UNIVERSITY OF SOUTHAMPTON

Faculty of Science

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Seasonal and spatial distribution of the mesozooplankton of Southampton Water with particular reference to the contribution of copepods and barnacle larvae to pelagic carbon flux.

by

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- Where I have quoted from the work of others, the source is always given. With the exception of such quotations, this thesis in entirely my own work;
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ABSTRACT

FACULTY OF SCIENCE
SCHOOL OF OCEAN AND EARTH SCIENCES
Doctor of Philosophy

Seasonal and spatial distribution of the mesozooplankton of Southampton Water with particular reference to the contribution of copepods and barnacle larvae to pelagic carbon flux.

By Erik Muxagata

In the past half century, a number of studies have described the general composition of the mesozooplankton of Southampton Water, highlighting aspects about the seasonality of the major components and identifying calanoid copepods and barnacle larvae as the major elements. Despite the number of studies, almost all knowledge about species composition, dominance and succession patterns of the mesozooplankton as a whole, is described from only a few studies, usually located at stations in the mid and lower estuary. It is clear that generalizations made for these stations will not reflect other parts of this estuary. Because of this, a 120 μm net-haul study comprising upper, mid and lower stations within Southampton Water was conducted over a period of 19 months, from 12/01/01 until 16/07/02, in order to critically re-evaluate the mesozooplankton community of the estuary, as well as to assess the importance of copepods and barnacle larvae to pelagic carbon fluxes. Additional biological and non-biological water column parameters were measured concurrently. A total of 144 different taxa were recorded within the zooplankton of Southampton Water during this study, with 92 identified to species, 30 to genus and 22 identified at a higher level. From these 31 were identified as holoplankton, 72 as meroplankton and 41 as tycoplankton, with 90 taxa recorded for the first time in Southampton Water. Numerically the zooplankton community was mainly composed of holoplankton forms (~69%), followed by meroplankton (~30%) and tycoplankton (~1%). Copepod nauplii were the most abundant holoplanktonic taxa, averaging 38% of all forms, followed by the calanoid *Acartia* spp. (31%), the cyclopoid *Oithona nana* (11%), the harpacticoid *Euterpina acutifrons* (11%) and the appendicularia *Oikopleura* sp. (5%). Barnacle larvae averaged 53% of the meroplanktonic forms, followed by polychaete (19%), gastropod (13%), bivalve (9%) and bryozoan larvae (3%). Harpacticoid copepods comprised 97% of the tycoplanktonic forms recorded. One unexpected finding of this study was the significant occurrence of the cyclopoid *Oithona nana* within the upper estuary, contrasting with previous studies where calanoids of the genus *Acartia* were considered the only dominant copepod form. Although present throughout the estuary, *O.nana* was clearly most abundant in the upper estuary where it presented a clear seasonal pattern, and was numerically the most abundant form from late-summer until early-winter, then replaced by copepod nauplii and *Acartia* spp. during mid-winter to late-spring, and by copepod nauplii, *Acartia* spp. and *E.acutifrons* during early to mid-summer. Barnacle larvae presented the same composition and seasonality reported in the past, with *Elminius modestus* the most abundant and frequent, and occurring throughout the year although it was outnumbered by *Balanus crenatus* from February to May. Of the remaining barnacle species found only *Balanus improvisus*, *Semibalanus balanoides* and *Verruca stroemia* were present in substantial numbers. Production of several copepod components was calculated, and an overall averaged production of 253.48 mg C m^{-3} yr^{-1} was estimated, with *Acartia* accounting for 55.6% of the production followed by *E.acutifrons* (16.0%), copepod nauplii (15.2%) and *O.nana* (13.2%). This previously unaccounted production may assist in readdressing the relatively low copepod secondary production previously estimated for Southampton Water. Production of barnacle larvae was also calculated and an overall averaged production of 32.80 mg C m^{-3} yr^{-1} was estimated, with *E.modestus* alone accounting for 54.7% followed by *B.crenatus* (35%), *B.improvisus* (6.7%), *S.balanoides* (3.1%) and *V.stroemia* (0.5%). Overall, production of barnacle larvae within Southampton Water is significantly lower than that of calanoid copepods contradicting previous assumptions that barnacle larvae could provide as much secondary production as calanoids. A new set of simple linear regression equations applicable to a range of crustacean zooplankton types are proposed for the preliminary estimation of production based primarily on the total number of organisms. Abundance, in conjunction with temperature, salinity and chlorophyll *a* pattern were also employed in the elaboration of multiple regression equations. Production values calculated by this new method were usually ±20% of the averaged value obtained by more conventional methods. When applied to an independent data set, differences of only ±7% were observed between production estimates using conventional and the new equations. The new estimated production values for barnacle larvae (meroplankton), *Acartia* (calanoid), *Oithona* (cyclopoid), *Euterpina* (harpacticoid) and copepod nauplii components of the mesozooplankton are integrated into an existing carbon-flux box-model for Southampton Water.

This work is dedicated to my family.

and to the memory of

Dr. Mónica Adelina Montú (1942 – 2003)

a wonderful person, friend e uma “criatura” linda that left us so early !!

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Chapter 1

General community structure.

1.1. Introduction.

Estuaries are areas in which seawater is gradually diluted by freshwater, creating a transition zone between the stability of the marine environments and the instability of the limnic ones (Kinne, 1967; Ketchum, 1983). The shallow nature of most of the estuaries, coupled with tidal mixing, freshwater run-off and anthropogenic interferences promotes a rapid cycling of resources, and consequently, makes the estuary more productive than the surrounding areas (Riley, 1967). This high productivity of estuarine areas is often reflected by its biota, that is present at least seasonally, as high abundances of plankton, benthos and nekton[1] (Riley, 1967; Haedrich, 1983; Wolff, 1983; Day Jr. *et al*., 1989), making these environments excellent nursery and feeding grounds for many important commercial species (Kinne, 1967; Haedrich, 1983; Ketchum, 1983; Day Jr. *et al*., 1989).

The term plankton includes communities of zooplankton, phytoplankton and bacterioplankton (Day Jr. *et al*., 1989). The subject of this study, the zooplankton, may be defined as the community of all phagotrophic organisms (Lenz, 2000), which includes representatives from most phyla of the animal kingdom.

Being so diverse, there are several different ways of classifying the zooplankton, with size and length/type of life history the most common way of doing so (Bougis, 1976; Omori & Ikeda, 1992; Lenz, 2000). Classifying by size is a well accepted way, and an example is shown in Table 1.

[1] Plankton, benthos and nekton are terms often used to classify groups of aquatic organisms according with their interactions with the environment where they live. The meaning of the word plankton comes from the greek "planktos" for "wanderer" or "drifter", which comprises those organisms that have very limited movement capabilities, so that its horizontal distribution is related mostly with the movement of the mass of water that the organism is in. Nekton also came from the greek term "nektos" for "swimming", and in contrast with plankton, are those animals with active free locomotion capabilities. Benthos (greek for "depth of the sea") refers to those organisms that live in/on the sediment at the bottom of a body of water (Perkins, 1974; Bougis, 1976; Wolff, 1983; Lenz, 2000).

Table 1. – Size ranges attributed to zooplankton organisms. Adapted from Bougis (1976), Omori & Ikeda (1992) and Lenz (2000).

Category	Length Size	Organisms
Nanozooplankton	2 − 20 μm	Nanoflagelates
Microzooplankton	20 − 200 μm	Foraminiferans, tintinids, rotifers, ciliates, crustacean nauplii and smaller copepods
Mesozooplankton	200 − 2000 μm	Adult forms of appendicularians, doliolids, chaetognaths, ctenophores and most crustaceans found in the plankton
Macrozooplankton (Includes some called Micronekton)	2 − 20 mm	Large specimens of hydromedusae, siphonophores, scyphomedusae, ctenophores, mysids, amphipods, copepods, fish larvae and euphausiids
Megazooplankton	>20 mm	Large scyphomedusae, siphonophores, thaliaceans

With reference to its life history, zooplankton can be divided in three wide categories: holoplankton, meroplankton and tycoplankton (Jeffries, 1967; Raymont, 1983; Omori & Ikeda, 1992). The term holoplankton are employed for those animals where all stages of its development lives in the water column throughout their entire life cycle, such as calanoid copepods, euphausiids and appendicularians. Meroplankton in contrast, represents that large array of animals that lives as free swimming planktonic (or planktic as recently suggested by Lenz (2000)) organisms only during part of their life, such as eggs and/or larval stages of benthic and nektonic species. The third group, tycoplankton, is a term employed especially in shallow estuaries for those animals, especially mysids and other crustaceans, that actively spend part of the day/night as plankton or even for those animals that are accidentally swept from the bottom, such as some harpacticoid copepods, gammarid amphipods, cumaceans, isopods and ostracods (Jeffries, 1967; Raymont, 1983).

Estuarine zooplankton can also be divided according to its period of residence/ retention within the estuary which will be dependent primarily on the balance between individual reproduction rates and loss due to tidal flushing and net river flow (Rogers, 1940; Perkins, 1974). Based on that it can be divided in three main components:

1. **Autochthonous populations**, the permanent residents, where the rate of reproduction exceeds the loss due to flushing and mortality and thus these animals are always present in estuaries;
2. **Temporary autochthonous**, or those introduced from neighbouring regions and capable of limited proliferation; usually with maintenance dependant upon reinforcements from the parent population;
3. **Allochthonous populations**, or those brought into the estuary either from the sea or river and unable to propagate, probably dying within the estuary.

Not withstanding these classifications, and based on selected studies that were performed along the entire axis of an estuary, it is possible to draw generalizations about the presence and abundance of typical estuarine zooplanktonic species. According to the

classical studies of Cronin *et al*., (1962) at the Delaware Bay (USA) and Bousfield *et al*.,(1975) in the St. Lawrence River (Canada), estuarine mesozooplankton communities are generally composed of holoplanktonic calanoid copepods, with mysids (tycoplankton), harpacticoid copepods (holo/tycoplankton), barnacle larvae (meroplankton) and cladocerans (holo/tycoplankton) also playing important roles. According to these reports, and also several other studies from tropical-temperate estuaries around the world (Haertel & Osterberg (1967) in the Columbia river (USA); Heinle (1972) in Chesapeake Bay (USA); Frolander *et al*.,(1973) in Yaquina Bay (USA); Reeve (1975) in Biscayne Bay (USA); Hulsizer (1976) in Narragansett Bay (USA); Hopkins (1977) in Tampa Bay, Turner (1982) in Long Island (USA); Montú (1980) in Lagoa dos Patos (Brazil); Hoffmeyer (2004) in Bahía Blanca (Argentina); Perissinotto *et al*.,(2000) in Eastern Cape (South Africa); Imabayashi & Endo (1986) in Hiroshima Bay; Ryan *et al*., (1986) in Killary Harbour (Ireland); Alcaraz (1983) in the ría of Vigo (NW. Spain); Soetaert & Van Rijswijk (1993) in the Westerschelde (NE Europe); Baretta & Malschaert (1988) in the Ems (Germany); Williams & Collins (1986) in the Bristol Channel (UK) and Raymont & Carrie (1964) in Southampton Water(UK)) estuarine mesozooplankton, regardless of life history and residence can also be divided in three groups, according to its apparent preferences.

- **Marine coastal species** which enter the estuary from the sea and are usually limited to regions influenced by the saltwater intrusion. They were represented mainly by oceanic/neritic calanoid copepods like *Calanus finmarchicus, Calanus hyperboreus, Labidocera aestiva, Centropages typicus*, *Centropages hamatus*, *Temora longicornis*, *Paracalanus parvus*, and *Pseudocalanus minutus*, the marine cladocerans *Penilia avirostris* and *Evadne nordmanni,* the barnacle larvae of *Balanus crenatus* and *Semibalanus balanoides*, the chaetognath *Sagitta setosa* and even euphausiids such as *Thysanoessa* spp.
- **Estuarine-endemic species** which can live within a wide range of estuarine conditions of temperature and salinity. These are typically represented by the calanoid copepods *Acartia tonsa*, *Acartia clausi*, *Acartia bifilosa*, *Acartia discaudata*, *Acartia margalefi*, *Eurytemora affinis*, the harpacticoids *Ectinosoma curticorne* and *Scottolana canadensis*, the cladoceran *Podon polyphemoides,* the barnacle larvae of *Balanus improvisus* and *Elminius modestus* and mysids like *Neomysis americana* and *Mesopodopsis slabberi* .
- **Freshwater species** which extend into the brackish water regions of the upper estuary. Exemplified by the cladocerans *Bosmina longirostris* and *Daphnia* sp.,

the calanoid copepod *Pseudodiaptomus coronatus,* the cyclopoid copepod *Cyclops viridis* and the amphipod *Gammarus fasciatus*.

Many others studies on estuarine zooplankton are available, and accommodating regional variations and different sampling methodologies most of them reports essentially the same species composition, or at least different species from the same genera, as the most abundant in estuaries. In addition the following species, *Parvocalanus crassirostris* (calanoid), *Oithona* spp viz. *O.similis* and *O.nana* (cyclopoid) and *Euterpina acutifrons* (harpacticoid), are small species which are being found to be quite abundant in estuaries where smaller mesh-size were employed (Reeve, 1975; Montú, 1980; Soetaert & Van Rijswijk, 1993; Hopcroft *et al*., 1998) as they were usually under-sampled by the 200 μm mesh-size recommended by the working party №.2 (WP2) of UNESCO as standard mesh-size for mesozooplankton sampling (Bé *et al*., 1968).

An exception are Australian estuaries that apart from the fact that *Acartia* spp. *Oithona* spp. and *Paracalanus* sp. are important constituents in the downstream reaches, provide a curious contrast in that there are no representatives of the genera that provides the bulk of euryhaline species in the main estuaries of other regions (viz. *Acartia* spp. and *Eurytemora* spp.) with *Gladioferen*s spp. and *Sulcanus conflictus* being present instead (Perkins, 1974; Miller, 1983).

It is clear therefore that, a mixture of holo, mero and tycoplanktonic organisms, to various degrees and proportions, characterize the zooplankton of estuaries (Jeffries, 1967; Raymont, 1983). The mixture will usually be dependent on a complex combination of water-column factors like temperature, salinity, degree of tidal mixing, flushing rates, advection, type of estuary, input of freshwater, concentration of dissolved gases, turbidity, light, nutrients and biological bottom-up/ top-down resource and predator pressure (Kinne, 1967; Perkins, 1974; Vernberg, 1983; Miller, 1983; Day Jr. *et al*., 1989).

Temperature and salinity are universally considered the most important non-biological factors regulating the distribution of zooplankton organisms in estuaries, since they often undergo considerable spatial and temporal fluctuations. These two factors will usually interact with each other, forcing and counteracting physiological and/or behavioural patterns from organisms, making estuaries extremely challenging and stressful habitats (Kinne, 1967). The ecological consequence of this is that any estuarine organism, regardless of its life story, will either have to be able to cope with substantial, perhaps extreme environmental changes and thrive even under sub-optimal conditions (Kinne, 1967; Vernberg, 1983; Miller, 1983) or be able to move to more favourable conditions or die.

This ability to cope with changeable conditions will be more noticeable in holoplanktonic organisms since they are permanently in the water column and more susceptible to the extreme variations. They will typically have characteristic behaviour patterns, rapid growth and reproduction rates, broad physiological tolerances, and in some cases, even resting eggs/stages (Perkins, 1974; Miller, 1983; Raymont, 1983; Mauchline, 1998). Such attributes have been reported in copepods of the genus *Acartia*, and explain why it is one of the most abundant genera within estuaries (Jeffries, 1967; Conover, 1979; Miller, 1983; Buskey, 1993), with congeners being found from nearly fresh to hypersaline waters and from 0 to 40 ºC, in clear or turbid estuaries from low to high latitudes (Day Jr. *et al*., 1989).

The meroplankton, in contrast, only spend a relatively brief, usually 2 – 4 weeks, but very specific time in the plankton, so they are usually found/released when productivity is high and conditions are favourable for survival and growth (Raymont, 1983). However, even they have, occasionally, to cope with extreme variations on tidal and perhaps on a seasonal basis, and so will also possess some physiological/behavioural mechanisms to make them more capable of adapting to changing conditions.

One of the most widely reported patterns of behaviour of zooplankton to remain in a relative fixed position within estuaries, and so avoid changeable and potentially detrimental conditions, is Selective Tidal Stream Transport (STST). STST had been reported mainly for meroplanktonic organisms (Olmi & Orth, 1995; Epifanio, 1995; Garvine *et al*., 1997; Garrison & Morgan, 1999) but has also observed in copepods (Jacobs, 1968; Trinast, 1975; Wooldridge & Erasmus, 1980; Hough & Naylor, 1991).

The tycoplankton are considered to be found in the plankton by accident, usually removed by force from its ideal niche, so its presence is usually neglected or considered occasional and of little importance to structuring the composition of the zooplankton community (Day Jr. *et al*., 1989).

Only few species seem to sustain optimum conditions in estuaries, and because of that it is considered that the richness of zooplanktonic populations in estuaries will increase towards the sea, mainly due to the contribution of meroplanktonic larvae and holoplanktonic copepods present in greater diversity in the relative stability offered by fully marine environments (Riley, 1967; Kinne, 1967; Perkins, 1974; Raymont, 1983; Day Jr. *et al*., 1989). Equally, within the main body of the estuary, where major environmental variations occur, zooplankton diversity is expected to be low with high abundances (Jeffries, 1967; Riley, 1967), and usually distributed in large patches (Jeffries, 1967; Raymont, 1983; Day Jr. *et al*., 1989). Holoplanktonic copepods are generally the main constituents of

these patches and, in general, the brackish upstream is characterised by *Eurytemora affinis,* and *Acartia tonsa,* with *Acartia* spp. (including *A.clausi*, *A.bifilosa* and *A.discaudata*) in the middle reaches and *Centropages hamatus, Temora longicornis, Paracalanus parvus* and *Pseudocalanus minutus* at the mouth, where the marine influence is more noticeable (Perkins, 1974). Small species like *Euterpina acutifrons* and *Oithona* spp. (*O.similis* and *O.nana*) are also expected to be among the dominant elements in those patches, and together with *Acartia* spp and *Eurytemora* sp. are almost always the greatest contributors to the total biomass (Jeffries, 1967; Conover, 1979; Miller, 1983; Raymont, 1983; Day Jr. *et al*., 1989; Buskey, 1993; Escaravage & Soetaert, 1995). However, other parts of the same estuary can also have patches where copepods are not the dominant component (Jeffries, 1967; Day Jr. *et al*., 1989), particularly close to areas where large concentrations of benthic animals could be supplying larvae and/or adults to the water column (Raymont, 1983).

In estuaries, as in other aquatic systems, the zooplanktonic organisms play a key role by grazing the primary production of the phytoplankton and bacterioplankton and transporting it, in terms of energy and matter, to different depths and ecosystems. This role could be either active, through daily vertical migrations, or even passive through the downward flux of faecal pellets. Because of this, zooplanktonic organisms are considered as the main link between primary production of the phytoplankton and bacterioplankton and the many important carnivores, including many commercial fish, at higher trophic levels (Buskey, 1993; Banse, 1995; Lenz, 2000). Not forgetting that zooplanktonic organisms also play a key role in nutrient cycling and remineralization (Day Jr. *et al*., 1989).

In Southampton Water, several authors have described the mesozooplankton populations of the estuary (Conover, 1957; Soares, 1958; Lance & Raymont, 1964; Raymont & Carrie, 1964; Bird, 1972; Barlow & Monteiro, 1979; Frid, 1984; Reubold, 1988; Zinger, 1989; Williams & Reubold, 1990; Geary, 1991; Lucas, 1993; Lucas & Williams, 1994; Lucas *et al*., 1995; Hirst, 1996; Castro-Longoria & Williams, 1996; Lucas *et al*., 1997; Castro-Longoria, 1998; Hirst *et al*., 1999; Chinnery, 2002; Muxagata *et al*., 2004), highlighting aspects of the basic spatial and temporal patterns of the major groups of the mesozooplankton.

From all of those, the work of Raymont & Carrie (1964) is the most taxonomically detailed, up to this date, and the one from which most of the species described for this estuary are known. In this work, the mesozooplankton of Southampton Water was

numerically dominated by barnacle nauplii throughout much of the year. Calanoid copepods were reported as the next most abundant group, particularly during the winter, when zooplankton abundance is at a minimum, and also during early-spring when calanoid copepods from the genus *Acartia* became the most abundant group. During summer-autumn, they also recognized the harpacticoid *Euterpina acutifrons* as an important component. Recently Hirst (1996) and other authors (Zinger, 1989; Lucas, 1993; Castro-Longoria, 1998) have presented a slightly different picture. In these studies almost the same group/species composition were identified, but the mesozooplankton was found to be primarily dominated by calanoid copepods from the genus *Acartia*, with barnacle nauplii numerically dominating only during short periods in early-spring (March - April) and summer (July - September). The major differences between the investigation of Raymont & Carrie (1964) and the recent ones can probably be attributed to different sampling gear and procedures.

Again, when most of those zooplanktonic studies are contrasted with the work of Raymont & Carrie (1964) it is clear that most of the studies characterized the zooplanktonic populations of this estuary based on:

1. the identification of the dominant holoplanktonic and meroplanktonic forms at "group" level (Bird, 1972; Reubold, 1988; Zinger, 1989),
2. or were only focused on detailed aspects of a specific group (Conover, 1957; Soares, 1958; Frid, 1984; Williams & Reubold, 1990; Lucas, 1993; Lucas & Williams, 1994; Lucas *et al*., 1995; Lucas *et al*., 1997; Hirst *et al*., 1999; Chinnery, 2002; Muxagata *et al*., 2004),
3. and/or were only based at a single station at the mouth (Conover, 1957; Soares, 1958; Hirst, 1996; Hirst *et al*., 1999), mid-section (Barlow & Monteiro, 1979) or at the head of the estuary (Geary, 1991; Castro-Longoria, 1998; Muxagata *et al*., 2004).

It is clear that some detailed general overview of the distribution, composition and abundance of the different species, as a community, along the estuary as a whole is needed.

Since rates, like reproduction, grazing, birth and death in zooplankton populations are performed at species level, any study related to fluxes in zooplanktonic communities requires detailed information about the spatial-temporal importance of species, abundances and biomasses before attempting to quantify any specific processes, like production and the rate of interactions with other trophic levels (Soetaert & Van Rijswijk, 1993). So, quantifying the different parameters related with species and understanding the processes controlling it within an ecosystem is a major objective of biological oceanography.

Abundance, biomass and production rates of some components of the pelagic community of Southampton Water are known, with ciliates (Leakey *et al*., 1992), bacteria (Antai, 1989), size-fractionated primary production (Iriarte & Purdie, 1994), gelatinous predators (Lucas *et al*., 1995; Lucas *et al*., 1997), calanoid copepods (Hirst, 1996; Hirst *et al*., 1999) already reported. The remaining major unresolved component in this estuary is the meroplankton. Detailed production studies of the meroplankton of this estuary are only available for few specific components, some gelatinous predators (Lucas *et al*., 1995; Lucas *et al*., 1997) and a single barnacle species, *Elminius modestus*, from data already published from this study (Muxagata *et al*., 2004). As said earlier, most of those zooplankton studies lack the in depth composition approach, spatial coverage or even both for generalizations. Despite of not being concerned with production, only the detailed work of Raymont & Carrie (1964) gives some overall qualitative-quantitative idea of almost all the species found within this estuary, from which generalizations on the importance of each holo, meroplanktonic species can be drawn. The problem is that this work is now more than 40 years old and major changes could have occurred to modify the overall zooplankton composition.

1.2. Aims of the study.

This study aims, therefore, to evaluate the contribution of holo-meroplanktonic components, but particularly barnacles, to the pelagic carbon flux of this estuary. Secondarily, as a consequence of the sampling strategy, it will monitor and re-evaluate the distribution, composition and abundance of the organisms found in zooplankton catches of Southampton Water on a taxonomically intensive approach, identifying and quantifying the dominant forms and comparing current patterns with earlier studies. Concurrent data on water column environmental variables will also be determined. The data generated in this study will allow a better evaluation of the estuarine zooplankton community of Southampton Water as a whole, and will also try to "fill the gaps" left by earlier studies.

Despite being concerned with the contribution of the major mesozooplankton components, the seasonality of minor/less abundant groups such as Decapoda, Amphipoda, Euphausiacea, Mysidacea, Isopoda, as well as other parasitic crustacean forms found in this estuary will also be described in detail. The study will therefore provide the first account of the distribution, composition and abundance of those crustacean components.

The work is divided in major sections, Chapter 1 will present the general methodology employed for collection, identification, and will present the general results of the analysis of the physico-chemical environmental variables. It will also introduce the importance of the different groups within the mesozooplankton.

Chapter 2 will be primarily focused in the seasonality and abundance of the different species of the holoplankton; while chapter 3 will be focused on the species of the meroplankton and tycoplankton.

Chapter 4 will highlight the seasonality of production of the different barnacle larvae present in this estuary, and apart from the recent published paper generated from data obtained during the present study (Muxagata *et al*., 2004 see this on Appendix I) this will be the first reported account of the contribution barnacle larvae to field production.

Chapter 5 will present the seasonality of production of the most important copepod species present in this estuary, particularly *Acartia*.

Chapter 6 will offer a new empirical way of estimating the production of some components within this estuary, as well as some general insights on pelagic community flux estimated from data available for this estuary.

Taxonomic intensive studies are not really appealing, but one must bear in mind that it is only through these kind of studies that the required data to detect any changes within the estuary is supplied; and when allied with retrospective studies it can also give some feedback concerning major environmental changes or even human impact on the environment.

1.3. Study Area.

Southampton Water is a shallow, partially mixed coastal plain estuary (Dyer, 1973) located on the South Coast of England (Hampshire, southern England), that discharge into the Solent (Figure 1).

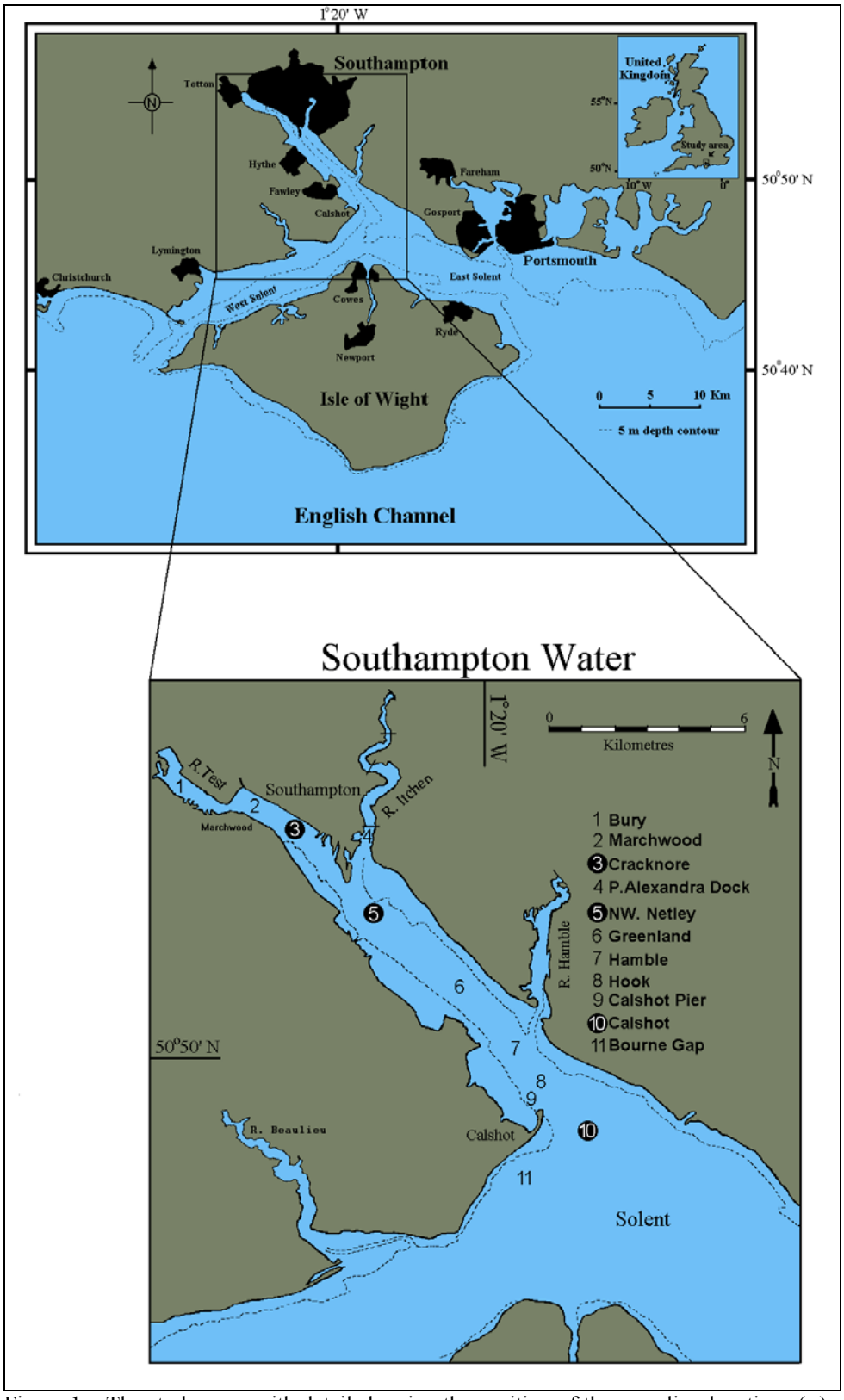


Figure 1 – The study area, with detail showing the position of the sampling locations (●) and sites of interest and/or sampled in previous studies.

At its head it is fed by the rivers Test and Itchen which border the industrialised city of Southampton, and near the mouth (~4 km) is the river Hamble (Figure 1). The largest rivers, Test and Itchen are chalk streams that pass through intensively farmed land (Howard *et al*., 1995), and have a mean annual discharge of 8.81 and 3.26 m^3 s^{-1}, respectively (Sylaios & Boxall, 1998). They are responsible for about 45% of the total inflow of freshwater into the Solent system (Webber, 1980), while the Hamble, with a mean annual discharge of 0.28 m^3 s^{-1}, constitutes a smaller input of freshwater (Sylaios & Boxall, 1998).

The estuary is a drowned river valley in nature ~11 Km in length and 1.9 - 2.5 km wide (Dyer, 1973; Webber, 1980; Dyer, 1982), running in a NW - SE direction. Broad intertidal mudflats with shingle and sand border the eastern side, with salt marshes on the western side. It is a shallow estuary, with depths usually between 1 - 8 m, except in the dredged shipping channel, where a maximum depth of ~13 m occurs. Southampton Water is essentially marine in character, with little salinity variation near the mouth and some stratification at the head of the estuary (Raymont & Carrie, 1964). This stratification at the head of the estuary depends on the state of the tide and the freshwater inflow.

The water temperature of Southampton Water varies with the season, with minima during the winter (T < 5 °C in December – February) and maxima during the summer (T > 17 °C June – August) (Raymont & Carrie, 1964; Leakey *et al*., 1992; Howard *et al*., 1995; Hirst, 1996). The tidal features of the Solent area are complex and are characterised by a "stand" of high water (also called double high water), during a period of 2 to 3 hours, where little tidal water movement occurs. The consequence of this double high water is to shorten the period of ebb to around 4 hours instead of 6 hours, which make ebb currents faster than the corresponding flood, and so flushing silt and contaminants in a seaward direction (Webber, 1980). Within Southampton Water the tidal range varies from 2 to 4m (Sylaios & Boxall, 1998).

A number of authors have reported the seasonal cycle of abundance, biomass and production rates for several components of the pelagic community of the Southampton Water. Ciliates were studied in detail by Leakey *et al*. (1992) and Kifle & Purdie (1993), bacteria by Antai (1989) while phytoplankton were the subject of several studies (Williams, 1980; Iriarte, 1991; Iriarte, 1993; Iriarte & Purdie, 1994; Howard *et al*., 1995). Based on those studies, Southampton Water can be considered as a productive estuary, with annual rates of primary production estimated as 177g C m^{-2} yr^{-1} and 130g C m^{-2} yr^{-1} at the middle and mouth respectively, with March and August being the most productive months (Iriarte & Purdie, 1994).

1.4. Materials and Methods.

1.4.1. Field Methodology.

During the period between 12/01/01 to 16/07/02, samples were collected (on board the University of Southampton boats RV "Bill Conway" and "Prince II") at three fixed sites, marked by permanent shipping buoys within Southampton Water (Figure 1). The geographic location and name of the buoys are given in Table 2.

Table 2. Fixed buoys and geographical positions of the sampling sites.

Buoy	Coordinates
Cracknore	50°53'93" N, 01°25'12" W
NW.Netley	50°52'28" N, 01°22'64" W
Calshot Spit	50°48'33" N, 01°17'52" W

These particular sampling stations where chosen because they were among the most sampled stations in previous studies, so it was decided to repeat these sites in order to compare the results of this work with the data from previous studies.

These sites were sampled on the same day, wherever possible, in association with the relatively extended 2 – 3 hour period of "slack water" at high tide. This procedure was done in order to attempt to sample the "same body of water", and also to standardize tidal influence (see Figure 2 showing the relative time in minutes to or from the first high water when sampling was performed).

Sampling frequency was carried out on a time scale that was comparable to the breeding and recruitment phases of the target species, and associated with boat availability and tide conditions (i.e. sometimes the high tide "falls" on a certain period of time when there is no boat available, so sampling were carried during boat availability i.e. flood or ebb. During this study 14% of the samples were collected during flood and 5% on ebb conditions).

For the target organisms, i.e. barnacles, moulting occurs at regular intervals and the metanauplius stage is usually reached within 3 – 4 weeks (Bassindale, 1936; Pyefinch, 1948b; Harms, 1984), followed by the cyprid stage. Because of that, a bimonthly sample programme was carried during the non-breeding season of the barnacles. During the breeding months a more focused and intensive sampling programme, involving a shorter sample frequency (3 – 4 times a month) was carried out. Later, following the analysis of the samples collected from October and November 2001 it was decided to collect only once a month between November 2001 until February 2002, resuming the more intensive

sampling effort (3 – 4 times a month) for samples collected from March 2002 until July 2002.

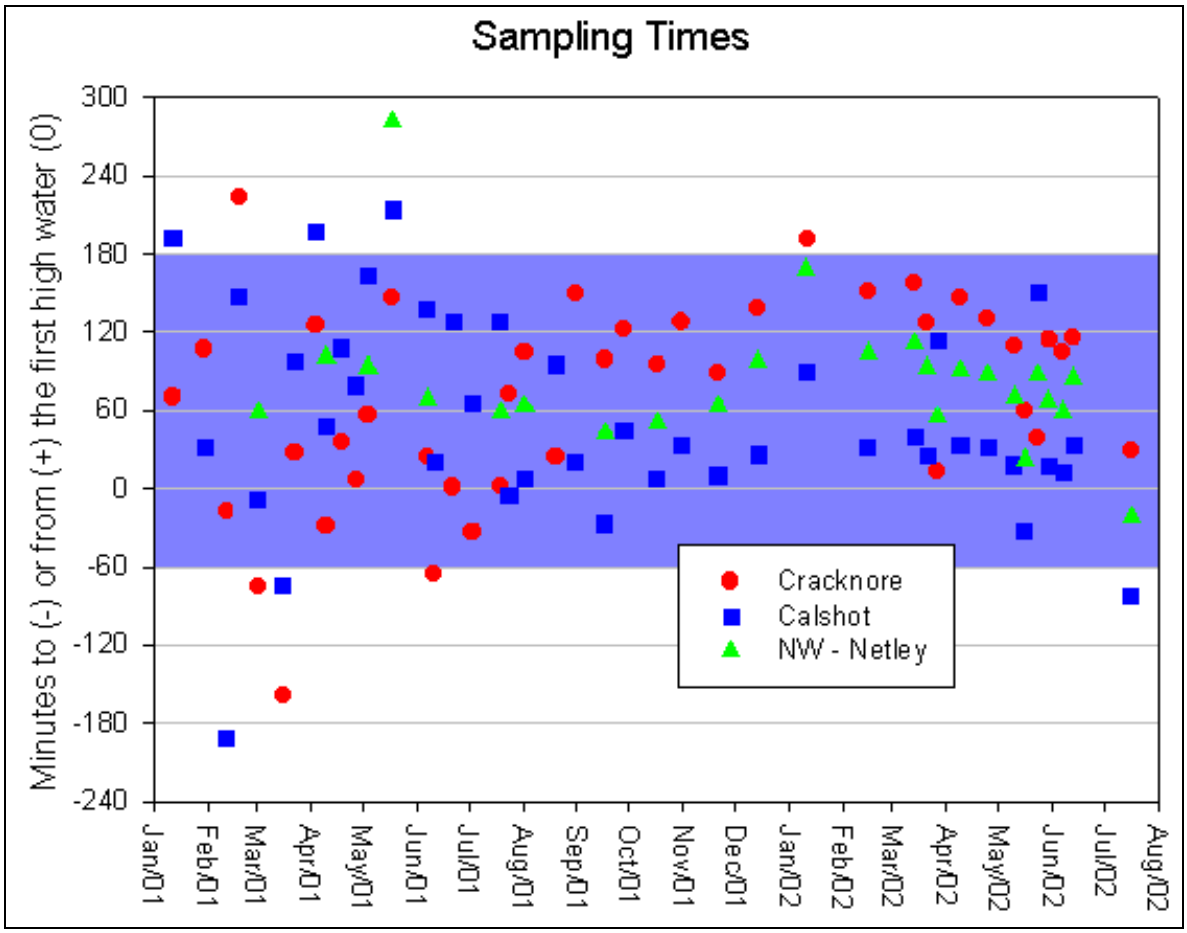


Figure 2 – Time when the sampling was carried out in the different station and months in relation the predicted time of the first high water at Southampton Water. Shaded area is the approximate duration of the "slack water" period.

Due to the amount of samples to be processed, and the labour-intensive task of sorting and identifying the species present, sampling at NW.Netley only started on March 2001. It was only sampled once a month until October 2001, after which it was sampled at the same frequency as the other sites (See Appendix II for dates, locations sampled and type of data gathered).

During the 19 month survey, on only one occasion (24/05/02) was it not possible to sample at Calshot due to extremely bad weather. On this particular date sampling was carried out at Hook Buoy (Figure 1), and since this buoy is fixed at ~1.35 nautical miles from Calshot Buoy, the data was computed as being from Calshot.

Mesozooplankton[2] samples were collected from 5m double oblique tows using conventional cod-end plankton net of 50 cm of mouth diameter and 120 μm mesh, with a towing speed around 2 knots. Towing times varied according to season, but was generally

[2] In this work and throughout the text when referring to mesozooplankton, it is good to have in mind that the 120μm mesh employed also collected a large parcel of microzooplanktonic organisms that usually would pass trough the conventional 200 μm mesh employed for mesozooplankton sampling (Bé *et al*., 1968).

5 - 10 min. during autumn – winter and 3 – 5 min. during spring – summer, in order to minimize phytoplankton clogging, sampling on average ~40 m^3 on each tow. Despite that some clogging could have occurred on 04/04/2001, 18/05/2001, 22/06/2001, 03/07/2001 and 02/08/2001 at Cracknore, 07/06/2002 and 02/08/2001 at NW.Netley and 18/05/2001 and 07/06/2001 at Calshot where ~6 m^3 were filtered instead of the average of 20 m^3 for ~3 min tows, but no attempt to correct the values was made. The volume of water filtered at each tow was estimated by a calibrated flowmeter (TSK - Tsurumi Seiki-Kosakusho and on very few occasions a Hydrobios) attached to the mouth of the net (See Appendix III a,b,c for field data).

After collection all samples were preserved in approximately 4% formaldehyde-seawater solution buffered with borax (Steedman, 1976) until processing.

At each station samples of water were collected with a 5 litre Niskin water bottle from surface (only on Cracknore site), 2 and 8 metres depth for chlorophyll *a* and dissolved oxygen analysis, following the procedures shown below:

- **Chlorophyll *a***: At each station/depth 2 samples of 60 ml of water were filtered through 2.5 cm glass microfibre filters (Whatman® GF/F) (Mantoura *et al*., 1997), using a 60 ml syringe with a filter holder attachment (Millipore – Swinnex 25). Each of the filter papers were then folded in half, wrapped in foil, sealed in labelled plastic bags and frozen (- 70°C) until processing.
- **Dissolved Oxygen**: At each station/depth 2 stoppered glass bottles were filled with water and immediately 1.0 ml of Manganous Chloride solution ($MnCl_2$) followed by 1.0 ml of Alkaline-Iodide solution (NaOH + KI) were added. The bottles were then stoppered, shaken and stored under water until analysis could take place (Strickland & Parsons, 1965).

Temperature and salinity measurements were obtained at 1m depth intervals at each station, using a digital field Thermo-salinometer (WTW – LF597-S) connected to a salinity-temperature probe. The results were expressed as temperature (°C) and salinity during the period of study (see Appendix IV a,b,c). Following the recommendations of UNESCO (1985), in this work the salinity will be expressed as an absolute value with no figures expressing salinity proportions. The temporal variability of temperature and salinity were drawn using SigmaPlot for Windows.

1.4.2. Laboratory Methodology.

1.4.2.1. Zooplankton.

In the laboratory, the zooplankton samples were concentrated in suitably sized containers, ensuring that the material will be in the proportion of 9 parts of fixative solution to 1 part of planktonic material (Steedman, 1976). When large quantities of gelatinous species were collected, those greater than ~5 mm were manually removed, counted and stored in a separate container. When large quantities of *Pleurobrachia pileus* were detected, they were also manually removed, counted, their gut content analysed and then stored in a separate container.

Because of the large number of organisms present in the samples, sub-samples of 0.4 to 12.5% of the original sample[3] were made using a Folsom plankton sample splitter (Appendix III a,b,c) after the removal of the large gelatinous species. According to Postel *et al.* (2000) sub-sampling with the Folsom splitter accounts for a coefficient of variation of 5-18%.

An average of 2558 organisms were counted and identified on each sub-sample. They were counted and initially identified in Bogorov tray chambers using a dissecting stereo-microscope (Wild MZ-5). When necessary, the identification and observation of detailed taxonomic features were made using a microscope. Mysidacea, Euphausiacea, Decapoda, Chaetognatha, Amphipoda, Isopoda, Cumacea, Vertebrata as well as rare and less abundant species were enumerated from the whole sample. The counting error, based on the number of all specimens counted following a Poisson distribution (Frontier, 1981; Postel *et al*., 2000), averaged ±10 % for all samples, with ± 6 % for the most abundant and ± 19 % for the less abundant ones. (See Appendix III a,b,c).

For comparison with other studies, the organisms present in the samples were initially identified to the following "grouping" levels: Gelatinous (Organisms belonging to Phylum Cnidaria and Ctenophora), Mollusca (the veligers of bivalves and gastropods pooled), Polychaeta, Chelicerata, Cladocera, Cirripedia, Copepoda, Ostracoda, Stomatopoda, Mysidacea, Isopoda, Amphipoda, Cumacea, Euphausiacea, Decapoda, Phoronida, Bryozoa, Chaetognatha, Echinodermata, Tunicata (Appendicularia and

[3] In estuarine research, sub-samples ranging from 0.5 to 10% are usual (McLaren & Corkett, 1981; Buskey, 1993; Hirst, 1996), but it should be noted that the size is entirely dependant to the researcher. The common sense is that the sub-samples should be large enough to permit a practical count of the animals in it; with the expectation that it will contain at least 100 individuals of the target species. This, according with a Poisson distribution, will result in counting errors around ± 20%, which is acceptable for zooplankton research (Frontier, 1981; Postel *et al*., 2000).

Ascidiacea pooled) and Pisces (larvae/ eggs of fish). Besides the fact that Foraminifera and Rotifera were noted in some samples, they were not counted in this investigation and the results presented here do not include them.

The Cnidaria, Ctenophora, Mollusca, Polychaeta, Chelicerata, Cladocera, Stomatopoda, Mysidacea, Isopoda, Amphipoda, Cumacea, Euphausiacea, Decapoda, Chaetognatha and Appendicularia present in the samples were identified to the lowest taxonomic level possible based on: (Apstein, 1901; Williamson, 1915; Webb, 1921; Lebour, 1928; Russell, 1939; Rammner, 1939; Lebour, 1940; 1943; Heegaard, 1948; Berrill, 1950; Russell, 1950; Nouvel, 1950; Forneris, 1957; Williamson, 1957; Jones, 1957a; Naylor, 1957a; Jones, 1957b; Naylor, 1957b; Jones, 1957c; Pike & Williamson, 1959; Williamson, 1960; Hannerz, 1961; Pike & Williamson, 1961; Russell, 1963; Newell & Newell, 1963; Scourfield & Harding, 1966; Williamson, 1967; Fretter & Pilkington, 1970; Mauchline, 1971; Pike & Williamson, 1972; Smirnov, 1974; King, 1974; Della Croce, 1974; Greve, 1975; Rice & Ingle, 1975a; 1975b; Le Roux, 1976; Makings, 1977; Russell, 1978; Fincham & Williamson, 1978; Lincoln, 1979; Mauchline, 1980; Ramírez, 1981; Stop-Bowitz, 1981; Emig, 1982; 1984; Montú & Gloeden, 1986; Isaac *et al*., 1990; Elliot *et al*., 1990; Pessani & Godino, 1991; Ingle, 1992; Paula, 1996; González-Gordillo *et al*., 1996; Martin, 2000; González-Gordillo & Rodríguez, 2000). The different species of Cnidaria, Polychaeta, and Amphipoda were, in the end, grouped, and only a list of species is presented.

Copepoda were identified to species based on: (Sars, 1903; 1905; van Breemen, 1908; Sars, 1911; 1916; 1918; 1921; Rose, 1933; Farran, 1948a; 1948b; Farran, 1951a; 1951b; 1951c; Isaac, 1975; Boxshall, 1977; Kabata, 1979; Björnberg, 1981; Huys & Boxshall, 1991; Piasecki, 1996; Boxshall & Montú, 1997; Bradford-Grieve, 1999; Bradford-Grieve *et al*., 1999; Boxshall & Halsey, 2004). Individuals were also subdivided in adults, copepodites and nauplii. Copepoda nauplii were, in the end, grouped together due to the almost impossible task of identifying then to species, or even orders, within a limited time frame.

Cirripedia were identified to species level based on: (Hoek, 1909; Bassindale, 1936; Veillet, 1943; Pyefinch, 1948a; Pyefinch, 1949; Knight-Jones & Waugh, 1949; Jones & Crisp, 1954; Crisp, 1962; Tighe-Ford *et al*., 1970; Turquier, 1972; Barker, 1976; Lang, 1980; Branscomb & Vedder, 1982; Dalley, 1984; Collis & Walker, 1994; Lee *et al*., 1998). They were also sorted to larval stage, in accordance with the definitions presented in Lang (1979).

The taxonomic system adopted in this work follows that of Howson & Picton (1997) for the species directory of the marine fauna and flora of the British Isles and surrounding seas. The results were expressed as number of organisms m^{-3} or percentages during the period of study. (Appendix III a,b,c shows the total animal abundance on each sampling day. Due to the large number of organisms present, this was synthesized showing only the most abundant on a species basis. Appendix V shows a picture of every single taxa observed during this investigation).

Graphics and statistical calculation were made using several software's, including Microsoft Excel, Sigma Plot for Windows, Statistica for Windows and Macromedia Freehand for Windows

1.4.2.2. Chlorophyll *a*.

The fluorometric technique introduced by Welschmeyer (1994) was used to determine chlorophyll *a* concentration. This particular method was chosen because it can provide sensitive measurements of extracted chlorophyll *a* free from the errors associated with conventional acidification techniques, ie, maximum sensitivity to Chlorophyll *a* without the interference of Chlorophyll *b* and phaeopigments. This method still maintains the higher sensitivity when compared with the spectrophotometric methods (Jeffrey & Welschmeyer, 1997).

Since the procedure for extraction of pigments was different from the reported literature for fluorometry (Yentsch & Menzel, 1963; Holm-Hansen *et al*., 1965) the extraction protocol is described:

- Soaking/Sonication[4]/Centrifugation: Frozen filters with material were placed in 8ml of 90% acetone in centrifuge tubes (Polypropylene centrifuge tubes of 13 ml with screw caps), sonicated for 30 s (sonicator set in 50%) with a VibraCell sonicator with the probe inserted directly into the solvent and then centrifuged for 10 min at 3000 rpm.

The fluorescence of the chlorophyll *a* extract was measured with a calibrated Turner Designs Fluorometer (Model 10 AU) fitted with a F4T4$_{1/2}$B2 (Type 10-089 Turner Designs Inc.) lamp as proposed by Welschmeyer (1994). The concentration of chlorophyll

[4] Wright *et al*. (1997) recommends sonication in dimethyl formamide for almost 100% of extraction, but due to the toxicity of this extractor it must be avoided. They also proposed sonication in methanol as an alternative, since methanol was the second most efficient extractor. However, since no fluorometric equations in methanol are available, this solvent cannot be used for extracted fluorometry (Wright & Mantoura, 1997).

a for each sample is calculated from the following equation (Jeffrey & Welschmeyer, 1997):

$$\text{Chlorophyll } a(\mu g\ l^{-1}) = \frac{KFvu}{Vs}, \quad (1)$$

where, K[5]= fluorescence sensitivity coefficient in extraction solvent, F = fluorescence response (no acidification), vu = Volume of acetone used for extraction (in millilitres), Vs= Volume of sample filtered (in millilitres).

The final chlorophyll *a* concentration for each stratum on each sample is then obtained by averaging the duplicate results (Appendix VI a,b,c). Differences between replicas varied and errors were calculated as a percentage of the mean averaged for all measurements; during this work it was around ± 3.9 %. The results were expressed as mg m^{-3} (equivalent to μg l^{-1}) of chlorophyll *a* during the period of study. The temporal variability of Chlorophyll *a* was drawn using SigmaPlot for Windows.

1.4.2.3. Dissolved oxygen.

The dissolved oxygen present on the samples was estimated by the Winkler method, using an end point detector and an automatic titrator (Dosimat 665 - Metrohm), connected to a chart recorder (Servoscribe), as described by Bryan *et al*. (1976).

The oxygen concentration in each sample was calculated as follows:

$$\text{Dissolved oxygen } (ml O_2 l^{-1}) = \left(\frac{AN10^3}{(V-2)4}\right)22.4, \quad (2)$$

where, A = volume of thiosulphate added (in ml), N = Normality of the thiosulphate, V = volume of the sample bottle (in ml).

For each station/depth the dissolved oxygen concentration were the averages of the two samples taken.

The oxygen concentration may be converted to units of mg $O_2 l^{-1}$ by multiplying by 1.4286 and to n moles l^{-1} by dividing by 22.4.

[5] In the fluorometer model employed in this study there is no need of this coefficient, since this fluorometer model gives straight readings (D. Purdie, pers. comm.)

Following Weiss (1970), the percentage of oxygen saturation could be calculated using the equation:

$$\ln C = A_1 + A_2\left(\frac{100}{T}\right) + A_3 \ln\left(\frac{T}{100}\right) + A_4\left(\frac{T}{100}\right) + S\left[B_1 + B_2\left(\frac{T}{100}\right) + B_3\left(\frac{T}{100}\right)^2\right], \qquad (3)$$

where, C = The solubility of oxygen in ml (STP) l^{-1} from water saturated air at a total pressure of one atmosphere, T = Absolute temperature. (Temperature of the sample in °C + 273.15), A's and B's = are constants (A_1 = -173.4292; A_2 = 249.6339; A_3 = 143.3483; A_4 = -21.8492; B_1 = -0.033096; B_2 = 0.014259; B_3 = -0.0017000).

This value of C gives the 100% saturation, when compared with the measured value the oxygen saturation is obtained.

The standard difference between replicas as a percentage of the mean averaged for all measurements was ± 1.2 % (Appendix VII a,b,c). The results were expressed as dissolved oxygen in ml l^{-1} or as percentages of saturation during the period of study. The temporal variability of dissolved oxygen and oxygen saturation were drawn using SigmaPlot for Windows.

1.4.2.4. Correlation Analysis.

Due to the oblique pattern of the zooplankton haul samplings, the data of temperature, salinity, chlorophyll *a*, and oxygen (dissolved and saturation) from each stratum of each station had to be averaged before any analysis could be made (Appendices III, V, VI). The Pearson's product-moment correlation coefficient *r* was used in order to measure the intensity of the association between the biotic and abiotic variables. To stabilize the variance of the data, zooplankton abundances were $\log_{10}(x+1)$ transformed and the average oxygen saturation and average Chl. *a* were $\log_{10}(x)$ transformed before analysis (Prepas, 1984; Zar, 1999; Clarke & Warwick, 2001). Usually, percentages are arcsine transformed, but this only applies when the percentages reflects proper probabilities (K. Clarke, pers. comm.). In the case where percentages values are considered a continuous variable, like the oxygen saturation values, other transformations can be used, i.e. $\log_{10}(x)$.

1.5. Results.

1.5.1. Temperature and salinity.

The temporal variability of the water temperature and salinity at three depths at the sampling stations during the period of study can be observed in Figure 3.

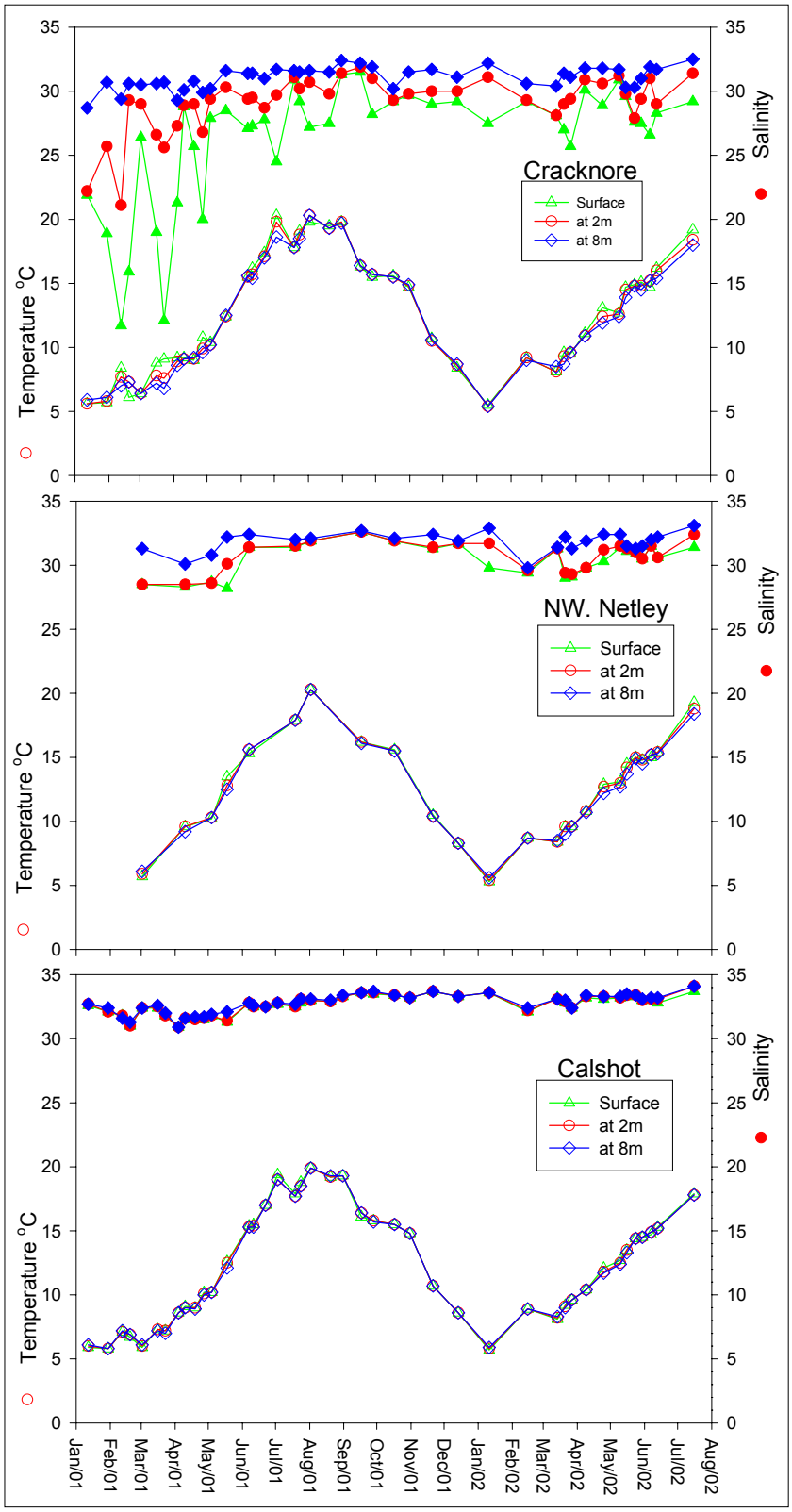


Figure 3 - Temporal variability of the temperature (open symbols) and salinity (solid symbols), at the three stations and depths in Southampton Water during 2001/02.

The temperature varied accordingly with season, with minima observed during the winter (December – February) and maxima from mid-summer through early autumn (July – September). The minimum temperature recorded during this investigation was 5.3 °C in January 2002 at NW.Netley, and the maximum 20.4 °C at Cracknore in August 2001. No remarkable differences of temperature with depth were observed, within any station. On some occasions slight differences of temperature in the surface layer at Cracknore were observed, but this never exceeded 2.3 °C. No differences in temperature were observed between stations, with the same pattern observed at the three locations (Figure 3).

Salinity, on the other hand, did not have any seasonal variation but showed an increasing gradient towards Calshot (Figure 3). There was some vertical stratification at NW Netley and particularly at Cracknore, where the lowest salinity values were recorded, with minimum values always in the surface layer and the salinity gradually increasing with depth. The minimum recorded value was 11.7 at Cracknore and a maximum of 34.1 at Calshot.

1.5.2. Dissolved oxygen.

Oxygen concentration and oxygen saturation for the three depths at Cracknore, and at 2 and 8 metres at NW.Netley and Calshot are illustrated in Figure 4.

Overall, in 2001 the oxygen concentration values of the depths and stations decreased from 7 - 8 ml l^{-1} in the beginning of the year to 5 – 6 ml l^{-1} in November 2001. During this period two peaks of >8.6 ml l^{-1}, in May and July, and another one of 7.4 ml l^{-1} in August were observed at Cracknore; with only one of >7.9 ml l^{-1} clearly discernible in May at NW.Netley and Calshot. From December 2001 values start to increase again, and by January 2002 concentrations again reach 7 - 8 ml l^{-1}, and again decline in spring towards July 2002. A slight increase was noted in April 2002 at all stations but no peaks, as in 2001, were observed. Usually the oxygen concentration were the same through the water column, exceptions occurring during the peaks of 2001 where oxygen concentrations were higher at the surface and 2 meters, compared with the values found at 8 meters.

In terms of saturation, values stayed between 90 and 100% throughout the 2001 – 2002 season at all stations. Peaks on February 2001 (115%), May 2001 (144%), July 2001 (164%), August 2001 (137%) and April 2002 (114%) were observed at Cracknore, while at NW.Netley and Calshot they were only observed on May 2001 (>128%), August 2001 (113%) and April 2002 (112%).

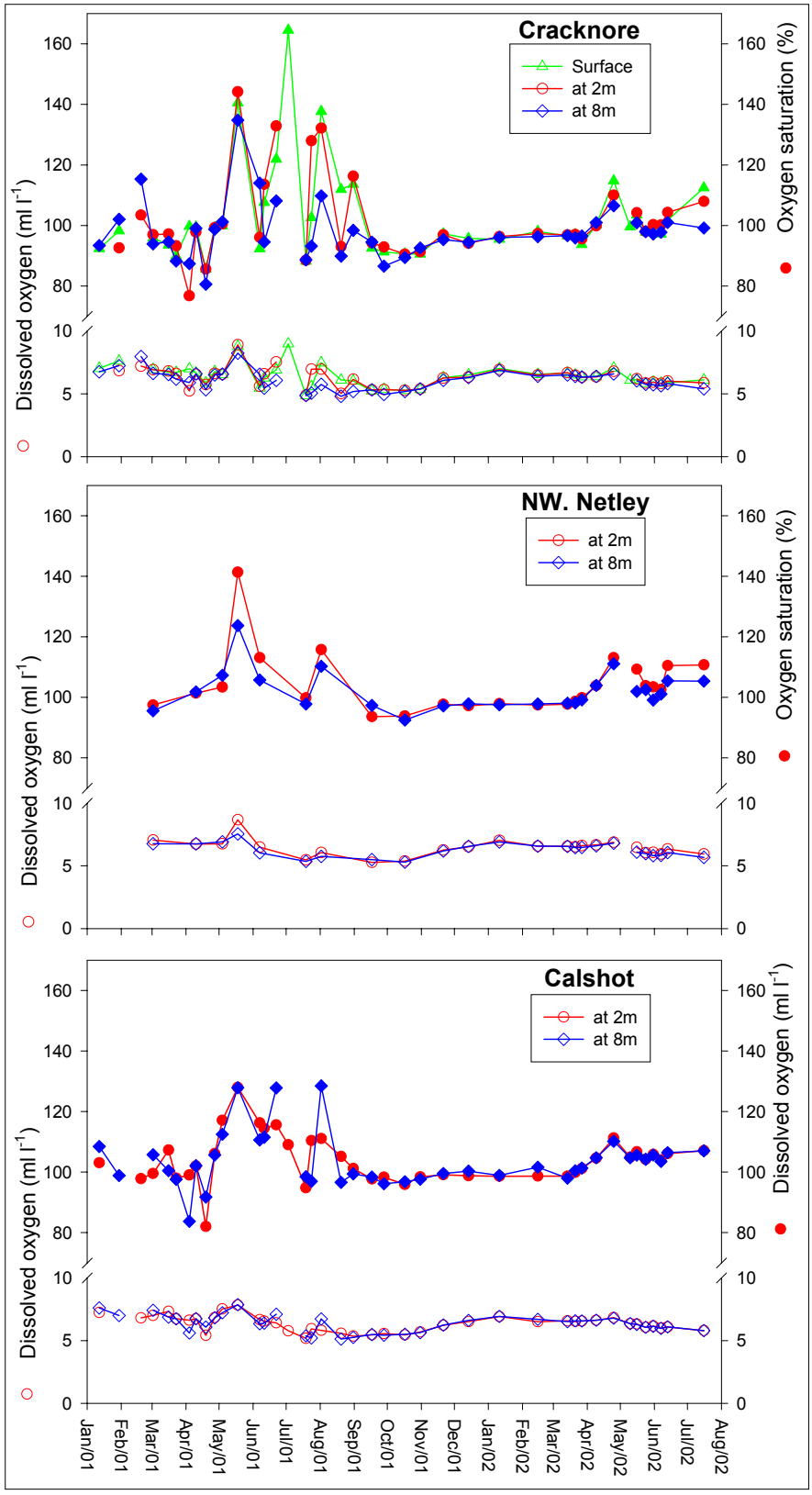


Figure 4 - Temporal variability of dissolved oxygen concentration (open symbols) and oxygen saturation (solid symbols) for the three stations in Southampton Water during 2001/02. A break in the plot indicates lack of data.

1.5.3. Chlorophyll *a*.

Measured chlorophyll *a* concentration for the three depths at Cracknore and 2 and 8 metres depths at NW.Netley and Calshot are shown in Figure 5.

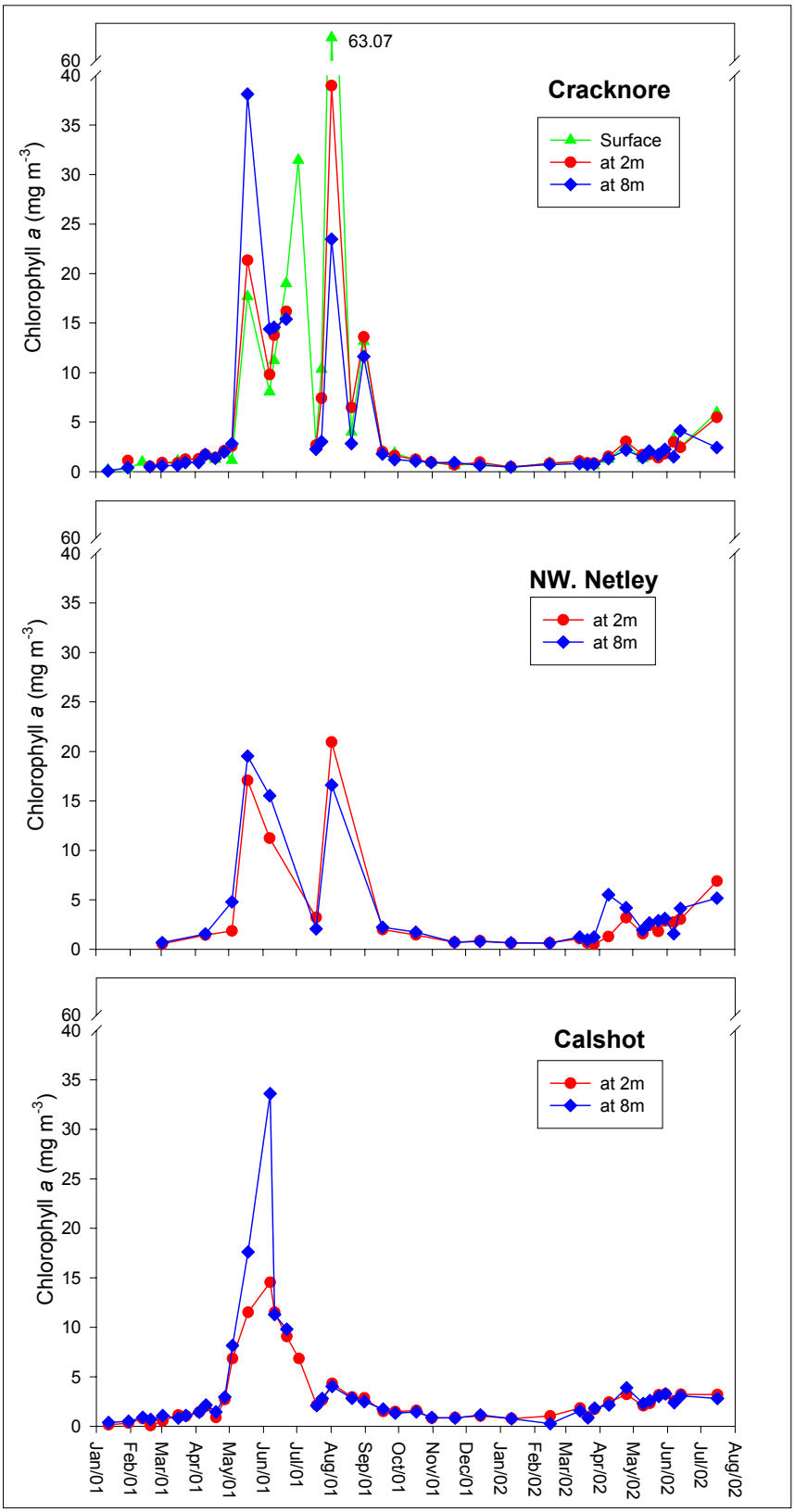


Figure 5 - Temporal variability in the concentration of Chlorophyll *a* at the three stations in Southampton Water during 2001/02. A break in the plot indicates lack of data.

It is clear that during winter 2001 the initial concentration of chlorophyll *a*, at all three sites, was usually <2 mg m^{-3} (Figure 5). After May, and until the end of August the concentration of chlorophyll *a* increased to an average of 15 mg m^{-3} in Cracknore, 13 mg m^{-3} in NW.Netley and 8 mg m^{-3} in Calshot, with four peaks being observed at Cracknore, two in N.W Netley and only one in Calshot. After this, in September, concentrations returned to values around or lower than 2 mg m^{-3}. In 2002 the chlorophyll *a* values started to increase slowly only after May, with no major peaks observed.

Generally, the level of chlorophyll *a* was uniform with depth during the low concentration period. However, during May and through September, the upper layers usually recorded higher concentrations (Figure 5).

1.5.4. Zooplankton.

During the present study 276,348 organisms were counted and identified at the 3 stations. A total of 144 different taxa were found within the zooplankton of Southampton Water during this study, with 92 identified to species, 30 to genus and 22 identified at a higher level. Of these 90 taxa are recorded for the first time within the zooplankton of this estuary (see the species with ★ in Table 3 – note that this list also includes 3 new taxa observed on samples of previous investigations). Only an overall list of species will be presented in this chapter, the results concerning each species/group will be detailed in Chapters 2 and 3.

A photographic record of most species/organisms identified during the present investigation can be seen in Appendix V (or on the attached CD, which presents a pdf file containing "The Mesozooplankton of the Solent-Southampton Water system: A photographic guide" which was elaborated from data obtained during the present investigation, and made available as Internal document No 97 of the Southampton Oceanography Centre (Muxagata & Williams, 2004 unpublished manuscript). Numbers in front of each taxa in Table 3 indicate the number of the picture in Appendix V.

Table 3- Taxa reported in the zooplankton of Southampton Water, with all previous records. (Part 1 of 4)

Phylum Protozoa
Class Sarcodina
Subclass Rhizopoda
Order Foraminifera
1-Unidentified (13,14)
Phylum Cnidaria
2-Unidentified (**15**)
Class Scyphomedusae
Order Samaeostomeae
Family Ulmaridae
3-*Aurelia aurita* (Linnaeus, 1758) (4,7,9,11,14,**15**)
Class Leptolida
Subclass Anthoathecatae
Order Capitata
Family Corynidae
4-*Sarsia* sp. (11,**15**)
Subclass Leptothecatae
Order Conica
Suborder Campanulinida
Family Phialellidae
5-*Phialella quadrata* (Forbes,1848) (11,**15**)
Order Proboscoida
Suborder Campanulariida
Family Campanulariidae
6-*Clytia hemisphaerica* (Linnaeus, 1767) (11,**15**)
7-*Obelia* sp. (11)
Phylum Ctenophora
Class Tentaculata
Order Cydippida
Family Pleurobrachiidae
8-*Pleurobrachia pileus* (O F Müller, 1776)(4,9,11,12,14,**15**)
Class Nuda
Order Beroida
Family Beroidae
Beroe sp. (7,11)
Phylum Mollusca
Unidentified (11)
Class Gastropoda
9-Veliger unidentified (4,11,13,14,**15**)
Order Mesogastropoda
Family Littorinidae
10-*Littorina littorea* (Linnaeus, 1758) (4,14)
Class Pelecypoda
11-Veliger unidentified (4,9,11,13,14,**15**)
Order Mytiloida
Family Mytilidae
Mytilus edulis Linnaeus, 1758 (4)
Class Cephalopoda
12-Unidentified ∗ (**16**)
Phylum Annelida
Class Polychaeta
13-Unidentified (4,9,11,13,14,**15**)
Order Phyllodocida
Family Syllidae
14-*Autolytus edwardsi* Saint-Joseph, 1886 (14,**15**)
Order Spionida
15-Unidentified spionidea larvae (**15**)
Family Spionidae
Polydora ciliata (Johnston, 1838) (5,6)
Polydora cornuta Bosc, 1802 (5)
Phylum Chelicerata
Class Arachnida
Subclass Acari
Order Acarina
16-Unidentified ∗(**15**)
Class Pycnogonida
Family Ammotheidae
17-*Achelia* sp. ∗ (**15**)
Family Nymphonidae
18-*Nymphon brevirostre* Hodge, 1863 ∗ (**15**)

Phylum Crustacea
Class Branchiopoda
Subclass Diplostraca
Order Cladocera
Unidentified (9)
Suborder Eucladocera
Superfamily Daphnioidea
Family Bosminidae
19-*Bosmina* sp. ∗(**15**)
Family Chydoridae
20-Unidentified ∗(**15**)
Family Daphniidae
21-*Daphnia* sp. ∗(**15**)
Superfamily Polyphemoidea
Family Polyphemidae
22-*Evadne nordmanni* Lovén,1836 (14,**15**)
Family Podonidae
23-*Podon* sp. (14)
Class Maxillopoda
Subclass Cirripedia
Unidentified (4,9,11,13)
Order Thoracica
Suborder Lepadomorpha
Family Lepadidae
24-*Conchoderma* sp. ∗(**15**)
Suborder Verrucomorpha
Family Verrucidae
25-*Verruca stroemia* (O F Müller, 1776) (2,**15**)
Suborder Balanomorpha
Superfamily Chthamaloideaa
Family Chthamalidae
26-*Chthamalus stellatus* (Poli, 1791)∗(**15**)
Superfamily Balanoidea
Family Archaeobalanidae
27-*Elminius modestus* Darwin, 1854 (2,6,10,**15**)
28-*Semibalanus balanoides* (Linnaeus, 1767) (1,2,6,**15**)
Family Balanidae
29-*Balanus crenatus* Bruguière, 1789 (2,6,**15**)
30-*Balanus improvisus* Darwin, 1854 (2,**15**)
Order Acrothoracica
Suborder Apygophora
Family Trypetesidae
31-*Trypetesa* sp. ∗ (**15**)
Order Rhizocephala
Suborder Kentrogonida
Family Sacculinidae
32-*Sacculina carcini* J.V. Thompson, 1836 (2,**15**)
Family Peltogastridae
33-*Peltogaster paguri* Rathke, 1842 (2,10,**15**)
Subclass Copepoda
34-Unidentified nauplii (11,13,**15**)
Order Calanoida
Unidentified (9,11)
Superfamily Diaptomoidea
Family Acartiidae
35- *Acartia bifilosa* (Giesbrecht, 1881) (1,4,13,14,**15**)
36-*Acartia tonsa* Dana, 1849 (1,4,14,**15**)
37-*Acartia clausi* Giesbrecht, 1889 (1,4,6,13,14,**15**)
38-*Acarita discaudata* (Giesbrecht, 1881) (1,4,6,13,14,**15**)
39-*Acartia margalefi* (Alcaraz, 1976) (13,14,**15**)
Acartia grani (G.O.Sars, 1904) (3,4)
Family Centropagidae
40-*Centropages hamatus* (Lilljeborg, 1853) (1,4,6,13,14,**15**)
41-*Centropages typicus* Kröyer, 1849 (13,14)
42-*Isias clavipes* Boeck, 1865 (14,**15**)
Family Parapontellidae
43-*Parapontella brevicornis* (Lubbock, 1857) (13,14,**15**)
Family Pontellidae
44-*Anomalocera patersoni* Templeton, 1837 (14,**15**)
45-*Labidocera wollastoni* (Lubbock, 1857) (14,**15**)
Family Temoridae
46-*Eurytemora affinis*[a] (Poppe, 1880) (4,11,13,14,**15**)
47-*Temora longicornis* (O F .Müller, 1795) (1,4,13,14,**15**)

Table 3- Taxa reported in the zooplankton of Southampton Water, with all previous records. (Part 2 of 4)

Phylum Crustacea (cont.)
Class Maxillopoda (cont.)
Subclass Copepoda (cont.)
Order Calanoida (cont.)
Superfamily Clausocalanoidea
Family Clausocalanidae
48-*Pseudocalanus elongatus*[b] (Boeck, 1864) (1,4,13,14,**15**)
Family Stephidae
49-*Stephos minor* (T Scott, 1892) (14)
50-*Stephos scotti* G O Sars, 1902 (14, **15**)
Superfamily Calanoidea
Family Calanidae
51-*Calanus helgolandicus*[c] (Claus, 1863) (1,4, 13,14,**15**)
Family Paracalanidae
52-*Paracalanus parvus* (Claus, 1863) (1,4,13, 14,**15**)
Superfamily Pseudocyclopoidea
Family Pseudocyclopiidae
53-*Pseudocyclopia* sp. ∗ (**15**)
Order Harpacticoida
54- Unidentified (9,11,13,**15**)
Suborder Polyarthra
Family Canuellidae
55-*Canuella* sp. (4,**15**)
Suborder Oligarthra
Superfamily Ectinosomatoidea
Family Ectinosomatidae
56-*Microsetella norvegica* (Boeck, 1864)∗(**15**)
Superfamily Tachidioidea
Family Harpacticidae
Harpacticus spp. (4)
Harpacticus flexus Brady & Robertson, 1873 (4, 13)
Zaus sp. (14)
Family Euterpinidae
57-*Euterpina acutifrons* (Dana, 1849) (4,6,13,14,**15**)
Family Peltidiidae
Alteutha sp. (14)
Family Tisbidae
58-*Sacodiscus* sp. ∗ (**15**)
59-*Tisbe* spp. ∗ (**15**)
Family Thalestridae
60-*Thalestris* sp.∗(**15**)
Order Cyclopoida
61-Unidentified (13,**15**)
Family Cyclopinidae
62-*Cyclopinoides littoralis* (Brady, 1872) ∗(**15**)
Family Notodelphydae
63-Unidentified ∗ (**15**)
64-*Notodelphys allmani* Thorell, 1859 (14)
Family Oithonidae
65-*Oithona nana*[d] Giesbrecht, 1892 (14,**15**)
66-*Oithona similis*[e] Claus, 1863 (4,13,14)
Order Poecilostomatoida[f]
Family Corycaeidae
67-*Corycaeus anglicus* Lubbock, 1855 (14, **15**)
Family Oncaeidae
68-*Oncaea* sp. ∗(**15**)
Oncaea similis G O Sars, 1918 (14)
Order Siphonostomatoida
69-Unidentified (14,**15**)
Family Asterocheridae
70-*Asterocheres* sp. ∗(**15**)
Family Caligidae
71-*Caligus elongatus* von Nordmann, 1832 ∗(**15**)
72-*Caligus minimus* Otto, 1821 ∗(**16**)
Family Cancerillidae
73-*Cancerilla tubulata* Dalyell, 1851∗(**15**)
Family Artotrogidae
74-*Bradypontius papillatus*[g] (T Scott, 1888)∗(**15**)
Order Monstrilloida
Unidentified (14)
Family Monstrillidae
Monstrilla sp. (13)
75-*Monstrilla conjunctiva* Giesbrecht, 1902 ∗(**15**)
76-*Monstrilla helgolandica* Claus, 1863 ∗(**15**)
77-*Cymbasoma*[h] *longispinosus* (Bourne, 1890)∗(**15**)
78-*Cymbasoma*[h] *rigidus* (I C Thompson, 1888)∗(**15**)
79-*Cymbasoma*[h] *thompsoni* Giesbrecht, 1892 ∗(**15**)
Class Ostracoda
80-Unidentified (13,14,**15**)
Class Malacostraca
Subclass Hoplocarida
Order Stomatopoda
Suborder Unipeltata
Family Squillidae
81-*Rissoides desmaresti* (Risso, 1816) ∗(**15**)
Subclass Eumalacostraca
Order Mysidacea
Unidentified (11)
Suborder Mysida
Family Mysidae
82- *Siriella armata* (H Milne-Edwards, 1837)∗ (**15**)
83- *Siriella clausii* (G O Sars, 1877)∗ (**15**)
84- *Anchialina agilis* (G O Sars, 1877)∗ (**15**)
85- *Gastrosaccus sanctus* (van Beneden, 1861)∗(**15**)
86- *Leptomysis lingvura* (G O Sars, 1866)∗(**15**)
87- *Mysidopsis gibbosa* G O Sars, 1864 ∗ (**15**)
88- *Acanthomysis longicornis*(H Milne-Edwards, 1837)∗(**15**)
89- *Mesopodopsis slabberi* (P J van Beneden, 1861)(4,14,**15**)
90- *Paramysis arenosa* (G O Sars, 1877) ∗(**15**)
Neomysis integer (Leach, 1814) (4)
91- *Schistomysis kervillei* (G O Sars, 1885)∗(**15**)
Order Isopoda
Suborder Gnathiidea
Family Gnathiidae
92- Unidentified praniza ∗ (**15**)
Suborder Valvifera
Family Idoteidae
93- *Idotea* sp. ∗ (**15**)
Suborder Epicaridea
94-Unidentified cryptonistic form ∗ (**15**)
Order Amphipoda
Unidentified (11,14)
Suborder Gammaridea
95-Unidentified (**15**)
Superfamily Leucothoidea
Family Amphilochidae
96-*Amphilochus manudens* Bate, 1862 ∗(**15**)
97-*Gitana* sp.∗(**15**)
Family Pleustidae
98-*Parapleustes* sp.∗(**15**)
Superfamily Corophioidea
Family Aoridae
99-*Aora gracilis* (Bate, 1857)∗(**15**)
Family Corophiidae
100-*Corophium* spp.∗(**15**)
Family Ischyroceridae
101-*Jassa* sp.∗(**15**)
Superfamily Eusiridae
Family Eusiridae
102-*Apherusa* spp.∗(**15**)
Superfamily Dexaminoidea
Family Dexaminidae
103-*Atylus vedlomensis* (Bate & Westwood, 1862)∗(**15**)
Superfamily Gammaroidea
Family Gammaridae
104-*Echinogammarus marinus* (Leach, 1815)∗(**15**)
Superfamily Melphidippoidea
Family Melphidippidae
Megaluropus agilis Hoek, 1889∗(**15**)

Table 3- Taxa reported in the zooplankton of Southampton Water, with all previous records. (Part 3 of 4))

Phylum Crustacea (cont.)
Class Malacostraca (cont.)
Subclass Eumalacostraca (cont.)
Order Amphipoda (cont.)
Suborder Gammaridea (cont.)
Superfamily Hadzioidea
Family Melitidae
Melita sp. ∗(**15**)
Superfamily Lysianassoidea
Family Lysianassidae
105-*Orchomene humilis* (Costa, 1853)∗(**15**)
Superfamily Synopioidea
Family Argissidae
Argissa hamatipes (Norman, 1869)∗(**15**)
Superfamily Phoxocephaloidea
Family Phoxocephalidae
106-*Parametaphoxus fultoni* (T Scott, 1890)∗(**15**)
Suborder Caprellidea
Superfamily Caprelloidea
Family Caprellidae
107- *Pariambus typicus* (Kröyer, 1845)∗(**15**)
Superfamily Phtisicoidea
Family Phtisicidae
108- *Phtisica marina* Slabber, 1769 ∗(**15**)
Order Cumacea
Family Pseudocumatidae
109-*Pseudocuma similis* G O Sars, 1900 ∗(**15**)
Subclass Eucarida
Order Euphausiacea
Family Euphausiidae
110-Unidentified (14,**15**)
111-*Meganyctiphanes norvegica* (M Sars, 1857) ∗ (**15**)
Order Decapoda
Unidentified (11)
Suborder Pleocyemata
Infraorder Caridea
Unidentified (9)
Superfamily Palaemonoidea
Family Palaemonidae
112-*Palaemon* spp.∗ (**15**)
113-*Palaemon elegans* Rathke, 1837 ∗(**15**)
Superfamily Alpheoidea
Family Alpheidae
114-*Alpheus glaber* (Olivi, 1792*)*∗(**15**)
115-*Athanas nitescens* (Leach, 1814*)*∗(**15**)
Family Hippolytidae
116-*Hippolyte* spp. ∗ (**15**)
117-*Thoralus cranchii* (Leach, 1817)∗(**15**)
Family Processidae
118-*Processa* sp. ∗(**15**)
Superfamily Crangonoidea
Family Crangonidae
119-*Crangon crangon* (Linnaeus, 1758)∗(**15**)
120-*Crangon bispinosus* (Hailstone, 1835)∗(**15**)
121-*Crangon trispinosus* (Hailstone, 1835)∗(**15**)
122-*Crangon fasciatus* (Risso, 1816)∗(**15**)
Infraorder Thalassinidea
Superfamily Thalassinoidea
Family Axiidae
123-*Axius stirhynchus* Leach, 1815 ∗(**15**)
Family Callianassidae
124-*Callianassa* sp. ∗(**16**)
Family Upogebiidae
125-*Upogebia* sp.∗(**15**)
Infraorder Palinura
Superfamily Palinuroidea
Family Scyllaridae
Scyllarus sp.[i] (6)
Infraorder Anomura
Unidentified (9,14)
Superfamily Paguroidea
Family Diogenidae
126-*Diogenes pugilator pugilator* (Roux, 1829)∗(**15**)
Family Paguridae
Unidentified (14)
127-*Anapagurus hyndmanni* (Bell, 1845)∗(**15**)
128-*Pagurus bernhardus* (Linnaeus, 1758)∗(**15**)
Superfamily Galatheoidea
Family Galatheidae
129-*Galathea squamifera* Leach, 1814 ∗(**15**)
Family Porcellanidae
130-*Pisidia longicornis* (Linnaeus, 1767) (6,14, **15**)
131-*Porcellana platycheles* (Pennant, 1777) ∗ (**15**)
Infraorder Brachyura
Unidentified (9,13,14)
Superfamily Leucosioidea
Family Leucosiidae
132-*Ebalia tuberosa* (Pennant, 1777)∗(**15**)
133-*Ebalia tumefacta* (Montagu, 1808)∗(**15**)
Superfamily Majoidea
Family Majidae
134-*Maja squinado* (Herbst, 1788)∗(**15**)
135-*Hyas* sp. ∗(**15**)
136-*Inachus* sp.∗(**15**)
137-*Macropodia* spp.∗(**15**)
138-*Pisa* sp.∗(**15**)
Superfamily Cancroidea
Family Corystidae
139-*Corystes cassivelaunus* (Pennant, 1777)∗(**15**)
Superfamily Portunoidea
Family Portunidae
140-*Liocarcinus* spp.∗(**15**)
Necora puber (Linnaeus, 1767) (2)
141-*Carcinus maenas* (Linnaeus, 1758)∗ (**15**)
Superfamily Xanthoidea
Family Xanthidae
142-*Pilumnus hirtellus* (Linnaeus, 1761)∗(**15**)
Superfamily Pinnotheroidea
Family Pinnotheridae
143-*Pinnotheres pisum* (Linnaeus, 1767)∗(**15**)
Phylum Phoronida
Family Phoronida
144-Actinotrocha unidentified* (**15**)
Phylum Bryozoa
145-Cyphonaute unidentified (4,13,14,**15**)
Phylum Chaetognatha
Unidentified (14)
Class Sagittoidea
Order Phragmorpha
Family Spadellidae
146-*Spadella cephaloptera* (Busch, 1851) ∗ (**15**)
Order Aphragmophora
Suborder Ctenodontia
Family Sagittidae
147-*Sagitta setosa* (J Müller, 1847) (4,5,11,12,**15**)
Phylum Echinodermata
Class Ophiuroidea
Order Ophiurida
Family Amphiuridae
148- *Amphipholis squamata* (Chiaje, 1828) ∗ (**15**)
Phylum Chordata
Subphylum Tunicata
Class Appendicularia
Order Copelata
Family Oikopleuridae
149-*Oikopleura* sp. (4,9,11,13,14,**15**)
Class Ascidiacea
150-Unidentified (9,13,14,**15**)

Table 3- Taxa reported in the zooplankton of Southampton Water, with all previous records. (Part 4 of 4))

Phylum Chordata (cont.)
Subphylum Pisces
Class Osteichthyes
151-Unidentified fish egg (3,9,11,14,**15**)
152-Unidentified fish larvae (3,9,11,13,14,**15**)
Family Gobiidae
Pomatoschistus minutus (Pallas, 1970) (8)

∗ Taxon reported for the first time within the zooplankton of this estuary

References:

1 = Conover (1957);
2 = Soares (1957);
3 = Lance &Raymont (1964);
4 = Raymont & Carrie (1964);
5 = Bird (1972);
6 = Barlow & Monteiro (1979);
7 = Reubold (1988);
8 = Hayes *et al.* (1989)
9 = Zinger (1989);
10 = Geary (1991);
11 = Lucas (1993);
12 = Frid *et al*. (1994)
13 = Hirst (1996);
14 = Castro–Longoria (1998);
15 = Present study.
16 = Personal observation on previous samples.

Note:
Other references are available on the Zooplankton of Southampton Water, but were based on data generated primarily from the references detailed above.

[a] *Eurytemora affinis* = *Eurytemora hirundoides* (Nordquist, 1888), see Busch & Brenning, 1992

[b] *Pseudocalanus elongatus* = Three forms of *Pseudocalanus minutus* were regarded as belonging to this genera *P. m. elongatus*; *P. m. major* and *P. m. gracilis* as described by Farran (1951). The species described by Conover (1957) as *P. minutus* were now known to be *P. m. elongatus* or simply *P. elongantus* as it is generally know nowadays.

[c] *Calanus helgolandicus* = Previous studies within this estuary misidentified *C. helgolandicus* as *Calanus finmarchicus* according to Hirst (1996). During this study the only Calanidae found here was *C. helgolandicus* according with the descriptions in Sars (1903).

[d] *Oithona nana* = *Oithona minuta* (Kritchaguine, 1873) as suggested by Hansson (1998).

[e] *Oithona similis* = *Oithona helgolandica* Claus, 1863 as indicated in Howson & Picton (1997).

[f] Poecilostomatoida = According to Boxshall & Halsey (2004) , Poecilostomatoida is not considered as a different order any more, with all families attributed to this order being part of the Cyclopoida. However, during this study it was decided to follow the old classification.

[g] *Bradypontius papillatus* = Howson & Picton (1997) includes *B. papillatus* into the family Dyspontiidae, but Boxshall & Halsey (2004) and references therein, includes *B.papillatus* into the Artotrogidae.

[h] *Cymbasoma* = Howson & Picton (1997) uses *Thaumaleus*, but this work followed Boxshall & Halsey (2004) and references therein, where *Thaumaleus* is not a valid genus with *Cymbasoma* being assigned.

[i] *Scyllarus* sp. = Barlow & Monteiro (1979) recorded the larvae of *Scyllarum* (?) spp. withim this estuary, but since no decapod is associated to this genera, I believe that in fact, this was a misprint error when they were referring to *Scyllarus* sp., probably, *Scyllarus arctus* since this is the only species that have been reported around (Bodo *et al*., 1965; Howson, 1987).

1.5.4.1. Total abundance.

Throughout the text when referring to seasonal averages, its important to note that spring is considered from 21st March to 20th June; Summer from 21st June to 20th September; Autumn from 21st September to 20th December and winter from 21st of December to 20th March.

As expected, the total zooplankton abundance varied with season (Figure 6) with the lowest abundances of organisms recorded during the winter at all three stations (averaging 1165 organisms m^{-3} in 2001 and 2940 organisms m^{-3} in 2002 for the three stations).

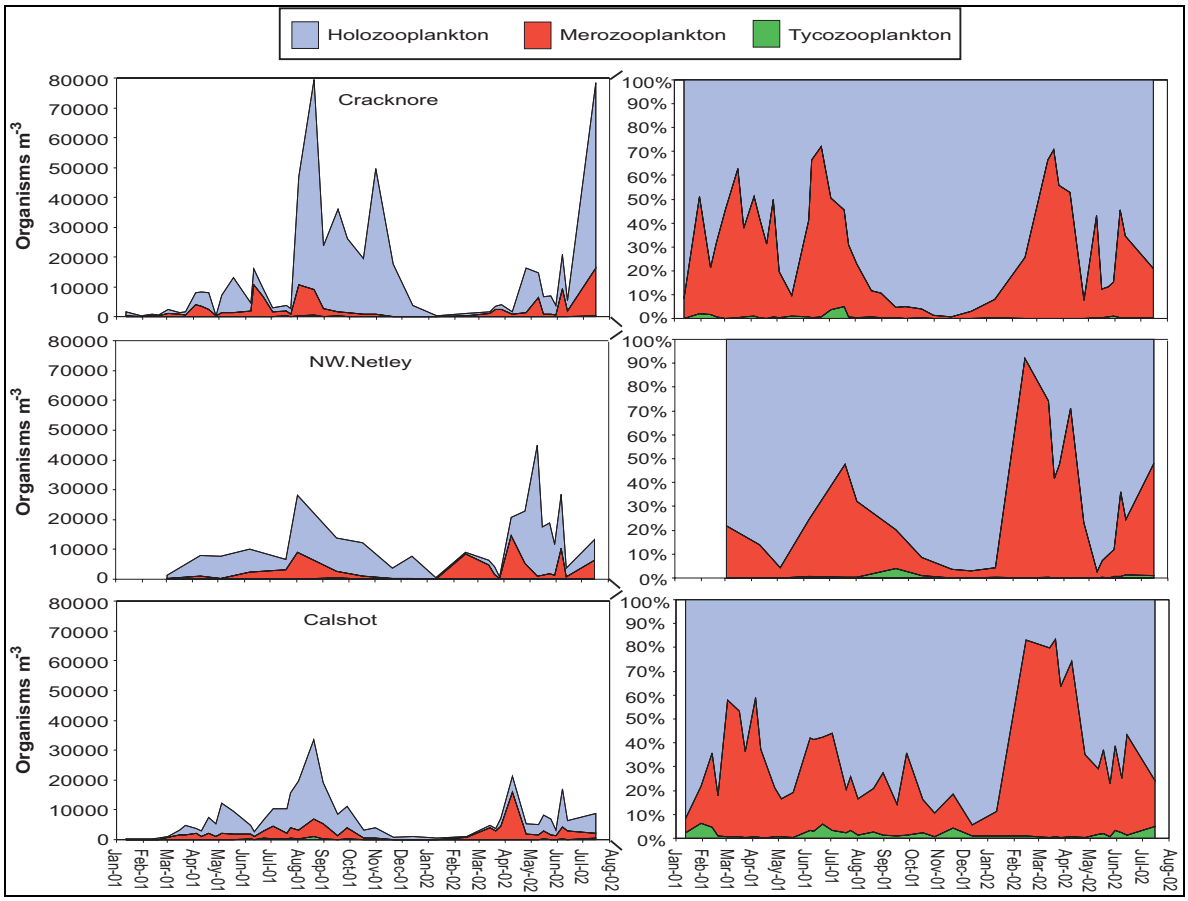


Figure 6. Temporal variability of the total abundance of zooplanktonic organisms at the three sites during 2001/02. Also shown is the percentage contribution of the holo, mero and tycoplankton on each station.

From early- spring numbers start to increase (spring averages of 7343 organisms m^{-3} in 2001 and 11376 organisms m^{-3} in 2002 for the three stations) reaching maximum values usually during the summer, where peaks of 79393, 28048, 33475 organisms m^{-3} were observed in August 2001 at Cracknore, NW.Netley and Calshot, respectively. During summer/01, large outbursts of animals were observed at Cracknore, where an average of

24728 organisms m^{-3} was maintained throughout the entire summer-autumn period at this station, with NW.Netley and Calshot presenting averages of 11986 and 11094 organisms m^{-3} for the same period, respectively.

The zooplanton community mainly comprised holoplanktonic organisms (~69% on average for the three stations), with meroplankton (~30%) abundant towards spring and summer. Tycoplanktonic organisms averaged ~1% and were much more abundant at Calshot (Figure 6).

Copepods comprised on average 95% of the holoplankton at the three stations, followed by appendicularians ~5%. The other components of the holoplankton, like euphausiids, ctenophores, cladocerans and chaetognaths only contributed with less than 1% fractions. (See Chapter 2).

Contrasting with the holozooplankton, the merozooplankton comprised a great number of organisms from different groups, such as crustacean decapod, stomatopod, barnacle larvae, parasitic copepods (cyclopoid, siphonostomatoid and monstrilloid) and isopod species; polychaete and mollusc larvae; gelatinous species (excluding the holoplanktonic ctenophore *Pleurobrachia pileus*); ascidian, bryozoan and phoronid larvae as well as fish larvae and eggs. Barnacle larvae averaged ~53 % of all meroplankton over the sample period at the three stations (Chapter 3). The tycoplankton were composed mainly of harpacticoid copepods, ~97% on average (several unidentified); with mysids, amphipods, cumaceans, isopods, ostracods and cladocerans together with the chaetognath *Spadella cephaloptera* completing the remaining fraction. (Chapter 3)

In order to be able to draw comparisons with previous investigations, the results presented in this chapter will only refer to "groups", and so only present a general overview of the zooplankton results. In this way it will act as an introduction to the dominant groups, and facilitate the presentation of the results from the generic/specific components of the holo, mero and tycozooplankton that are presented in Chapters 2 and 3. Based on this, the zooplankton component can be divided into its major components, where Copepoda averaged ~66%, Cirripedia ~18%, Polychaeta ~5%, Urochordata ~4%, Mollusca ~5%, and all the other groups, pooled under "remaining groups", ~2% for all stations over the sample period.

From Figure 7, it is clear that Copepoda constitute the major fraction the zooplankton at the three sites, with overall averages for the whole season of 10280, 8811, 4498 organisms m^{-3} followed by Cirripedia (1032, 2132, 1657 organisms m^{-3}), Mollusca (830, 668, 579 organisms m^{-3}), Urochordata (475, 529, 461 organisms m^{-3}) and Polychaeta (616, 339, 118 organisms m^{-3}) at Cracknore, NW.Netley and Calshot, respectively.

Usually, averaged abundances of each component were higher inside the estuary than at its mouth, particularly for Copepoda and Polychaeta.

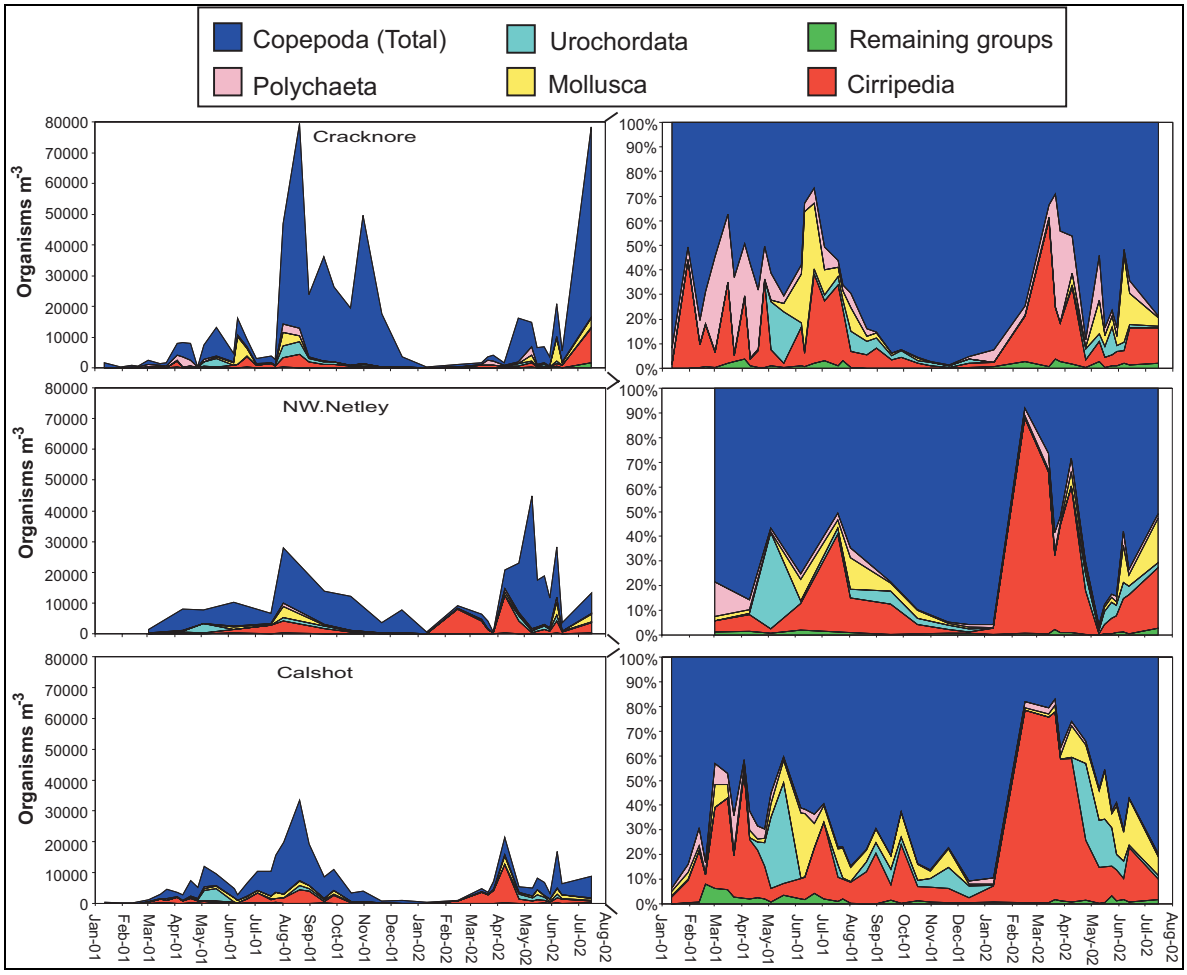


Figure 7. Temporal variability of the total abundance of Copepoda, Polychaeta, Urochordata, Mollusca, Cirripedia and all the other groups (remaining groups) at the three sites during 2001/02.

On a general basis, the abundance of each component varied with season (Figure 7). The lowest abundances of organisms were recorded during the winter at all three stations, with the exception of NW.Netley where an early outburst of barnacle larvae in 2002 increased the overall abundance at this station. From early-spring numbers of each component start to increase, reaching a spring maxima usually between April-June. Summer-autumn usually had the highest abundance values for each zooplankton component.

Although the dominant group, copepods is a broad category, and can easily be sub-divided with regard to the Order to which the species belong as: Calanoida, Harpacticoida, Cyclopoida, Poecilostomatoida, Siphonostomatoida, Monstrilloida and Copepoda nauplii.

In this study only Calanoida and Poecilostomatoida were comprised exclusively of holoplanktonic species, while Siphonostomatoida and Monstrilloida, in contrast, are composed only of meroplanktonic forms. Cyclopoida contain mainly holoplanktonic

species, but a small percentage of meroplanktonic forms were included (<1%). Harpacticoida, in comparison, are composed of 93% holoplanktonic and 7% tycoplanktonic forms.

The temporal abundance distribution of Copepoda from these 6 orders + nauplii, as well as the temporal variation of the percent contribution of each order + nauplii for the 19 month sample period can be seen in Figure 8.

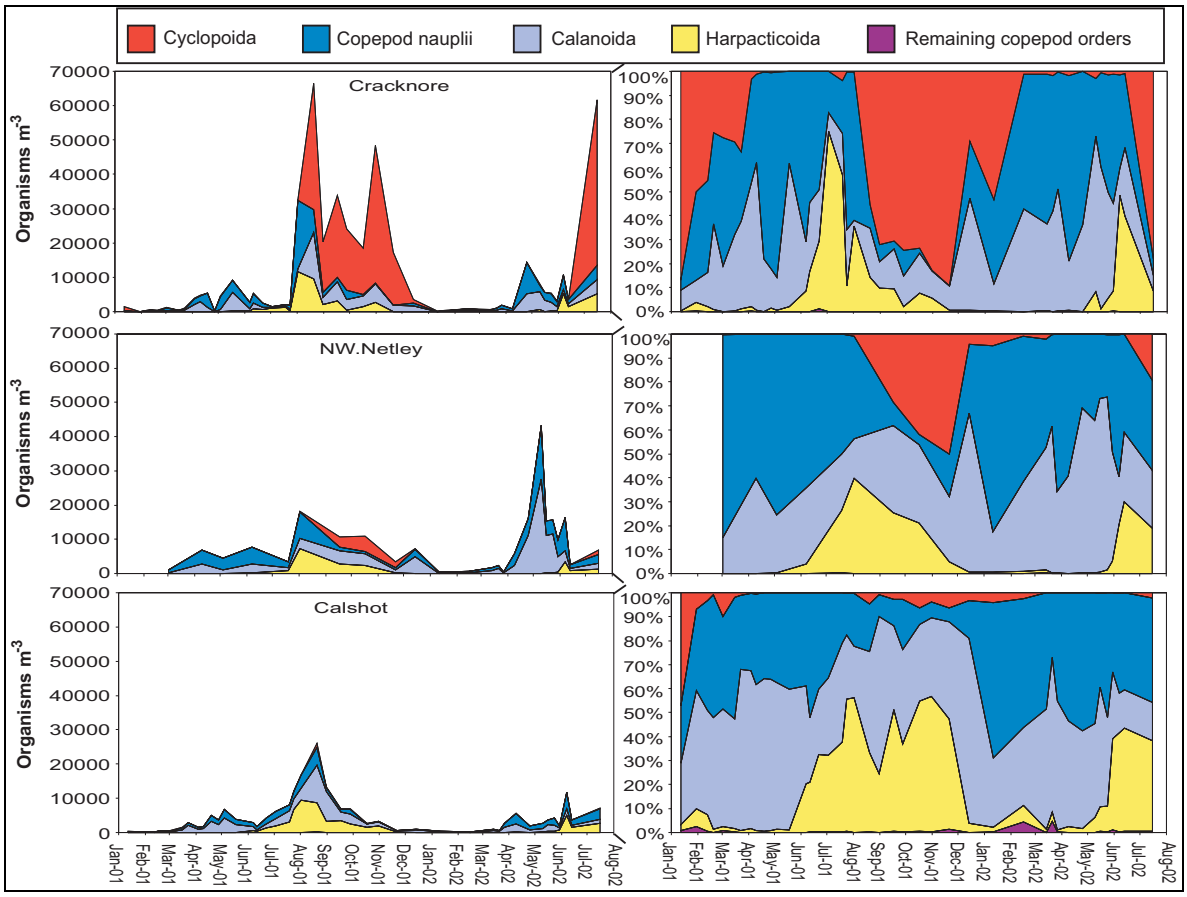


Figure 8. Temporal variability of the total abundance of the different Copepoda orders at the three sites during 2001/02.

From Figure 8 it is easy to see that only Calanoida and copepod nauplii follow the overall spring-summer pattern of abundance, with Cyclopoida and Harpacticoida presenting a summer-autumn pattern. Due to their low abundance values, Poecilostomatoida, Siphonostomatoida and Monstrilloida had to be pooled as "Remaining copepod orders", and their contribution was only noticeable during the winter, particularly at Calshot. Cyclopoida presented the highest abundances of a single order in the estuary at Cracknore during the summer-autumn months of 2001, but its importance was clearly confined to the inner reaches of the estuary and diminished towards the mouth of the estuary. In terms of total numerical dominance, Calanoida with an average for the whole season and stations of 2609 organisms m^{-3} was followed by Copepoda *nauplii* (2244

organisms m^{-3}), Cyclopoida (1891 organisms m^{-3}), Harpacticoida (1111 organisms m^{-3}) and "remaining Copepoda" (8 organisms m^{-3}).

1.5.4.2. Correlation analysis.

The physico-chemical environmental variables were correlated against each other, and with the total abundance of holo, mero and tycoplanktonic organisms (Table 4). Temperature was positively correlated with salinity, and both were positively correlated with chlorophyll *a* and negatively with dissolved oxygen. Oxygen saturation was positively correlated with temperature and chlorophyll *a*. Total abundances of holo, mero and tycoplanktonic organisms also showed positive correlations with temperature and chlorophyll *a*.

Table 4. Pearson's product-moment correlation of biotic and abiotic parameters from data collected at the three stations. Correlations in red are significant at $p<0.05$, and shaded at $p<0.01$, ns = not significant.

	T °C	S	Chl.*a*	O_2	O_2 Sat	Holo	Mero	Tyco
T °C	1.00	0.33	0.70	-0.57	0.37	0.68	0.57	0.77
S		1.00	0.19	-0.24	ns	0.24	ns	0.46
Chl.*a*			1.00	ns	0.72	0.49	0.57	0.59
O_2				1.00	0.54	-0.49	-0.31	-0.43
O_2 Sat					1.00	ns	0.21	0.32

1.6. Discussion.

1.6.1. Temperature and salinity.

The temperature and salinity results of this investigation are in agreement with the values reported during other studies in this estuary (Raymont & Carrie, 1964; Zinger, 1989; Kifle, 1992; Leakey *et al*., 1992; Iriarte, 1993; Lucas, 1993; Iriarte & Purdie, 1994; Hirst, 1996; Castro-Longoria, 1998; Hirst *et al*., 1999).

The only significant aspect of the temperature-salinity distribution, other than the seasonality of temperature, is the surface salinity stratification at Cracknore. This stratification is normal and reflects the partially mixed nature of this estuary. This is a broad estuary classification however, within the same estuary different mixing regimes in different areas can be seen (Dyer, 1973). Dyer (1973) and Ketchum (1983) discussed the types of mixing regimes that can occur in different areas of an estuary, and in this respect Southampton Water can be arbitrarily divided in two distinct zones. A well-mixed zone with almost no temperature and salinity variation with depth, that is generally found at mid-estuary and is more established towards Calshot at the mouth of the estuary. In contrast, a weak/partially stratified zone, with some surface temperature and salinity stratification, is usually found at the head of the estuary at Cracknore, and can sometimes be detected towards mid-estuary at NW.Netley

It is important to note that the very clear stratification found mostly at the beginning of the study at Cracknore could, in part, be explained by the fact that sampling was carried out after extensive flooding that occurred at the end of 2000, but without corroborative data this is only speculation.

1.6.2. Dissolved oxygen.

Normally, dissolved oxygen concentrations lie within the range of 1 - 6 ml l^{-1}, with a theoretical maximum of 14 ml l^{-1} (at 30 of salinity) (Perkins, 1974). During this investigation the value of dissolved oxygen ranged from 5 – 9 ml l^{-1} and, as expected, it was inversely correlated with both temperature and salinity. In a temperate estuary like Southampton Water with little salinity variation along the main axis, oxygen concentration usually reflects the seasonality of temperature. However, several other factors are likely to influence the concentration of oxygen within an estuary, like the input of well-oxygenated

waters, photosynthesis, re-aeration, pollution and respiratory consumption by the animals, all of which in turn, make dissolved oxygen results difficult to interpret.

By a simple superposition of the figures between Chl. *a* and dissolved oxygen a well-marked pattern can be identified, but no significant correlation between these two parameters were observed. An alternative is to express the oxygen concentration is in terms of oxygen saturation, and when this was correlated with Chl *a* strong positive correlation were evident.

1.6.3. Chlorophyll *a*.

Typical values of chlorophyll *a* in Southampton Water are reported to be 1 – 2 mg m^{-3} in the winter and 10 – 20 mg m^{-3} during the summer, with values above 40 mg m^{-3} during the peak of a bloom (Williams, 1980). The present values are within these limits, and agree with most chlorophyll *a* data reported previously for this estuary (Iriarte, 1991; Leakey *et al*., 1992; Iriarte, 1993; Kifle & Purdie, 1993; Iriarte & Purdie, 1994; Howard *et al*., 1995; Ali, 2003). Considering that values around 1 – 10 mg m^{-3} are reported as normal for other inshore and estuarine environments (Raymont, 1980), the values reported here indicate the potentially productive nature of Southampton Water, since production values of 130-177 g C $m^{-2}yr^{-1}$ have been reported by Iriarte & Purdie (1994) in a season when lower levels of chlorophyll *a* were detected.

In Southampton Water spring and summer blooms are common, with the diatoms *Skeletonema costatum* and *Guinardia delicatula* usually blooming during spring (max. 10 – 40 mg. m^{-3}) with ciliates like *Mesodinium rubrum* during summer (max 40 – 60 mg. m^{-3}) (Antai, 1989; Iriarte, 1991; Leakey *et al*., 1992; Kifle & Purdie, 1993; Ali, 2003). The seasonal pattern of the chlorophyll *a* concentration observed in this investigation during 2001 also showed this spring – summer pattern, but in 2002 no distinguishable pattern was observed. It was probable that a single summer bloom might be detected later, since chlorophyll *a* values were starting to rise toward the end of the sampling survey. This different temporal pattern cannot be interpreted as unusual, since single summer blooms have been reported within this estuary (Williams, 1980).

Phytoplankton species identification was not part of the present study, but it is important to note that the early peak in May (17 – 38 mg. m^{-3} in 18/05/02) was associated with a massive bloom of *Phaeocystis* sp. (D. Purdie pers. comm.). *Phaeocystis* sp. is a colonial prymnesiophyte algae previously reported in this estuary (Iriarte, 1991; Iriarte &

Purdie, 1994). Copepods are known to consume this alga, but it has been reported as having toxic effects on other fauna (Mauchline, 1998).

Chlorophyll *a* concentrations were positively correlated with all the other factors tested with the exception of dissolved oxygen, suggesting that the amount of available food is strongly linked with temperature, and an important driving factor of total zooplanktonic abundances. Care should be taken when interpreting these results, since rates truly occur at species level, which will be investigated in more detail in the following chapters.

1.6.4. Zooplankton.

In terms of overall general composition, the results presented here lie somewhat between the recent studies (Zinger, 1989; Lucas, 1993; Hirst, 1996; Castro-Longoria, 1998) and that of Raymont & Carrie (1964). The general similarity, that Copepoda is the dominant form followed by Cirripedia with some seasonal contribution of other meroplanktonic forms is clear. However, when examining the components making up the Copepoda differences/similarities between this study and the others arise.

During this survey, Cirripedia were observed throughout the year, but only dominated the plankton composition in short bursts, usually during spring. Calanoida were the dominant form of Copepoda during late-winter through late-spring at all three stations, with late-spring to early-summer being dominated by harpacticoids. From mid-summer through to early-winter these two, plus cyclopoids at the inner stations, occur together.

Attention should be drawn, however, to the two ends of the estuary, where contrasting situations are seen. At the mouth of the estuary, exemplified by Calshot, almost no cyclopoids were recorded and the summer-autumn period was clearly dominated by calanoids and harpacticoids. At Cracknore, cyclopoids clearly dominate the summer-autumn period, outnumbering all other organisms pooled. Based on this, a generalistic abundance pattern of copepods within this estuary during this survey might be best illustrated by the NW.Netley composition depicted in Figure 8, where cyclopoids have an intermediate importance.

From the results presented here, the major differences between this study and previous ones lies in the fact that when Copepoda were broken down to orders, it was not only composed by calanoids, with other orders like cyclopoids and harpacticoids outnumbering calanoids on particular seasons/locations (see above). Harpacticoids and cyclopoids, on average, were also most abundant even than barnacle larvae that had been previously considered as the second most abundant form after calanoids. Despite that, it is

felt that most of these differences can clearly be explained by differences in methodologies and sampling gears employed.

It was suggested earlier that probably the major differences highlighted between the early investigation of Raymont & Carrie (1964) compared with the more recent studies might be attributed to the use of different gear and sampling procedures, since Raymont & Carrie (1964) employed pumps while the majority of the remaining studies, including this one, utilized nets, albeit of different mesh sizes. Pumps are known to obtain discrete samples, although usually filtering smaller volumes when compared with towed nets (Omori & Ikeda, 1992; Sameoto *et al*., 2000). Thus, one could assume that differences between the recent studies and that of Raymont & Carrie (1964) could be due to differences based from counts of samples represented by small volumes. Supporting this is that even when similar mesh sizes is employed elsewhere, pump collected samples usually gave values of abundances 8 times higher than the net samples (Bousfield *et al*., 1975). However, this would account mainly for differences in abundance, with the different proportions of organisms probably due to other causes. Mesh sizes is certainly a factor, since retention of a particular organism by a particular mesh clearly depends of the organisms largest cross-section (Bé *et al*., 1968). Raymont & Carrie (1964) employed ~158 μm meshes in conjuction with a pump, while other studies employed towed nets with meshes within 100 – 220 μm. The use of meshes only ~30% bigger (i.e. 220 μm) than that employed by Raymont & Carrie (1964) almost completely under-sampled harpacticoids and copepod nauplii in the investigations carried out by Lucas (1993) and Castro-Longoria (1998) in this estuary, and this clearly would change the proportions of each component. Another thing that one must bear in mind is that the more shallow and protected nature of the sampling locations of Raymont & Carrie (1964) i.e. Marchwood and Calshot Pier (Figure 1) could be a place of natural accumulation/ release of barnacle nauplii.

Despite harpacticoids being noted in high numbers by Raymont & Carrie (1964), Hirst (1996) and Zinger (1989) during the summer-autumn months, they were not recorded in investigations where coarser mesh-size were employed (Lucas, 1993; Castro-Longoria, 1998), its importance was somehow excluded and/or ignored in the overall generalizations made for this estuary.

The occurrence of cyclopoids within Southampton Water is a recent feature, since they were only detected in significant numbers by Castro-Longoria (1998) at Bury Buoy (Figure 1), but due to the coarse mesh used the importance of this component, like harpacticoids, were clearly underestimated. Based on the fact that even with a 220μm mesh Castro-Longoria (1998) was able, at least, to detect this group, its complete absence from

previous studies indicates/suggests that this group only recently appeared, probably after the 1985-1987 or 1990-1991 samplings carried out at the inner estuary by Zinger (1989), and Lucas (1993), respectively.

In terms of total zooplankton numbers, the results presented here agree with previous investigations, where the inner estuary stations usually presented higher abundances. However, numbers presented in this study should only be compared with those of Zinger (1989) and Hirst (1996) where similar sampling devices were used (Figure 9).

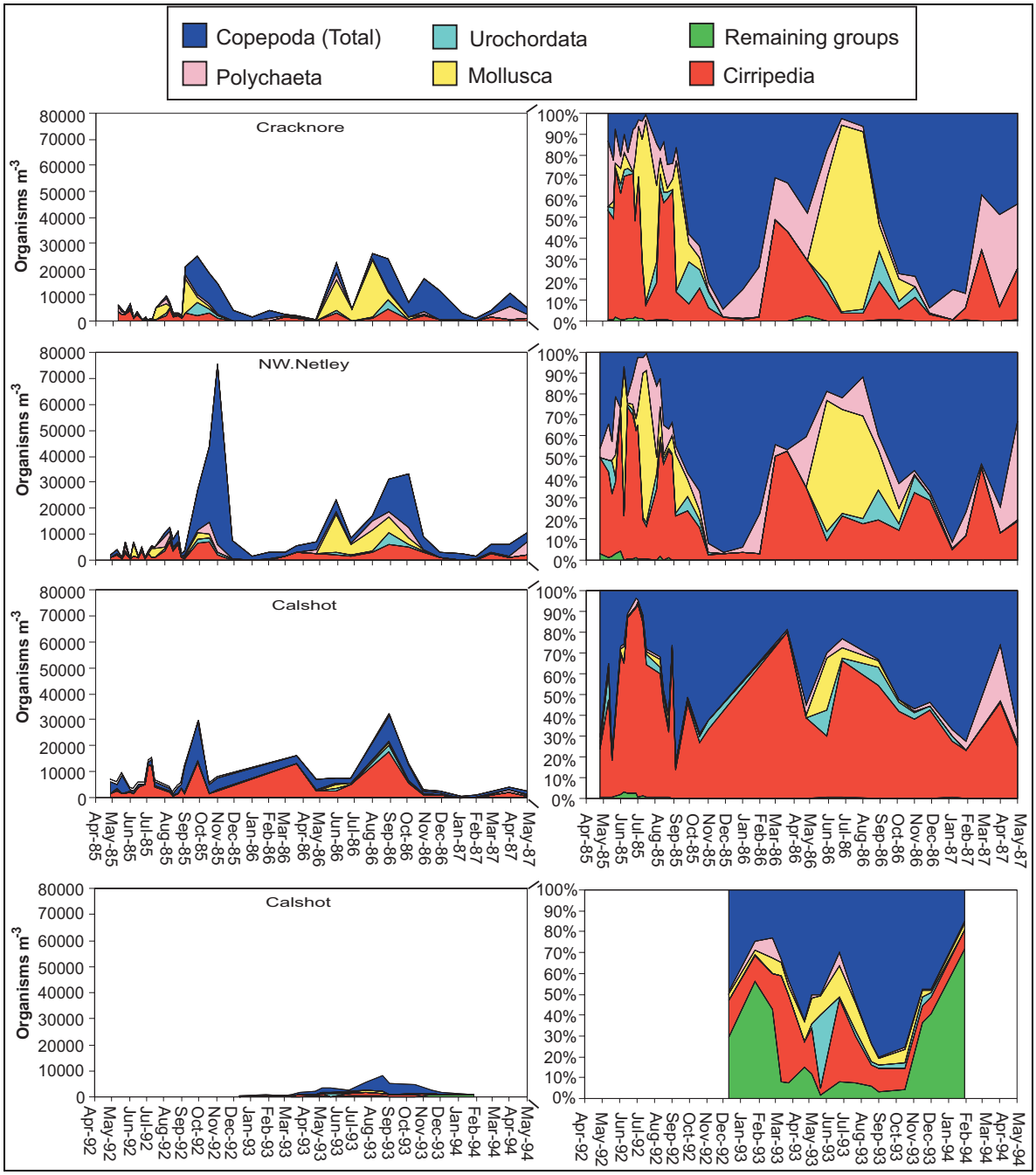


Figure 9. Temporal variability of the total abundance of Copepoda, Polychaeta, Urochordata, Mollusca, Cirripedia and all the other groups (remaining groups) at the three sites during 1985-1987 and 1992-1994, draw from the data of Zinger (1989) and Hirst (1996), respectively. (Temporal scale from the data of Hirst was extended for a better comparison with the data of Zinger).

When comparing the general composition indentified in the present study with those of Zinger (1989) and Hirst (1996) (Figure 9), the same major groups were observed, with similar seasonality. If we assume that cyclopoids did not occurred before 1990's, and that the slight finer mesh, of 100 μm, used by Zinger (1989) would efficiently capture more bivalve veligers, the results presented here are quite similar with that of 1985-1987. Differences in this case, would certainly be due to the contribution of cyclopoids and inter-annual variability. During the present study copepods had a total average of 7863 organisms m^{-3} for the three stations with maxima of 66531, 43164 and 26084 organisms m^{-3} at Cracknore, NW.Netley and Cracknore, respectively. These values are greater than the total average of 4007 organisms m^{-3}, and maxima of 16518, 69322, 15114 organisms m^{-3} at the same stations reported by Zinger (1989), and even the 1604 organisms m^{-3} average reported at Calshot by Hirst (1996). The removal of the cyclopoid component from the present study will bring total copepod values down to an overall average of 5980 organisms m^{-3} , and closer to the overall values observed by Zinger (1989)

Hirst's (1996) values are unusually low and this could, in part, be explained by his temporal coverage, where sampling occurred usually once a month and clearly missed some major peak abundances. However, it is clear that Hirst's samples must have been analysed/sampled in a different manner to other studies, since the "remaining groups" accounted for an uncharacteristic 22% of the total community, with Foraminifera accounting, on average, for 54% of this group, and 15% of the total zooplankton community.

Straightforward comparisons between numbers of different organisms obtained in different investigations are clearly simplistic, especially when several biotic and abiotic factors will determine the amount of a particular species within an estuary. However, since no major differences were observed among the environmental parameters currently measured when compared to the previous studies, it could be assumed that the influences of these variables would be the same/similar in all investigations. Equally, as sampling occurred during the same period of slack water at high tide in all investigations, this might standardize to some degree the variability introduced by tidal mixing, flushing and advection and allow comparisons between the studies. Since general trends are quite similar for several components any differences in spatial and/or temporal patterns of density might therefore be attributed primarily to different sampling efforts/methodologies and inter-annual variability.

In this study copepod nauplii were not identified to Order, but if they were sampled correctly, this group will clearly constitute the major component of any copepod analysis.

Only limited conclusions can be made from zooplankton data at the level of identification presented in this chapter and this serves primarily as a basis for the introduction of the species constituents in following chapters. Comparisons with other estuarine systems will also be drawn in following chapters, taking advantage of the more detailed identifications.

1.7. Chapter Conclusions.

- Temperature, Salinity, Chlorophyll a and Dissolved Oxygen results are in agreement with previous studies within this estuary.
- Overall, copepod nauplii and Calanoida were the numerically dominant copepod forms within this estuary for most of the seasons, with harpacticoids and cyclopoids becoming as important as calanoids from early-summer and throughout autumn.
- At the inner estuary, cyclopoids outnumber all other copepod orders together from late-summer to late-autumn.
- Barnacle larvae are the most abundant meroplanktonic component, followed by Mollusca, Urochordata and Polychaeta.
- Allowing for inter-annual variability and the occurrence of cyclopoids at the inner station, the current study compares well with previous investigations that employed similar sized meshes.

Chapter 2

The holoplankton of Southampton Water.

2.1. Introduction.

Over the past 48 years, the zooplankton community of Southampton Water have been the subject of several published reports (Conover, 1957; Raymont & Carrie, 1964; Lance & Raymont, 1964; Barlow & Monteiro, 1979; Williams & Reubold, 1990; Lucas & Williams, 1994; Lucas *et al*., 1995; Castro-Longoria & Williams, 1996; Lucas *et al*., 1997; Hirst *et al*., 1999; Muxagata *et al*., 2004), together with unpublished M.Sc. and Ph.D. reports (Soares, 1958; Bird, 1972; Frid, 1984; Reubold, 1988; Zinger, 1989; Geary, 1991; Lucas, 1993; Hirst, 1996; Castro-Longoria, 1998; Chinnery, 2002). Although differing in detail, these studies indicated that calanoid copepods from the genus *Acartia*, are the dominant holoplanktonic element in this estuary.

Acartia is represented in Southampton Water by 6 different species and according to Conover (1957), Raymont & Carrie (1964) and Hirst (1996) three of them establish a clear seasonal succession, with *A.bifilosa* the commonest species early in the year and until July when both *A.discaudata* and *A.clausi* become common, with *A.bifilosa* only reappearing in November-December. Three other *Acartia* species have also been recorded within Southampton Water: *A.tonsa* and *A.margalefi* towards the inner reaches, and *A.grani* (= *Paracartia grani*) that has been reported only in the 1960's (Conover, 1957; Raymont & Carrie, 1964; Lance & Raymont, 1964; Castro-Longoria & Williams, 1996; Hirst, 1996; Castro-Longoria, 1998; Hirst *et al*., 1999).

Of the remaining holoplanktonic calanoid species found within Southampton Water in significant numbers, *Centropages hamatus* is the next most abundant followed by *Temora longicornis*, *Paracalanus parvus, Pseudocalanus elongatus* and *Eurytemora affinis* (*affinis*) (Raymont & Carrie, 1964; Hirst, 1996; Castro-Longoria, 1998). Several other holoplanktonic calanoid copepod species were also reported to occur sporadically, and usually in very low numbers, with *Centropages typicus*, *Calanus helgolandicus* and *Parapontella brevicornis* among them (Raymont & Carrie, 1964; Hirst, 1996; Castro-Longoria, 1998). Castro-Longoria (1998) also recorded the presence of *Labidocera*

wollastoni, *Anomalocera patersoni*, *Isias clavipes*, *Stephos minor* and *Stephos scotti* in the Solent area, but stated that this species could occasionally be found within Southampton Water.

Among other copepod orders, the cyclopoids *Oithona similis* and *Oithona nana*, the harpacticoid *Euterpina acutifrons* and the poecilostomatoids *Corycaeus anglicus* and *Oncaea similis* are the remaining holoplanktonic copepods reported within Southampton Water (Raymont & Carrie, 1964; Hirst, 1996; Castro-Longoria, 1998).

Pleurobrachia pileus (Ctenophora), *Evadne nordmanii* and *Podon* sp. (Cladocera), *Sagitta setosa* (Chaetognatha) and *Oikopleura* spp. (Urochordata) represent the remaining holoplanktonic species that has been observed within the estuary (Raymont & Carrie, 1964; Lucas, 1993; Castro-Longoria & Williams, 1996). A summary of all previously reported species within the mesozooplankton of Southampton Water, as well as the findings of this study is summarized on Table 3 (Chapter 1). (Pictures of most of them can be seen on Appendix V, or in the enclosed cd containing a copy of the photographic zooplankton guide of the Solent – Southampton Water).

With so many species described, the generalization that calanoids from the genus *Acartia* are the dominant form is quite simplistic. Within the entire estuary other holoplanktonic components, like copepod nauplii, harpacticoids and cyclopoids have been recorded to outnumber calanoids in different seasons and locations (see Chapter 1). One of the problems in assessing the statement is that most of the knowledge about species composition, dominance and succession of holoplanktonic species throughout Southampton Water comes from Conover (1957), and principally Raymont & Carrie (1964). These studies remained the sole source of specific information until studies on *Pleurobrachia pileus* and *Sagitta setosa* (Lucas, 1993) and "copepods" (Hirst, 1996; Castro-Longoria, 1998; Hirst *et al*., 1999) were reported some 30 years later. Of these, only Lucas (1993) and Castro-Longoria (1998) give any information on what is occurring in the inner reaches of the estuary, but they employed net mesh sizes > 200 μm that would have under-sampled/missed the overall contribution of other zooplankton components, like copepod nauplii and harpacticoids.

It is clear that the historical generalizations based on studies that under-sampled some components and/or were based on data primarily from a single station, Calshot, at the mouth of the estuary (Conover, 1957; Hirst, 1996; Hirst *et al*., 1999) would not be expected to reflect other parts of this estuary. It is well known that abundance is usually higher within the estuary, while the diversity of zooplankton increases towards the sea (Riley, 1967; Miller, 1983). Since Calshot is marine in nature, it should have smaller

abundances and higher diversity when compared with Cracknore, within the inner reaches of the estuary. These general differences of abundances have already been presented in Chapter 1, and also observed in the studies of Raymont & Carrie (1964) and Castro-Longoria (1998) at Marchwood and Bury Buoy, respectively, but not truly investigated.

As pointed out most of the knowledge of species distribution and composition throughout this estuary is based on the study of Raymont & Carrie (1964), and as this work is now 41 years old, changes may well have modified the overall zooplankton composition in this estuary. In line with this argument is the recent report by Castro-Longoria (1998) of the cyclopoid *Oithona nana* in significant numbers toward the innermost part of Southampton Water. Previously, cyclopoids were notable absentees from the zooplankton record, and on the very few occasions when they were found, they were individuals of *Oithona similis* (Raymont & Carrie, 1964; Hirst, 1996).

While the zooplankton community structure of temperate estuaries is variable on a seasonal/annual basis it usually follows a pattern that repeats year after year (Day Jr. *et al*., 1989). Major changes in species composition have been usually attributed to climate changes and/or human activities (Soetaert & Van Rijswijk, 1993; Uye, 1994). Therefore knowledge of zooplankton composition, distribution and abundance, and the processes controlling it through time is vital and one of the major objectives of biological oceanography. Detection of any changes within an estuary, allied with retrospective studies can also give some feedback concerning major environmental changes or even human impact on the environment and can provide the baseline necessary for advanced studies and general theories/models concerning the zooplankton of this or any other estuary. So, in order to further extend the knowledge about the holoplankton of Southampton Water, a taxonomically detailed investigation of its components were carried out to observe the general/main trends on the composition, distribution and abundance of those components.

2.2. Materials and Methods.

The methodology employed for collection and identification of the different species has been fully described in Chapter 1.

2.2.1. Data analysis.

As in the previous chapter, Pearson's product-moment correlation coefficient *r* was used in order to measure the intensity of the association between the biotic and abiotic variables. To stabilize the variance of the data, zooplankton abundances were $\log_{10}(x+1)$ transformed, and the average oxygen saturation and average Chl. *a* were $\log_{10}(x)$ transformed before analysis (Prepas, 1984; Zar, 1999; Clarke & Warwick, 2001).

In order to further investigate the relationship between samples collected at different stations and seasons, a Bray-Curtis similarity matrix was constructed using all holoplaktonic species abundances after a $\sqrt{x+0.5}$ transformation. This transformation was chosen instead of $\log_{10}(x+1)$ in order to adjust the influence of numerically dominant species and so allowing for the contribution of "intermediate" species without losing information about the dominant ones.

Ordination was done by non-metric multi-dimensional scaling (MDS), with plots being calculated using the PRIMER 5 package (Clarke & Warwick, 2001). MDS plots were chosen to illustrate the results as they allow a more informative visualisation of the configuration of distances between stations than the corresponding dendrogram from the cluster analyses (Appendix VIII). Clustering does not display their inter-relations in a continuous scale, with many possible re-arrangements of the samples being possible. MDS plots attempt to satisfy all conditions imposed by the ranks of the similarity matrix, so it usually elaborates a "map" of the relative spatial distribution of the samples in a specified number of dimensions (Clarke & Warwick, 2001). Summarizing, MDS will place two samples closer and/or further apart according to their similarities, i.e. if sample "a" is more similar to "c" than "b", than sample "a" will be closer to "c" then to "b" in the plot. The theory and computations behind MDS can be found in (Kruskal, 1964; Clarke & Warwick, 2001). The stress factor is a measure of the stress required to force a two-dimensional representation upon the similarity matrix, where values <0.01 indicates a perfect representation and >0.3 indicates that the points were probably arbitrarily placed. Stress values between 0.2 and 0.3 should be discarded, while values <0.2 gives potentially useful picture (Clarke & Warwick, 2001). Values close to 0.2 should be cross-checked against

those obtained from an alternative technique (i.e. Cluster analysis), while those close to 0.1 or below corresponds to a good ordination, with no real prospect of misleading interpretations. Accordingly MDS plots were checked for consistency against dendrograms of station/season (Appendix VIII) from the cluster analysis performed on the same Bray-Curtis similarity matrix, using the group average linkage rule (= UPGMA Sneath & Sokal, 1973). After the MDS ordination was established, its relation with biological/environmental measures was visualized by superimposing bubble plots onto the ordination.

2.2.2. Other studies.

Since most of the information on this estuary is based on unpublished Ph.D. dissertations, raw data from previous investigations were compiled and graphs redrawn in order to have a better understanding when discussing/comparing results. This was already introduced in the previous chapter and will be used to substitute extensive comments on some species and/or groups.

2.3. Results.

During the present survey, a total of 31 taxa were observed among the holoplankton of this estuary, with 24 identified to species, 5 to genus and 2 to order/class (Table 5). Of these, 6 taxa are reported for the first time within this estuary. Numbers in front of each taxon, indicates the number of its picture on Appendix V.

Table 5. Holoplanktonic taxa observed in the zooplankton of Southampton Water during the present investigation. (For more details see Table 3 – Chapter 1).

Phylum Ctenophora
- 8-*Pleurobrachia pileus* (O F Müller, 1776)

Phylum Crustacea

Subclass Diplostraca

Order Cladocera
- 19-*Bosmina* sp. *
- 21-*Daphnia* sp. *
- 22-*Evadne nordmanni* Lovén,1836

Subclass Copepoda
- 34-Unidentified nauplii

Order Calanoida
- 35- *Acartia bifilosa* (Giesbrecht, 1881)
- 36-*Acartia tonsa* Dana, 1849
- 37-*Acartia clausi* Giesbrecht, 1889
- 38-*Acarita discaudata* (Giesbrecht, 1881)
- 39-*Acarita margalefi* (Alcaraz, 1976)
- 40-*Centropages hamatus* (Lilljeborg, 1853)
- 42-*Isias clavipes* Boeck, 1865
- 43-*Parapontella brevicornis* (Lubbock, 1857)
- 44-*Anomalocera patersoni* Templeton, 1837
- 45-*Labidocera wollastoni* (Lubbock, 1857)
- 46-*Eurytemora affinis* (Poppe, 1880)
- 47-*Temora longicornis* (O F Müller, 1795)
- 48-*Pseudocalanus elongatus* (Boeck, 1864)
- 50-*Stephos scotti* (G O Sars, 1902)
- 51-*Calanus helgolandicus* (Claus, 1863)
- 52-*Paracalanus parvus* (Claus, 1863)
- 53-*Pseudocyclopia* sp. ★

Order Harpacticoida
- 56-*Microsetella norvegica* (Boeck, 1864)★
- 57-*Euterpina acutifrons* (Dana, 1849)

Order Cyclopoida
- 65-*Oithona nana* Giesbrecht, 1892

Order Poecilostomatoida
- 67-*Corycaeus anglicus* Lubbock, 1855
- 68-*Oncaea sp.* ★

Subclass Eucarida

Order Euphausiacea
- 110-Unidentified
- 111-*Meganyctiphanes norvegica* (M Sars, 1857) ★

Phylum Chaetognatha

Order Aphragmophora
- 147-*Sagitta setosa* (J Müller, 1847)

Phylum Chordata

Order Copelata
- 149-*Oikopleura* sp.

★ Taxon reported for the first time within the holoplankton of this estuary

2.3.1. Total abundances.

As pointed out in chapter 1, copepods comprised the majority of the holoplankton at the three stations, followed by appendicularians. Again, if we divide the holoplankton in all its major components, copepod nauplii averages 38, 43 and 33% of the total holoplankton followed by Calanoids (26, 38 and 40%), Harpacticoids (9, 7, 16%), Cyclopoids (24, 6, 3%) and Appendicularia (3, 5 and 7%) at Cracknore, NW. Netley and Calshot, respectively, with Poecilostomatoida, and others (Cladocera, Euphausiids, Ctenophora and Chaetognatha pooled) averaging less than 1% (Figure 10).

Since only the genus *Oikopleura* (probably *O.dioica*) was observed in Southampton Water during this study, the temporal variability of abundance and composition is the same as that presented in Figure 10 under the heading Appendicularia. Overall, this species was almost absent during the winter months, with abundances < 1 organisms m^{-3} (Table 6), but during spring its abundance started to increase, remaining abundant until late autumn (spring-autumn average of 699, 602 and 557 organisms m^{-3} in 2001 for Cracknore, NW.Netley and Calshot respectively). In a single year, two peaks were observed at each station during this investigation, one in May 2001 (2736, 3032 and 3954 organisms m^{-3} at Cracknore, NW.Netley and Calshot respectively) and other in August 2001 (4079, 921, 1362 organisms m^{-3} Cracknore, NW.Netley and Calshot respectively).

Holoplanktonic harpacticoids were represented by only two species, *Microsetella norvegica* and *Euterpina acutifrons*. Since only a single individual of *M.norvegica* was observed on January 2001, *E.acutifrons* averages >99.99% of all harpacticoids depicted on Figure 10, at all the three sites. *E.acutifrons* is found all year round (Table 6) but it usually appears in significant numbers in plankton catches during April-May, becoming abundant during mid-summer (August) were peaks of 11346, 7125 and 9115 organisms m^{-3} were observed at Cracknore, NW. Netley and Calshot respectively. From mid-summer and throughout autumn, this species maintains abundances usually above 1000 organisms m^{-3} until the end of October (Table 6), when it averaged 11, 26 and 42% of the holoplankton at Cracknore, NW.Netley and Calshot respectively. After this period its abundance on plankton catches starts to decline with very few individuals (< 4 organisms m^{-3}) being observed during winter (Figure 10 and Table 6).

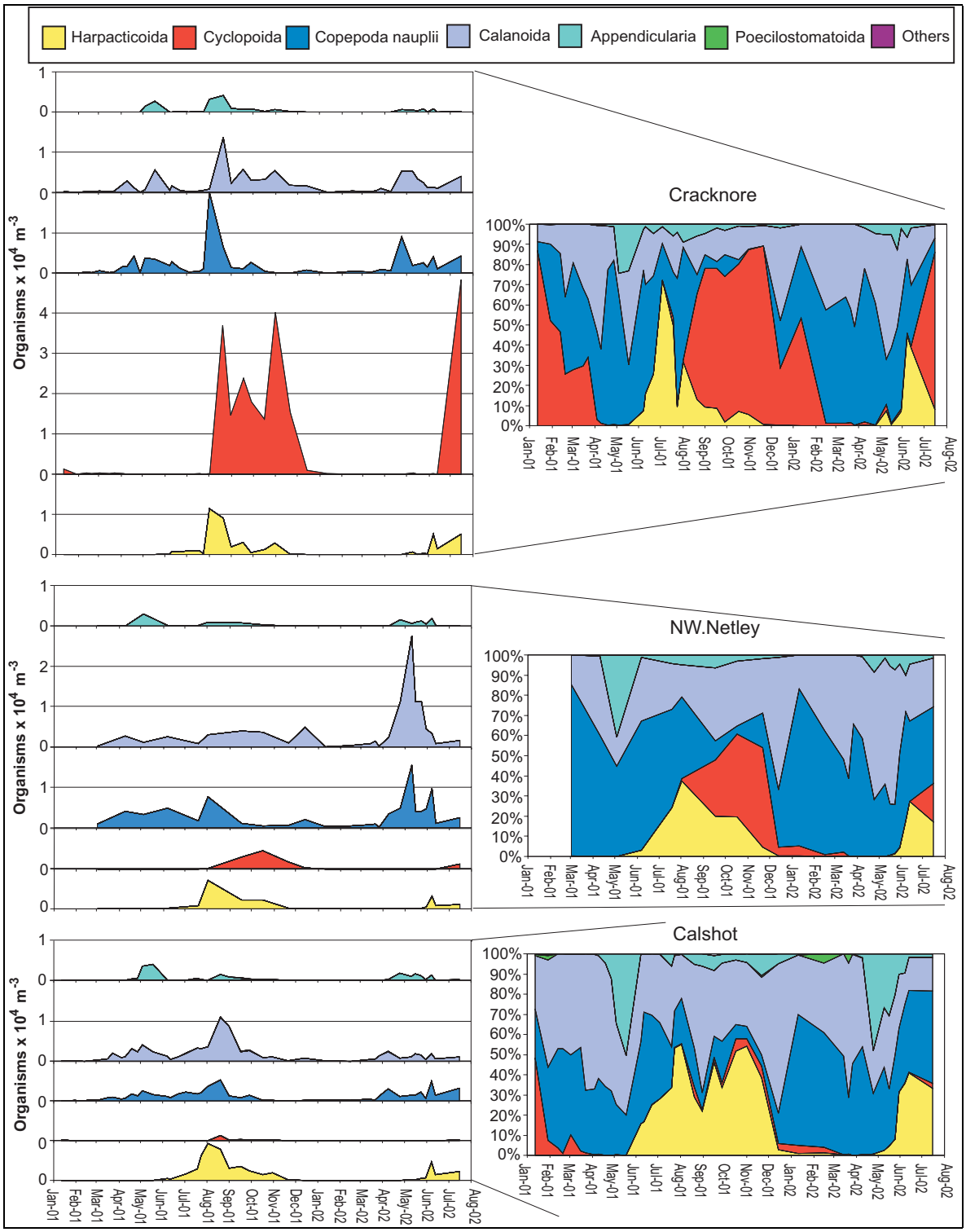


Figure 10. Temporal variability and seasonal contribution of the different Holoplanktonic groups at Cracknore, NW. Netley and Calshot during 2001/02. (Note that abundance interval indicates 10000 organisms m^{-3}).

Holoplanktonic cyclopoids were found all year round at all the three stations (Figure 10 and Table 6) especially during summer-autumn and extending until early-winter. Despite this, they were detected in high numbers only within the inner reaches of Southampton Water where, between late-summer to early-winter, they became the dominant group at Cracknore (Figure 10). *Oithona nana* was the only holoplanktonic cyclopoid copepod recorded in Southampton Water and occurred in 77% of all samples (Table 6). At Cracknore this species occurred in 90% of the samples and accounted for 51% of the total holoplanktonic copepods. *O.nana* occurred in low abundances from mid-winter through to mid-summer, but from late-summer until late-autumn *O.nana* accounted for 61% of all copepods, averaging 18192 organisms m^{-3}, with peaks of 36916, 23880 and 40092 organisms m^{-3} in August, September and October/November 2001 respectively, and 48199 organisms m^{-3} in July 2002. This high abundance starts to decline by November/December, reaching the winter–spring low values around January/February. At NW. Netley and Calshot *O. nana* accounted numerically for only 5.5% and 1.5% of the total holoplanktonic copepods at these stations, with late-summer to late-autumn averages of 1970 and 236 organisms m^{-3}, representing 26% and 3.8% of all holoplanktonic copepods at NW.Netley and Calshot, respectively (Figure 10).

Copepod nauplii (Figure 10) were clearly the most abundant holoplanktonic group within this estuary. Despite being found all year round (Table 6), they were usually present with high abundances from spring through to autumn (Figure 10). Small peaks in May (>2500 organisms m^{-3}), followed by larger ones in July-August (>5000 organisms m^{-3}) were observed at the three stations.

Despite being the most diverse order found in the holoplankton of Southampton Water, with 17 taxa recorded during this investigation, the genus *Acartia* alone averaged 93, 94 and 81% of the calanoid composition at Cracknore, NW. Netley and Calshot, respectively (Figure 11). Apart from *Acartia*, only *Centropages hamatus, Temora longicornis, Eurytemora affinis, Pseudocalanus elongatus* and *Paracalanus parvus* had minor, seasonal contributions (Figure 11).

Centropages hamatus averaged 2, 4 and 10% of the calanoids composition at Cracknore, NW. Netley and Calshot, respectively (Figure 11). They were usually found all year round (Table 6), and usually recorded in high numbers from late-spring to late-autumn with two major peaks of abundance, one in May-June and another one in August at all three stations.

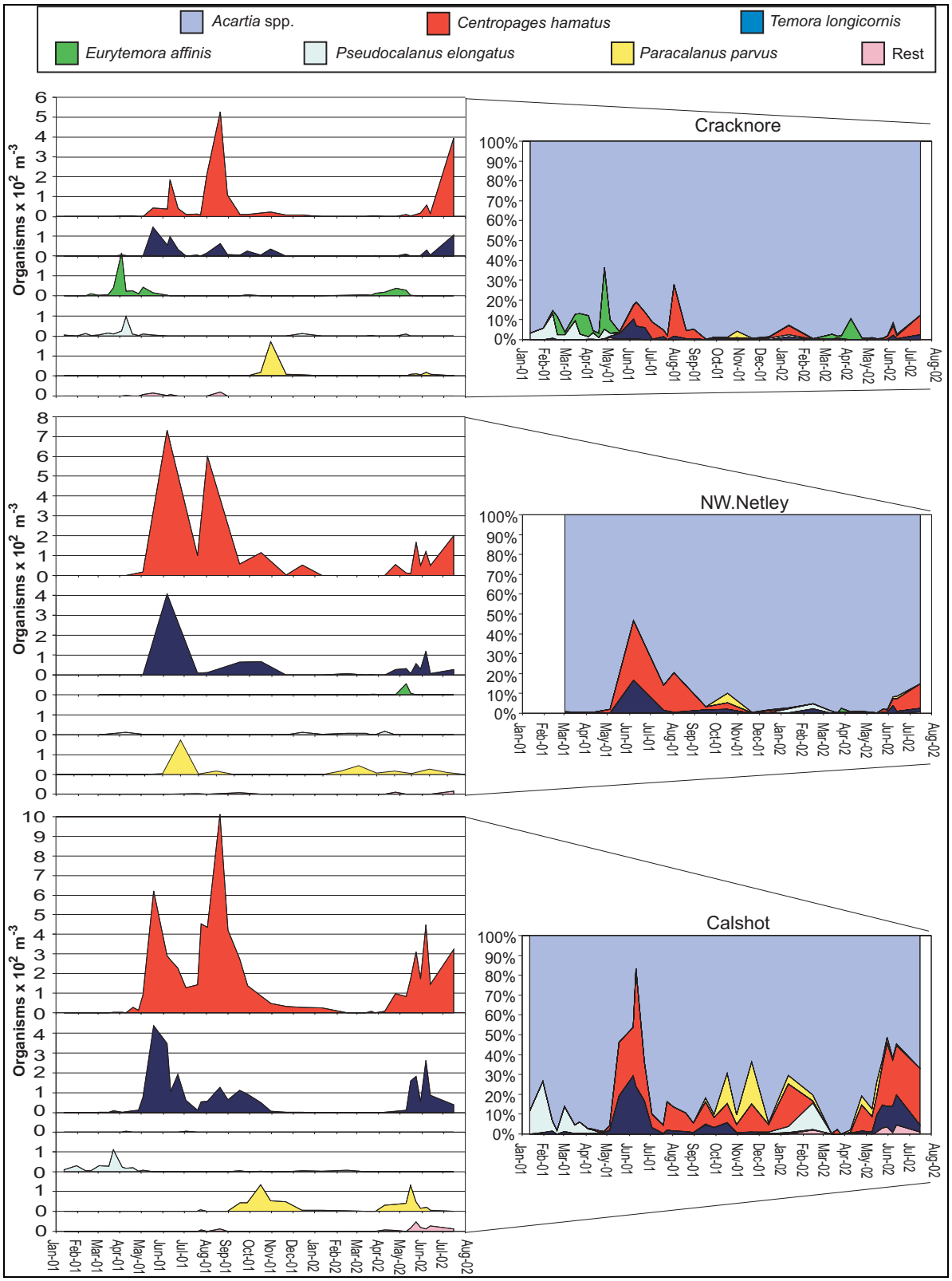


Figure 11. Temporal variability and seasonal contribution of abundant calanoid species at Cracknore, NW. Netley and Calshot during 2001/02. The seasonality of abundance of *Acartia* was omitted for a better view of the variability of the other species, but note that the abundance of some species at some stations were too low to appear in the graphic (Note that abundance interval indicates 100 organisms m^{-3}).

Usually, *C.hamatus* was more abundant towards Calshot where it averaged 156 organisms m^{-3} for the whole season, than at Cracknore where on average 42 organisms m^{-3} were observed (Figure 11). *Temora longicornis* was the third most abundant calanoid, averaging 1, 1 and 4% of the calanoids composition of Cracknore, NW. Netley and Calshot respectively. This species was found all year round (Table 6), but was usually detected from late-spring to late-autumn and was much more abundant in spring when peaks of 147, 408 and 439 organisms m^{-3} were recorded at Cracknore, NW.Netley and Calshot respectively (Figure 11). *Pseudocalanus elongatus* had a very marked pattern of seasonality, usually occurring in high numbers only during winter – spring when peaks of 97, 17 and 110 organisms m^{-3} were observed at Cracknore, NW.Netley and Calshot respectively (Figure 11), although it was also present in catches from September to June (Table 6). *Eurytemora affinis* was only abundant at the innermost stations of the estuary from late-winter to early-summer, particularly at Cracknore where it averaged 2% of the calanoids and presented a maximum of 217 organisms m^{-3} in April 2001 (Figure 11). *Paracalanus parvus* was usually found from late-summer to early-winter in 2001, however in 2002 it was also present during late-winter to early-summer (Figure 11). Maximum abundances of *P.parvus* recorded were 172, 175 and 133 organisms m^{-3} in October 2001 at the three stations respectively.

During this investigation only 5 of the 6 congeneric species of *Acartia* previously reported within Southampton Water were found. Abundances and overall contribution during 2001/02 are shown in Figure 12, where it is clear that the "combined" copepodite stages of *Acartia* are the most abundant form, averaging 73, 81 and 71% of the total *Acartia* composition at Cracknore, NW.Netley and Calshot, respectively.

Figure 12 illustrates that the total abundance of *Acartia* is, as expected, strongly influenced by the copepodite stages. When several congeneric species are present at the same period copepodite stage identification is very difficult because of the great resemblance of the early stages. Therefore identification of copepodite stages at species level was not possible in the time frame of the study. Generally, the total abundance of *Acartia* was relatively low through winter, with overall averages for the three stations, of 164 and 265 organisms m^{-3} being observed during 2001 and 2002, respectively. During spring, the average abundance increased to 1626 organisms m^{-3} in 2001 and 3429 organisms m^{-3} in 2002, with maximum of 5297 organisms m^{-3} in May 2001 at Cracknore, 27331 organisms m^{-3} in May 2002 at NW.Netley and 3908 organisms m^{-3} in May 2001 at Calshot. In both years, abundances fell abruptly around early-summer before increasing again in mid-summer, when peaks of 12925, 3820 and 9805 organisms m^{-3} were observed

at Cracknore, NW.Netley and Calshot respectively. A Summer-Autumn average of 2766 organisms m^{-3} was recorded for all three stations in 2001.

Since this is the most studied calanoid group within this estuary, the seasonality of occurrence of the adults of each species is highlighted to better understand any possible pattern between them. Of the five species recorded, *A.margalefi*, *A.discaudata* and *A.clausi* were found throughout the year at all three stations. *A.margalefi* and *A.tonsa* were more abundant towards the inner reaches of the estuary while *A.bifilosa* and *A.clausi* were more common at the mouth.

Acartia margalefi was the commonest species during winter at Cracknore and NW.Netley, although barely detected at Calshot. Overall winter averages of 10, 13 and 1 organisms m^{-3}, were observed for each station, respectively. During spring, *A.margalefi* averaged 140, 149 and 7 organisms m^{-3}, with peaks of 631, 1478 and 28 organisms m^{-3} observed at Cracknore, NW.Netley and Calshot, respectively (Figure 12). During summer-autumn, *A.margalefi* presented averaged abundances of 357, 72 and 50 organisms m^{-3} with peaks of 2682, 173 and 140 organisms m^{-3} at Cracknore, NW.Netley and Calshot respectively, becoming the dominant adult form at Cracknore during this season (Figure 12).

A.discaudata presented winter averages of 1, 14 and 8 organisms m^{-3} for Cracknore, NW.Netley and Calshot respectively. During spring *A.discaudata* numbers increased to averages of 314, 606 and 156 organisms m^{-3} at Cracknore, NW.Netley and Calshot (peaks of 2302, 2956 and 394 organisms m^{-3} observed for each station respectively) making it the most abundant spring species at Cracknore and NW.Netley. During summer-autumn it averaged 197, 266 and 570 organisms m^{-3} (peaks of 781, 863 and 3563 organisms m^{-3}) for the three stations, respectively. *A.discaudata* was also the most abundant adult form during this period at NW. Netley and Calshot (Figure 12).

A.bifilosa had winter averages of 3, 13 and 55 organisms m^{-3} at Cracknore, NW.Netley and Calshot, and was clearly more abundant than the others species at Calshot. During spring, as with the other species, its numbers increased to averages of 150, 76 and 314 organisms m^{-3} (peaks of 1137, 291 and 1009 organisms m^{-3}) at the three stations, and again it clearly dominate the catches of Calshot. During summer-autumn it almost disappears, being caught sporadically only towards the end of the season (Figure 12).

A.clausi was particularly abundant during the summer-autumn where it averaged 37, 24 and 69 organisms m^{-3} (peaks of 370, 116 and 436 organisms m^{-3}) for the three stations respectively (Figure 12). Despite being found in each month, very low abundances were recorded from January to May (Table 6).

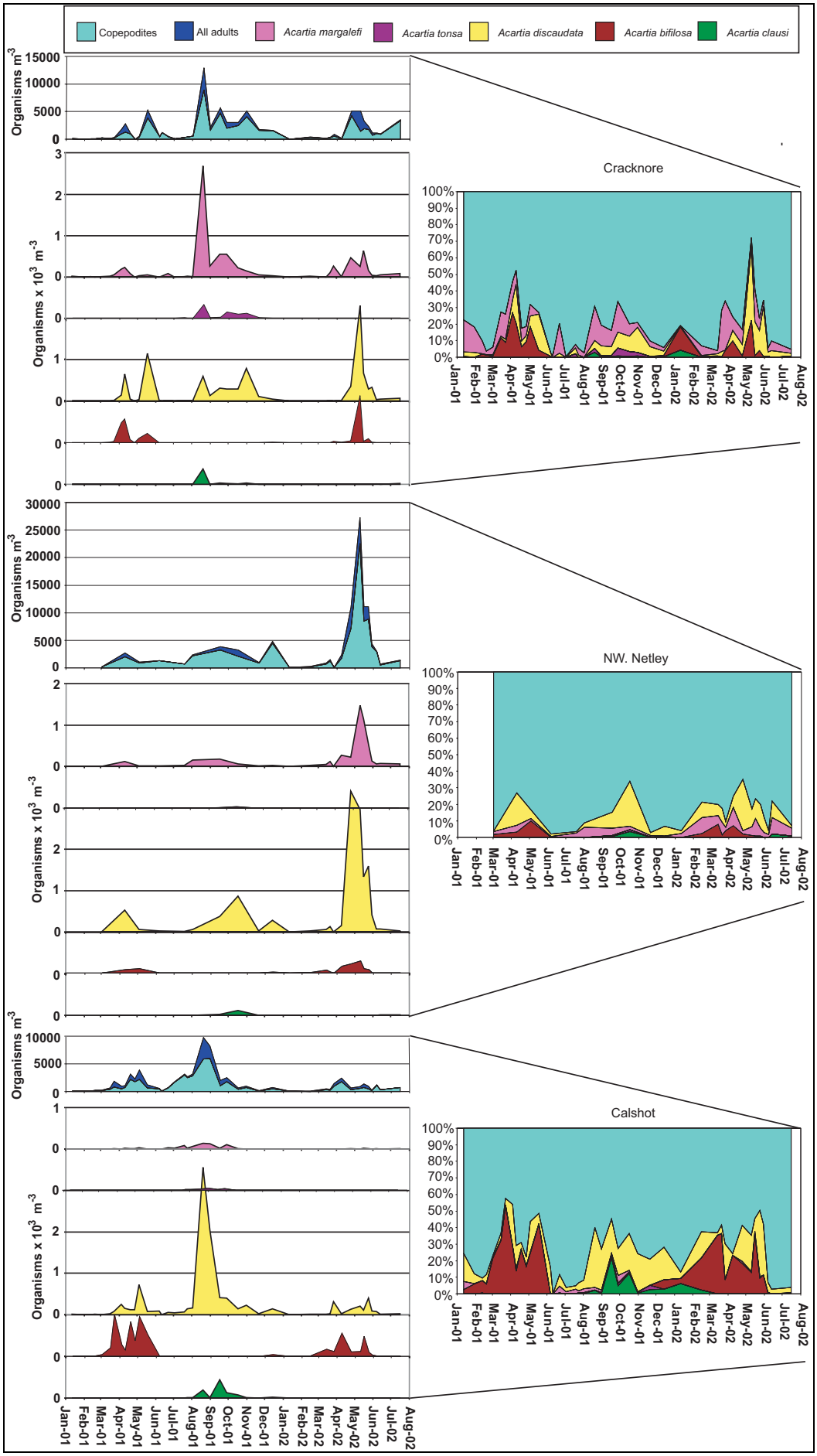


Figure 12. Temporal variability and seasonal contribution of the different *Acartia* species at Cracknore, NW. Netley and Calshot during 2001/02. (Note that abundance interval of adults indicates 1000 organisms m^{-3}).

A.tonsa was recorded at the three stations only from July to November (Table 6), presenting summer-autumn averages of 56, 9 and 16 organisms m^{-3} at Cracknore, NW.Netley and Calshot, respectively. Substantial numbers were only recorded at Cracknore, where a peak of 329 organisms m^{-3} was observed (Figure 12).

Table 6. Seasonal occurrence of holoplanktonic species in Southampton Water, with the frequency of occurrence (FO) of each taxa. Where ■ = Cracknore; ▲= NW. Netley, ● = Calshot. Colour shades indicate average abundances where, = 0, = 0.001 – 0.01, = 0.01 – 0.1, = 0.1 – 1.0, = 1.0 – 10, = 10 – 100, = 100 – 1000 and = ≥ 1000 organisms m^{-3}.

Species	J	F	M	A	M	J	J	A	S	O	N	D	FO
Ctenophora													
Pleurobrachia pileus	●	●		■▲●	■▲●	■▲●	■▲●	■ ●	■	■▲●			41%
Cladocera													
Bosmina sp.											■		1%
Daphnia sp.		■		■	■								4%
Evadne nordmanni		▲											1%
Copepoda													
Copepoda nauplii	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	100%
Acartia copepodites	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	100%
Acartia bifilosa	■ ●	■▲●	■▲●	■▲●	■▲●	■ ●						■▲●	59%
Acartia tonsa							■ ●	■ ●	■▲●	■▲●	■▲●		19%
Acartia clausi	■▲●	■▲●	■	▲	■▲	■▲●	■▲●	■ ●	■▲●	■▲●	■▲●	■▲●	41%
Acarita discaudata	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	96%
Acarita margalefi	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲	■▲	87%
Centropages hamatus	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	87%
Isias clavipes				▲●	■▲●		●	■ ●	▲●	▲●	●		16%
Parapontella brevicornis			■ ●	■▲●	■▲●	■ ●	■▲●	■ ●	■▲●	■▲●			43%
Anomalocera patersoni					●								1%
Labidocera wollastoni					▲●			▲●	■ ●				6%
Eurytemora affinis	■	■▲	■▲	■▲●	■▲●	■	●		■				31%
Temora longicornis	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■ ●	■▲●	92%
Pseudocalanus elongatus	■▲●	■▲●	■▲●	■▲●	■▲●	■▲			■ ●	■ ●	■ ●	■▲●	65%
Stephos scotti	▲		●			■							4%
Calanus helgolandicus	●	▲		■▲●	■▲●	▲	■	●	■ ●	■			24%
Paracalanus parvus	■▲●	■▲●	▲●	■▲●	■▲●	■▲●	●		■▲●	■▲●	■▲●	■▲●	44%
Pseudocyclopia sp.			■	■		●							3%
Microsetella norvegica	■												1%
Euterpina acutifrons	■▲●	▲●	▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	76%
Oithona nana	■▲●	■▲●	■▲●	■ ●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	77%
Corycaeus anglicus	●	●	▲						■ ●	●	●		8%
Oncaea sp.	■ ●	■▲●	■ ●	■ ●	▲		■▲●	●		■ ●	●		25%
Euphausiacea													
Unidentified Euphausiacea	▲●	●	■▲●	■▲●	■▲●							■	27%
Meganyctiphanes norvegica	●			●						●	■		4%
Chaetognatha													
Sagitta setosa	■▲●	■▲●	■▲●	■▲●	▲●	■▲	▲●	●	■▲●	■▲●	■ ●	■▲●	48%
Appendicularia													
Oikopleura sp	■ ●	▲	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	81%

Of the minor calanoid copepod contributors, *Parapontella brevicornis* was usually found from spring until mid-autumn with abundances rarely exceeding 10 organisms m^{-3} (Table 6). *Isias clavipes* was also found during this period, but usually at abundances below 1 organism m^{-3} (Table 6). *Calanus helgolandicus* was usually recorded from January to October and, like *I.clavipes,* it usually presented abundances below 1 organism m^{-3} (Table 6). The remaining calanoids, *Anomalocera pattersoni*, *Labidocera wollastoni*, *Stephos scotti* and *Pseudocyclopia* sp. were only found sporadically. Among the poecilostomatoids, *Corycaeus anglicus* was usually found at NW.Netley and Calshot at

very low abundance (<1 organism m^{-3}) during autumn-winter. *Oncaea* sp. was recorded from January to October, usually with abundances above 1 organism m^{-3} and achieving a maximum of 35 organisms m^{-3} recorded at Calshot in August 2001 (Table 6).

Among the remaining holoplanktonic species recorded during the present investigation, cladocerans were only recorded a few times, and in very low abundances (never exceeding 2 organisms m^{-3}), and were only represented by three taxa. The freshwater species *Bosmina* sp and *Daphnia* sp were only found at Cracknore while *Evadne nordmanni,* a marine species, was found only once at NW.Netley (Table 6).

The ctenophore *Pleurobrachia pileus* was found from January to October (Table 6), but was relatively abundant in June, with abundances > 1 organism m^{-3} recorded. It was usually much more abundant at Cracknore (peak of 20 organisms m^{-3} recorded in June 2001). Gut contents of *P.pileus* were also analysed and it was observed that of the 1230 individuals captured at the three stations (88% at Cracknore), 34% of them had from 1 to 38 animal prey items inside their gut (phytoplankton was also observed in large quantities but was not quantified). A total of 24 different prey types were identified (Table 7), with Copepoda averaging 71, 84 and 73% of the total number of items identified from *P.pileus* collected from Cracknore, NW.Netley and Calshot, respectively. Although some variation in the composition of the diet was observed, it usually reflected *in situ* mesozooplankton composition.

Table 7. Averaged percentage composition of prey items in *Pleurobrachia pileus* found at each site.

Type of Prey	Cracknore	NW. Netley	Calshot
Unidentified barnacle nauplii	20.30	13.40	14.86
Unidentified barnacle cypris	1.36	0.50	1.35
Sacculina carcini	0.14	0.00	0.00
Copepoda nauplii	13.76	18.86	9.46
Unidentified Copepoda.	2.72	1.24	2.7
Acartia discaudata (adults)	1.50	0.50	0.00
Acartia bifilosa (adults)	0.27	0.00	0.00
Acartia spp. (copepodites+adults)	31.74	49.14	22.97
Pseudocalanus elongatus (copepodites+adults)	0.41	0.00	0.00
Eurytemora affinis (copepodites+adults)	0.00	0.25	0.00
Temora longicornis (copepodites+adults)	1.23	0.99	4.05
Centropages hamatus (copepodites+adults)	0.14	0.74	0.00
Unidentified Harpacticoida (copepodites+adults)	0.27	0.00	1.35
Euterpina acutifrons (copepodites+adults)	18.66	12.66	31.08
Tisbe sp. (copepodites+adults)	0.14	0.00	0.00
Oithona nana (copepodites+adults)	0.41	0.00	0.00
Unidentified siphonostomatoida (copepodite)	0.00	0.00	1.35
Decapoda larvae	1.23	0.25	4.05
Unidentified Crustacea	0.82	0.00	1.35
Gastropoda Veliger	2.18	1.24	4.05
Bivalve Veliger	1.23	0.00	0.00
Oikopleura sp.	0.68	0.00	0.00
Polychaeta	0.68	0.25	1.35
Ant (Terrestrial)	0.14	0.00	0.00

Euphausiid nauplii were usually found from October to March and always at low abundances (Table 6) at all three stations. A total of 3 furcilia and 1 caliptopis of *Meganyctiphanes norvegica* were identified in the samples.

The chaetognath *Sagitta setosa* was also a minor component of the holoplankton, and despite being found all year round it was only relatively abundant (>1 organism m^{-3}) in September and October, when abundances up to 62 organisms m^{-3} were recorded. It was found throughout the estuary, but tended to be more abundant and frequent at Calshot.

2.3.2. Statistical analysis.

Correlations between biotic and abiotic factors that could be forcing spatial and temporal patterns in the species distribution can be seen in Table 8.

Table 8. Pearson's product-moment correlation of biotic and abiotic parameters from data collected at the three stations. Correlations in red are significant at p<0.05, and shaded at p<0.01, ns = not significant.

Species	T °C	S	Chl.*a*	O_2	O_2Sat%
Acartia discaudata	0.35	0.34	ns	-0.38	ns
Acartia bifilosa	-0.46	ns	ns	0.38	ns
Acartia margalefi	0.43	ns	ns	-0.42	ns
Acartia tonsa	ns	ns	ns	-0.59	-0.24
Acartia clausi	0.42	0.29	ns	-0.54	ns
Acartia Copepodites	0.53	0.27	0.34	-0.46	ns
Pseudocalanus elongatus	-0.65	-0.26	-0.40	0.35	-0.26
Temora longicornis	0.65	0.45	0.60	-0.33	0.32
Centropages hamatus	0.79	0.53	0.65	-0.42	0.36
Isias clavipes	ns	0.22	ns	ns	ns
Paracalanus parvus	0.20	0.36	ns	-0.32	ns
Eurytemora affinis	-0.21	-0.43	ns	ns	ns
Calanus helgolandicus	ns	ns	0.20	ns	0.25
Labidocera wollastoni	0.25	ns	ns	ns	ns
Anomalocera pattersoni	ns	ns	ns	ns	ns
Parapontella brevicornis	0.30	ns	0.26	ns	ns
Stephos scotti	ns	ns	ns	ns	ns
Pseudocyclopia sp.	ns	ns	ns	ns	ns
Oithona nana	ns	ns	-0.25	-0.48	-0.38
Oncaea sp.	ns	0.32	ns	ns	ns
Corycaeus anglicus	ns	ns	ns	ns	ns
Euterpina acutifrons	0.91	0.43	0.56	-0.60	0.27
Microsetella norvegica	ns	ns	ns	ns	ns
Copepod nauplii	0.54	ns	0.60	-0.25	0.27
Euphausiid larvae	ns	ns	ns	ns	ns
Meganycthiphanes norvegica	ns	ns	ns	ns	ns
Daphnia sp.	ns	-0.23	ns	ns	ns
Evadne nordmanii	ns	ns	ns	ns	ns
Bosmina sp.	ns	ns	ns	ns	ns
Pleurobrachia pileus	0.24	ns	0.30	ns	ns
Sagitta setosa	ns	0.24	ns	-0.31	ns
Oikopleura sp:	0.64	0.29	0.50	-0.38	0.22

As expected, temperature, salinity and chlorophyll were positively correlated with those species abundant during spring – autumn (e.g. *C.hamatus*, *T.longicornis*,

E.acutifrons, *Oikopleura* sp.) and negative for those peaking during winter-spring (e.g. *P.elongatus*). Contrasting with this was the negative correlation found for *O. nana* with chlorophyll. Dissolved oxygen was usually negatively correlated with those species present during spring – autumn and positively with those peaking during winter – spring, while oxygen saturation was the opposite.

MDS ordination plots, based on Bray-Curtis similarities of species abundances from all samples collected for all stations show a clear seasonal pattern (Figure 13 a) but with apparently no distinction between the three sites in terms of holoplanktonic composition, with all sites intermingling together in a big cluster (Figure 13 b), with the exception of a cluster composed mainly by summer-autumn samples of Cracknore (Figure 13 a,b).

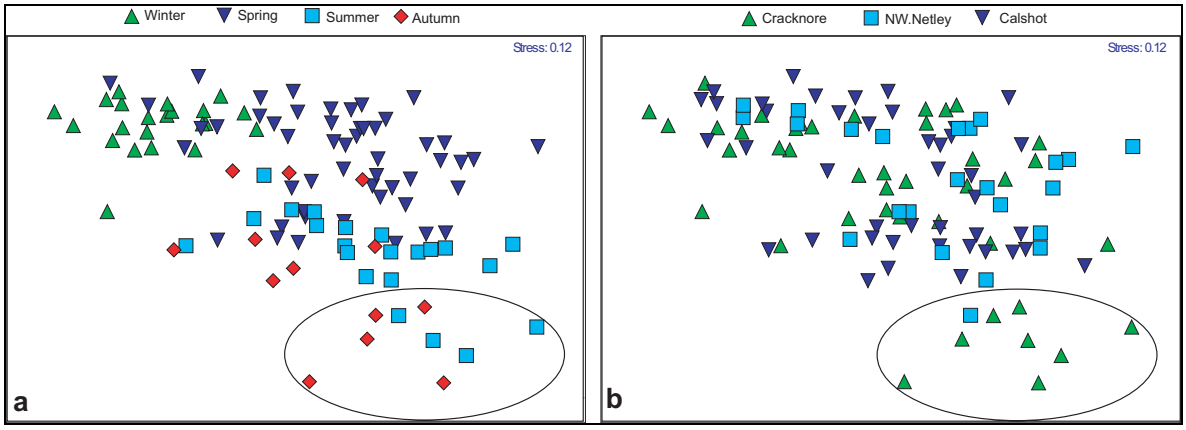


Figure 13. MDS ordinations of the 108 samples, based from Bray-Curtis similarities on square root transformed abundances of all holoplanktonic organisms, found in the zooplankton of Southampton Water during 2001/02. Indicated in the figure is an apparent distinctive cluster indicating spatial differentiation of some Cracknore samples.

When the relative abundance of each species was superimposed over the MDS ordination (Figure 14 a to r), the seasonality of occurrence of several species is clear. Species shown in Figures a to d had a winter-spring pattern, while species shown on Figures e to j and p to r had a spring-summer and k to o had a summer-autumn distribution.

From Figure 14 it is also clear that the summer-autumn cluster of Cracknore samples highlighted on Figure 13 is clearly due to the contribution of *O.nana* (Figure 14 o).

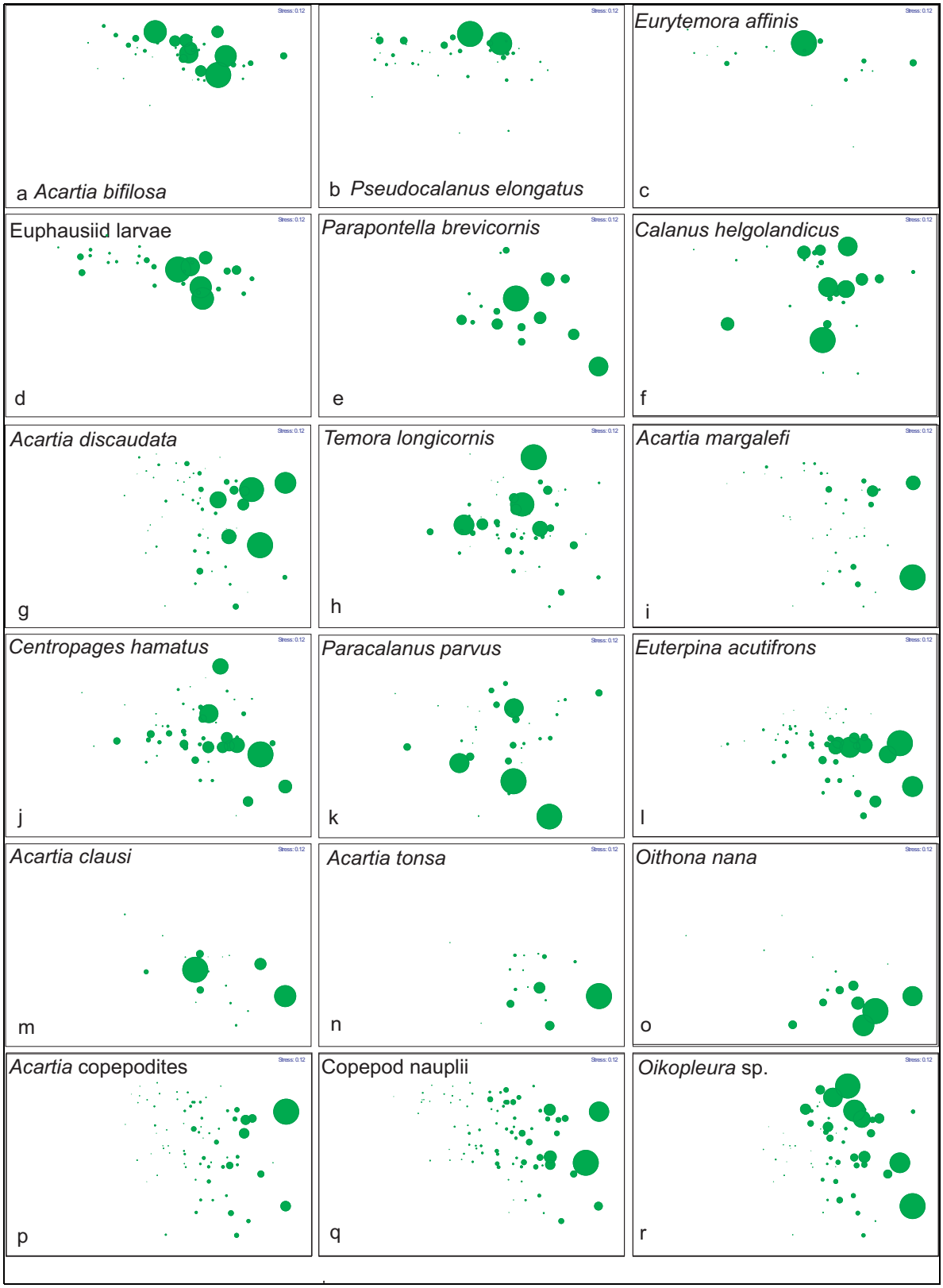


Figure 14. MDS of the three sites, as in Figure 13, with superimposed circles representing relative species abundances at the three sites. (Note that abundances are in the same proportional scale for a clearer evaluation of patterns).

By superimposing the physico-biological parameters measured on the MDS presented on Figure 13 (Figure 15), it is clear that temperature, dissolved oxygen and chlorophyll clearly follows the seasonal pattern in Figure 13 and when contrasted with the patterns of the species presented on Figure 14 its easy to identify which are responsible for some patterns presented by the different holoplanktonic species.

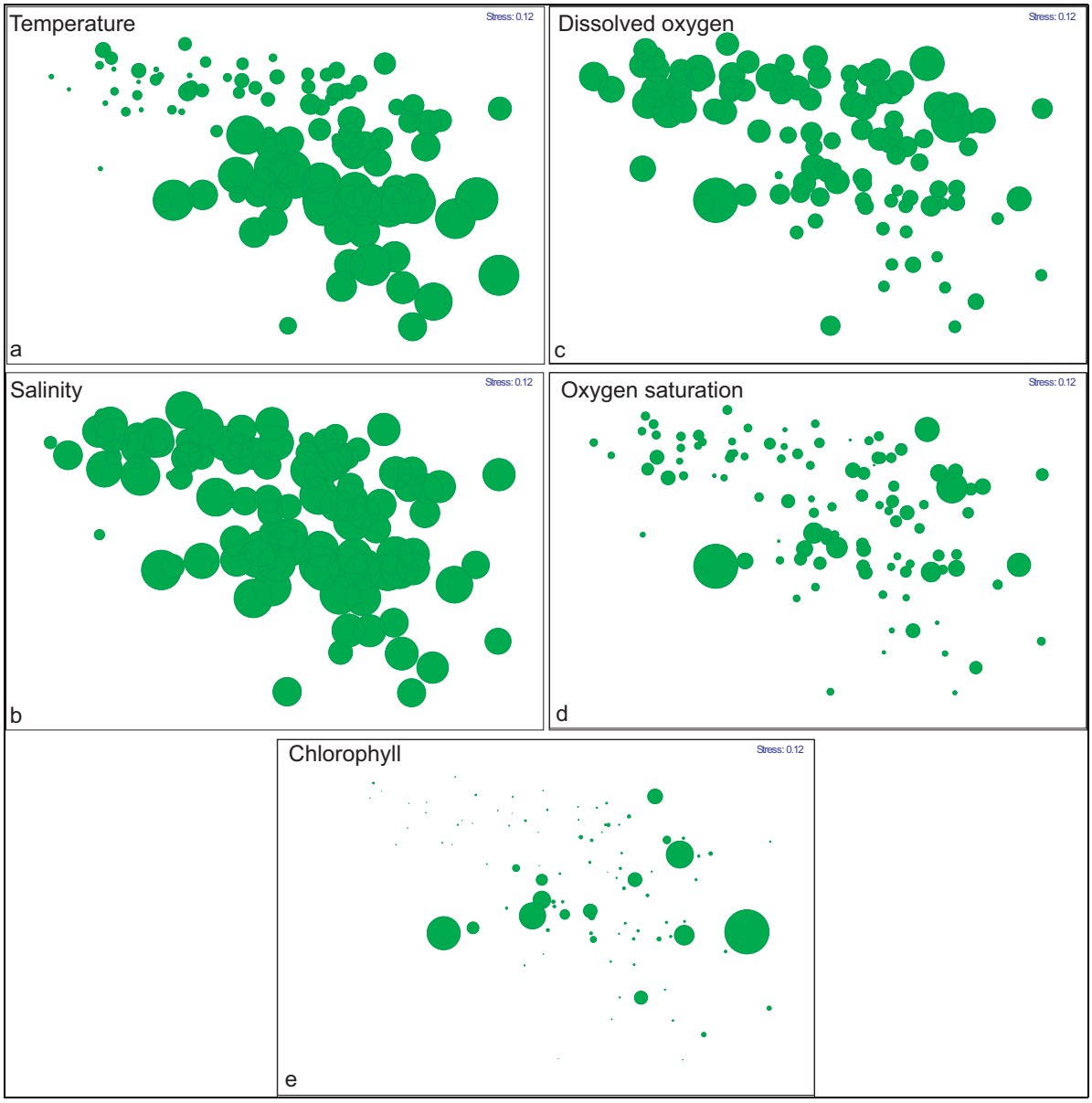


Figure 15. MDS of the three sites, as in Figure 13, with superimposed circles representing the range of values of the physico-chemical parameters of all three sites. (Note that concentrations are in the same proportional scale for a clearer evaluation of patterns).

2.4. Discussion.

Calanoids have been always considered the dominant holoplanktonic form within estuaries (Jeffries, 1967; Conover, 1979; Miller, 1983; Buskey, 1993) and until the present study it was also the dominant form reported within Southampton Water. Generalizing, in terms of overall major species composition and seasonal occurrences, the results presented here agree with those presented by Raymont & Carrie (1964), Hirst (1996) and Castro-Longoria (1998), with *Acartia* being the most abundant calanoid form and only *C.hamatus*, *T.longicornis; P.parvus; P.elongatus* and *E.affinis* of the remaining calanoid species with some minor/major importance depending on the seasons and/or location. This is also similar to what is observed in other North-European estuaries (Baretta & Malschaert, 1988; Soetaert & Van Rijswijk, 1993; Irigoien & Castel, 1995).

In terms of total numbers both Hirst (1996) and Castro-Longoria (1998) presented raw data for each *Acartia* species individually, however the results presented here can only be compared with those of Hirst (1996) which sampled with a comparable mesh size. Based on this, the results presented here contrast with those of Hirst (1996), where his total values never exceeded 1665 organisms m^{-3} (Figure 16). As pointed out in Chapter 1, this could be a reflection of the lack of temporal coverage, since sampling only occurred once a month. However, the numbers presented in that study are even lower than from samples collected with a coarser meshes, 220 μm, that have also been collected only once a month (Castro-Longoria, 1998). This would indicate that it was either a year of unusually lower abundance, or that some kind of under-estimation occurred.

Unexpectedly, the total numbers of *Acartia* presented here are comparable with those of Castro-Longoria (1998), collected with 220 μm mesh at different stations and tide conditions. Despite the fact that the general composition reflected the coarser mesh i.e. were mainly composed of adult forms, it was surprising to note that the abundances of some adults reported by her were usually 2 to 5 times higher than the values recorded in the present study (Figure 16). Of course inter-annual variability, the composition at different stations and different tide conditions could be responsible for this although these differences were only observed in the spring samples. The remaining samples, usually with similar or lower values to the present study, suggest that the finer mesh nets employed during this investigation may have been clogged by the high concentration and/or type of phytoplankton during spring (See probable dates on section 1.4.1. on Chapter 1), thereby underestimating abundances and partially explaining the differences in abundances of adults found between the two studies.

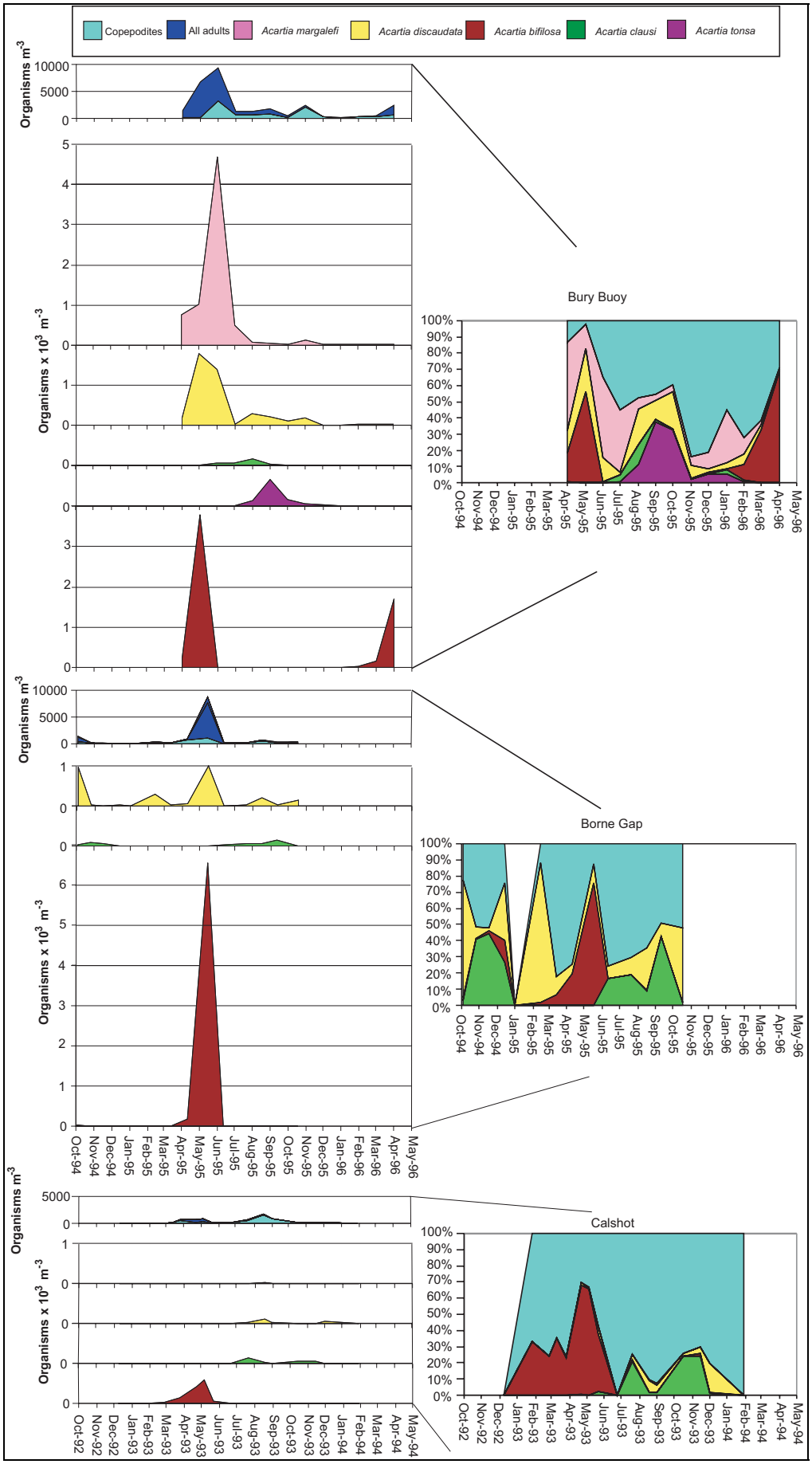


Figure 16. Temporal variability and seasonal contribution of *Acartia* species at Bury Buoy and Bourne Gap during 1994/96 and Calshot in 1992/94 from the raw data of Castro-Longoria (1998) and Hirst (1996), respectively. (Note that abundance interval of adults indicates 1000 organisms m^{-3}). Data for different depth strata were averaged.

Supporting this is the fact that during spring 2002 no phytoplankton bloom was present to clog the nets and volumes filtered (Appendix III) as well as abundances of adults were usually higher than those reported for the spring of 2001 at the inner stations (Figure 12). At Calshot however, abundances of *Acartia* during the spring of both years were similar, suggesting that nets were only clogged at the inner stations where the bloom of *Phaeocystis* sp. in 2001 was more evident.

Conover (1957) was the first to indicate a successional pattern among the different *Acartia* species in this estuary, particularly at Calshot. Although differing in detail, Raymont & Carrie (1964) and Hirst (1996) endorsed this suggestion. Based on Conover (1957) and Raymont & Carrie (1964) it was observed that usually at the beginning of the year *A.discaudata* is the commonest species, with the occasional appearance of *A.clausi* and *A.bifilosa*. During February and until March *A.bifilosa* begins to replace *A.discaudata*, and from March to early July *A.bifilosa* clearly dominates the *Acartia* populations, with few *A.discaudata* and *A.clausi* coexisting during this period. From July-August both *A.discaudata* and *A.clausi* became common again, with *A.bifilosa* almost disappearing from the zooplankton catches after August. Hirst (1996) also observed this pattern, but additionaly reported the presence of *A. bifilosa* during November-December, and also stated that this species is the commonest during the first 5 months of the year at the mouth of the estuary (Figure 16).

Recently, Castro-Longoria (1998) in a specific study of the *Acartia* populations in the Solent–Southampton Water system reported that while *A.discaudata, A.clausi* and *A.bifilosa* are the dominant forms in the Solent (and consequently at Calshot), no clear succession pattern was observed among them, either in the Solent or further up the estuary. Castro-Longoria (1998) also reported the co-occurrence of *A.tonsa* and *A.margalefi* in addition to the other three species (Figure 16). Despite not observing any succession, Castro-Longoria (1998) reports that almost all species coexisted, with each one having a single sequential seasonal maximum between late-spring and early autumn, with *A.bifilosa* peaking on May, *A.discaudata* in May/June, *A.margalefi* in June, *A.clausi* in August and *A.tonsa* in September (Figure 16).

The results of the current study agree, in part, with those of Castro-Longoria (1998), since no clear succession pattern was observed among the different *Acartia* species, and all species were seen coexisting and usually peaking at the same time (Figure 12). In contrast with her results, during this investigation at least two peaks of abundance were recorded for some species in a single season, one in spring and another one/two during summer-autumn (Figure 12). This should probably be a reflection of the higher

sampling frequency carried out during this study, where two to three samples were collected during summer-autumn, while only single monthly samples were collected in the previous studies (Hirst, 1996; Castro-Longoria, 1998). Raymont & Carrie (1964) also observed this pattern of two peaks of abundance usually at the inner stations, and attributed the later peak to *A.discaudata*.

Based on all previous records (Conover, 1957; Raymont & Carrie, 1964; Hirst, 1996; Castro-Longoria, 1998) it is clear that, some seasonal and spatial preferences occurs within this estuary, with *A.margalefi* and *A.tonsa* occurring and attaining higher abundances preferably in the inner reaches with *A.clausi* and *A.bifilosa* at the mouth. In terms of seasonality, it is clear that *A.bifilosa* is a winter-spring form while *A.clausi* and *A.tonsa* are autumn ones. *A.margalefi* and *A.discaudata* are present through the year, but occurs in elevated numbers during spring-summer (Figures 12 and 14).

Throughout the world, but especially in estuaries, harbours and semi-enclosed areas where changeable environmental conditions occur, the species living within those systems must be able to deal with those changes. They can occur by physiologically tolerating a wide range of temperature and salinity conditions, by being able to move to more favourable locations, having rapid growth and reproduction rates, or through the production of dormant stages/eggs for unfavourable periods (Raymont & Carrie, 1964; Kinne, 1967; Miller, 1983; Hairston & Munns, 1984; Castro-Longoria, 1998; Chinnery, 2002). The genus *Acartia* is certainly one that meets these requirements, since it has been reported that congeners can found from nearly fresh to hypersaline waters and from 0 to 40 ºC, in clear or turbid estuaries from low to high latitudes (Day Jr. *et al*., 1989) resulting in it being one of the most abundant elements within estuaries (Jeffries, 1967; Conover, 1979; Miller, 1983; Buskey, 1993), with as many as 9 congeneric species presenting spatial and seasonal patterns of abundances have been reported in the Cochin Backwater, a monsoonal estuarine lagoon in Kerala, India (Tranter & Abraham, 1971).

Temperature and salinity have been identified as the main factors behind spatial and seasonal occurrence of *Acartia* congeners in estuaries (Jeffries, 1962; 1967; Tranter & Abraham, 1971; Wooldridge & Melville-Smith, 1979; Greenwood, 1981; Alcaraz, 1983; Castro-Longoria, 1998), but food utilization, high growth rates and characteristic behaviours are also important (Tranter & Abraham, 1971; Greenwood, 1981; Miller, 1983; Castro-Longoria, 1998; Chinnery, 2002). The correlations with temperature (Table 8) confirm the overall seasonal occurrence/preferences of most species (also shown on MDS plots in Figures 14 a,g,i,m,n,p). Salinity would be expected to have a significant negative correlation with *A.margalefi* and *A.tonsa* but was not. Examining MDS plots depicted in

Figures 13, 14 and 15 it is possible to observe that both *A.margalefi* and *A.tonsa* high abundances (Figure 13 i and n) were restricted to samples at Cracknore and NW. Netley (Figure 13 b) of relatively lower salinities (Figure 15 b). It has also been reported that these two species are often restricted to environments of low salinity (Lance, 1964; Alcaraz, 1976; Alcaraz, 1983; Escaravage & Soetaert, 1995; Irigoien & Castel, 1995; Castro-Longoria & Williams, 1996) supporting the occurrence of these two species at higher abundances towards the inner reaches of the estuary, where salinity oscillations were more evident (Figure 3 – Chapter 1). The complete absence of *A.bifilosa*, *A.tonsa* and to some extent of *A.clausi* adults from plankton catches of this estuary at certain seasons was also expected, since those species produces resting eggs to avoid some adverse conditions (Castro-Longoria, 1998; Chinnery, 2002).

Acartia congeners are often reported to occur in seasonal successions where usually one congener is abundant during winter-spring and another in summer-autumn (Conover, 1956; Jeffries, 1962; Jeffries, 1967; Herman *et al*., 1968; Hulsizer, 1976; Wooldridge & Melville-Smith, 1979). Patterns similar to the one observed during the present study, with one or more *Acartia* species coexisting within the total range of estuarine salinity and temperature have also been observed (Tranter & Abraham, 1971; Greenwood, 1981; Turner, 1982; Alcaraz, 1983; Baretta & Malschaert, 1988; Kimmerer, 1993). Of these, Alcaraz (1983) and Baretta & Malschaert (1988) recorded almost the same species in the ría of Vigo in Spain and at the Ems estuary between Germany and The Netherlands, respectively. At Vigo *A.discaudata*, *A.clausi, A.margalefi* and *A.grani* were also observed coexisting, with the first three occurring all year round and with similar spatial segregation to the present study, i.e. *A.discaudata* being predominantly found within the estuary, with *A.margalefi* and *A.grani* predominantly at the fresher end and *A.clausi* at the marine one (Alcaraz, 1983). In contrast, Baretta & Malschaert (1988) in the Ems show that although *A.discaudata*, *A.clausi, A.tonsa, A.bifilosa* and *Acartia sp.* were seen coexisting for most of the year, *A.tonsa* and *A.bifilosa* were clearly the dominant species and occurred throughout the year.

Allowing for regional differences and the particularities of each estuary the *Acartia* component reported in Southampton Water is similar to that that reported in other North-European estuaries (Alcaraz, 1983; Williams & Collins, 1986; Baretta & Malschaert, 1988; Soetaert & Van Rijswijk, 1993; Irigoien & Castel, 1995), with any one of *A.discaudata*, *A.bifilosa, A.clausi, A.tonsa* and *A.margalefi* being the most abundant form in particular localities and/or seasons.

In an attempt to view the seasonal/spatial pattern of *Acartia* within Southampton Water more clearly, the species/pair of species responsible for most of the abundance encountered at each station and/or season were grouped, and a summary can be seen in Table 9 where the importance of *A.discaudata* is evident, as it appears as a dominant/co-dominant on 10 out of 15 possible combinations.

Table 9. Overall seasonal/spatial pattern of dominance of *Acartia* species within Southampton Water, based on the average values for each season.

Station	Winter	Early Spring	Late Spring	Summer	Autumn
Cracknore	*A.margalefi*	*A.margalefi* *A.bifilosa*	*A.discaudata* *A.bifilosa*	*A.margalefi*	*A.margalefi* *A.discaudata*
NW.Netley	*A.margalefi* *A.discaudata* *A.bifilosa*	*A.margalefi* *A.discaudata*	*A.discaudata* *A.bifilosa*	*A.margalefi* *A.discaudata*	*A.discaudata*
Calshot	*A.bifilosa*	*A.bifilosa*	*A.discaudata* *A.bifilosa*	*A.discaudata*	*A.discaudata*

Chinnery (2002) reports that *A.discaudata* has the same hatch success and assimilation efficiency over the range of temperatures and salinities found at this estuary (i.e. 5 – 20 ºC and salinities higher than 23 on average), and so, it is possible to infer that with enough food supply it should be able to reproduce all year round, so reflecting its continuous presence in the water column. Castro-Longoria (1998) indeed reported that *A.discaudata* is capable of producing eggs within the range of temperature and salinity observed for this estuary, with the rate being clearly temperature dependant. At 5 ºC it produced less than 1 egg $♀^{-1}d^{-1}$, with rates increasing to 2.6 and 4.9 eggs $♀^{-1}d^{-1}$ at 10 and 20 ºC respectively. From Table 9 however, is clear that under particular circumstances/seasons other congeners are able to overshadow the importance of *A.discaudata* at some seasons/stations. The pattern presented in Table 9 is only a summary/abstraction, since no single simplistic pattern can summarize the different combination of five *Acartia* species coexisting with seasonal/spatial preferences and different life strategies. Future monitoring studies should explore this further, as well as establish which factors apart from temperature and salinity control the seasonal/spatial distribution of *Acartia* species. Inter-annual patters with other dominance patterns may also occur since, potentially, *A.discaudata, A.bifilosa, A.clausi* and possibly *A.margalefi* can hatch and survive within the range of salinity and temperature conditions encountered in Southampton Water (Chinnery, 2002).

In addition to trying to match calanoid abundances recorded by different investigators, in different years, using different sampling methodologies and with different taxonomic skills, a question occurs concerning the situation observed in 2002 (Figure 5 – Chapter 1), specifically, what supported the relatively high copepod abundances recorded during spring when no early phytoplankton bloom was recorded?

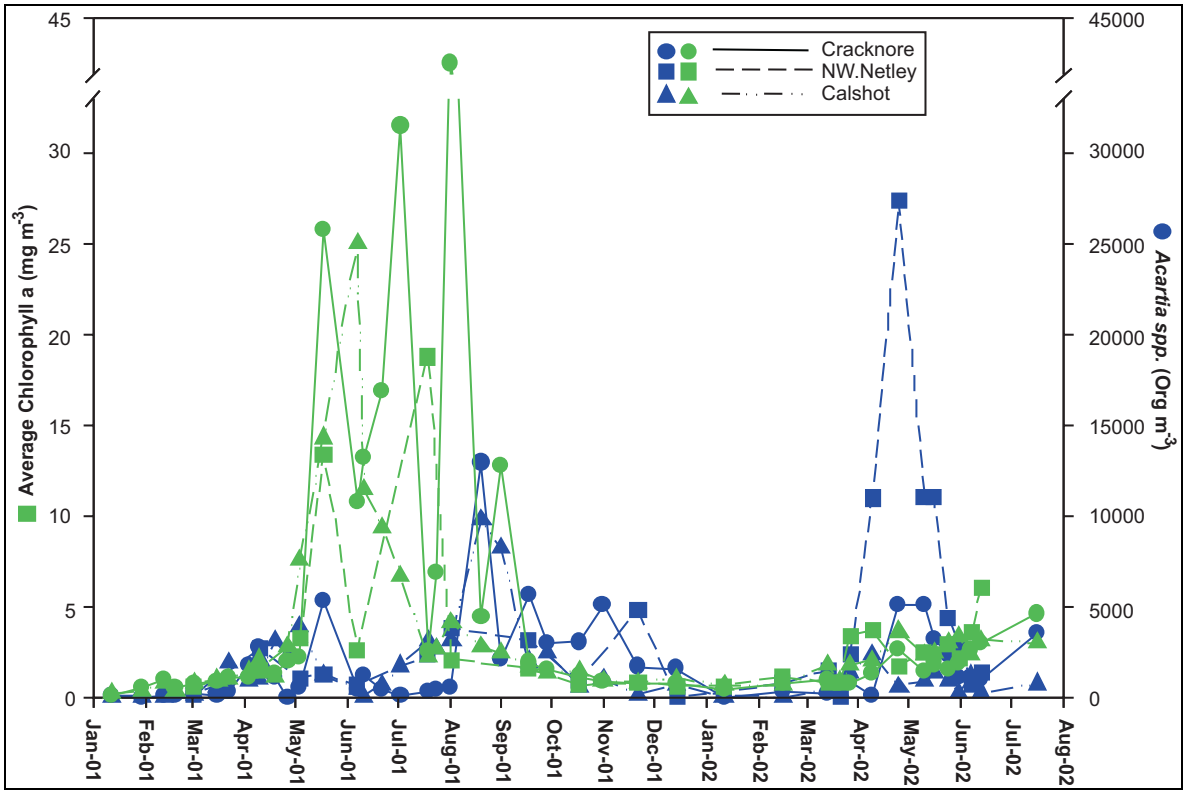


Figure 17. Seasonal pattern of Chlorophyll a concentration and *Acartia* spp. abundance at the three stations during 2001/02.

The answer to this is not straightforward particularly as no data for an in-depth analysis is available. At the moment, based on data provided by this study and from previous reports (Hirst, 1996; Castro-Longoria, 1998), it is possible to say that a spring peak in chlorophyll is usually followed by a peak of *Acartia* abundance. However, despite the fact that no chlorophyll peaks were recorded during 2002 (Figure 17) the general spring pattern of *Acartia* abundance was repeated at all three stations (see also Figure 12), together with a massive peak at NW. Netley.

This could imply that the chlorophyll levels reported in spring 2002, i.e <5 mg m^{-3}, are enough to support the spring copepod abundances (Figure 17). Chlorophyll levels of <2 mg m^{-3} are matched by abundances of *Acartia* well over 3000 organisms m^{-3} on average, at Cracknore and NW.Netley from September to December (Figure 17) assuming that *Acartia* (mainly *A.discaudata* and *A.margalefi*) only graze on diatoms and ciliates, the main producers of chlorophyll reported for Southampton Water (Iriarte, 1991; Leakey *et al*., 1992; Kifle & Purdie, 1993; Iriarte, 1993; Iriarte & Purdie, 1994; Howard *et al*., 1995; Ali, 2003). However other, unaccounted food sources, could also be being utilized by these copepods, possible detritus, bacterio-aggregates, flagellates and even earlier copepod stages, since all have been indicated as alternative food sources for this genus (Day Jr. *et al*., 1989; Mauchline, 1998).

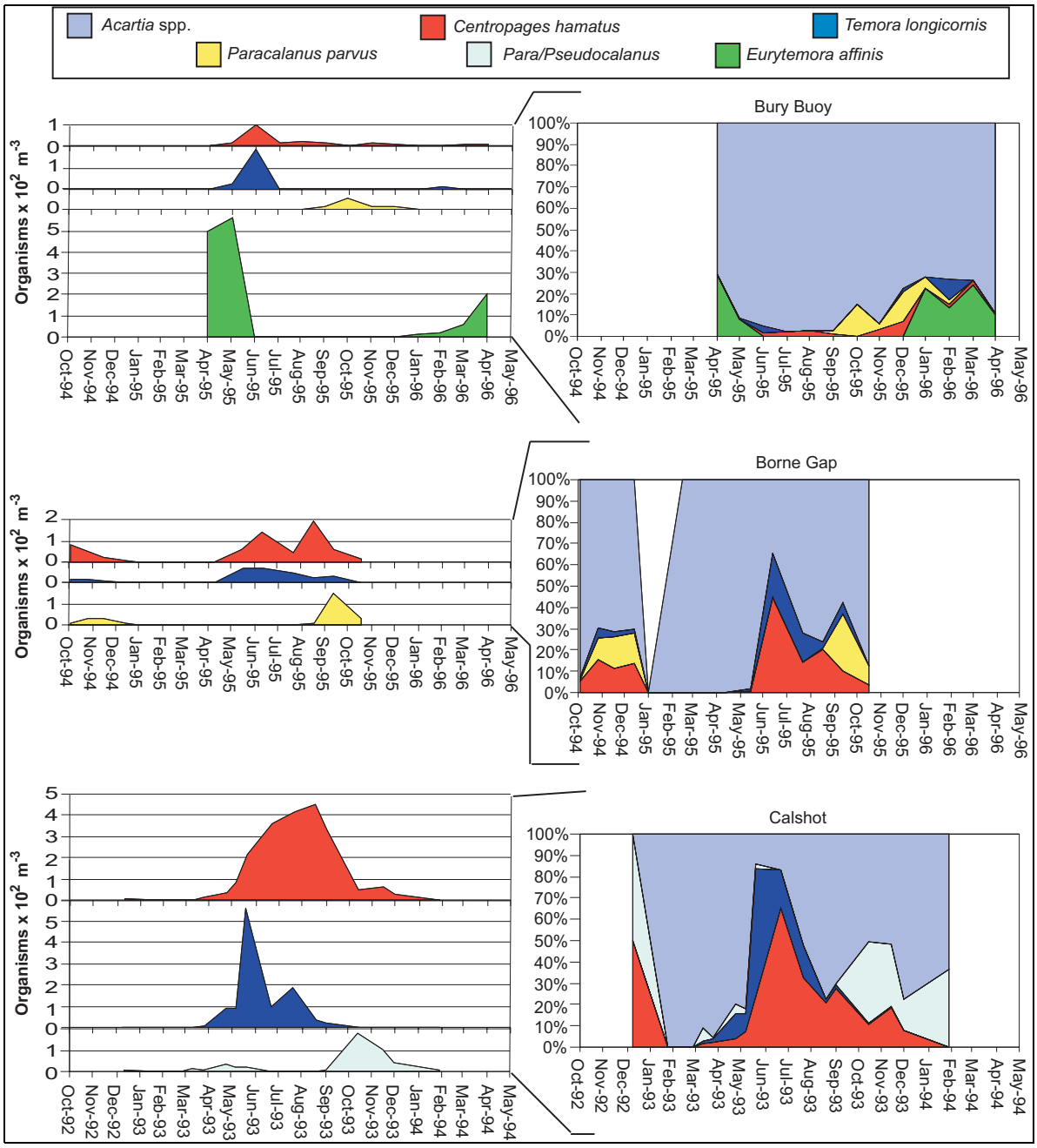


Figure 18. Temporal variability and seasonal contribution of the most abundant calanoid species at Bury Buoy and Bourne Gap during 1994/96 and Calshot in 1992/94 from the raw data of Castro-Longoria (1998) and Hirst (1996), respectively. The seasonality of abundance of *Acartia* was omitted for a better view of the variability of the other species (Note that abundance interval indicates 100 organisms m^{-3}). Data for different strata were averaged.

Other than *Acartia*, only *C.hamatus, T.longicornis, P.parvus, P.elongatus* and *E.affinis* were present with some importance, contributing up to 80 % of the calanoid fraction on some occasions (Figure 11). From these, *C.hamatus* and *T.longicornis* were found throughout the year but especially during spring-autumn where peak abundances were seen. Usually both species presented higher abundances towards the mouth of the estuary. *P.parvus* and *P.elongatus* also had higher abundances towards the mouth, with

P.parvus usually found during autumn and *P.elongatus* in winter-spring. *E.affinis*, in contrast, was confined to the inner reaches of the estuary and usually found during spring. Correlations with environmental parameters (Table 8) and MDS plots (Figure 14) clearly reflect these patterns, with the only anomalous result being the negative correlation of *P.elongatus* with salinity.

In terms of abundance, the values recorded here (Figure 11) are surprisingly similar to those of Hirst (1996), and again it raises the question of why only *Acartia* abundances were so low in that study. Reflecting the coarser mesh used by Castro-Longoria (1998) the values reported by her were anticipated to be lower than the present study, perhaps with the exception of *E.affinis* which, as an estuarine copepod, is expected to be in higher numbers further up the estuary at Bury Buoy (Figure 18).

Nothing different/unusual was observed in the occurrence and distribution of these species during this investigation, with seasonal and spatial patterns similar to those reported previously in this estuary (Figure 18) (Raymont & Carrie, 1964; Hirst, 1996; Castro-Longoria, 1998) and other north European estuaries (Baretta & Malschaert, 1988; Soetaert & Van Rijswijk, 1993). These species are also typical constituents of the English Channel and North Sea zooplankton (Digby, 1950; Bodo *et al*., 1965; Evans, 1977).

Euterpina acutifrons is a widespread neritic species (Rose, 1933; Björnberg, 1981) inhabiting a range of estuaries (Hopkins, 1977; Montú, 1980; Roper *et al*., 1983; Baretta & Malschaert, 1988; Soetaert & Van Rijswijk, 1993; Hopcroft *et al*., 1998; Dunbar & Webber, 2003; Hoffmeyer, 2004). It has been reported within Southampton Water several times (Raymont & Carrie, 1964; Hirst, 1996; Castro-Longoria, 1998), and always with a seasonal summer-autumn occurrence. Zinger (1989) reported an average of 561, 938 and 1170 harpacticoid organisms m^{-3} occurring from August through November, at Cracknore, NW.Netley and Calshot, with a maximum of 3834 organisms m^{-3} at NW.Netley in October. Hirst (1996), sampling at the mouth of the estuary, recorded *E.acutifrons* with an average of 1955 organisms m^{-3} for the same period (August-November), with maximum of 2524 organisms m^{-3} also in October. Raymont & Carrie (1964) reported a maximum of 10900 organisms m^{-3}, at Marchwood, with *E.acutifrons* and occurring mostly during August and lasting until October-November with abundances over 1000 organisms m^{-3} being reported. This species was substantially under-sampled by mesh-size greater than 200 μm, reflecting the low numbers of harpacticoids reported by Lucas (1993) and Castro-Longoria (Castro-Longoria, 1998).

The results presented here approach closely those of Raymont & Carrie (1964) and clearly indicate little change in distribution pattern and seasonality in the past 43 years. The differences noted with the data of Hirst (1996) and Zinger (1989) could probably be attributed to a different sampling effort and inter-annual variability. Significant correlations were obtained between *E.acutifrons* and environmental parameters (Table 8, also shown on the MDS plot on Figure 14 l) reflecting that the species was only abundant during the warm, saline and most productive period of the year, although it can be found throughout the year at Calshot. Despite the fact that *O.nana* overshadowed the numeric importance of this species at Cracknore during the summer-autumn season, it is clear that *E.acutifrons,* at least numerically, has the same impact as calanoids during summer-autumn through the entire estuary. *E.acutifrons* is also found at relative high abundances (up to 45000 organisms m^{-3}) in other north European estuaries (Baretta & Malschaert, 1988; Soetaert & Van Rijswijk, 1993), but surprisingly its significance is usually ignored or it is relegated as a minor component. Clearly more attention should be drawn to this species in the future, especially as it is clearly underestimated by coarser meshes.

Probably the major difference noted between previous reports and this study was the appearance of cyclopoids, particularly *Oithona nana*, within the upper estuary, and its progressive elimination towards the mouth of the estuary (Figure 10). *O.nana* is a widespread neritic species, commonly found in The Atlantic (Björnberg, 1981; Bradford-Grieve *et al*., 1999), Pacific, Indian, Mediterran, Red Sea (Rose, 1933), sea lochs in Scotland (Lampitt, 1979), the English Channel (Digby, 1950) and on tropical-temperate estuaries elsewhere (Reeve, 1975; Montú, 1980; Soetaert & Van Rijswijk, 1993; Hopcroft *et al*., 1998). The late-summer pattern of occurrence observed in this study is quite similar to that reported in the Westerschelde (Soetaert & Van Rijswijk, 1993) and Killary Harbour (Ryan *et al*., 1986).

This species was first recorded in Southampton Water in 1995/96 by Castro-Longoria (1998), but due to the 220 μm mesh used most of *O.nana* nauplii and earlier copepodite forms were not collected, resulting in an underestimation of the impact that *O.nana* has on total copepod abundance in this estuary. Its absence in previous studies of the zooplankton of Southampton Water could also be due, to some degree, to the larger mesh-size used in other studies, in fact, the absence of *O.nana* within Southampton Water was specifically mentioned by Raymont and Carrie (1964) who expected it to be plentiful since it was abundant off the Isle of Wight (Figure 1 – Chapter 1). Perkins (1974) attributed this absence to the shallow nature of coastal plain estuaries, although this is

unlikely since it has been reported in other shallow estuaries elsewhere (Reeve, 1975; Montú, 1980; Hopcroft *et al*., 1998).

Investigations that employed finer mesh-size (Reeve, 1975; Montú, 1980; Ryan *et al*., 1986; Roff *et al*., 1988; Hopcroft *et al*., 1998; Richard & Jamet, 2001) usually ranked *O.nana* among the most abundant species. Reeve (1975) attributed 50% of the total copepod biomass of Card Sound in southern Florida to *O.nana* alone, while Lampit (1978) in a sea loch on the west coast of Scotland, indicates that it can amount up 67% of the biomass as dry weight (90 % in terms of numbers). Ryan *et al*. (1986) considered *O. nana* as the most abundant copepod in the Irish inlet of Killary Harbour, with abundances over 50000 organisms m^{-3}, similar to those of the present investigation, being reported. In contrast, in the Westerschelde, Soetaert & Van Rijswik (1993) reported maximum values of 12000 organisms m^{-3}. The widespread acceptance and use of 200 μm mesh as the standard net for mesozooplankton (Bé *et al*., 1968) should, however, be reconsidered as the importance of oithonids and other small copepod species in zooplankton catches is being reassessed (Kiørboe & Nielsen, 1994; Nielsen & Sabatini, 1996; Hopcroft *et al*., 1998; Gallienne & Robins, 2001; Hansen *et al*., 2004). In the particular case of *O.nana*, Richard & Jamet (2001) reported that over 80% of adults and copepodites can pass through a 200μm mesh.

Zinger (1989) and Hirst (1996) studies are the only previous investigations carried out in Southampton Water where similar nets to the present study were employed, i.e. 100 – 120 μm mesh. Of these two, only Hirst (1996) reported the occurrence of any cyclopoid at all, and, despite the fact that overall copepod densities reported by him (Figure 9 – Chapter 1) were much lower than in the present study, the proportion of cyclopoids (~2.7%) and seasonality of occurrence at Calshot were very similar to the values presented here. This would suggest that the identification of those cyclopoids as *Oithona similis* by Hirst (1996), could be in error. A definitive answers for the "sudden" appearance of *O.nana* in Southampton Water must certainly include the possibility that they have been either ignored or under-sampled by particular sampling devices/protocols, although this is unlikely since *O.nana* had been systematically recorded in every investigation since 1995 (J.A.Williams pers. comm.) in abundances up to 1507 organisms m^{-3}, even when 220μm mesh were employed (Castro-Longoria, 1998). Its complete absence in previous studies indicates/suggests that the species appeared after the 1985-1987 or 1990-1991 samplings carried out by Zinger (1989), and Lucas (1993) respectively, both of which included inner-estuarine sampling sites which are the most probable place for this species to be found in high numbers.

The recent occurrence of this species is possibly related to environmental or biological changes in this estuary. Richard & Jamet (2001) indicate *O.nana* to be a suitable species to act as a biological indicator of anthropogenic perturbed systems, and the negative correlation with dissolved oxygen could be related to this, but further studies and other parameters should be measured in order to further investigate this. Changes in copepod composition, where smaller and more numerous organisms replace large species that had been previously detected, have been associated with increasing eutrophication in other planktonic communities (Zaitsev, 1992; Uye, 1994). In Tokyo Bay, Uye (1994) suggested that nutrient loading promoted a shift from diatoms to flagellates and thus favoured *O.davisae* that feeds well on flagellates (Uchima & Hirano, 1986). At the present moment no data indicating such changes are available in Southampton Water, but this should clearly be addressed in future investigations.

Anyway, it is clear that *O.nana* is now established within this estuary and is found throughout the year at the inner stations, with maxima usually occurring during summer-autumn months and minima in spring. Of the environmental factors measured (Table 8), chlorophyll *a* and dissolved oxygen (concentration and % saturation) showed a significant negative correlation ($P<0.05$) with the abundance of *O.nana*, while MDS plot highlighted the spatial preference.

The impact of grazing could, of course, produce this kind of relationship with chlorophyll. While *O.nana* peaked at Cracknore around 20 days after the last major peak of chlorophyll *a* and could indeed have grazed phytoplankton down, it also maintained high abundances, >13000 organisms m^{-3}, for more than three months after the last phytoplankton bloom, when chlorophyll *a*. concentrations were, on average, 1.19 mg m^{-3} (Figure 19).

This would suggest that an additional/alternative feeding strategy to phytoplankton grazing could be part/all of the answer to its high numbers in late-autumn and early-winter. Lampitt & Gamble (1982) reported that *O.nana* is a raptorial feeder with an opportunistic diet, able to consume particulates from detritus to phytoplankton and including the earlier stages of calanoid nauplii, and even copepodite stages (Lampitt, 1979). This, allied with a low metabolic demand, could explain its high numbers in low phytoplankton concentrations (Lampitt & Gamble, 1982). Although no significant correlation was found between copepod nauplii and *O. nana* the potential value of nauplii as a food resource cannot be ruled out since the mesh employed in this investigation clearly under-sampled copepod nauplii. *O.nana,* however, strongly correlated ($r = 0.34$, $p<0.01$) with the smallest copepodite stages of *Acartia* reported here, i.e. 288 – 360 μm prosome length (Chapter 5),

and these are within the upper size limit that can be eaten by *O. nana* (Lampitt & Gamble, 1982). Further investigation is clearly required regarding what is maintaining this large community in Southampton Water before any further comment, as no data on other possible food sources are available. Certainly there is a growing body of literature suggesting that oithonids consume other food material in preference to diatoms. Uchima & Hirano (1986) demonstrated that *O.davisae* does not feed on diatoms but preferably on motile flagellates, while Nakamura & Turner (1997) report that *O.similis* has a diet based on autotrophic/heterotrophic (dino)flagellates, ciliates and nauplii, with heterotrophic dinoflagellates and ciliates as its main food source. Additionally, González & Smetacek (1994) reported that *O.similis* can meet 20 to 30% of its daily carbon requirement by faecal matter alone, and also point out that on the Weddel Sea (Antarctica) *Oithona* could subsist and reproduce entirely from faecal material. Either way it is clear that *Oithona* plays an important role in pelagic food webs, possibly being responsible for reprocessing faecal material and/or making nano, microflagelates and ciliates available to higher trophic levels.

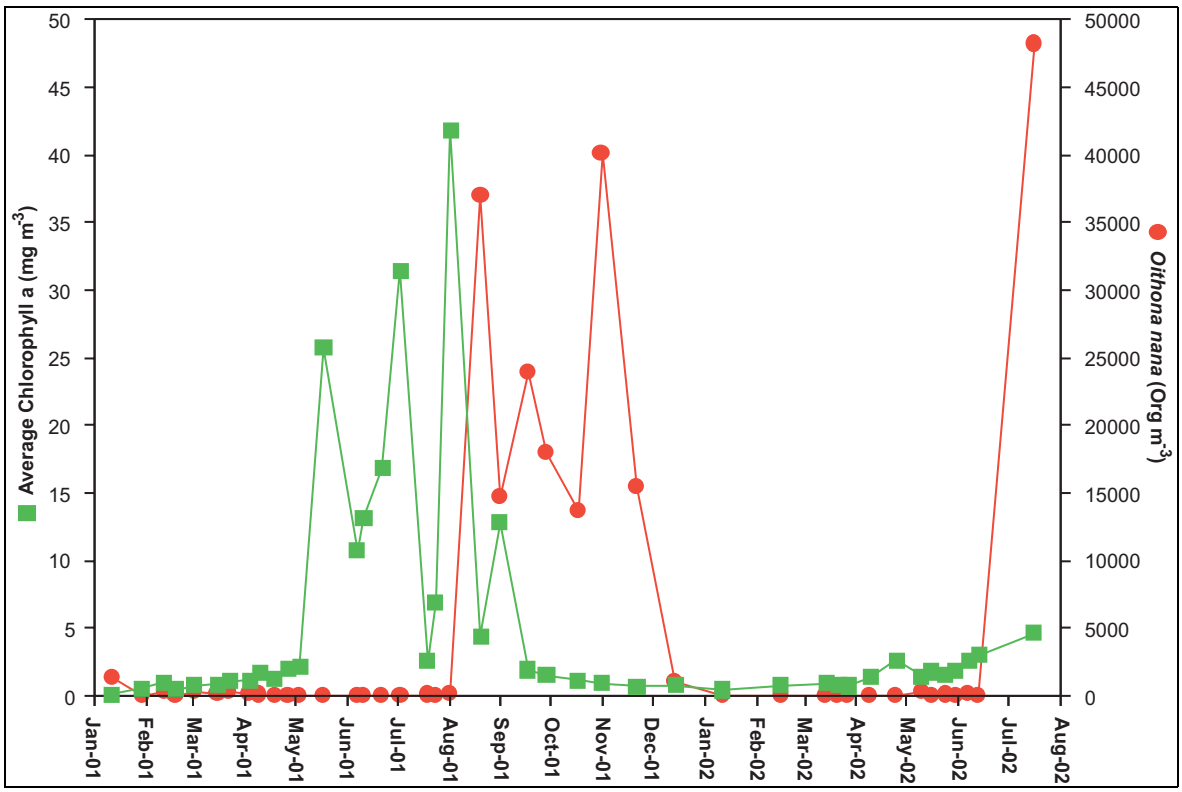


Figure 19. Seasonal pattern of Chlorophyll a concentration and *Oithona nana* abundance at Cracknore in 2001/02.

The importance of *O.nana* is clearly reflected by the Cracknore data during the present study, where it represented 50% of total copepods and had a biomass equivalent to

a total of 752 mg C m^{-3} (Chapter 5), or 76% of the total biomass of *Acartia* spp. (991 mg C m^{-3} – Chapter 5) for the same period. *Acartia*, in turn, represented only 18% of the total copepods and 96% of the calanoids at Cracknore (Figure 11). Even allowing for its low relative importance in the lower estuary, where the total biomass of *O. nana* were only 9 mg C m^{-3} i.e. 1.03% of the biomass of *Acartia* spp (873 mg C m^{-3} – Chapter 5), this previously unconsidered abundance/biomass, together with copepod nauplii and *E.acutifrons,* can go some way to explain the low copepod secondary production estimate within Southampton Water (Hirst *et al*., 1999), which was exclusively based on calanoid copepods (see Chapter 5).

Increases in the knowledge of the biology and ecology of oithonids is a current "hot topic" in pelagic ecology, since its potential role was clearly underestimated by coarser meshes employed in earlier studies. Recently, oithonids together with other small species, were proposed at the Marine Zooplankton Colloquium 2 (Paffenhöfer *et al*., 2001) as a potential topic for future studies because its occurrence in vast numbers can clearly affect processes underlying marine ecosystems function.

Of the remaining holoplanktonic groups, only *Oikopleura* had high abundances, with the numbers recorded during this survey higher than any previous estimates and approaching those of Zinger (1989) for total Urochordates. *Oikopleura* is a relatively small organism and if caught without its mucus capsule the smaller forms can clearly pass through the coarser mesh-size employed by Lucas (1993) and Castro-Longoria (1998), resulting in the relative low numbers reported by them, where a maximum of 1091 organisms m^{-3} were reported by Castro-Longoria (1998) in May 1995. Hirst (1996), employing a 118 μm mesh, reported values similar to those of Lucas (1993) and Castro-Longoria (1998) recording a maximum of 1172 organisms m^{-3} in May 1993. In contrast to Castro-Longoria (1998), who suggested that *Oikopleura* had an inconsistent distribution pattern within this estuary, the results presented here and in other studies indicate that *Oikopleura* was always found within Southampton Water with peaks of abundance during May. During the present study another peak in August, in addition to the May peak (>3000 organisms m^{-3}), was observed at the three stations. These values and the pattern of seasonality are similar to those reported by Ryan *et al*., (1986) at Killary Harbour, where a peak of 3054 organisms m^{-3} was reported early in June. In the Westerschelde maximum abundances of 8000 organisms m^{-3} in July have been reported (Soetaert & Van Rijswijk, 1993). Hansen & Anderson (1962) also found a maximum of 3500 organisms m^{-3} during August at Bloden Ground, while Paffenhöfer (1976) also found greatest numbers of

O.dioica in June-July in the southern North-Sea, with a maximun of 8500 organisms m^{-3}. In other estuaries *O.dioica* was observed with averaged abundances of 7364 organisms m^{-3} (peak of 11343 organisms m^{-3}) at Tampa Bay (Hopkins, 1977), while at North Inlet (South Carolina) averaged values of 9581 organisms m^{-3} (peak of 20072 organisms m^{-3}) have been reported (Costello & Stancyk, 1983). At the Avon-Heathcote estuary (New Zealand) maximum of 548 organisms m^{-3} were reported.

In the present study, the abundance of *Oikopleura* was significantly correlated with chlorophyll (Table 8) and this is clearly illustrated in the MDS plots (Figure 14 r and Figure 15 e). The size of population is, in part, clearly linked with the occurrence of phytoplankton blooms since abundances were much lower in spring 2002 when compared with 2001 when blooms occurred. Appendicularians are important and efficient filter feeders, and with the aid of their mucus capsules they are capable of filtering and retaining particles as small as nanoplankton (Esnal, 1981). (It has been reported that these houses can be produced in 5 to 240 minutes (Esnal, 1981; Raymont, 1983), and with *Oikopleura dioica* having a life cycle between 3 - 5 days (22 ºC) and 10 - 12 days (14 °C) this can result in the production of up to 8 houses per day (Fenaux, 1976). The production of this mucopolysaccharide capsule is one of the most important factors about the biology of these organisms, because in bloom conditions these capsules became easily clogged and then abandoned by the animal, which will secret another one. The discarded capsules become a potentially concentrated source of energy as it contains mucus, detritus, phytoplankton and bacteria that otherwise would remain unavailable. Esnal (1981) and Raymont (1983) report that several zooplanktonic organisms benefit from this rich food source including copepods, euphausiids and fish).

Little attention has been given to this group in Southampton Water so far, but as seen in Figure 9 (Chapter 1) and Figure 10 they are clearly important during their peak season, in addition to which discarded capsules will clearly boost the significance of this group to overall energy flow within the mesozooplankton community.

The "gelatinous" predators *Sagitta setosa* (Chaetognatha) and *Pleurobrachia pileus* (Ctenophora) were reported previously by several zooplanktonic studies (Zinger, 1989; Lucas, 1993; Hirst, 1996; Castro-Longoria, 1998), and were the subject of specific studies within this estuary (Frid, 1984; Lucas, 1993; Frid *et al*., 1994). Despite the difference in mesh sizes, the abundance and seasonal/spatial distribution of *P.pileus* found during this investigation agrees with that reported by Lucas (1993), where *P.pileus* was usually found from April to October, and peaking in June, with abundances up to 20 organisms m^{-3}. Spatially it was usually much more abundant at Cracknore compared with

the other two stations. At Killary Harbour, Ryan *et al*., (1986) observed *P.pileus* at similar abundances with up to 26 organisms m^{-3} being reported in May however, a second peak of 75 organisms m^{-3} were also observed in September. In contrast to ctenophores, *S.setosa* was observed in higher abundances, up to 62 organisms m^{-3}, and found throughout the year. Like previous investigations, it was more abundant and frequent at Calshot and usually found from September to October. Again, mesh sizes is considered the cause of the higher abundances and frequency of occurrence of *S.setosa* in this study. At Killary Harbour, where finer meshes (90 µm) were employed, Ryan *et al*., (1986) observed similar *S.setosa* abundances with up to 55 organisms m^{-3} being reported in early November. Baretta & Malschaert (1988), sampling with a 200 µm mesh net, only reported 5 organisms m^{-3} in the Ems estuary.

Ctenophores and chaetognaths are active predators and can be responsible for the large-scale depredation of zooplankton in some areas (Boltovskoy, 1981a; Raymont, 1983; Båmstedt, 1998; Kasuya *et al*., 2000). Despite the fact that simplistic inverse correlations between copepods and these predators have been reported (Fraser, 1962; 1970; Deason & Smayda, 1982), no significant correlation was observed during the present study. However, the decline in *Acartia* abundance during early-summer could be related with the peak abundance of *P.pileus* by simple superposition of abundance graphs at Cracknore, where it was more abundant (Figure 20).

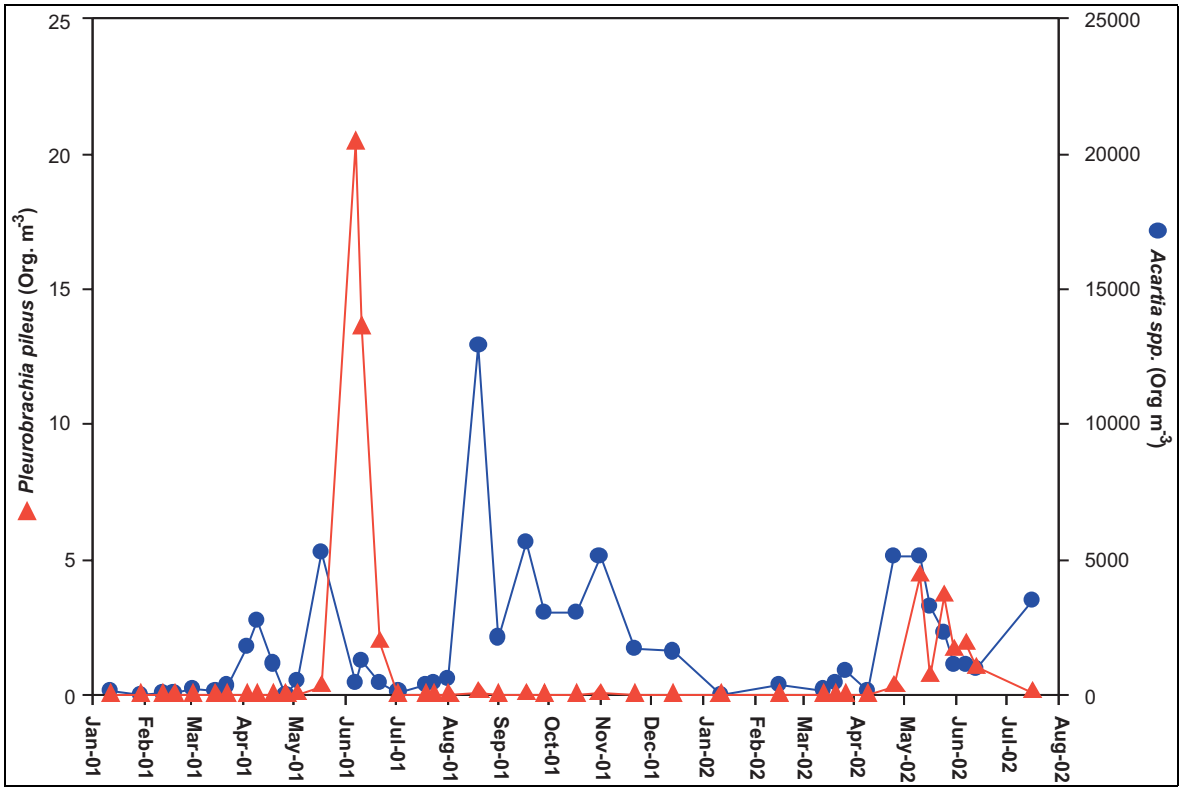


Figure 20. Seasonal pattern of abundance of *Pleurobrachia pileus* and *Acartia spp.* at Cracknore in 2001/02.

Analysis of the gut contents of *P.pileus* indicates that *Acartia* spp. is the main prey item, but *E.acutifrons*, copepod nauplii and barnacle nauplii are also important in the diet. Despite their relatively low abundance, the real impact the two predators can have on the zooplankton of this estuary should be investigated further.

Of the remaining copepods found, *Anomalocera pattersoni*, *Labidocera wollastoni* and *Stephos scotti* had been previously reported by Castro-Longoria (1998) at abundances lower than 1 organism m^{-3} within the Solent, and were probably brought into the estuary in water from the English Channel. The occurrences of *Calanus helgolandicus* and *Corycaeus anglicus* within this estuary are probably due to the same processes. *Isias clavipes* and *Parapontella brevicornis* were also reported by Castro-Longoria (1998) as an occasional occurrence, but despite the low abundances found in this study both showed a seasonal pattern within the estuary.

Six new taxa are reported for the first time within the holoplankton of Southampton Water. *Bosmina* sp. and *Daphnia* sp. are freshwater species and were certainly brought into the estuary by riverine input. *Microsetella norvegica* is a widespread neritic harpacticoid copepod that was probably transported into the estuary from the English Channel, where it is known to occur (Rose, 1933; Raymont, 1983). Little is known about the distribution of *Pseudocyclopia* sp. and apart from its record, no further comments can be made. Attention should also be drawn to the occurrence of *Oncaea* sp., which, like *Oithona nana,* is a small species that has been consistently under-sampled by meshes of small size and was identified by the marine Zooplankton Colloquium 2 (MZC2) as a potential species for future studies (Paffenhöfer *et al*., 2001).

The euphausiid *Meganyctiphanes norvegica* is also identified for the first time within this estuary, however unidentified specimens were observed previously in the Solent region by Castro-Longoria (1998). During the present study only three late furcilia and one caliptopis stage of *M. norvegica* were caught on different occasions at Calshot and Cracknore, although unidentified nauplii of euphausiids were found on a regular basis further into the estuary at Cracknore and NW. Netley. *Meganyctiphanes norvegica* was also reported by Williams & Collins (1986) in the inner reaches of the Bristol Channel and also in Killary Harbour (Ryan *et al*., 1986). The occurrence of euphausiids in these shallow waters is remarkable, since they are usually of open water distribution (Mauchline, 1980; Raymont, 1983; Mauchline, 1984).

Podon sp., *Acartia grani*, *Centropages typicus*, *Stephos minor*, *Oithona similis* and *Oncaea similis* had previously been reported within the holoplankton of this estuary and

surrounding areas but were not observed in this study. Of these, *A.grani* is a Mediterranean species that was only reported in the 1950's (Raymont & Carrie, 1964; Lance & Raymont, 1964). *Podon* sp., *C.typicus*, *S.minor*, *Oncaea similis* and *Oithona similis* were reported at Calshot and in the Solent, usually on single occasions and at very low abundances. Their prior occurrence within Southampton Water clearly indicates the occasional/regular incursion of species usually found in the English Channel (Rose, 1933; Digby, 1950; Raymont, 1983; Green *et al*., 1993).

Estuaries which do not drain completely during ebb tides have a characteristic zooplankton composition, which will be a reflection of the interaction of physical, biological and environmental factors, allied with the chance of organisms being caught, or not, by particular sampling artefacts or surveys (Raymont & Carrie, 1964; Perkins, 1974; Soetaert & Van Rijswijk, 1993). Accordingly, it can be said (Perkins, 1974) that these estuarine plankton can be summarized into three main components:

1 - Autochthonous populations; the permanent residents or those organisms always present in the estuary.

2 - Temporary autochthonous; those introduced from neighbouring regions and capable of limited proliferation, although dependant upon reinforcement from the parent population.

3 - Allochthonous populations; those brought into the estuary either from the sea or river which are unable to propagate and probably dying rapidly within the estuary.

The holoplankton of Southampton Water can be considered with respect to these categories and also according to its origin as indicated in Table 10.

Table 10. Autochthonous and allochthonous holoplanktonic populations of Southampton Water, with all previous records and origin.

Autochthonous	Temporary autochthonous	Allochthonous
Acartia discaudata (E/M)†	*Pseudocalanus elongatus* (M)	*Labidocera wollastoni* (M)
Acartia margalefi (E)	*Isias clavipes* (M)	*Anomalocera pattersoni* (M)
Acartia clausi (E/M) †	*Paracalanus parvus* (M)	*Stephos scotti* (M)
Acartia bifilosa (E/M)	*Eurytemora affinis* (E)	*Pseudocyclopia sp.* (M)
Acartia tonsa (E)	*Calanus helgolandicus* (M)	*Corycaeus anglicus* (M)
*Temora longicornis** (E/M) †	*Parapontella brevicornis* (M)	*Microsetella norvegica* (M)
*Centropages hamatus** (E/M) †	*Oncaea* sp. (M)	*Meganycthiphanes norvegica* (M)
Oithona nana (E/M) †	*Pleurobrachia pileus* (M)	*Daphnia sp.*(F)
Euterpina acutifrons (E/M) †	*Sagitta setosa** (M)	*Evadne nordmanii* (M)
	*Oikopleura sp**(E/M) †	*Bosmina sp.*(F)
		Podon sp. (M)
		Centropages typicus (M)
		Oithona similis (M)
		Oncaea similis (M)
		Acartia grani (M)
		Stephos minor (M)

Highlighted species are known to produce resting eggs, so they can be temporarily "absent" from the water column.
* species that were found throughout the year, and not clear if autochthonous or temporary autochthonous.
† species of marine origin, but since they were present at this estuary all year round (E/M) was attributed.
(E) = Estuarine; (M) = Marine; (F) = Fresh Water

This division presented in Table 10 is clearly arbitrary and only considers the patterns observed during this study. This clearly reflects the marine nature of Southampton Water, since several "marine" species were considered "estuarine" inhabitants. The results presented here are in line with classical estuarine studies in which the estuarine holoplankton communities are generally composed of calanoid copepods of the genus *Acartia* and/or *Eurytemora* (Conover, 1956; Jeffries, 1962; Cronin *et al*., 1962; Jeffries, 1967; Haertel & Osterberg, 1967; Heinle, 1972; Frolander *et al*., 1973; Bousfield *et al*., 1975; Reeve, 1975; Hulsizer, 1976; Wooldridge & Melville-Smith, 1979; Alcaraz, 1983; Baretta & Malschaert, 1988; Buskey, 1993). However, when considering studies where a finer mesh-size was employed (Reeve, 1975; Hopkins, 1977; Montú, 1980; Turner, 1982; Ryan *et al*., 1986; Soetaert & Van Rijswijk, 1993; Hopcroft *et al*., 1998; Hoffmeyer, 2004) estuarine holoplankton communities in addition to *Acartia* and *Eurytemora,* will also be dominated in some seasons and/or locations by the calanoid *Parvocalanus crassirostris*, the cyclopoid *Oithona* spp (viz. *O.similis, O.nana* and *O.colcarva*) and the harpacticoid *Euterpina acutifrons*. These reports clearly reflect Southampton Water, since at some seasons and locations, other components like *E.acutifrons* and *O.nana* clearly overshadow the numerical importance of *Acartia* (Table 11).

Table 11. Overall seasonal/spatial pattern of dominance of holoplanktonic forms within Southampton Water, based on the averaged value for each season. For the dominance of each *Acartia* species see Table 9.

Station	**Winter**	**Spring**	**Summer**	**Autumn**
Cracknore	*O.nana* Copepod nauplii	*Acartia* spp. *Copepod nauplii*	*O.nana*	*O.nana*
NW.Netley	Copepod nauplii	*Acartia* spp. Copepod *nauplii*	*E.acutifrons*. Copepod *nauplii*	*Acartia* spp. *O.nana*
Calshot	*Acartia* spp. Copepod *nauplii*	*Acartia* spp. Copepod *nauplii*	*E.acutifrons*. *Acartia spp.*	*E.acutifrons*. *Acartia spp.*

As proposed in Chapter 1, attention should be drawn to the two "ends" of this estuary, where contrasting situations are seen. At the mouth of the estuary, exemplified by Calshot, virtually no cyclopoids were recorded, with winter-spring dominated by *Acartia* spp. and copepod nauplii while the summer-autumn period was defined by *Acartia* spp. and *E.acutifrons*. At the head, at Cracknore, the cyclopoid *O.nana* clearly dominates the summer-autumn period, even outnumbering all other organisms summed. Therefore the overall pattern of copepods within the estuary as a whole might, simplistically, be best illustrated by the NW.Netley composition depicted in Figure 10, not forgetting that almost all calanoids are *Acartia* spp., harpacticoids *E.acutifrons* and all cyclopoids *O.nana*.

2.5. Chapter Conclusions

- 31 taxa were recorded among the holoplankton, with 6 taxa being reported for the first time within this estuary.

- Apart from *Acartia,* very few calanoids had any numerical importance, with *C.hamatus*, *T.longicornis, P.parvus, P.elongatus* and *E.affinis* having some significance during their respective seasons.

- Five *Acartia* species were recorded coexisting during this study; with *A.margalefi*, *A.discaudata* found throughout the year while *A.tonsa* and *A.clausi* was found during summer-autumn and *A.bifilosa* in winter-spring. *A.margalefi* and *A.tonsa* were more abundant at the inner reaches, while *A.clausi* and *A.bifilosa* at the mouth. *A.discaudata* was found at high abundances throughout the estuary.

- Contrary to previous studies, no simplistic species succession in the *Acartia* species was observed, with all species co-existing and peaking almost at the same periods.

- Other than calanoids, copepod nauplii, *Oikopleura* (Urochordata), *E.acutifrons* (Harpacticoida) and *O.nana* (Cyclopoida) had high abundances, even outnumbering *Acartia* in different seasons and locations. *Acartia* only dominated zooplankton samples throughout the estuary during spring.

- *E.acutifrons* had a consistent pattern of abundance at all three stations, peaking during summer, and maintaining high numbers throughout autumn.

- *O.nana* was observed in substantial numbers only towards the inner reaches of this estuary, where it clearly dominates from late-summer to early-winter.

- Correlations between biological and non-biological environmental variables reflect the seasonal patterns observed.

Chapter 3

The mero and tycoplankton of Southampton Water.

3.1. Introduction.

As already pointed out in previous chapters, the major constituents of the zooplankton community of Southampton Water have been described (Conover, 1957; Soares, 1958; Raymont & Carrie, 1964; Lance & Raymont, 1964; Bird, 1972; Barlow & Monteiro, 1979; Frid, 1984; Reubold, 1988; Zinger, 1989; Williams & Reubold, 1990; Geary, 1991; Lucas, 1993; Lucas & Williams, 1994; Lucas *et al*., 1995; Hirst, 1996; Castro-Longoria & Williams, 1996; Lucas *et al*., 1997; Castro-Longoria, 1998; Hirst *et al*., 1999; Chinnery, 2002; Muxagata *et al*., 2004). Despite the number of studies, only the holoplankton are described in any detail, with the meroplankton and tycoplankton either being virtually ignored, relegated to broad taxonomic groups or only included on lists of "occurrence".

Apart from the work of Raymont & Carrie (1964) and the Ph.D theses of Hirst (1996) and Castro-Longoria (1998) where several mero and tycoplanktonic species were briefly reported, only barnacle larvae (Soares, 1958; Muxagata *et al*., 2004) and gelatinous predators (Williams & Reubold, 1990; Lucas, 1993; Lucas & Williams, 1994; Lucas *et al*., 1995; Lucas *et al*., 1997) are reported in detail, with the composition, seasonality and abundance of the different species given.

This lack of study is probably due to the fact that apart from Cirripedia, Mollusca and Polychaeta that have some substantial contribution (Chapter 1), the remaining meroplankton and tycoplankton species only constitute a small fraction of the zooplankton of Southampton Water. Because of this they were often combined within a "general" group in the zooplankton of the estuary (Zinger, 1989; Lucas, 1993; Hirst, 1996; Castro-Longoria, 1998), with no specific details being given.

Decapods can be used as an example of the magnitude of the lack of information for this zooplankton fraction. It is well known that decapods, as a whole, contain potentially commercial species, but despite this importance, and the fact that more than 50 species are reported on the French side of the English Channel (Bodo *et al*., 1965; Martin, 2000), the occurrence of larvae of only three species, *Necora* (*Portunus*) p*uber*,

Scyllarum(?) spp. and *Pisidia (Porcellana) longicornis* (Barlow & Monteiro, 1979; Castro-Longoria, 1998) have been described so far, with no data on other constituents or any general seasonality. Information on other groups, such as the minor elements of the tycoplankton or even commensal and parasitic species, that have a short, free-living planktonic form at some stage of their life cycle, could be expected to be even more problematic. Surprisingly, the occurrences of the parasitic meroplankton species *Sacullina carcini, Peltogaster paguri, Notodelphys allmahi* and *Monstrilla* sp. and tycoplankton *Harpacticus* spp, *Canuella* sp., *Zaus* sp., *Altheuta* sp., *Mesopodopsis slaberri* and *Neomysis integer* have been reported in several species list of Southampton Water (Soares, 1958; Raymont & Carrie, 1964; Hirst, 1996; Castro-Longoria, 1998; Muxagata *et al*., 2004) and more frequently than species of decapod, mollusc and polychaete. However, apart from barnacle larvae and gelatinous predators, no critical detail is available regarding the distribution and seasonality of any of the remaining mero-tycoplanktonic species.

This is not a particular feature of Southampton Water. Specific information on invertebrate larvae in plankton catches are usually scarce and confined to broad taxonomic groups, with the exception of decapod and mollusc larvae (Lebour, 1947; Sankarankutty, 1975; Wehrtmann, 1989) that have been described in more detail because they have some representatives of commercial importance (Raymont, 1983). Usually in estuarine studies, invertebrate larvae are relegated to broader taxonomic groups (Hopkins, 1977; Turner, 1982; Williams & Collins, 1986; Imabayashi & Endo, 1986; Baretta & Malschaert, 1988; Kimmerer, 1993; Soetaert & Van Rijswijk, 1993; Hoffmeyer, 2004) with usually only holoplanktonic copepods being described in any detail. This absence of data on invertebrate larvae is of concern considering that several species have meroplanktonic larvae that can be seasonally abundant. Basic studies about the distribution, abundance and composition of meroplanktonic larvae can provide a unique source of data to be used in the management, monitoring and/or exploitation of these resources, or even to assess human/environmental impacts. Such data, allied with retrospective studies, can also be used to investigate recruitment of new commercial populations as well as to study dispersal and colonization of new environments; identify reproductive regions and seasons; predict future captures and estimate the size and health of parental populations (Boschi, 1981; Wehrtmann, 1989). In fact, since rates in zooplankton populations originate at species level, information about the spatial-temporal importance of species is vital before any attempt to quantify and model specific processes (Soetaert & Van Rijswijk, 1993).

Considering these points, the objective of the present chapter is to evaluate the contribution of mero and tycoplanktonic species, especially crustaceans, within the estuary,

and so offer a baseline reference of most of the species that compose this group together with their seasonality of occurrence in the zooplankton.

3.2. Materials and Methods.

The methodologies employed for collection and identification of the different species are fully described in Chapter 1.

3.2.1. Data Analysis.

As in the previous chapter, Pearson's product-moment correlation coefficient *r* was used to measure the intensity of the association between the biotic and abiotic variables. To stabilize the variance of the data, zooplankton abundances were $\log_{10}(x+1)$ transformed, and the average oxygen saturation and average Chl. *a* were $\log_{10}(x)$ transformed before analysis (Prepas, 1984; Zar, 1999; Clarke & Warwick, 2001).

In order to further investigate the relationship between samples collected at different stations and seasons, a Bray-Curtis similarity matrix was constructed using all meroplanktonic taxa abundances after a $\sqrt{x+0.5}$ transformation. This transformation was chosen in order to adjust the influence of numerically dominant species and allow for the contribution of "intermediate" species without losing information about the dominant ones. Ordination was done by non-metric multi-dimensional scaling (MDS), with plots calculated using the PRIMER 5 package (Clarke & Warwick, 2001) in the same form described in Chapter 2.

3.2.2. Other studies.

As with the previous chapter, raw data of previous investigations of Southampton Water were compiled and graphs redrawn with the same standards and scales used in this study, in order to form a clearer understanding when discussing/comparing results.

3.3. Results.

A total of 113 taxa were identified, consisting of 72 meroplanktonic and 41 tycoplanktonic forms. Of these, 84 are new records for the zooplankton of Southampton Water (species with * and ** in Table 12), although most of them have been observed as

adults in the benthos of Southampton Water and the Solent (Barnes *et al*., 1973; Hibbert, 1975; Thorp, 1980; Rowe, 1999; Guyard, 2000; Collins & Mallinson, 2000) (species with ** on Table 12). Numbers in front of each taxon, indicates the number of its picture on Appendix V.

Table 12. Meroplankton (M) and tycoplankton (T) taxa observed in the zooplankton of Southampton Water during the present investigation. (For more details see Table 3 – Chapter 1).

Phylum Cnidaria
- 2-Unidentified (M)
- 3-*Aurelia aurita* (M)
- 4-*Sarsia* sp. (M)
- 5-*Phialella quadrata* (M)
- 6-*Clytia hemisphaerica*(M)

Phylum Mollusca
- 9-Gastropod Veliger unidentified (M)
- 11-Bivalve veliger unidentified (M)

Phylum Annelida
- 13-Unidentified Polychaeta (M)
- 14-*Autolytus edwardsi* (M)
- 15-Unidentified spionidea larvae (M)

Phylum Chelicerata

Order Acarina
- 16-Unidentified Acari* (T)
- 17-*Achelia* sp. ** (T)
- 18-*Nymphon brevirostre* ** (T)

Phylum Crustacea

Order Cladocera
- 20-Unidentified Chydoridae* (M)

Subclass Cirripedia

Order Thoracica
- 24-*Conchoderma* sp. * (M)
- 25-*Verruca stroemia* (M)
- 26-*Chthamalus stellatus** (M)
- 27-*Elminius modestus* (M)
- 28-*Semibalanus balanoides* (M)
- 29-*Balanus crenatus* (M)
- 30-*Balanus improvisus* (M)

Order Acrothoracica
- 31-*Trypetesa* sp. *(M)

Order Rhizocephala
- 32-*Sacculina carcini* (M)
- 33-*Peltogaster paguri* (M)

Subclass Copepoda

Order Harpacticoida
- 54- Unidentified (T)
- 55-*Canuella* sp. ** (T)
- 58-*Sacodiscus* sp.* (T)
- 59-*Tisbe* spp.* (T)
- 60-*Thalestris* sp.* (T)

Order Cyclopoida
- 61-Unidentified (M)
- 62-*Cyclopinoides littoralis* * (M)
- 63-Unidentified notodelphydae * (M)

Order Siphonostomatoida
- 69-Unidentified (M)
- 70-*Asterocheres* sp. *(M)
- 71-*Caligus elongatus* * (M)
- 73-*Cancerilla tubulata* * (M)
- 74-*Bradypontius papillatus** (M)

Order Monstrilloida
- 75-*Monstrilla conjunctiva* * (M)
- 76-*Monstrilla helgolandica* * (M)
- 77-*Cymbasoma longispinosus** (M)
- 78-*Cymbasoma rigidus** (M)
- 79-*Cymbasoma thompsoni** (M)

Class Ostracoda
- 80-Unidentified ostracod (T)

Subclass Hoplocarida

Order Stomatopoda
- 81-*Rissoides desmaresti* ** (M)

Subclass Eumalacostraca

Order Mysidacea
- 82- *Siriella armata* ** (T)
- 83- *Siriella clausii* ** (T)
- 84- *Anchialina agilis** (T)
- 85- *Gastrosaccus sanctus* * (T)
- 86- *Leptomysis lingvura* **(T)
- 87- *Mysidopsis gibbosa* * (T)
- 88- *Acanthomysis longicornis* *(T)
- 89- *Mesopodopsis slabberi* (T)
- 90- *Paramysis arenosa* ** (T)
- 91- *Schistomysis kervillei* ** (T)

Order Isopoda
- 92- Unidentified praniza* (T)
- 93- *Idotea* sp. ** (T)
- 94-Unidentified cryptonistic form *(M)

Phylum Crustacea

Order Amphipoda
- 95-Unidentified (T)
- 96-*Amphilochus manudens* * (T)
- 97-*Gitana* sp.* (T)
- 98-*Parapleustes* sp.* (T)
- 99-*Aora gracilis** (T)
- 100-*Corophium* spp. ** (T)
- 101-*Jassa* sp.* (T)
- 102-*Apherusa* spp. ** (T)
- 103-*Atylus vedlomensis* **(T)
- 104-*Echinogammarus marinus* **(T)
- *Megaluropus agilis* * (T)
- *Melita* sp. * (T)
- 105-*Orchomene humilis**(T)
- *Argissa hamatipes*.* (T)
- 106-*Parametaphoxus fultoni* ** (T)
- 107- *Pariambus typicus* ** (T)
- 108- *Phtisica marina* ** (T)

Order Cumacea
- 109-*Pseudocuma similis* *(T)

Order Decapoda

Infraorder Caridea
- 112-*Palaemon* spp. ** (M)
- 113-*Palaemon elegans* * (M)
- 114-*Alpheus glaber* ** (M)
- 115-*Athanas nitescens* ** (M)
- 116-*Hippolyte* spp. ** (M)
- 117-*Thoralus cranchii* ** (M)
- 118-*Processa* sp. ** (M)
- 119-*Crangon crangon* ** (M)
- 120-*Crangon bispinosus* ** (M)
- 121-*Crangon trispinosus* ** (M)
- 122-*Crangon fasciatus* ** (M)

Infraorder Thalassinidea
- 123-*Axius stirhynchus* ** (M)
- 125-*Upogebia* sp. ** (M)

Infraorder Anomura
- 126-*Diogenes p.pugilator* ** (M)
- 127-*Anapagurus hyndmanni* ** (M)
- 128-*Pagurus bernhardus* ** (M)
- 129-*Galathea squamifera* ** (M)
- 130-*Pisidia longicornis* (M)
- 131-*Porcellana platycheles* ** (M)

Infraorder Brachyura
- 132-*Ebalia tuberosa* * (M)
- 133-*Ebalia tumefacta* ** (M)
- 134-*Maja squinado* ** (M)
- 135-*Hyas* sp. ** (M)
- 136-*Inachus* sp.** (M)
- 137-*Macropodia* spp.** (M)
- 138-*Pisa* sp.** (M)
- 139-*Corystes cassivelaunus* **(M)
- 140-*Liocarcinus* spp.** (M)
- 141-*Carcinus maenas** (M)
- 142-*Pilumnus hirtellus* ** (M)
- 143-*Pinnotheres pisum* ** (M)

Phylum Phoronida
- 144-Actinotrocha unidentified* (M)

Phylum Bryozoa
- 145-Cyphonaute unidentified (M)

Phylum Chaetognatha

Order Phragmorpha
- 146-*Spadella cephaloptera* * (T)

Phylum Echinodermata

Order Ophiurida
- 148- *Amphipholis squamata* ** (T)

Phylum Chordata

Class Ascidiacea
- 150-Unidentified (M)

Class Osteichthyes
- 151-Unidentified fish egg (M)
- 152-Unidentified fish larvae (M)

* Taxon reported for the first time in the zooplankton of Southampton Water
** Reported within the benthos of the surrounding area.

As most of the knowledge about the benthic species occurring in this estuary and surrounding area is sparse, and based on unpublished reports and personal observations, the species that could be supplying adults and/or larvae to the zooplankton, apart from barnacles and fish, are summarized in Table 13.

Table 13. Benthic organisms found in the Southampton Water and the Solent (Part 1 of 3).

Phylum Mollusca

Class Polyplacophora

Acanthochitona crinita (Pennant, 1777) (6,7)
Lepidochitona cinerea (Linnaeus, 1767) (6,7)
Leptochiton asellus (Gmelin, 1791) (1,6,7)

Class Gastropoda

Order Archaeogastropoda

Diodora graeca (Linnaeus, 1758) (6,7)
Tricolia pullus (Linnaeus, 1758) (6,7)
Gibbula cineraria (Linnaeus, 1758) (1,3)
Gibbula umbilicalis (da Costa, 1778) (6,7,8)
Calliostoma zizyphinum (Linnaeus, 1758) (6,7)

Order Patellogastropoda

Patella depressa Pennant, 1777 (2)
Patella ulyssiponensis Gmelin, 1791 (2)

Order Mesogastropoda

Lacuna crassior (Montagu, 1803) (1)
Lacuna vincta (Montagu, 1803) (6,7)
Littorina littorea (Linnaeus, 1758) (1)
Hydrobia ulvae (Pennant, 1777) (8)
Crepidula fornicata (Linnaeus, 1758) (1,2,3,6,7)
Trivia monacha (da Costa, 1778) (1,6,7)

Order Neogastropoda

Nucella lapillus (Linnaeus, 1758) (1,3)
Ocenebra erinacea (Linnaeus, 1758) (1,6,7)
Buccinum undatum Linnaeus, 1758 (1,3,6,7)
Neptunea antiqua (Linnaeus, 1758) (1,2)
Hinia reticulata (Linnaeus, 1758) (1,2,3,6,7,8)
Hinia incrassata (Ström, 1768) (6,7)

Order Anaspidea

Akera bullata O F Müller, 1776 (1)

Order Nudibranchia

Goniodoris castanea Alder & Hancock, 1845 (6,7)
Doto coronata (Gmelin, 1791) (1)
Acanthodoris pilosa (Abildgaard, 1789) (1,6,7)
Onchidoris bilamellata (Linnaeus, 1767) (1,6,7)
Archidoris pseudoargus (Rapp, 1827) (1)

Class Pelecypoda

Order Mytiloida

Mytilus edulis Linnaeus, 1758 (1,2,6,7,9)
Modiolus modiolus (Linnaeus, 1758) (1)

Order Nuculoida

Nucula spp. (2,8)
Nucula nitidosa Winckworth, 1930 (1,3,6,7)
Nucula nucleus (Linnaeus, 1758) (6,7)

Order Ostreoida

Ostrea edulis Linnaeus, 1758 (1,2,3,6,7,9)
Chlamys varia (Linnaeus, 1758) (1,6,7)
Aequipecten opercularis (Linnaeus, 1758) (1,6,7)

Order Veneroida

Cerastoderma edule (Linnaeus, 1758) (1,2,6,7,8,9)
Cerastoderma glaucum (Poiret, 1789) (2,9)
Parvicardium ovale (G B Sowerby II, 1840) (6,7)
Parvicardium exiguum (Gmelin, 1791) (1)
Spisula elliptica (Brown, 1827) (6,7)
Lutraria angustior Philippi, 1844 (6,7)
Lutraria lutraria (Linnaeus, 1758) (6,7)
Solen marginatus Pulteney, 1799 (2)
Ensis siliqua (Linnaeus, 1758) (2)
Ensis ensis (Linnaeus, 1758) (2)
Abra nitida (O F Müller, 1776) (1,9)
Tapes decussatus (Linnaeus, 1758) (2,9)
Tapes rhomboides (Pennant, 1777) (2)
Tapes aureus (Gmelin, 1791) (9)
Venerupis senegalensis (Gmelin, 1791) (9)
Macoma balthica (Linnaeus, 1758) (9)
Scrobicularia plana (daCosta, 1778) (9)
Mercenaria mercenaria (Linnaeus, 1758) (2,8,9)
Petricola pholadiformis Lamarck, 1818 (2,9)

Order Myoida

Corbula gibba (Olivi, 1792) (6,7)
Mya truncata Linnaeus, 1758 (2)
Mya arenaria Linnaeus, 1758 (2)
Barnea candida (Linnaeus, 1758) (1)
Pholas dactylus (Linnaeus, 1758) (3)

Class Cephalopoda

Sepia officinalis Linnaeus, 1758 (1)

Phylum Annelida

Class Polychaeta

Order Phyllodocida

Aphrodita aculeata Linnaeus, 1758 (1,6,7)
Harmothoe sp. (8)
Gattyana cirrosa (Pallas, 1766) (6,7)
Lepidasthenia argus Hodgson, 1900 (6,7)
Lepidonotus squamatus (Linnaeus, 1767) (6,7)
Lepidonotus clava (Montagu, 1808) (6,7)
Pholoe inornata Johnston, 1839 (6,7,8)
Sthenelais boa (Johnston, 1839) (1,6,7)
Sthenelais limicola (Ehlers, 1864) (6,7)
Eteone longa (Fabricius, 1780) (1,6,7,8)
Mysta picta (Quatrefages, 1866) (6,7)
Anaitides mucosa (Oersted, 1843) (6,7,8)
Eulalia viridis (Linnaeus, 1767) (6,7)
Eumida bahusiensis Bergstrom, 1941 (8)
Eumida sanguinea (Oersted, 1843) (8)
Eumida sp. (8)
Glycera tridactyla Schmarada, 1861 (8)
Glycera sp.
Glycinde nordmanni (Malmgren, 1866) (6,7)
Kefersteinia cirrata (Keferstein, 1862) (8)
Syllidia armata Quatrefages, 1866 (8)
Ehlersia cornuta (Rathke, 1843) (8)
Syllis sp. (8)
Syllis gracilis Grube, 1840 (8)
Streptosyllis websteri Southern, 1914 (6,7,8)
Syllides benedicti Banse, 1971 (8)
Typosyllis armillaris (O F Müller, 1771) (6,7)
Exogone hebes (Webster & Benedict, 1884) (8)
Exogone naidina Oersted, 1845 (8)
Sphaerosyllis sp. (8)
Sphaerosyllis erinaceus Claparède, 1863 (8)
Autolytus sp. (6,7,8)
Hediste diversicolor (O F Müller, 1776) (2)
Neanthes irrorata (Malmgren, 1867) (2)
Nereis longissima Johnston, 1840 (2,8)
Nereis pelagica Linnaeus, 1761 (1)
Perinereis cultrifera (Grube, 1840) (6,7,8)
Platynereis dumerilii (Audouin & Milne-Edwards, 1834) (1,6,7,8)
Websterinereis glauca (Claparède, 1870) (8)
Nephtys caeca (Fabricius, 1780) (2,8)
Nephtys assimilis Oersted, 1843 (8)
Nephtys hombergii Savigny, 1818 (1,6,7,8)
Nephtys incisa Malmgren, 1865 (2)
Nephtys cirrosa Ehlers, 1868 (6,7,8)
Nephtys sp. (6)

Order Eunicida

Lysidice ninetta Audouin & Milne-Edwards, 1833 (6,7)
Marphysa sanguinea (Montagu, 1813) (6,7)
Paarougia caeca (Webster & Benedict, 1884) (8)
Protodorvillea kefersteini (McIntosh, 1869) (8)

Order Orbiniida

Scoloplos armiger (O F Müller, 1776) (6,7,8)
Aricidea minuta Southward, 1956 (8)

Order Spionida

Poecilochaetidae serpens Allen, 1904 (8)
Polydora sp. (6,8)
Polydora caeca (Oersted, 1843) (8)
Polydora ciliata (Johnston, 1838) (8)
Pseudopolydora antennata (Claparède, 1870) (8)
Pseudopolydora pulchra (Carazzi, 1895) (8)
Pygospio elegans Claparède, 1863
Spio armata Thulin, 1957 (6,7)
Spio decorata Bobretzky, 1870 (8)
Spio martinensis Mesnil, 1896 (8)
Spiophanes bombyx (Claparède, 1870) (8)
Apelochaeta ssp. (8)
Aphelochaeta marioni (Saint-Joseph, 1894) (8)
Cirriformia tentaculata (Montagu, 1808) (1,8)

Table 13. Benthic organisms found in the Southampton Water and the Solent (Part 2 of 3).

Phylum Annelida (cont.)
- **Class Polychaeta (cont.)**
  - **Order Spionida (cont.)**
    - *Caulleriella bioculata* (Keferstein, 1862) (6,7)
    - *Caulleriella alata* (Southern, 1914) (8)
    - *Caulleriella zetlandica* (McIntosh, 1911) (8)
    - *Chaetozone* sp. (6)
    - *Chaetozone gibber* Woodham & Chambers, 1994 (8)
    - *Chaetozone setosa* Malmgren, 1867 (8)
    - *Tharyx* sp. (8)
    - *Tharyx killariensis* (Southern, 1914) (8)
  - **Order Flabelligerida**
    - *Pherusa plumosa* (O F Müller, 1776) (1,2)
  - **Order Capitellida**
    - *Capitella capitata* (Fabricius, 1780) (8)
    - *Notomastus latericeus* M Sars, 1851 (8)
    - *Arenicola* sp. (8)
    - *Arenicola marina* (Linnaeus, 1758) (3)
    - *Clymenura* sp. (8)
    - *Euclymene oerstedii* (Claparède, 1863) (6,7,8)
  - **Order Opheliida**
    - *Ophelia bicornis* Savigny, 1818 (2)
    - *Ophelia rathkei* McIntosh, 1908 (2)
    - *Scalibregma inflatum* Rathke, 1843 (2)
  - **Order Terebellida**
    - *Polycirrus* sp. (6,7)
    - *Ampharete* sp. (6,7)
    - *Lagis koreni* Malmgren, 1866 (6,7)
    - *Amphitritides gracilis* (Grube, 1860) (1)
    - *Lanice conchilega* (Pallas, 1766) (1,3,6,7,8)
    - *Eupolymnia nebulosa* (Montagu, 1819) (1,6,7)
    - *Sabellaria spinulosa* Leuckart, 1849 (1,6,7)
    - *Melinna palmata*(Grube, 1869 (2,6,7)
    - *Terrebellides stroemi* M Sars, 1835 (2)
    - *Thelepus cincinnatus* (Fabricius, 1780) (1)
  - **Order Sabellida**
    - *Sabella pavonina* Savigny, 1820 (2,6,7)
    - *Sabella* spp. (3)
    - *Hydroides* sp. (8)
    - *Hydroides ezoensis* Okuda (8)
    - *Branchiomma bombyx* (Dalyell, 1853) (1)
    - *Laonome kroyeri* Malmgren, 1866 (1)
    - *Pomatoceros triqueter* (Linnaeus, 1758) (6,7,8)
    - *Pomatoceros lamarcki* (Quatrefàges, 1866) (8)

Phylum Crustacea
- **Class Maxillopoda**
  - **Subclass Copepoda**
    - **Order Harpacticoida**
      - *Asellopsis intermedia* (T Scott, 1895) (8)
      - *Canuella perplexa* T Scott & A Scott, 1893 (8)
      - *Halectinosoma* sp. (8)
      - *Rhizothrix* sp. (8)
    - **Order Poecilostomatoida**
      - *Hersiliodes* sp. (8)
- **Class Malacostraca**
  - **Subclass Hoplocarida**
    - **Order Stomatopoda**
      - *Rissoides desmaresti* (Risso, 1816) (4)
  - **Subclass Eumalacostraca**
    - **Order Mysidacea**
      - *Siriella armata* (H Milne-Edwards, 1837) (6,7)
      - *Siriella clausii* (G O Sars, 1877) (6,7)
      - *Gastrosaccus spinifer* (Goës, 1864) (6,7)
      - *Leptomysis gracilis* (G O Sars, 1864) (6,7)
      - *Leptomysis lingvura* (G O Sars, 1866) (6,7)
      - *Leptomysis mediterranea* G O Sars, 1877 (6,7)
      - *Mysidopsis angusta* G O Sars, 1864 (6,7)
      - *Paramysis arenosa* (G O Sars, 1877) (6,7)
      - *Praunus neglectus* (G O Sars, 1869) (6,7)
      - *Schistomysis kervillei* (G O Sars, 1885) (6,7)
      - *Schistomysis ornata* (G O Sars, 1864) (6,7)
      - *Schistomysis spiritus* (Norman, 1860) (6,7)
    - **Order Isopoda**
      - *Gnathia oxyuraea* (Liljeborg) (6,7)
      - *Limnoria lignorum* (Rathke, 1799) (2)
      - *Limnoria tripunctata* (Menzies, 1957) (2)
      - *Limnoria quadripunctata* Holthuis, 1949 (2)
      - *Sphaeroma serratum* (Fabricius, 1787) (1)
      - *Sphaeroma monodi* Bocquet Hoestlandt & Levi, 1954 (8)
      - *Idotea linearis* (Pennant, 1777) (1,6,7)
      - *Idotea baltica* (Pallas, 1772) (1,6,7)
      - *Athelges paguri* (Rathke, 1843) (6)
    - **Order Tanaidacea**
      - *Tanaissus lilljeborgi* Stebbing, 1891 (8)
    - **Order Cumacea**
      - *Vaunthompsonia cristata* Bate, 1858 (6,7)
      - *Bodotria pulchella* (G O Sars, 1879) (8)
      - *Bodotria scorpioides* (Montagu, 1804) (8)
      - *Iphinoe trispinosa* (Goodsir, 1843) (6,7)
      - *Eudorellopsis deformis* (Kroeyer, 1846) (8)
      - *Diastylis bradyi* Norman, 1879 (6,7)
      - *Diastylis rathkei typica* (Kröyer, 1841) (6,7)
      - *Diastylis rugosa* G O Sars, 1865 (6,7)
      - *Nannastacus unguiculatus* (Bate, 1859) (6,7)
      - *Pseudocuma longicornis* (Bate, 1858) (6,7)
    - **Order Amphipoda**
      - *Apherusa ovalipes* Norman & T Scott, 1906 (6,7)
      - *Gammarellus angulosus* (Rathke, 1843) (6,7,8)
      - *Monoculodes carinatus* (Bate, 1856) (6,7)
      - *Perioculodes longimanus* (Bate & Westwood, 1868) (6,7)
      - *Pontocrates arenarius* (Bate, 1858) (6,7,8)
      - *Pontocrates altamarinus* (Bate & Westwood, 1868) (6,7)
      - *Amphilochus neapolitanus* Della Valle, 1893 (8)
      - *Leucothoe incisa* Robertson, 1892 (6,7,8)
      - *Leucothoe lilljeborgi* Boeck, 1861 (8)
      - *Leucothoe procera* Bate, 1857 (8)
      - *Leucothoe* sp. (8)
      - *Iphimedia eblanae* Bate, 1857 (6,7)
      - *Ampithoe rubricata* (Montagu, 1808) (6,7)
      - *Urothoe brevicornis* Bate, 1862 (6,7)
      - *Urothoe poseidonis* Reibisch, 1905 (8)
      - *Parametaphoxus fultoni* (T Scott, 1890) (8)
      - *Harpinia pectinata* G O Sars, 1891 (6,7)
      - *Lysianassa ceratina* (A O Walker, 1889) (6,7)
      - *Atylus guttatus* (Costa, 1851) (6,7)
      - *Atylus vedlomensis* (Bate & Westwood, 1862) (6,7)
      - *Atylus swammerdamei* (H Milne-Edwards,1830) (6,7,8)
      - *Dexamine spinosa* (Montagu, 1813 (6,7,8)
      - *Ampelisca aequicornis* Bruzelius, 1859 (6,7)
      - *Ampelisca brevicornis* (Costa, 1853) (6,7,8)
      - *Ampelisca diadema* (A Costa, 1853) (3,6,7)
      - *Ampelisca macrocephala* Liljeborg, 1852 (6,7)
      - *Ampelisca tenuicornis* Liljeborg, 1855 (6,7)
      - *Ampelisca typica* (Bate, 1856) (6,7)
      - *Ampelisca* sp. (6)
      - *Siphonoecetes striatus* Myers & McGrath, 1979 (6,7)
      - *Bathyporeia elegans* Watkin, 1938 (6,7)
      - *Bathyporeia guilliamsoniana* Bate, 1856 (6,7,8)
      - *Bathyporeia pelagica* (Bate, 1856) (6,7)
      - *Bathyporeia sarsi* Watkin, 1938 (8)
      - *Echinogammarus marinus* (Leach, 1815) (6,7)
      - *Gammarus locusta* (Linnaeus, 1758) (6,7,8)
      - *Gammarus* sp. (8)
      - *Cheirocratus* sp. (8)
      - *Abludomelita obtusata* (Montagu, 1813) (7)
      - *Maera othonis* (H Milne-Edwards,1830) (6,7)
      - *Melita palmata* (Montagu, 1804) (6,7,8)
      - *Ericthonius* sp. (8)
      - *Ericthonius punctatus* (Bate, 1857) (8)
      - *Aora gracilis* (Bate, 1857) (8)
      - *Corophium arenarium* Crawford, 1937 (8)
      - *Corophium sextonae* Crawford, 1937 (6,7)
      - *Corophium volutator* (Pallas, 1766) (1)
      - *Pariambus typicus* Kröyer, 1845) (8)
      - *Phtisica marina* Slabber, 1789 (8)

Table 13. Benthic organisms found in Southampton Water and the Solent (Part 3 of 3).

Phylum Crustacea (cont.)

Subclass Eumalacostraca (cont.)

Order Decapoda

Infraorder Caridea

Palaemon longirostris H Milne-Edwards, 1837 (4)
Palaemon serratus (Pennant, 1777) (4)
Alpheus glaber (Olivi, 1792) (6,7)
Athanas nitescens (Leach, 1814) (1,6,7)
Eualus occultus (Lebour, 1936) (6,7)
Hippolyte varians Leach, 1814 (6,7)
Hippolyte sp. (4)
Thoralus cranchii (Leach, 1817) (5,7)
Processa nouveli holthuisi Al-Adhub & Williamson, 1975 (6,7)
Pandalina brevirostris (Rathke, 1837) (4,5,6,7)
Pandalus montagui Leach, 1814 (4)
Crangon allmanni Kinahan,1857 (6,7)
Crangon crangon (Linnaeus, 1758) (1,4,6,7,8)
Crangon bispinosus neglecta (Hailstone, 1835) (6,7)
Crangon trispinosus (Hailstone, 1835) (6,7)
Crangon fasciatus (Risso, 1816) (5,6,7)

Infraorder Astacidea

Homarus gammarus (Linnaeus, 1758) (1,4)

Infraorder Palinura

Palinurus elephas (Fabricius, 1787) (4)

Infraorder Thalassinidea

Axius stirhynchus Leach, 1815 (5)
Upogebia deltaura (Leach, 1815) (5)

Infraorder Anomura

Diogenes pugilator pugilator (Roux, 1829) (6,7)
Anapagurus chiroacanthus (Liljeborg, 1856) (6,7)
Anapagurus hyndmanni (Bell, 1845) (4,6,7)
Pagurus bernhardus (Linnaeus, 1758) (1,3,4,6,7,8)
Pagurus cuanensis Bell, 1845 (4,6,7)
Pagurus spp (3)
Galathea squamifera Leach, 1814 (3,4,6,7)
Galathea intermedia Liljeborg, 1851 (1,6,7)
Galathea strigosa (Linnaeus, 1767) (1)
Pisidia longicornis (Linnaeus, 1767) (1,3,4,5,6,7)
Porcellana platycheles (Pennant, 1777) (4)

Infraorder Brachyura

Ebalia tumefacta (Montagu, 1808) (2,6,7)
Ebalia sp (4,5)
Maja squinado (Herbst, 1788) (4,6,7)
Hyas coarctatus Leach, 1815 (1)
Inachus dorsettensis (Pennant, 1777) (1)
Inachus leptochirus Leach, 1814 (6,7)
Inachus phalangium (Fabricius, 1775) (4,6,7)
Macropodia deflexa Forest, 1978 (6,7)
Macropodia linaresi Forest & Z Alvarez, 1964 (5,6,7)
Macropodia rostrata (Linnaeus, 1761) (1,3,6,7)
Macropodia sp. (4,8)
Pisa tetraodon (Pennant, 1777) (1,3,4)
Corystes cassivelaunus (Pennant, 1777) (2,6,7)
Pirimela denticulata (Montagu, 1808) (2)
Cancer pagurus Linnaeus, 1758 (1,4,6,7)
Liocarcinus arcuatus (Leach, 1814) (1,4,5,6,7,8)
Liocarcinus depurator (Linnaeus, 1758) (1,4,6,7)
Liocarcinus holsatus (Fabricius, 1798) (1,6,7)
Liocarcinus pusillus (Leach, 1815) (2,5,6,7)
Liocarcinus spp (3,6,7)
Necora puber (Linnaeus, 1767) (4,6,7)
Carcinus maenas (Linnaeus, 1758) (1,2,4,8)
Portumnus latipes (Pennant, 1777) (2,6,7)
Goneplax rhomboides (Linnaeus, 1758) (4)
Pilumnus hirtellus (Linnaeus, 1761) (1,4,5,6,7)
Brachynotus sexdentatus (Risso, 1826) (6,7)
Pinnotheres pisum (Linnaeus, 1767) (1,2,6,7)

Phylum Chelicerata

Class Pycnogonida

Anoplodactylus pygmaeus (Hodge, 1864) (8)
Nymphon brevirostre Hodge, 1863 (6,7)
Nymphon gracile Leach, 1814 (6,7)
Nymphon rubrum (Hodge, 1865) (6)
Achelia echinata Hodge, 1864 (6,7)

Phylum Bryozoa

Class Gymnolaemata

Order Ctenostomatida

Alcyonidium gelatinosum (Linnaeus, 1761) (1)
Alcyonidium spp. (3)
Amathia lendigera (Linnaeus, 1758) (1)

Order Cheilostomatida

Flustra foliacea (Linnaeus, 1758) (1,3)
Bugula turbinata Alder, 1857 (3)
Bugula spp. (3)

Phylum Echinodermata

Class Asteroidea

Order Velatida

Crossaster papposus (Linnaeus, 1767) (1)

Order Spinulosida

Henricia sanguinolenta (O F Müller, 1776) (1)

Order Forcipulatida

Asterias rubens Linnaeus, 1758 (1)

Class Ophiuroidea

Order Ophiurida

Ophiura sp. (4)
Ophiothrix fragilis (Abildgaard, 1789) (1,6,7)
Amphipholis squamata (Chiaje, 1829) (6,7)

Class Echinoidea

Order Echinoida

Psammechinus miliaris (Gmelin, 1778) (1)

Class Holothurioidea

Order Dendrochirotida

Thyone fusus (O F Müller, 1776) (1)

Phylum Chordata

Class Ascidiacea

Order Enterogona

Clavelina lepadiformis (O F Müller,1776) (1,3)
Archidistoma aggregatum Garstang, 1891 (1)
Morchellium argus (Milne-Edwards, 1841) (1,3)
Sidnyum sp. (1)
Diplostoma listerianum (Milne-Edwards, 1841) (1)
Ciona intestinalis (Linnaeus, 1767) (1,3)
Perophora listeri Forbes, 1848 (1)
Ascidiella aspersa (O F Müller,1776) (1)
Ascidia conchilega O F Müller,1776 (1)

Order Pleurogona

Styela clava Herdman, 1882 (1,2,3)
Polycarpa pomaria (Savigny, 1816) (1)
Polycarpa scuba Monniot, 1970 (1,3)
Dendrodoa grossularia (van Beneden, 1846) (1,3)
Botryllus schlosseri (Pallas, 1766) (1)
Botrylloides leachi (Savigny, 1816) (1)
Molgula occulta Kupffer, 1875 (1)

Underlined species were observed within Southampton Water

References:
1 = Barnes *et al.*, (1973);
2 = Thorp (1980);
3 = Collins & Mallinson (2000);
4 = Mallinson (Pers. Com.);
5 = Widiawari (Pers. Com.)
6 = Axelsson (Pers. Com);
7 = Guyard (2000);
8 = Rowe (1999);
9 = Hibbert (1975);

3.3.1. Meroplankton.

After copepods, barnacle larvae were numerically the second most abundant group found in the mesozooplankton of Southampton Water during 2001-2002 (Figure 7 – Chapter 1). They averaged 45, 57 and 57% of the meroplankton at Cracknore, NW.Netley and Calshot, respectively; contributing up to 95% on some occasions (Figure 21).

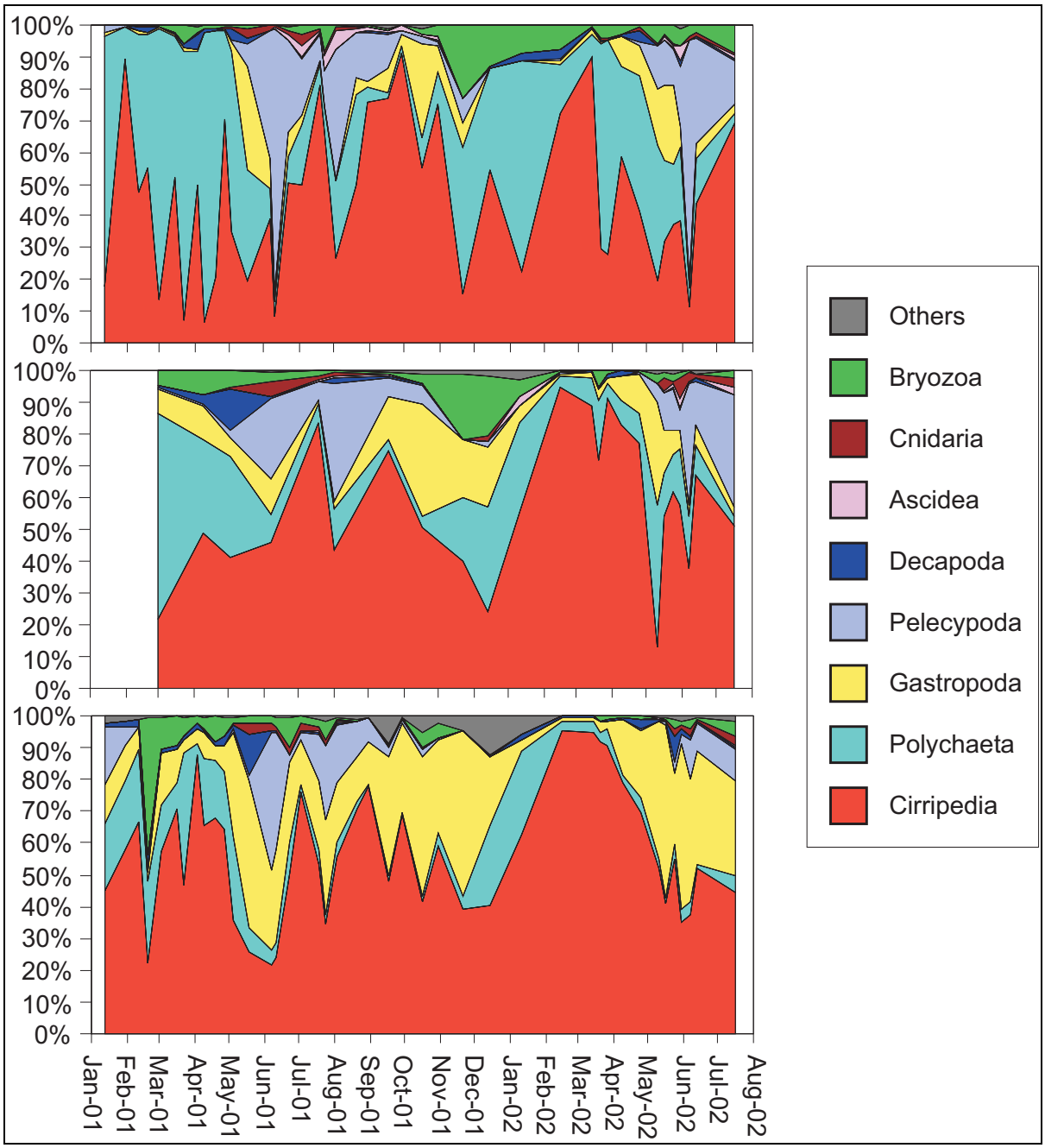


Figure 21. Seasonal contribution of the different meroplankton groups at Cracknore (Top), NW. Netley (Middle) and Calshot (Bottom) during 2001/02.

Polychaeta, Gastropoda, Pelecypoda (bivalves), Ascidia, Cnidaria, Bryozoa, and Decapoda complete the remaining major meroplanktonic contributors that had substantial

numerical contributions (Figure 21). The remaining meroplanktonic groups/species were considered minor contributors and were grouped under the heading "Others" in Figure 21. Apart from the barnacles and decapods that were detailed to species, the remaining major contributors were only accounted as groups, with a few species of polychaetes and cnidarians identified (Table 12) but not quantified.

After barnacles, polychaetes were the next in abundance with larvae present in the plankton throughout the whole period (Table 14), and averaging 32, 17 and 9% of the meroplankton at Cracknore, NW.Netley and Calshot, respectively. Lower abundances were usually observed during autumn and winter and maxima from early-spring to late-summer. Peaks of abundance in April (3140 organisms m^{-3}) and August (2696 organisms m^{-3}) were observed at Cracknore where polychaetes were much more abundant when compared with abundances at the other stations (Figure 22).

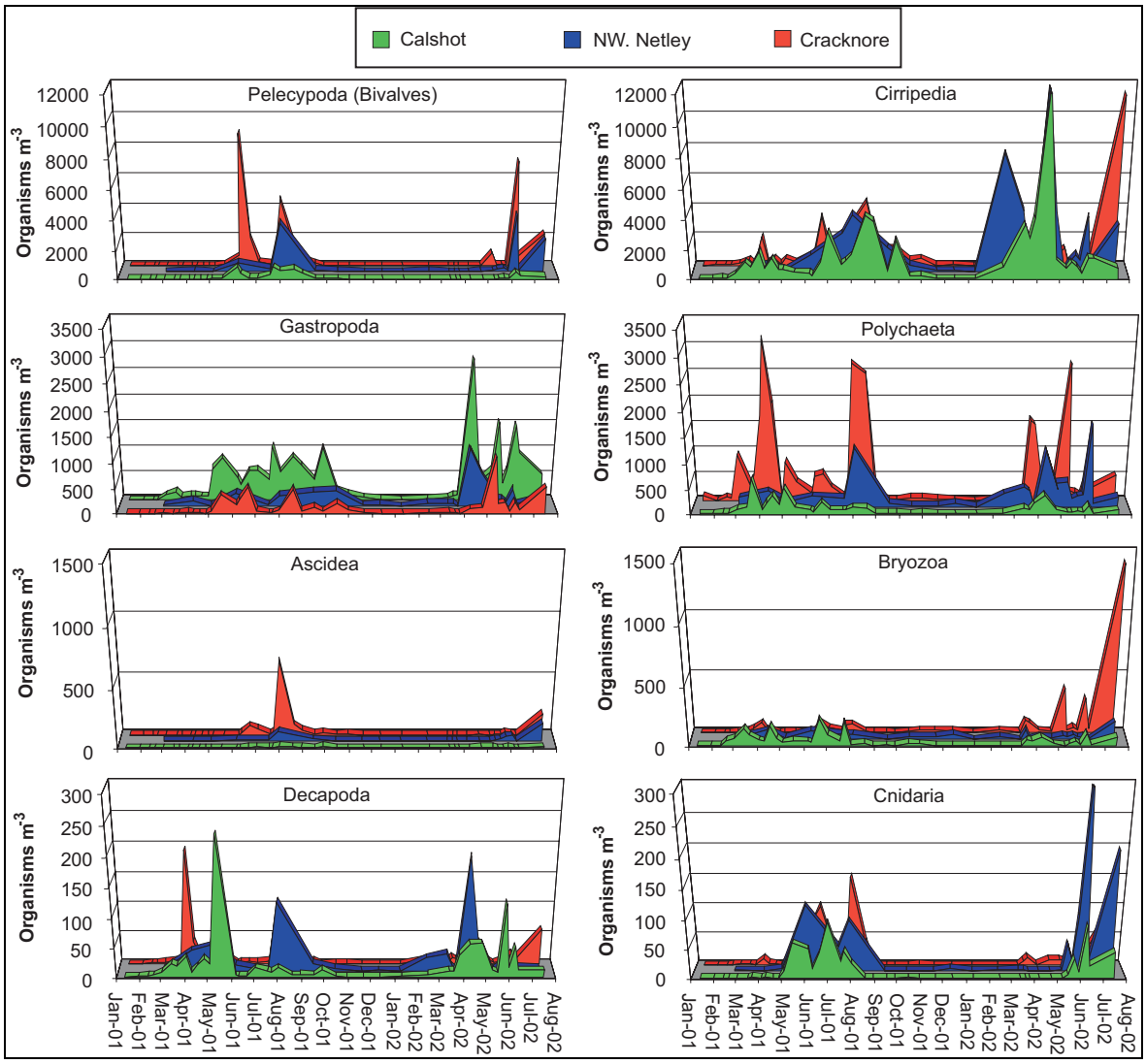


Figure 22. Temporal variability of the major meroplanktonic groups at Calshot, NW. Netley and Cracknore during 2001/02. (Note that figures are on different scales, and that the order of stations is changed for the Gastropoda)

Mollusca were differentiated into veligers of bivalves and gastropods and both, like Polychaeta, were present in plankton catches throughout the entire sample period (Table 14). Bivalves had a marked "seasonality", where high abundances were only observed from May to August, with peaks observed in June-July (more than 6000 organisms m^{-3} at Cracknore) and August. Like polychaetes, bivalves were more abundant in the inner estuary, with abundances gradually decreasing towards the mouth of the estuary, averaging 11, 9 and 7% of the meroplankton composition at Cracknore, NW.Netley and Calshot, respectively. Gastropods, in contrast, were much more abundant at Calshot with abundance diminishing towards the inner estuary. Several peaks of abundance were recorded from late spring throughout autumn, with a maximum of 2748 organisms m^{-3} in April 2002 at Calshot (Figure 22). Gastropods averaged 7, 10 and 21% of the meroplankton at Cracknore, NW.Netley and Calshot, respectively

Bryozoans were also observed at higher abundances inside the estuary than at the mouth. Cyphonaute larvae were recorded throughout the year at abundances usually >1 organism m^{-3} (Table 14), with a peak abundance of 1414 organisms m^{-3} at Cracknore in July 2002 (Figure 22). They usually averaged 3% of the meroplankton at each station. Ascidians were usually observed from May through to November (Table 14), and were relatively abundant from June to September, peaking in August (636 organisms m^{-3}). Abundances were much higher at the inner stations than at the mouth (Figure 22). Overall, ascidians averaged 0.7, 0.5 and 0.1% of the meroplankton at Cracknore, NW.Netley and Calshot, respectively. Cnidarians were mainly noted from February to October, with peak abundances observed from May through to August (Table 14). The maximum abundance recorded was 325 organisms m^{-3} observed at NW.Netley in July 2002 (Figure 22). Cnidarians usually averaged ~1% of the meroplankton at each station.

Table 14. Seasonal occurrence of the major meroplanktonic groups in Southampton Water, with the frequency of occurrence (FO) of each taxa. Where ■ = Cracknore; ▲= NW. Netley, ● = Calshot. Colour shades indicates average abundances, where, = 0, = 0.001 – 0.01, = 0.01 – 0.1, = 0.1 – 1.0, = 1.0 – 10, = 10 – 100, = 100 – 1000 and = ≥ 1000 organisms m^{-3}.

Species	J	F	M	A	M	J	J	A	S	O	N	D	FO
Major contributors													
Cirripedia (total)	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	100%
Decapoda (total)	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	100%
Cnidaria (total)		■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■	■▲●		▲	81%
Bivalve veliger (total)	■ ●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■	▲	78%
Gastropod veliger (total)	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	▲●	98%
Polychaeta (total)	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	100%
Unidentified Bryozoa (total)	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	90%
Unidentified ascidian (total)	▲		■▲	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■	■		47%

During this study 10 species of Cirripedia were identified, and Figure 23 illustrates the temporal abundance distribution of the most abundant ones at Southampton Water. Of those, *Elminius modestus* was the most numerically abundant, occurring in the plankton throughout the year and found in every single sample, averaging between 56-60% of barnacle larvae at each station. This species typically had lower abundances in winter, with averages of 36, 58 and 47 organisms m^{-3} at Cracknore, NW.Netley and Calshot. During spring its abundance began to increase with averages of 351, 558 and 320 organisms m^{-3} at the same stations, and with a maximum of 1037 organisms m^{-3} in May 2002 at Cracknore. Maximum abundances were recorded during the summer-autumn months (July to December) with averages of 1053, 1299 and 1512 organisms m^{-3}, and a maximum of 9940 organisms m^{-3} in July 2002 at Cracknore. From autumn its abundance gradually declines towards the winter values (Figure 23).

The second most abundant species, *Balanus crenatus*, presented a marked seasonal pattern of abundance (Figure 23). It was most abundant during late-winter and early-spring, with winter-spring averages of 175, 1130 and 1149 organisms m^{-3} at Cracknore, NW.Netley and Calshot. Apart from Cracknore, abundances were much higher at NW.Netley and Calshot in 2002, with peaks up to 11963 organisms m^{-3} in April. During winter-spring *B.crenatus* averaged 36, 50 and 49 % (or 24, 36 and 33% during the entire sampling period) of the barnacles at Cracknore, NW.Netley and Calshot, respectively. Occasionally, very few larvae of this species were found during summer-autumn.

Balanus improvisus also had a very marked seasonal pattern of abundance (Figure 23). It usually appeared during summer-autumn, with averages of 339, 148 and 16 organisms m^{-3}, at Cracknore, NW.Netley and Calshot respectively, and was much more abundant and frequent at the inner stations, where a peak of 1767 organisms m^{-3} were recorded at Cracknore in 2002. This species was present in relative very low numbers during the winter and spring, with averages of 0.4, 0.8 and 0.1 organism m^{-3} recorded at the three stations during winter compared with 52, 29 and 4 organisms m^{-3} during spring. *B.improvisus* was absent from samples between mid-autumn to early-winter (November – January) averaging 10, 3 and 1% of the barnacles during the entire sampling period at Cracknore, NW.Netley and Calshot, respectively.

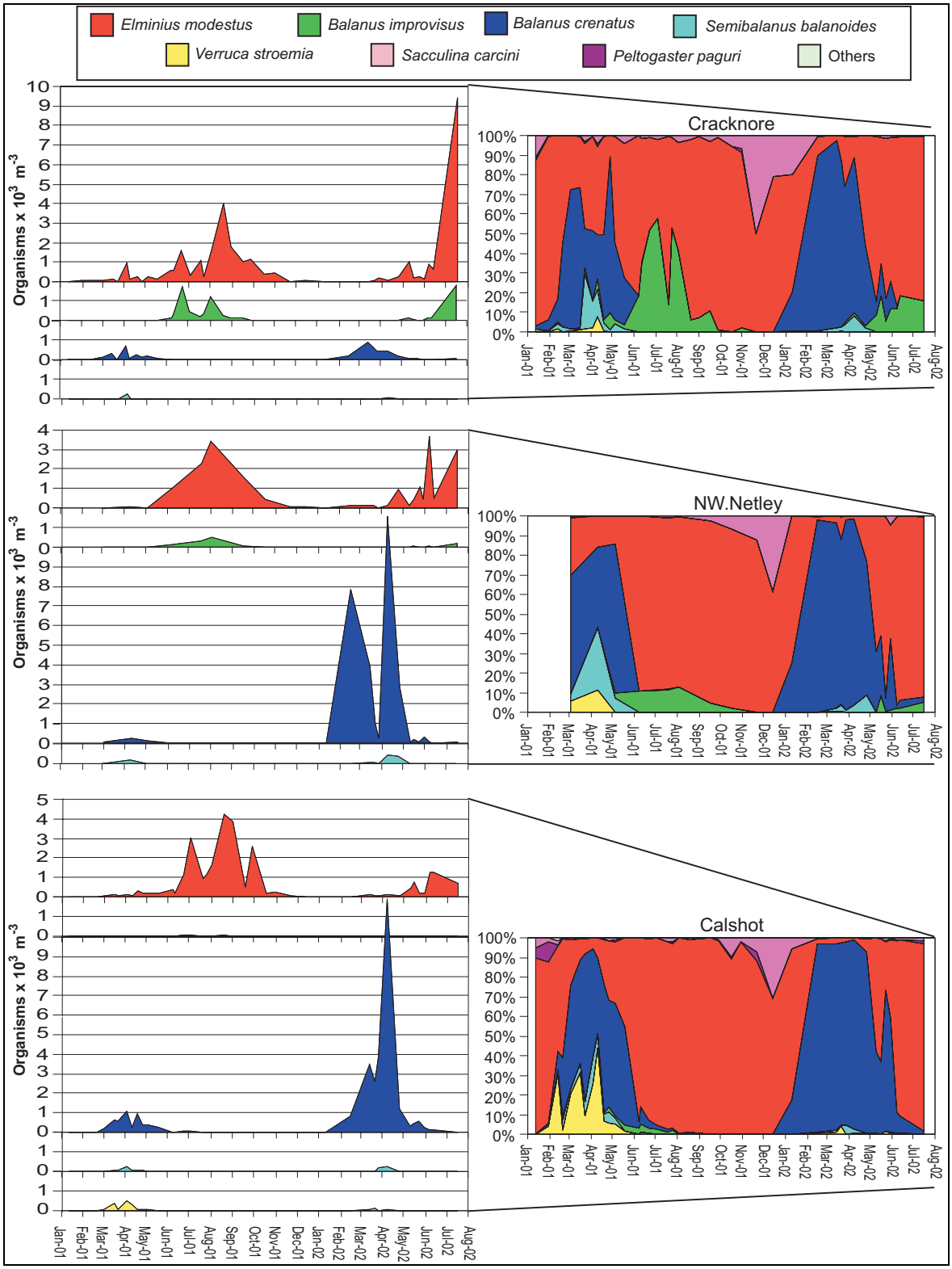


Figure 23. Temporal variability and seasonal contribution of barnacle larvae at Cracknore, NW. Netley and Calshot during 2001/02. (Note that abundance interval indicates 1000 organisms m^{-3} and that the temporal variability of *S.carcini*, *P.paguri* and others are not shown due to the low abundances)

Semibalanus balanoides and *Verruca stroemia* expressed the same pattern of distribution as *B.crenatus*, but at much lower abundances. A maximum of 441 organisms m^{-3} were recorded for *S.balanoides* in April 2002 at NW.Netley and 486 organisms m^{-3} for *V.stroemia* in April 2001 at Calshot (Figure 23). Both completely disappear from the plankton from June to February. While *S.balanoides* was observed at apparent similar abundances at all three stations throughout the sample period *V.stroemia* was clearly more abundant in 2001 compared with 2002, particularly at Calshot. During the entire sampling period *S.balanoides* averaged 2-3% of the barnacle composition at each station while *V.stroemia* accounted for <1, 1 and 5% of the barnacles at Cracknore, NW.Netley and Calshot, respectively.

The remaining barnacle species, *Sacculina carcini, Peltogaster paguri*, *Chthamalus stellatus, Conchoderma* sp. and *Trypetesa* sp. were present at very low abundances. The parasitic species *S.carcini* and *P.paguri* were found throughout the year, with abundances up to of 106 organisms m^{-3} observed for *S.carcini* in August 2001 and 19 organisms m^{-3} for *P.paguri* in February 2002 (Table 15). Only single individuals of *Chthamalus stellatus, Trypetesa sp.* and *Conchoderma* sp. were observed in a few samples (Table 15).

Table 15. Seasonal occurrence of Cirripedia larvae species found in Southampton Water, with the frequency of occurrence (FO) of each taxa. Where ■ = Cracknore; ▲= NW. Netley, ● = Calshot. Colour shades indicates average abundances, where, = 0, = 0.001 ⌐ 0.01, = 0.01 ⌐ 0.1, = 0.1 ⌐ 1.0, = 1.0 ⌐ 10, = 10 ⌐ 100, = 100 ⌐ 1000 and = ≥ 1000 organisms m^{-3}.

Species	J	F	M	A	M	J	J	A	S	O	N	D	FO
Trypetesa sp.							●						1%
Conchoderma sp.				▲									1%
Chthamalus stellatus			■	▲									2%
Elminius modestus	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	100%
Verruca stroemia	■	■ ●	■▲●	■▲●	●	●	●						38
Semibalanus balanoides	■ ●	■▲●	■▲●	■▲●	■▲●	▲							44%
Balanus crenatus	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■ ●					77%
Balanus improvisus	■	■ ●	■▲	■▲●	■▲●	■▲●	■▲●	■▲●	■▲	■▲			62%
Peltogaster paguri	■ ●	■▲●	■▲●	■▲●	■ ●	■ ●	■ ●		●	■ ●	●	▲	37%
Sacculina carcini	■ ●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	72%

During the present survey a total of 16102 decapod larvae were recorded at the three stations, averaging only 1% of the total meroplankton at each station (Figure 21). Decapod larvae do not generally constitute a large fraction of the mesozooplankton of Southampton Water only averaging 0.25% of the total mesozooplankton, with maximum abundances never exceeding 250 organisms m^{-3} (Figure 22).

A total of 31 decapod taxa were identified (but not staged), belonging to four infraorders (Table 12). Figure 24 indicates the abundance of each infraorder at each station, and it is clear that brachyuran larvae are the most abundant form, averaging 92% of all decapod larvae found.

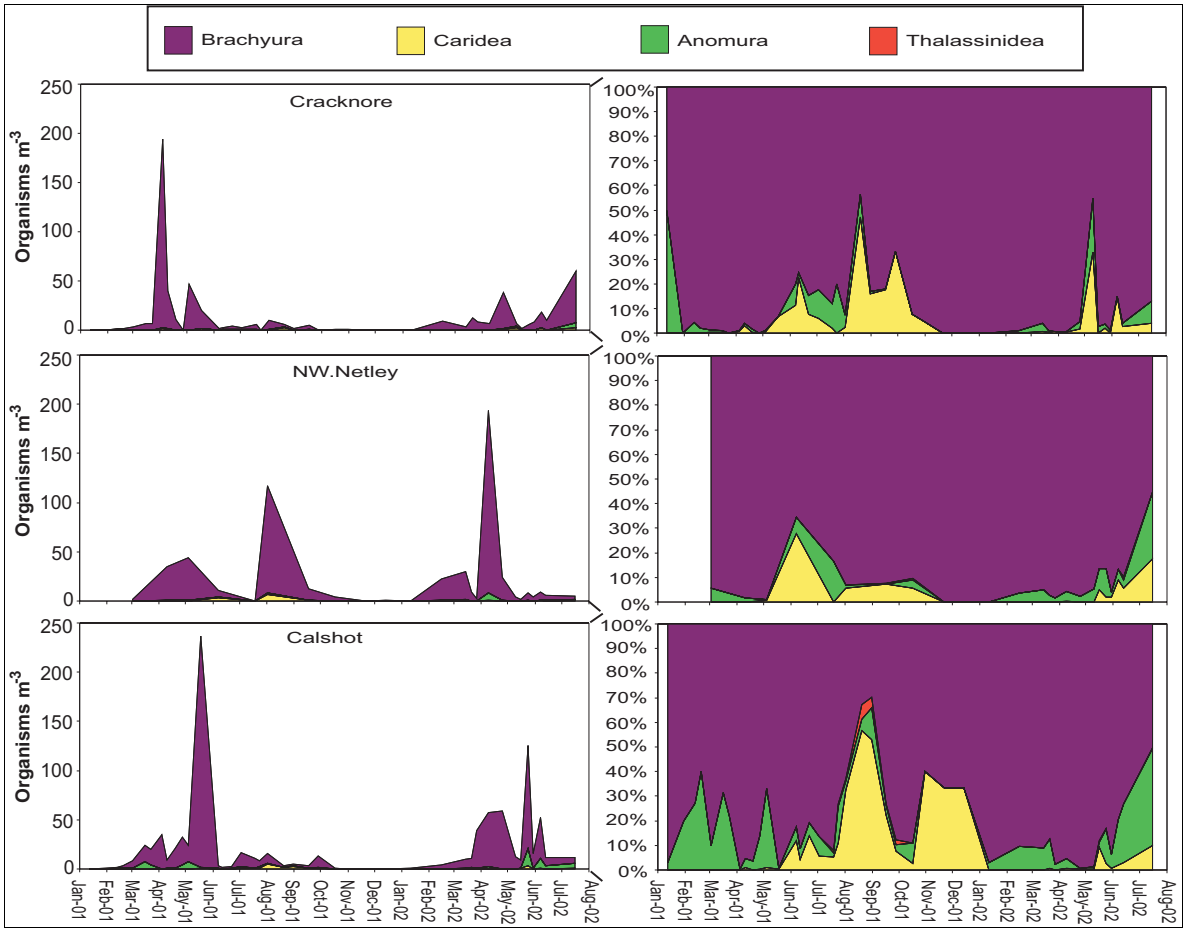


Figure 24. Temporal variability and seasonal contribution of the different Decapoda infraorders at Cracknore, NW. Netley and Calshot during 2001/02.

In terms of individual contribution, *Carcinus maenas*, *Liocarcinus* spp., *Pagurus bernhardus, Crangon crangon, Pisidia longicornis* and *Macropodia* spp. are the most numerically common and abundant and together account for 98% of all decapod larvae found in Southampton Water. The temporal and spatial abundance of these species can be seen in Figure 25. Of all species found, only the brachyuran *C.maenas* had any numerical importance in catches at all stations (Figure 25), accounting, on average, for 78, 66 and 53% of the decapods at Cracknore, NW Netley and Calshot, respectively. *C.maenas* larvae were found throughout the year (Table 16), but were more abundant during spring, particularly in April when maximum abundances of 191, 182 and 39 organisms m^{-3} were recorded at Cracknore, NW. Netley and Calshot, respectively.

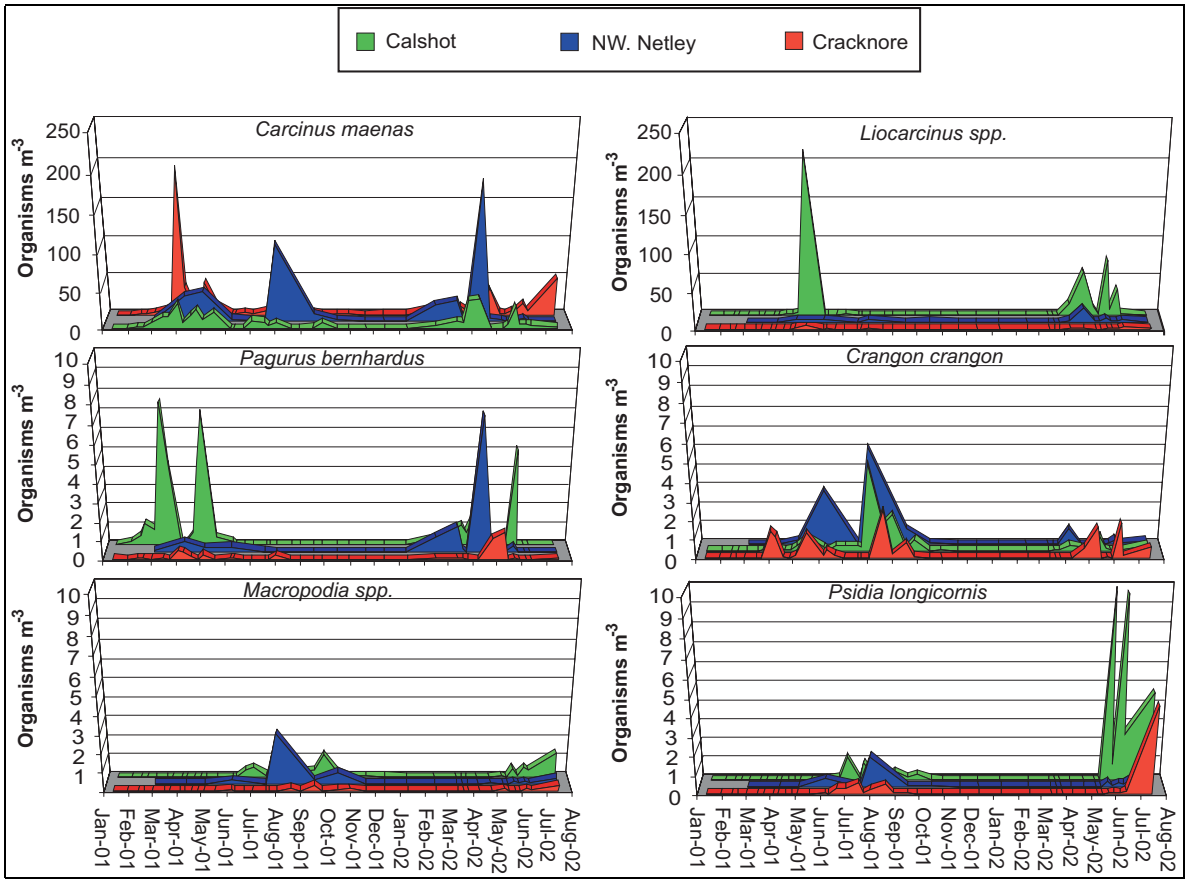


Figure 25. Temporal variability of the six most abundant Decapoda species at Calshot, NW. Netley and Cracknore during 2001/02. (Note that the top 2 graphs are on a different scale and that the order of stations were changed for *Carcinus maenas* and *Crangon crangon*).

Liocarcinus-type larvae were the second most common decapod larvae, and were more abundant at Calshot than at the inner sites (Figure 25). In contrast to *C.maenas*, relative high abundances of *Liocarcinus*-type larvae were concentrated in May (Table 16). *Macropodia* spp. were relatively common during May to October (Table 16), averaging 0.24 organisms m^{-3} at all three stations during this period, with a maximum of 2.7 organisms m^{-3} observed at NW. Netley in August 2001. *Crangon crangon* was the only caridean of numerical importance in Southampton Water during the investigation (Figure 25). It usually occurred from April to September, with peak abundance of 5.2 organisms m^{-3} during the summer (Table 16). Among the anomurans, *Pagurus bernhardus* and *Pisidia longicornis* were the only species with abundances greater than 1 organism m^{-3}. The temporal abundance variability of *P. bernhardus* and *P. longicornis* is illustrated on Figure 25, with both species being more abundant towards Calshot and NW. Netley during spring and summer, respectively (Table 16).

Of the remaining species found, only 5, *Pilumnus hirtellus, Pinnotheres pisum, Galathea squamifera*, *Thoralus cranchii* and *Hyppolite* spp. were recorded with

abundances higher than 1 organism m^{-3} at a single sample. The seasonal appearance of each species, together with its averaged abundance within the estuary, is shown in Table 16. *Pilumnus hirtellus, Pinnotheres pisum* and *Galathea squamifera* have a marked seasonal occurrence in the zooplankton of Southampton Water, with the first two occurring from June to October and *G.squamifera* from January to June. All three were usually more abundant towards Calshot, with *P.hirtellus* presenting abundances as high as 1.8 organisms m^{-3} and *P.pisum* and *G.squamifera* 1.2 and 2.7 organisms m^{-3}, respectively. Larvae of *Thoralus cranchii* and *Hippolyte* spp. were commonly found from May to December (Table 16) with maxima of 1.8 and 1.3 organisms m^{-3} for each species being recorded at Calshot and NW. Netley respectively.

Table 16. Seasonal occurrence of Decapoda larvae found in Southampton Water, with the frequency of occurrence (FO) of each taxa. Where ■ = Cracknore; ▲= NW. Netley, ● = Calshot. Colour shades indicates average abundances, where, = 0, = 0.001 – 0.01, = 0.01 – 0.1, = 0.1 – 1.0, = 1.0 – 10, = 10 – 100, = 100 – 1000 and = ≥ 1000 org. m^{-3}.

Species	J	F	M	A	M	J	J	A	S	O	N	D	FO
Palaemon elegans							●	▲●					3%
Palaemon spp.					●	▲	■	■					7%
Alpheus glaber							●						2%
Athanas nitescens						■▲	■▲●	■▲●	■▲●				12%
Hippolyte spp.			■ ●	■▲●	■▲	■▲●	■▲●	■▲●	■ ●	■▲●	●	●	28%
Thoralus cranchii			■	■	■▲●	■▲●	■▲●	■ ●	▲●	▲			24%
Processa sp.						▲	■ ●	●	●				9%
Crangon crangon			■ ●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●			56%
Crangon bispinosus					●	●		●		■▲●			7%
Crangon trispinosus			■	■	■ ●	▲	●	●	●				10%
Crangon fasciatus					▲●	■▲●	■▲●	▲●	▲				19%
Axius stirhynchus							●	●					2%
Upogebia sp.					■ ●	▲	●	●	▲●	▲			13%
Diogenes p.pugilator							■	●					2%
Anapagurus hyndmanni			●	●	■▲●			■ ●	●	▲●			12%
Pagurus bernhardus	■ ●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲	■ ●					58%
Galathea squamifera	●		■▲●	■▲●	■▲●	▲							31%
Pisidia longicornis					■▲●	■▲●	■▲●	■▲●	■▲●	▲●			36%
Porcellana platycheles						▲●	■▲●	▲●					11%
Ebalia tuberosa					▲●	▲	●		●	▲●			8%
Ebalia tumefacta									●	▲●			4%
Maja squinado							●						2%
Hyas sp.		●	●	●	●								4%
Inachus sp						■	●			●			3%
Macropodia spp				▲	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	●	●	35%
Pisa sp						●	●						3%
Corystes cassivelaunus		●	▲●	■▲●	■▲●								17%
Liocarcinus spp			■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲	▲	■▲	69%
Carcinus maenas	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	98%
Pilumnus hirtellus						■▲●	■▲●	■▲●	■▲●	■▲●			23%
Pinnotheres pisum						■▲	■▲●	■▲●	▲●	▲			19%
Megalopas (Brachyura)					■▲●	■▲●	■▲●	■ ●	●	■▲			30%

Considering the remaining species, all of which showed individual average sample abundances < 1 organism m^{-3}, *Hyas* sp. and *Corystes cassivelaunus* only occurred early in the season, in January-June. Apart from these, the remaining species usually presented a pattern of appearance during May to August (Table 16) with a few species, *Ebalia tuberosa*, *E.tumefacta*, *Crangon bispinosus*, *C.trispinosus, Anapagurus hyndmanni* and *Upogebia* sp., also extending into October. Generally, most decapods were usually found

towards the mouth of the estuary at Calshot, where consistent tidally-associated salinity variation is minimal (Figure 3 - Chapter 1). Similarly, many of the species that were recorded at all three sites (Table 16) had highest abundances at Calshot.

Apart form the groups/species mentioned, all the remaining meroplanktonic forms identified were considered as minor contributors (Table 17) and were grouped together as "Others" in Figure 21. With the exception of the Chydoridae (Cladocera), *Cyclopinoides littoralis* (copepod), *Rissoides desmaresti* (stomatopod), Actinotrocha larvae (Phoronida) and fish larvae and eggs, all the remaining minor contributors of the meroplankton are regarded as parasitic and/or commensal taxa. Only *C.littoralis*, unidentified copepodites of Siphonostomatoida, unidentified cryptonistic isopods and unidentified fish larvae and eggs were recorded frequently enough to present any pattern based on presence throughout the year along the entire estuary (Table 17). *Cyclopinoides littoralis* were usually found from January to October on a consistent basis while unidentified copepodites of Siphonostomatoida and cryptonistic isopods were found all year round, but more abundantly from July to September. Fish eggs were usually found from December to July while larvae from February to October (Table 17). The remaining species/taxa were only caught sporadically and predominantly at Calshot (Table 17) toward the mouth of the estuary.

Table 17. Seasonal occurrence of the minor meroplanktonic species/groups in Southampton Water, with the frequency of occurrence (FO) of each taxa. Where ■ = Cracknore; ▲= NW. Netley, ● = Calshot. Colour shades indicates average abundances, where, = 0, = 0.001 ⌐ 0.01, = 0.01 ⌐ 0.1, = 0.1 ⌐ 1.0, = 1.0 ⌐ 10, = 10 ⌐ 100, = 100 ⌐ 1000 and = ≥ 1000 organisms m^{-3}.

Species	J	F	M	A	M	J	J	A	S	O	N	D	FO
Cladocera													
Unidentified Chydoridae				■				■					2%
Copepoda													
Unidentified Cyclopoida	■ ●	■	▲	■ ●	■ ●		■▲●	■ ●			●	●	9%
Cyclopinoides littoralis	■▲●	■ ●	■▲●	■▲	■▲●	■ ●	■ ●	■ ●	●	■▲●			30%
Unidentified Notodelphydae		●						●			●		2%
Unidentf.Siphonostomatoida	■ ●	■▲●	■▲●	■ ●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	▲●	■▲	73%
Asterocheres sp.	●			●			●						4%
Caligus elongatus	●												1%
Cancerilla tubulata	●												1%
Badypontius papillatus			●				●						2%
Monstrilla conjunctiva	●	●											2%
Monstrilla helgolandica									▲				1%
Cymbasoma longispinosus									●				1%
Cymbasoma rigidus					●			●	●				3%
Cymbasoma thompsoni					■▲	●	■	■	▲	▲			7%
Isopoda													
Unidentified cryptonistic	▲●	▲●	■▲●	●	■▲●	▲●	●		●	■▲●	●	▲●	68%
Stomatopoda													
Rissoides desmaresti							▲●	●					3%
Phoronida													
Unidentified Actinotrocha			■ ●										3%
Pisces													
Unidentified fish egg	●	■▲●	■▲●	■▲●	■▲●	■ ●	■ ●					▲	56%
Unidentified fish larvae		■ ●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■ ●			70%

3.3.2. Tycoplankton.

Tycoplanktonic species only averaged 0.6, 0.5 and 1.8% of the total zooplankton at Cracknore, NW.Netley and Calshot, respectively but contributing up to 6% on some occasions (Figure 6 – Chapter 1). Harpacticoid copepods comprised 97% of the tycoplankton found, with unidentified individuals recorded throughout the year with high abundances found particularly from June to September (Table 18).

Table 18. Seasonality of occurrence of Tycoplanktonic species/groups in Southampton Water, with the frequency of occurrence (FO) of each taxa. Where ■ = Cracknore; ▲= NW. Netley, ● = Calshot. Colour shades indicates average abundances, where, = 0, = 0.001 ⌐ 0.01, = 0.01 ⌐ 0.1, = 0.1 ⌐ 1.0, = 1.0 ⌐ 10, = 10 ⌐ 100, = 100 ⌐ 1000 and = ≥ 1000 organisms m^{-3}.

Species	J	F	M	A	M	J	J	A	S	O	N	D	FO
Chelicerata													
Unidentified Acari							●						1%
Achelia sp.							●						1%
Nymphon brevirostre						▲			▲				2%
Harpacticoida													
Unidentified Harpacticoida	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■ ●	92%
Canuella sp.	■ ●	■ ●		■	●	▲●	■▲●	■ ●			●		15%
Sacodiscus sp.	●		▲					■					3%
Tisbe spp.	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■▲●	■ ●	■▲●	●	●	▲●	62%
Thalestris sp.	●	■ ●	■▲●	■▲●	■▲●	▲●	●	■ ●					32%
Isopoda													
Unidentified praniza								●					1%
Idotea sp.				■									1%
Cumacea													
Pseudocuma similis	●		▲●	●		●	●	●					12%
Ostracoda													
Unidentified Ostracoda	■▲●	●	■ ●	■ ●	■	■ ●	■▲●	■ ●	■▲	■▲			34%
Mysidacea													
Siriella armata							●	●	●	●			6%
Siriella clausii								●		●			2%
Anchialina agilis	●									●			2%
Gastrosaccus sanctus								●					1%
Leptomysis lingyura				●									1%
Mysidopsis gibbosa							●	●					2%
Acanthomysis longicornis				●			●						2%
Mesopodopsis slabberi	■ ●	▲●	■ ●	■ ●	■▲	●	■ ●	■ ●	■▲●	■▲●	▲●	■▲●	38%
Paramysis arenosa	●												1%
Schistomysis kervillei	●		▲										2%
Amphipoda													
Gammaridea (Total)	■ ●	●	■▲●	▲●	■▲●	■▲●	■▲●	■ ●	■▲●	■▲●	■ ●	■ ●	55%
Unidentified	●		■ ●	▲●	▲	■▲●	■▲●	■ ●	■▲●	■▲●		●	29%
Amphilochus manudens			▲					■ ●		●			4%
Gitana sp.								●					1%
Parapleustes sp.							●						1%
Aora gracilis				●	●	■			■				4%
Corophium spp.	■ ●				■	▲	■▲	■	■▲	▲	■		14%
Jassa sp.			■	●		■▲●	■	■ ●	■ ●	▲●		■	16%
Apherusa spp.						●	●	●		●		●	8%
Atylus vedlomensis		●	●	●	●	●	▲●	●		●		●	17%
Echinogammarus marinus						●				●			3%
Megaluropus agilis								●					1%
Melita sp.								●		●			2%
Orchomene humilis	●	●	●					●		●	●		6%
Argissa hamatipes								●					1%
Parametaphoxus fultoni								●					1%
Pariambus typicus			●										1%
Phtisica marina							●	■ ●	■	●			6%
Chaetognatha													
Spadella cephaloptera			●									●	2%
Echinodermata													
Amphipholis squamata								●					1%

With the exception of all harpacticoids, ostracods, *Mesopodopsis slabberi*, *Corophium* spp., *Jassa* sp. and *Phitisica marina,* most of the taxa reported within the estuary were restricted to Calshot (Table 18).

Of the organisms identified to species, only *Canuella* sp, *Tisbe* spp., *Thalestris* sp., *M.slabberi, Corophium* spp., *Jassa* sp. and *A.vedlomensis* were reported with some regularity, probably reflecting some seasonal pattern within this estuary. *Tisbe* spp. was found throughout the year on a consistent basis while *Canuella* sp. and *Thalestris* sp. were usually found from January to August. *Canuella* sp. was more abundant in summer and *Thalestris* sp. in winter-spring. *Mesopodopsis slabberi* were also found throughout the year, but clearly more abundant during spring and autumn. *Corophium* spp., *Jassa* sp. and *A.vedlomensis* were usually found from June to October (Table 18).

3.3.3. Statistical analysis.

Correlations between biotic and abiotic factors that could act as potential forcing factors for the distribution patterns highlighted in different species are presented in Table 19 (Only taxa with 5% or greater frequency of occurrence were considered). As expected, temperature was positively correlated with those species abundant during spring – autumn (e.g. *E.modestus*, *B.improvisus*, *E.acutifrons*, *P.longiornis, P.hirtellus*.) and negative for those peaking during winter-spring (e.g. *B.crenatus*, *S.balanoides*, *V.stroemia, P.bernhardus*). Salinity and Chlorophyll were also positively correlated with most species abundant during spring – autumn. Dissolved oxygen was usually negatively correlated with those species present during spring – autumn, and positively with those peaking during winter – spring, while oxygen saturation was the opposite (Table 19).

Table 19. Pearson's product-moment correlation of biotic and abiotic parameters collected at the three stations. Correlations in red are significant at p<0.05, and shaded at p<0.01, ns = not significant. Only shown organisms that presented any significant correlation.

Species/groups	T °C	S	Chl.*a*	O_2	O_2Sat%
Polychaeta (total)	ns	-0.31	0.36	ns	ns
Gastropoda (total)	0.62	0.55	0.57	-0.29	0.35
Bivalvia (total)	0.84	0.22	0.69	-0.40	0.39
Ascidian (total)	0.76	ns	0.55	-0.39	0.29
Cnidaria (total)	0.59	ns	0.68	ns	0.49
Bryozoan (total)	0.30	ns	0.32	ns	ns
Elminius modestus	0.84	0.27	0.61	-0.56	0.22
Balanus crenatus	-0.36	ns	ns	0.31	ns
Balanus improvisus	0.69	ns	0.66	-0.29	0.32
Semibalanus balanoides	-0.47	ns	ns	0.30	ns
Verruca stroemia	-0.41	ns	ns	0.26	ns
Sacculina carcini	0.55	ns	0.26	-0.48	ns
Pagurus bernhardus	-0.28	ns	ns	0.27	ns
Crangon vulgaris	0.42	ns	0.39	ns	0.21
Liocarcinus spp.	ns	0.25	0.41	ns	0.41
Macropodia spp.	0.51	0.35	0.25	-0.36	ns
Pilumnus hirtellus	0.37	0.31	ns	-0.37	ns
Psidia longicornis	0.40	0.29	0.25	-0.22	ns
Porcellana platycheles	0.34	0.20	ns	-0.20	ns
Pinnotheres pisum	0.38	0.20	ns	-0.22	ns
Thoralus cranchii	ns	0.20	ns	ns	ns
Crangon trispinosus	0.25	0.26	ns	-0.26	ns
Crangon fasciatus	0.33	0.27	0.22	ns	ns
Anapagurus hyndmani	ns	0.20	ns	ns	0.23
Athanas nitescens	0.37	ns	0.20	-0.28	ns
Processa sp	0.38	0.23	ns	-0.22	ns
Upogebia sp	0.34	0.30	ns	-0.32	ns
Cymbasoma thompsoni	ns	ns	0.34	ns	0.25
Canuella sp.	0.35	0.14	0.29	ns	ns
Pseudocuma similis	ns	0.28	ns	ns	ns
Siriella armata	0.26	0.22	ns	-0.23	ns
Mesopodopsis slaberri	ns	ns	ns	-0.35	-0.23
Corophium spp.	0.31	ns	0.28	ns	ns
Jassa sp.	0.34	ns	ns	-0.24	ns
Apherusa spp.	0.31	0.24	ns	ns	ns
Atylus vedlomensis	0.32	0.28	ns	ns	0.20
Orchomene humilis	ns	0.23	ns	ns	ns
Phitisica marina	0.25	ns	ns	-0.31	ns

MDS ordination plots, based on Bray-Curtis similarities of meroplankton and tycoplankton species/groups abundances from all samples and for all stations show a clear cyclic seasonal pattern (Figure 26 a), with a slight distinction between Calshot and NW.Netely/Cracknore in terms of mero-tycoplanktonic composition during spring and summer (Figure 26 b). When only spring-summer samples where selected for analysis, the spatial differentiation is more evident (Figure 26 c and d).

Considering the mesozooplankton as a whole, the holoplankton was also added to the analyses (Figure 26 e and f) and the cyclic seasonal pattern was still clear, someway between Figures 26 (a) and Figure 13 (a - Chapter 2). Again, all sites were intermingled together in a big cluster, with only the cluster composed by summer-autumn samples of Cracknore shown of Figure 13 (Chapter 2) being evident (Figure 26 e).

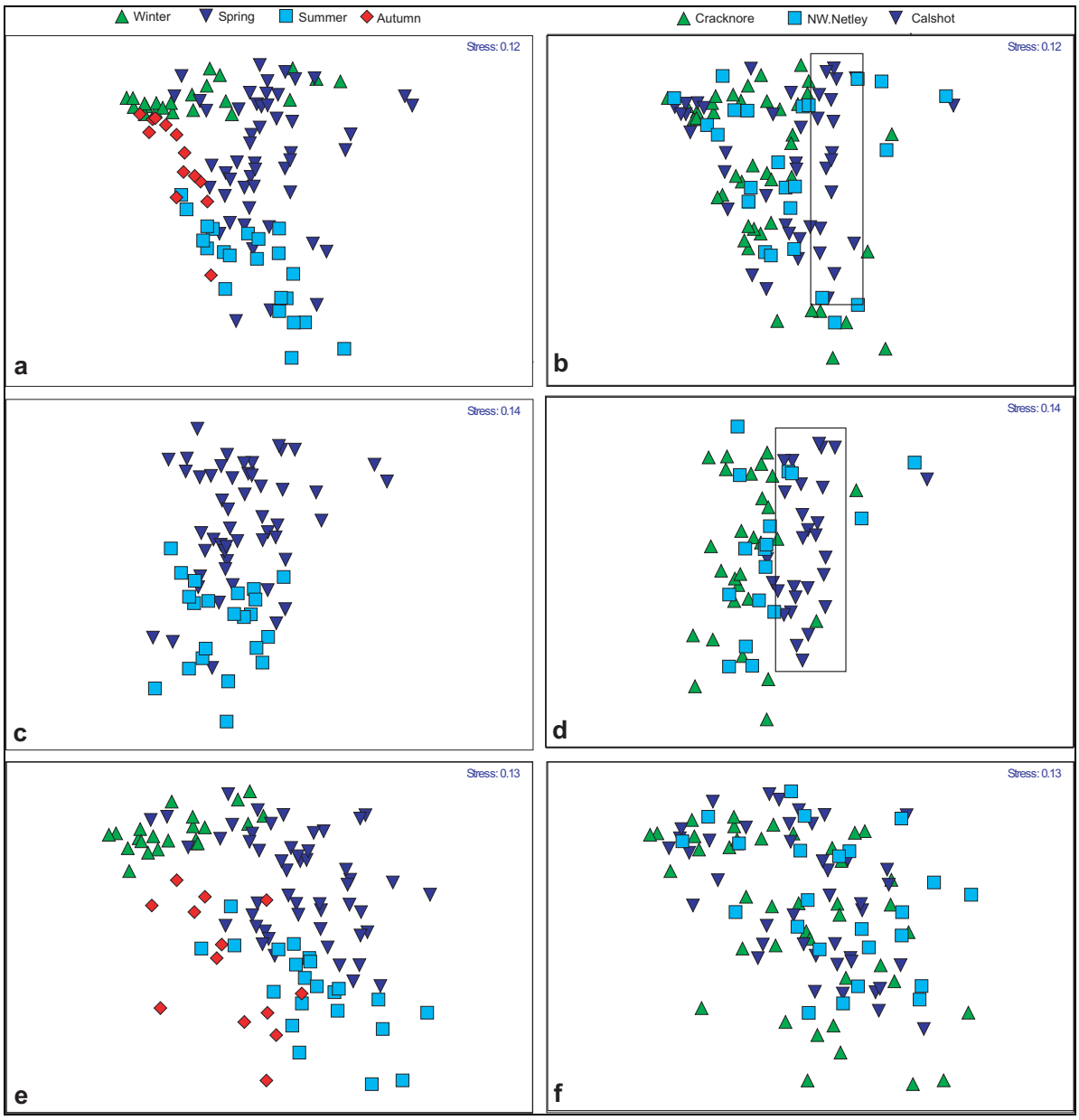


Figure 26. MDS ordinations of the 108 samples, based from Bray-Curtis similarities on square root transformed abundances of all mero-tycoplanktonic organisms (a and b), and only considering spring-summer samples (c and d). Also included is the MDS for all organisms (holo, mero and tycoplankton) found in all samples of the zooplankton of Southampton Water during 2001/02 (e and f). Indicated in Figure b and d is an apparent cluster indicating spatial differentiation of Calshot spring-summer samples.

When the relative abundance of each species/groups (Figure 27 a to r) was superimposed over the MDS ordination (Figure 26 a and b), it is easy to follow the seasonal occurrence of several species. Species/groups shown in Figure 27 a to d were found at the inner stations during spring-summer, while e to j found at the three sites during spring-summer. Species/groups k to p were found primarily at Calshot during spring-summer, and r shows the distribution of *Tisbe* spp which was found over the entire estuary throughout the year and at similar abundance.

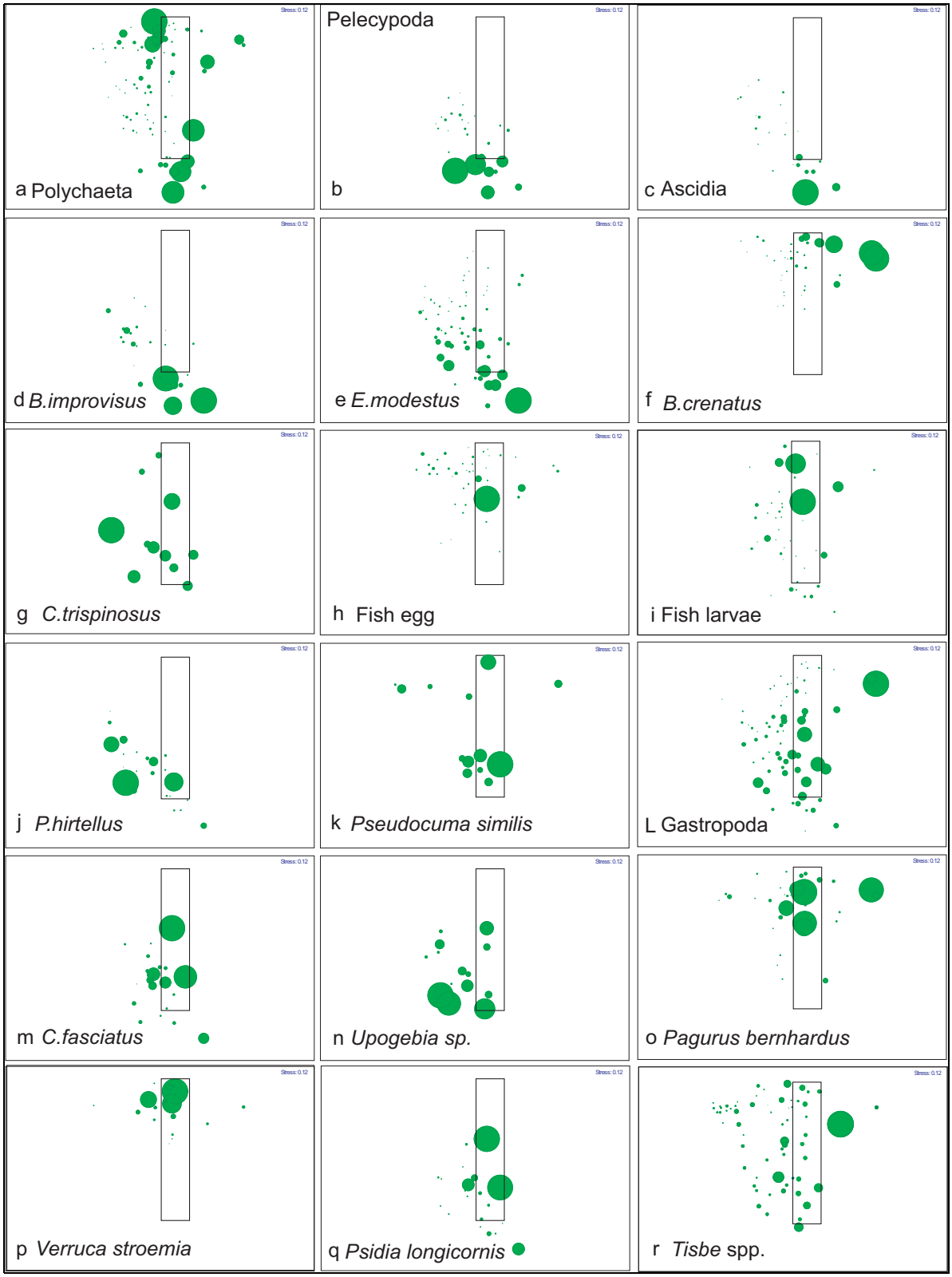


Figure 27. MDS of the three sites, as in figure 26 (a and b), with superimposed circles representing relative species/group abundances at the three sites. Marked area indicates Calshot spring-summer samples. (Note that abundances are in the same proportional scale for a clearer evaluation of patterns).

By superimposing the physico-biological parameters measured onto the same MDS plot presented in Figure 26 (a and b), it is clear that temperature is responsible for most of the pattern presented by the mero and tycoplankton (Figure 28).

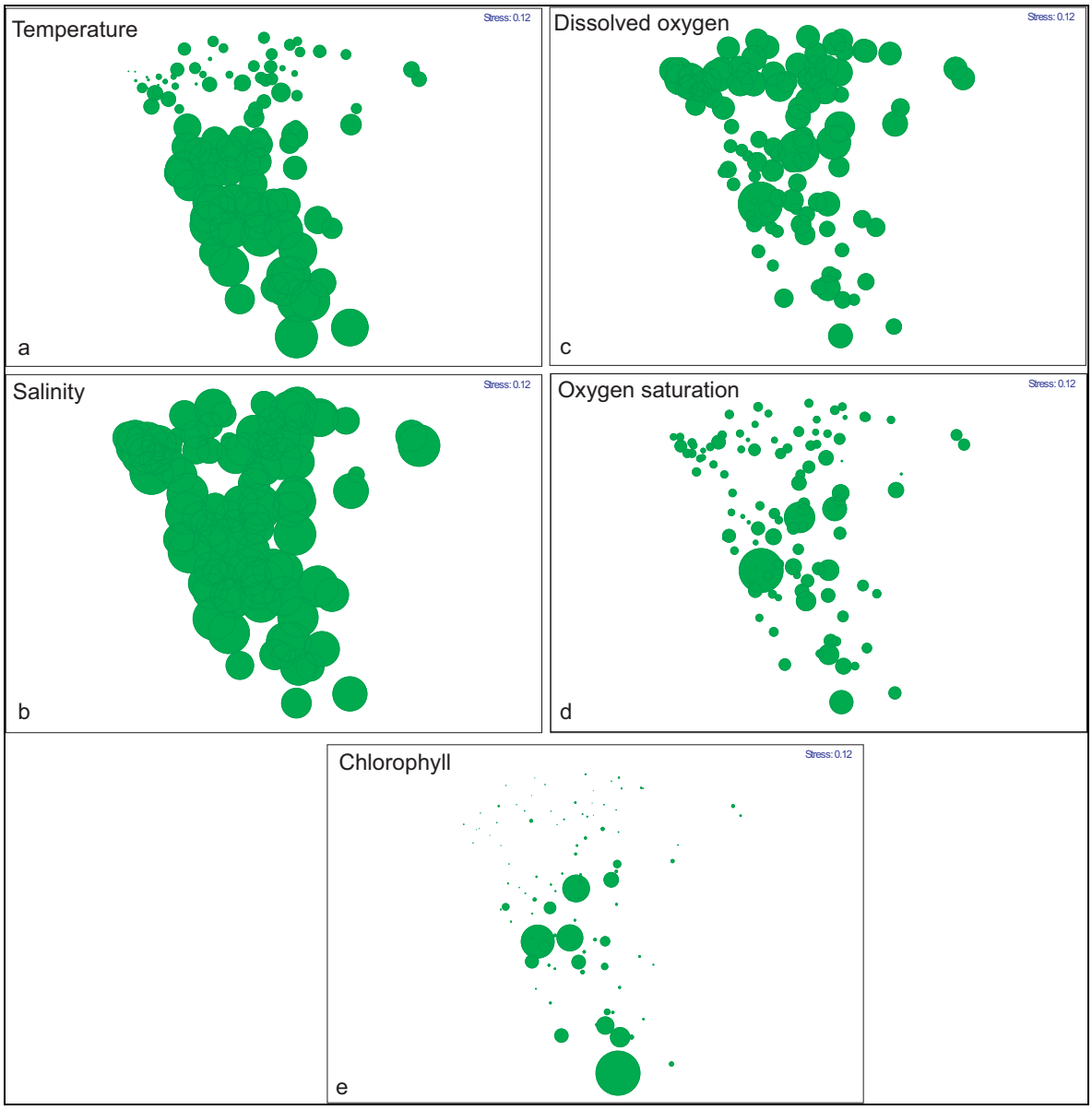


Figure 28. MDS of the three sites, as in Figure 26 (a and b), with superimposed circles representing the range of values of the physico-chemical parameters of all three sites. (Note that concentrations are in the same proportional scale for a clearer evaluation of patterns).

3.4. Discussion.

Before discussing each component of the mero-tycoplankton fraction of Southampton Water, it is necessary to point out that both meroplankton and tycoplankton compositions of each estuary will be different. The composition and seasonality of invertebrate larvae are clearly dependant on the sampling devices utilized and

particularities of the distribution and composition of the parental benthic population in the near vicinity, which in turn will be a reflection of several aspects, like type of sediments, presence/absence of hard substrates, health of the parent populations, recruitment and even socio-economical aspects of the surrounding human communities that could be exploiting particular species.

As an example, Bousfield *et al*., (1975) in the St. Lawrence estuary (Canada) reports tycoplanktonic harpacticoid copepods, followed by barnacle larvae and mysids to be the most abundant mesozooplankton component after holoplanktonic copepods when collecting with pumps and retained on ~158 μm meshes. Hopkins (1977) in Tampa Bay (USA) reports a meroplankton fraction mainly composed by bivalve veligers, followed by barnacle larvae, polychaetes and gastropods veligers when employing towed nets of 74 μm of mesh-size. In Long Island (USA), Turner (1982) recorded polychaetes, bivalves, gastropods and echinoderm larvae as the main constituents when employing towed nets of 73 μm of mesh-size. In the estuary of Lagoa dos Patos (Brazil) Montú (1980) observed barnacle larvae as the most abundant meroplanktonic organism reaching densities even higher than all holoplanktonic copepods, followed by decapod larvae as the second most abundant meroplanktonic form using 200 μm towed nets. Perissinotto *et al*., (2000) reports unidentified harpacticoid copepods (possible tycoplanktonic) as the dominant form of the mero-tycoplankton fraction, followed by polychaetes in the Nyara estuary (South Africa) when employing two nets of 90 and 200 μm mesh-size. Soetaert & Van Rijswijk (1993) report bivalve larvae as the most abundant component within the meroplankton of the Westerchelde estuary (NW Europe), followed by polychaetes, barnacles, cyphonautes, gastropods and equinoderm larvae when collecting with pumps and retaining them on 55 μm meshes. Baretta & Malschaert (1988) in the Ems estuary (NW Europe) report similar overall composition, with barnacle larvae followed by polychaetes as the most abundant components after holoplanktonic copepods when employing 200 μm towed nets.

So, contrary to what was seen in the holoplankton where estuaries from different locations and latitudes present almost similar species composition, the meroplankton and tycoplankton compositions are usually different, with different components of both groups usually ranking second after holoplanktonic copepods.

Based on the results presented here, Cirripedia were the most abundant component of the mero - tycoplankton fraction of Southampton Water, followed by Polychaeta, Gastropoda, Pelecypoda (bivalves), Ascidia, Cnidaria, Bryozoa and Decapoda. All other components, including all tycoplanktonic organisms, were considered to have a minor numerical contribution.

3.4.1 Cirripedia.

As with most meroplanktonic organisms, barnacle nauplii usually have a very short planktonic life, although they can represent a large proportion of the total zooplankton on a seasonal time scale (Figure 7 – Chapter 1). In terms of species composition, only Soares (1958), Raymont & Carrie (1964) and Geary (1991) have reported on barnacle larvae within Southampton Water. Soares (1958) sampled at Calshot Pier, a station at the mouth of Southampton Water (Figure 1 – Chapter 1), recording the nauplii of both *Semibalanus balanoides* and *Balanus crenatus* as the most abundant forms during spring and *Elminius modestus* during the summer. Raymont & Carrie (1964) offered a very general picture of the distribution of the dominant species over the entire estuary based on Soares (1958) results. Geary's (1991) results from Cracknore should be compared cautiously with the present study, as only summer-autumn samples were available and all individuals found in the summer were assumed to be *E. modestus*.

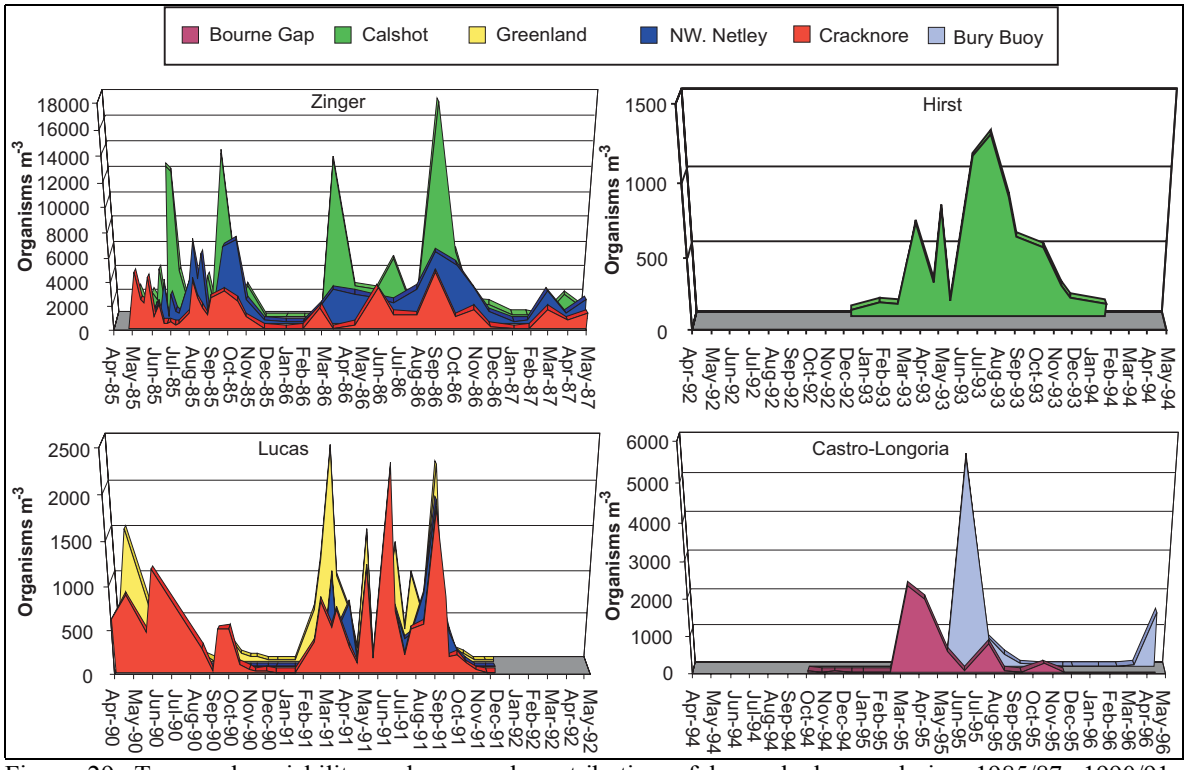


Figure 29. Temporal variability and seasonal contribution of barnacle larvae during 1985/87, 1990/91, 1992/94 and 1994/96 from the raw data of Zinger (1989), Lucas (1993), Hirst (1996) and Castro-Longoria (1998) at different stations in Southampton Water and the Solent. (Note that temporal scale of Hirst, Lucas and Castro-Longoria data was extended for a better comparison with the 1985-1987 results. Figures are also on different scales. Data for different depth strata were averaged, and data obtained with meshes larger than 220 µm are not included).

In terms of total barnacle larvae abundance the values reported here concur with those presented by Zinger (1989) for the same stations, the only differences being the

relative size of the summer-autumn peaks (Figure 29). Again, Hirst's (1996) values were unusually low, even lower than the values presented by Lucas (1993) and Castro-Longoria (1998) where a coarser mesh were used (Figure 29).

Zinger (1989) reported that barnacles and calanoids represented, on average, 37% each of the total zooplankton composition at the three stations considered, whereas in the present study barnacles and calanoids represented on average only 18 and 23.5%, respectively, of the total zooplankton. This difference could partly be explained if Zinger (1989) had included copepod nauplii as calanoids in her raw values, but, as can be clearly seen in Figure 29, the period studied had very high numbers of barnacle larvae.

The species recorded during the present study indicated the same composition and seasonal pattern as the study of Soares (1958) (Figure 30), although *Semibalanus balanoides, Balanus crenatus, Balanus improvisus* and *Peltogaster paguri* presented higher abundance values at Calshot when compared with the present study. In contrast, *Elminius modestus, Verruca stroemia* and *Sacculina carcini* occured at higher abundances in the current survey.

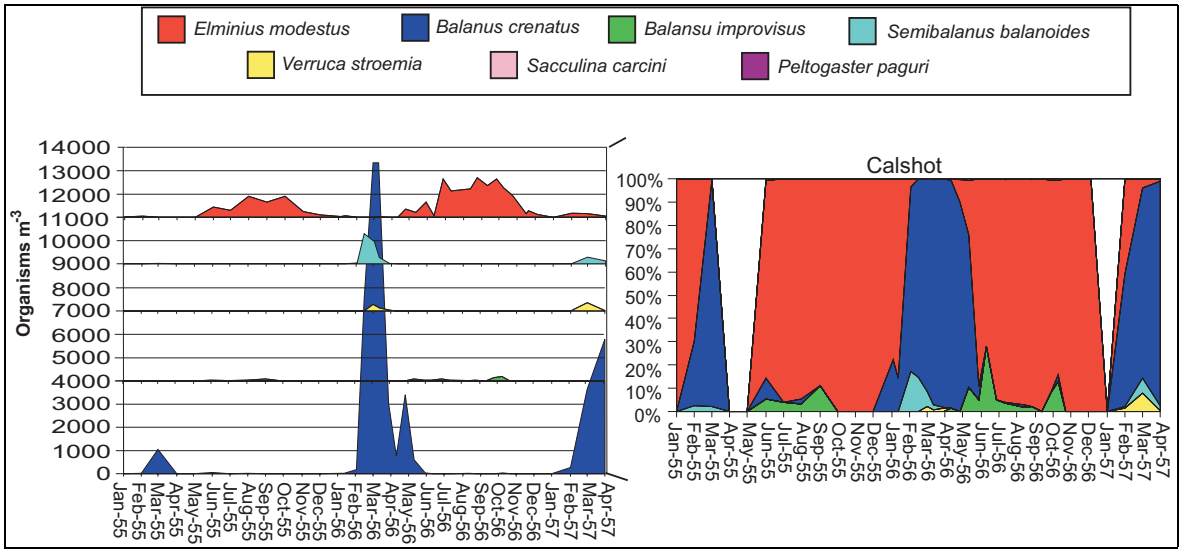


Figure 30. Temporal variability and seasonal contribution of each barnacle larvae species during 1955/57, from the raw data of Soares (1958) at Calshot (Note that scale shoul be re-initiated at the base of each category).

These differences could be due, in part, to the different locations and sampling gear used. Raymont & Carrie (1964) report that higher abundances of both *S.balanoides* and *B.crenatus* were commonly found at Calshot in the spring compared with Marchwood (Figure 1 – Chapter 1), with the opposite occurring for *E.modestus* during the summer. Supporting this observation, is the idea that both *E.modestus* and *B.improvisus* could be more tolerant to lower salinities than the other two, as they are common inhabitants of brackish water regions in several British estuaries (Jones & Crisp, 1954) with *B.improvisus*

clearly a brackish species elsewhere (Montú, 1980; Baretta & Malschaert, 1988), and the results presented here confirms that.

Peltogaster paguri and *Sacculina carcini* are endoparasites of decapods and have a short free, non-feeding, planktonic stage, and their occurrence is related to the presence of the infected benthic host within the estuary. Adult *Peltogaster paguri* have been reported to infect pagurid crabs, such as *Pagurus bernhardus*, *Pagurus cuanensis*, *Anapagurus chiroachantus* and *Anapagurus laevis* while *Sacculina carcini* is reported in portunid and pirimelid crabs (Hansson, 1998). In Southampton Water the larvae of both *P.paguri* and *S.carcini* were found freely in the plankon almost all year round, with the larvae of *S. carcini* being particularly abundant at times (Muxagata *et al*., 2004). (A single specimen of *P.bernhardus* infected by *P.paguri* was observed late in 2002 from pagurids collected in the estuary (Pers. obs.)).

Chthamalus stellatus, Trypetesa sp. and *Conchoderma* sp. are reported for the first time within Southampton Water. *Conchoderma*, possibly *C.auritum* has been reported settled on "Very Large Crude Oil Carriers" (VLCCs) (Dalley, 1984) and its occurrence here could clearly be associated with this. *Trypetesa sp.* is a burrowing barnacle usually found in the shells of gastropod molluscs (Turquier, 1967; Turquier, 1972).

Figure 23 and Table 15 clearly show the general seasonal breeding pattern presented by the different barnacle species in Southampton Water. Generalizing, in the beginning of the year larvae of *E.modestus* dominate the composition of barnacles in the mesozooplankton. It is then replaced in numerical dominance by *B.crenatus* larvae from February to May, with *S.balanoides* and some *V.stroemia* also occurring. At the innermost station, Cracknore, *B.improvisus* begins to replace *B.crenatus* from May and then co-dominates along with *E.modestus*. From July to January *E.modestus* is typically the dominant barnacle larvae in the estuary. A remarkable feature is the strong percent composition of *Sacculina carcini* during late-autumn (Figure 23), but this is clearly a reflection of the low total numbers of barnacle larvae found. In contrast with the copepods (Chapter 2) where a major change is observed in the composition of holoplanktonic species, no major changes have apparently occurred in the barnacle populations of the estuary in the past half century, with the same composition and seasonality being reported in all the, albeit few, studies.

Correlations with temperature confirmed the seasonal occurrence of most species, being positive for those more abundant during summer (*E.modestus*, *B.improvisus* and *S.carcini*), and negative for those peaking during winter-spring (*S.balanoides*, *B.crenatus* and *V.stroemia*). This was also shown on the MDS plots (Figure 27 d,e,f,p). Chlorophyll

was positively correlated with those peaking during summer (also shown on MDS plots). The secondary production of the different barnacle species is described in Chapter 4, together with more detailed information on stage composition patterns.

Specific information on barnacle larvae abundance in estuaries seems scarce, with Bousfield (1955) and Bousfield *et al*., (1975) reporting the seasonality of occurrence and abundance of *B.improvisus* and *B.crenatus* larvae at the Miramichi and St.Lawrence estuary (Canada), and Montú (1980) indicating that *B.improvisus* larvae can overwhelm copepods during spring and summer at Lagoa dos Patos (Brazil). Studies carried out in North European estuaries (Isaac, 1979; Ryan *et al*., 1986; Williams & Collins, 1986; Baretta & Malschaert, 1988; Soetaert & Van Rijswijk, 1993) only mentioned barnacle larvae as a broad taxonomic group, with a few describing the overall species composition and even fewer giving any detail of specific seasonality and/or abundance patterns. In this respect, Baretta & Malschaert (1988) report that the barnacle larvae composition found in the Ems estuary is mainly composed of *S.balanoides, B.crenatus, B.improvisus* and *E.modestus* with a total abundance of 3365 organisms m^{-3} reported in June at the inner estuary and so, approaching to the summer values reported at this estuary in 2001 when a maximum of 3346 organisms m^{-3} were observed at Cracknore (maximum of 12415 organisms m^{-3} were observed in April 2002 at Calshot). In the Bristol Channel *S.balanoides, B.crenatus, C.stellatus, V.stroemia* and *E.modestus* larvae were all reported, with *E.modestus* clearly dominating summer samples, but no density values were given (Isaac, 1979; Williams & Collins, 1986). Ryan *et al*., (1986) in Killary harbour report abundances of barnacle larvae reaching 7197 organisms m^{-3} in April. While Soetaert & Van Rijswijk (1993) recorded abundance up to 45000 organisms m^{-3} in pump collected samples from the Westerchelde. At Tampa Bay, Hopkins (1977) reported maxima of 4600 organisms m^{-3} in May while Perissinotto *et al*., (2000) reported averages of 5848 organisms m^{-3} in March at the Nyara estuary. At the Avon-Heathcote estuary (New Zealand), Roper *et al*.,(1983) observed maximum of 1172 barnacle larvae m^{-3}.

3.4.2 Polychaeta.

Polychaeta were present throughout the year although most proeminently from spring to early autumn (Figure 22). Although not identified to species, several different forms were clearly present and the discrete peaks possibly reflect the breeding of species reported for the area (Table 13). (Pictures of some of the different forms can be seen in the zooplankton guide (Muxagata & Williams, 2004) included as a pdf file in the attached CD).

When compared with previous studies (Figure 31), the values presented here were lower than those of Zinger (1989) but much higher than those of Lucas (1993), Hirst (1996) and Castro-Longoria (1998). Again, Hirst's (1996) values were unusually low, even lower than the values presented by Lucas (1993) and Castro-Longoria (1998) where a coarser mesh were used (Figure 31).

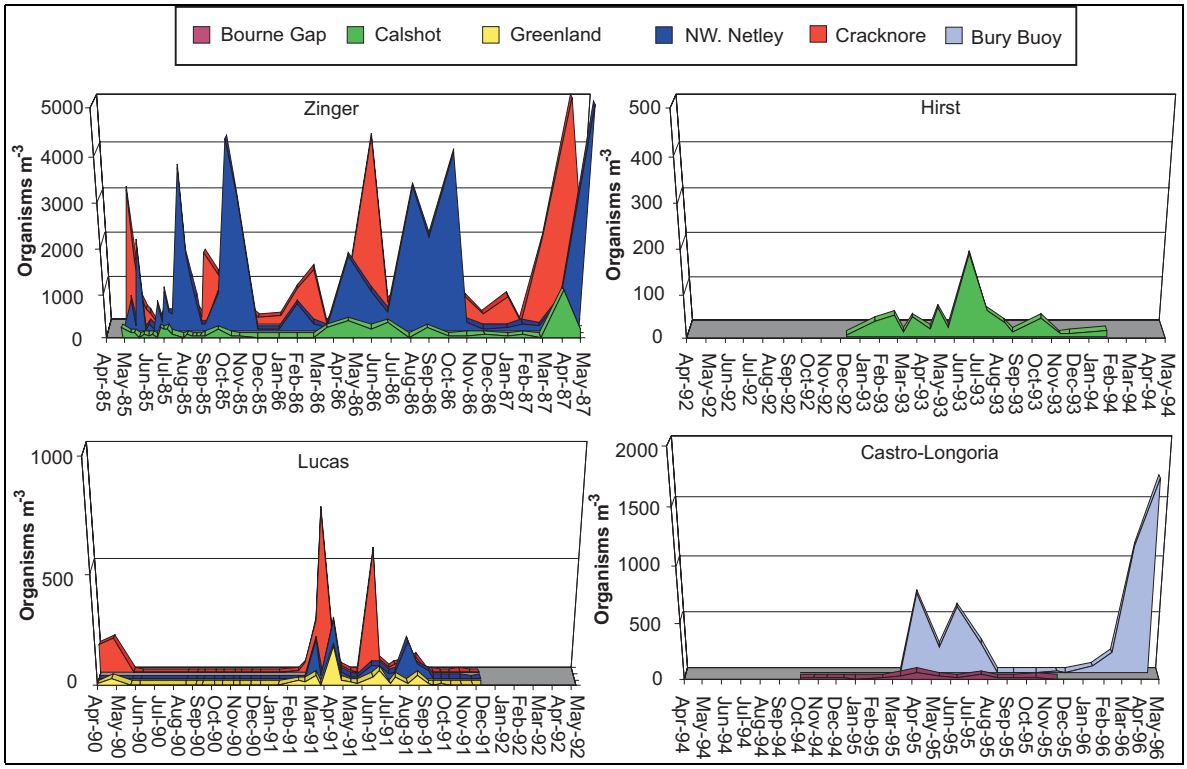


Figure 31. Temporal variability and seasonal contribution of polychaete larvae during 1985/87, 1990/91, 1992/94 and 1994/96 from the raw data of Zinger (1989), Lucas (1993), Hirst (1996) and Castro-Longoria (1998) at different stations in Southampton Water and the Solent. (Note that temporal scale of Hirst, Lucas and Castro-Longoria data was extended for a better comparison with the 1985-1987 results. Figures are also on different scales. Data for different depth strata were averaged, and data obtained with meshes larger than 220 µm are not included).

Not much can be deduced from data at this level however, from the results presented on Figures 22 and 31, the pattern of higher abundances in the upper estuary is clear and consistent, suggesting that polychaete larvae remain essentially confined within the inner reaches of Southampton Water, with a limited dispersal into the Solent (exemplified by the Bourne Gap values). A negative correlation of polychaetes with salinity reflects the higher abundances into the estuary. This is the second most abundant meroplanktonic group, and with so many species described in the benthos of the surrounding region (Table 13), a more in-depth analysis of species composition needs to be made.

Comparing the maximum value of 3140 organisms m^{-3} reported during this study at the inner estuarine station of Cracknore (Figure22), in April, with those reported in north

European estuaries it is possible to observe some similarities, especially with the report of Baretta & Malschaert (1988), that also reported higher abundances of polychaetes in the inner reaches of the Ems estuary, also in April, where a maxima of 1111 organisms m^{-3} were reported. At Killary harbour Ryan *et al*., (1986) found that polychaetes abundance could reach 7639 organisms m^{-3} in June, while Soetaert & Van Rijswijk (1993) report abundances, collected by pump, of up to 242000 organisms m^{-3} in the Westerchelde. In estuaries elsewhere, Hopkins (1977) reported maxima of 3800 organisms m^{-3} in August at Tampa Bay, while in Long Island Turner (1982) observed polychaetes reaching 3770 organisms m^{-3} in June. At the Nyara estuary Perissinotto *et al*., (2000) reported averages of 7437 organisms m^{-3} in March. Roper *et al*.,(1983) found maximum of 1283 polychaetes m^{-3} in the Avon-Heathcote estuary (New Zealand).

3.4.3 Mollusca.

Both pelecypod and gastropod veligers were found throughout the year in the estuary, and when compared with the previous studies of Zinger (1989), Lucas (1993), Hirst (1996) and Castro-Longoria (1998) the number of bivalves recorded here was, as with polychaetes, usually lower than in Zinger (1989) and much higher than those of Hirst (1996) (Figure 32). The coarser mesh employed in some earlier studies (Lucas, 1993; Castro-Longoria, 1998) will undoubtedly be the reason for the complete absence of bivalve veligers in these studies. By contrast, gastropod larvae were usually recorded at higher abundances during this investigation than at these earlier studies (Figure 32).

It is clear that, like polychaetes, the number of bivalve larvae is substantially higher within the upper reaches of the estuary than at its mouth. Gastropod larvae, in contrast, present the inverse pattern and are more abundant towards Calshot and the Solent, where Castro-Longoria (1998) reported peaks of 2670 organisms m^{-3} at Bourne Gap (Figure 1 – Chapter 1).

No attempt to identify the larvae of molluscs was made, but the July peak of bivalves reported here (Figure 22) coincides with the reported peak of *Mytilus* by Raymont & Carrie (1964). The gastropod *Crepidula fornicata* is reported as the most abundant species in the Solent (Barnes *et al*., 1973; Guyard, 2000).

It is relatively straightforward to identify the main breeding season of both bivalves and gastropods and more or less pinpoint larval release. The two major peaks of bivalves (Figure 22) probably reflect the release of two species, while the numerous peaks presented by gastropods could be related with the breeding of several of the species reported (Table 13). This can only be answered after detailed species analyses.

Since both groups have potentially important commercial species, a more in-depth analysis at species level should be made in the future, as well as a clarification of which mechanisms are confining bivalve larvae within Southampton Water and "restricting" dispersal into the Solent. Significant correlations with all environmental variables measured were achieved, but at a group level it is very difficult to interpret the results.

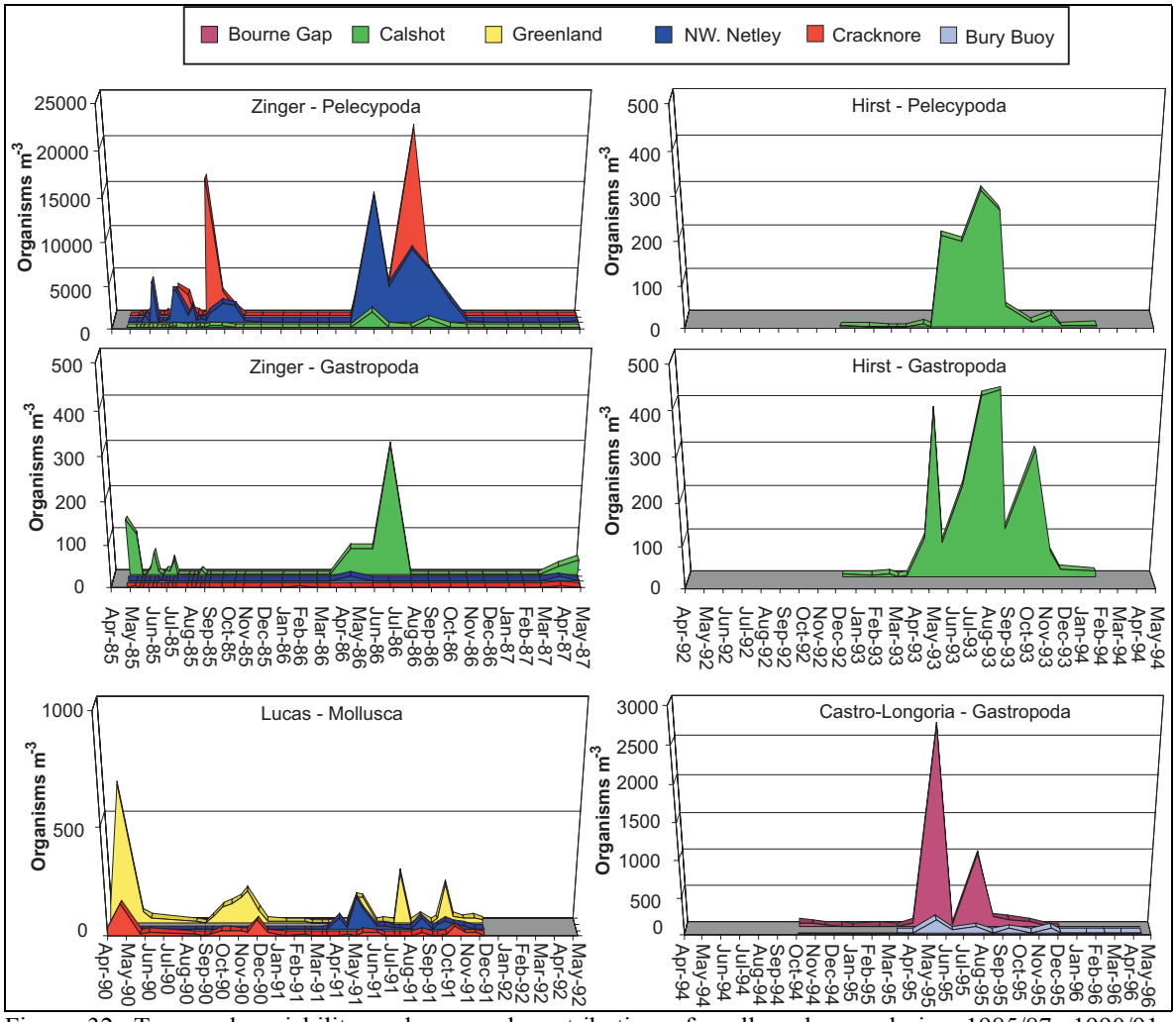


Figure 32. Temporal variability and seasonal contribution of mollusc larvae during 1985/87, 1990/91, 1992/94 and 1994/96 from the raw data of Zinger (1989), Lucas (1993), Hirst (1996) and Castro-Longoria (1998) at different stations in Southampton Water and the Solent. (Note that temporal scale of Hirst, Lucas and Castro-Longoria data was extended for a better comparison with the 1985-1987 results. Figures are also on different scales. Data for different depth strata were averaged, and data obtained with meshes larger than 220 μm are not included).

Comparing the maximum abundances of 2784 and 8878 organisms m^{-3} observed for gastropods and bivalves at this estuary, Ryan *et al*., (1986) found in Killary harbour that gastropods presented maximum abundances of 11783 organisms m^{-3}, while bivalves attained even higher abundances of 31388 organisms m^{-3}. Ryan *et al*., (1986) attributed these abundances to the gastropod *Turritella communis* and to the bivalve *Mytilus edulis*.

Soetaert & Van Rijswijk (1993) usually recorded higher abundances of bivalves (up to 96000 organisms m^{-3}) at the mouth of the Westerchelde, while gastropods were usually found at mid-estuary (maximun of 3000 organisms m^{-3}). Hopkins (1977) reported maxima of 15500 bivalves m^{-3} and 3300 gastropods m^{-3} in Tampa Bay while in Long Island Turner (1982) observed maxima of 112485 bivalves m^{-3} and 4685 gastropods m^{-3}. Roper *et al*.,(1983) reports maximum of 402 bivalves m^{-3} and 1010 gastropods m^{-3} in the Avon-Heathcote estuary (New Zealand).

3.4.4 Bryozoa and Ascidia.

Previous reports of cyphonaute larvae within Southampton Water have been made by Raymont & Carrie (1964), Hirst (1996) and Castro-Longoria (1998) recording numbers mainly at the mouth of the estuary and in the Solent, where abundances up to 432 organisms m^{-3} have been reported (Castro-Longoria, 1998). During this study however, cyphonaute larvae were commonly found, occurring in 90% of samples, and presenting an average of 44 organism m^{-3} for the entire season and throughout the estuary. By contrast to Castro-Longoria (1998), maximum abundances, up to 1414 organisms m^{-3} were reported inside the estuary, possibly indicating the recent presence of bryozoan colonies near Cracknore. Good correlation with environmental variables is clear, but at a "group" level it is very difficult to interpret the results. At Killary harbour Ryan *et al*., (1986) reported bryozoans in Feruary, April, May, June and September with a maximum of 422 organisms m^{-3}. Soetaert & Van Rijswijk (1993) recorded bryozoans, with densities up to 10000 organisms m^{-3}, at the mouth of the Westerchelde in April. Hopkins (1977) reported an average of 173 bryozoans m^{-3} over the entire season (maxima of 880 organisms m^{-3} in August) and throughout the estuary in Tampa Bay. Roper *et al*.,(1983) reports maximum of 72 bryozoans m^{-3} in the Avon-Heathcote estuary (New Zealand).

Ascidian larvae were only previously reported in Southampton Water by Hirst (1996), with maximum abundances up to 30 organism m^{-3} at Calshot. Similar abundances are observed for this station in the present study (Figure 33), but with abundances usually much higher inside the estuary. Despite the fact that ascidians were not identified to species, the seasonal occurrence of ascidian larvae in Southampton Water plankton is in agreement with the reported pattern of breeding of *Ciona intestinalis* and *Dendrodoa grossularia* (Table 13) in southern Britain waters, which usually extends from March/April to November (Raymont, 1983). In the current study maximum abundances occurred from June to September, with a peak reported on August (636 organisms m^{-3}), the same period

reported by Holmes (1968 cited in Raymont, 1983) as the breeding period of the immigrant species *Styela clava* within Southampton Water. Ascidian larvae may also be confined within the estuary (Figure 22) and this should be investigated. At Killary harbour Ryan *et al*., (1986) reported ascidians at a maximum of 37 organisms m^{-3} while Roper *et al*.,(1983) reports maximum abundances of only 5 organisms m^{-3} in the Avon-Heathcote estuary (New Zealand).

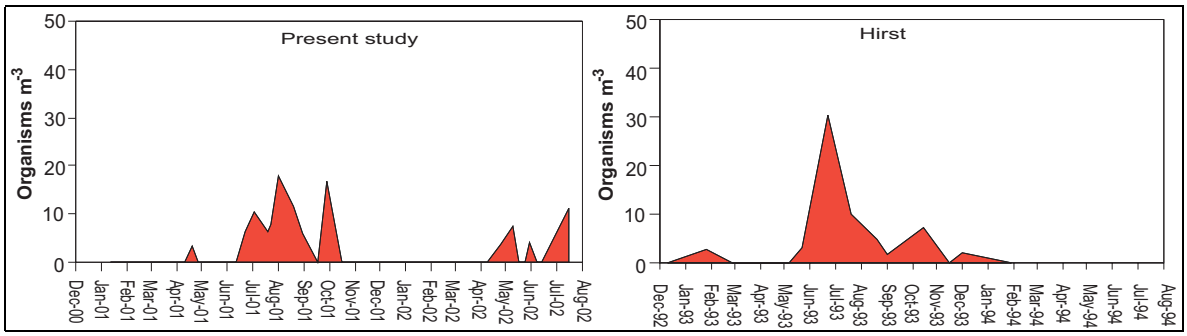


Figure 33. Temporal variability and seasonal contribution of ascidian larvae at Calshot during 2001/02 and 1992/94 from the raw data of Hirst (1996). (Note that temporal scale of Hirst data was extended from February 1994 to August 1994 for a better comparison with the 2001-2002 results. Data of ascidian for the remaining stations is shown on Figure 22 on a different scale).

3.4.5 Cnidaria.

Cnidarians are one of the few meroplanktonic "groups" where information is available (Williams & Reubold, 1990; Lucas, 1993; Lucas & Williams, 1994; Lucas *et al*., 1995; Lucas *et al*., 1997). In terms of total abundances the values reported here are in agreement of those presented by Zinger (1989) and, as expected, much higher than those of Lucas (1993) who used a 220µm mesh (Figure 34).

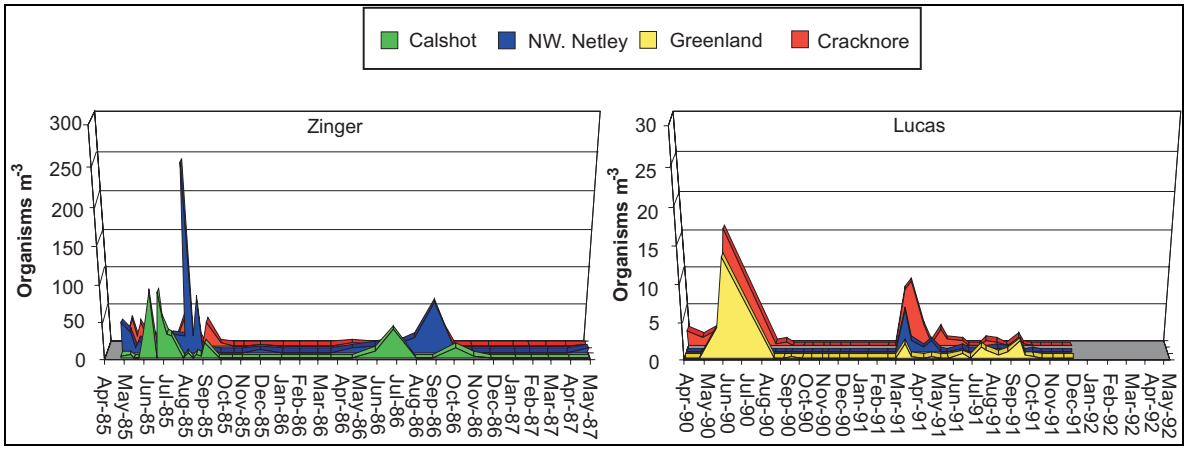


Figure 34. Temporal variability and seasonal contribution of Cnidaria during 1985/87 and 1990/91 from the raw data of Zinger (1989) and Lucas (1993), respectively. (Note that temporal scale of Lucas data was extended from December 1991 to May 1992 for a better comparison with the 1985-1987 results. Figures are also on different scales. Data for different depth strata were averaged, and data obtained with meshes larger than 220 µm were not included).

Considering species composition, the same species reported by Lucas (1993) are currently recorded, however, several unidentified species were found that were not accounted in previous studies. (The seasonal occurrence and pictures of identified and unidentified cnidarians can be seen on the zooplankton guide (Muxagata & Williams, 2004) included as a pdf file in the attached CD).

Cnidarians are recognized as important predators and often present a inverse correlation with copepods and fish, the main components of their diet (Ramírez & Zamponi, 1981). Because of that they can seriously affect fish stocks by either consuming the fish or its main prey (Möller, 1978; Purcell, 1985).

Despite the fact that no negative correlation was observed between cnidarians and copepods, by comparison of the numerical abundance patterns of cnidarians and calanoid copepods, Figure 35, it is clear that the "peak" of cnidarian presence matches with the late-spring decline experienced by some *Acartia* species, the main spring calanoid genus (Chapter 2). This suggests that cnidarians, together with *Pleurobrachia* (Chapter 2), could be one of the factors structuring the early-summer decline of *Acartia* reported in the previous chapter. However, it must be remembered that clogging by phytoplankton could also be the reason for this decline (Chapter 2).

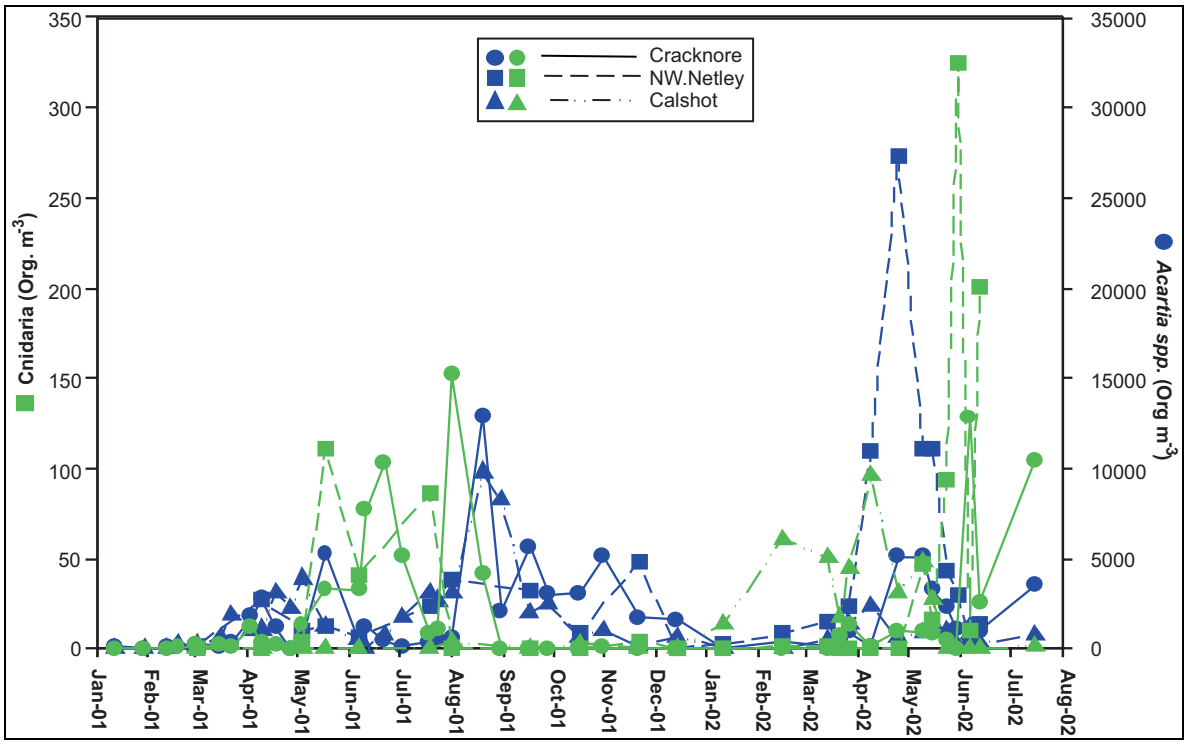


Figure 35. Seasonal pattern of abundance of Cnidaria and *Acartia spp.* at Southampton Water in 2001/02.

3.4.6. Decapoda.

Despite the fact that decapod larvae abundance was relatively low, with an overall average of 19.34 organisms m^{-3}, the results presented here were close to the average decapod abundance of 8.16, 16.76, 7.01 and 26.77 larvae m^{-3} presented by Zinger (1989), Lucas (1993), Hirst (1996) and Castro-Longoria (1998) respectively, in other studies of the estuary (Figure 36). This was unexpected, since the larger mesh-size used by Lucas (1993) and Castro-Longoria (1998) might be expected to capture a greater number of these relatively motile individuals. The total abundance data presented here are, however, comparable with the results of Grabe (2003) at New Hampshire where an average of 21.3 decapod larvae m^{-3} were recorded with a mesh of 505 µm, and with data on shrimp at Helgoland where an average of 1.48 carideans m^{-3} (this study recorded an average of 0.53 carideans m^{-3}) were collected with a 500 µm mesh (Wehrtmann, 1989).

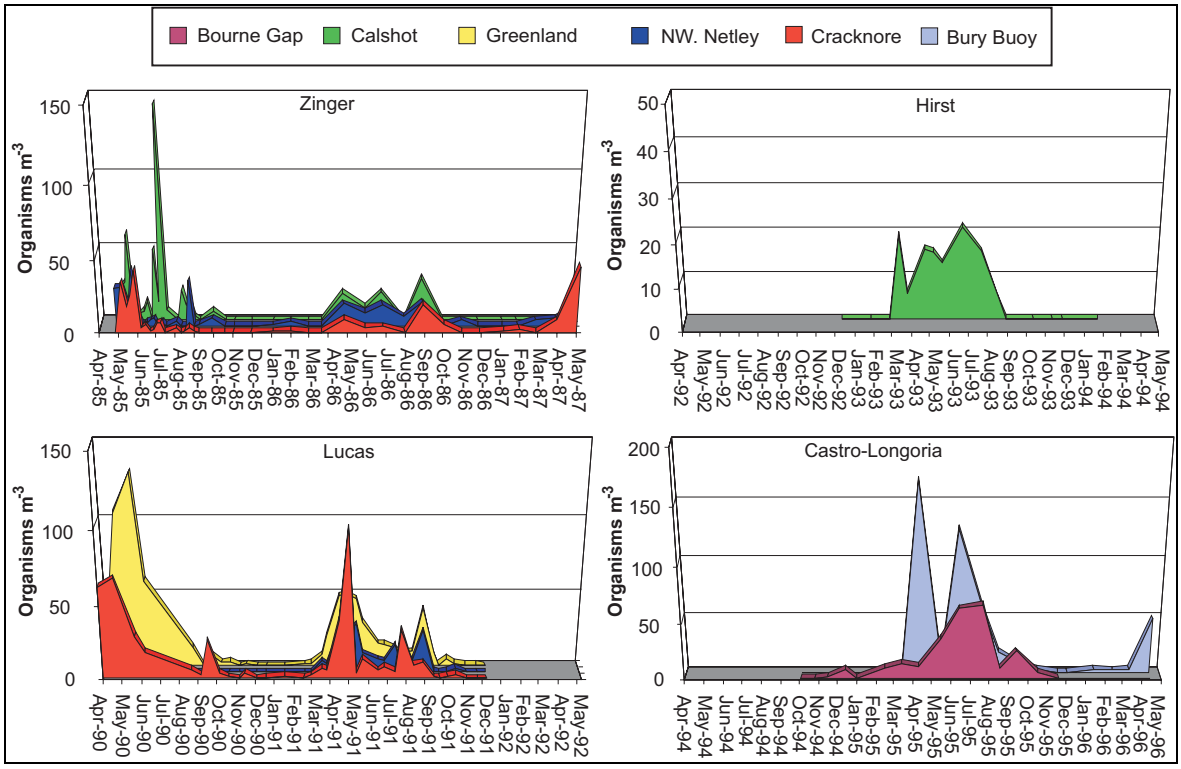


Figure 36. Temporal variability and seasonal contribution of larvae of Decapoda during 1985/87, 1990/91, 1992/94 and 1994/96 from the raw data of Zinger (1989), Lucas (1993), Hirst (1996) and Castro-Longoria (1998) at different stations in Southampton Water and the Solent. (Note that temporal scale of Hirst, Lucas and Castro-Longoria data was extended for a better comparison with the 1985-1987 results and figures are on a different scale). Data for different depth strata were averaged, and data obtained with meshes larger than 220 µm are not included.

Total abundance data presented here are also comparable with the results found on other estuaries where finer meshes were employed. At Killary harbour Ryan *et al*., (1986) reported two main peaks of abundance with a 97 µm mesh net, one in April (up to 104

organisms m^{-3}) and another in August (197 organisms m^{-3}). Hopkins (1977) sampling with a 74 μm mesh net reported a maxima of 190 larvae m^{-3} in Tampa Bay, while in Long Island Turner (1982), using a 73 μm mesh, observed a maxima of ~100 larvae m^{-3}. In the estuary of Lagoa dos Patos (Brazil) Montú (1980) observed a maxima of 198 larvae m^{-3} when sampling with a 200 μm mesh net.

Information on specific decapod larvae seasonality, composition and abundance from the surrounding area are presented by Lebour (1947), Bodo *et al*., (1965) and Martin (2000) but, unfortunately, no clear indication of the mesh-size employed were given. However, based on the similarities of the abundance results obtained with different mesh-sizes (shown above) those studies can still be compared.

Of the present species recorded, the brachyuran *C.maenas* was the most abundant and found throughout the year in significant numbers at each station, usually during spring and summer. Lebour (1947) associated this with the fact that adults breed in any month, but highest larval concentrations are usually expected for spring-summer, when peaks of more than 40 larvae m^{-3} have been reported around the UK (Ryan *et al*., 1986; Martin, 2000). These current data support the suggestion of Barnes *et al*.,(1973) that *C.maenas* is the dominant crab species in the Solent - Southampton Water system. Lebour (1947), Bodo *et al*., (1965) and Martin (2000) also recorded the persistent appearance of *C.maenas* larvae in the zooplankton off Plymouth, Roscoff and North Coast of France respectively.

Liocarcinus spp. and *N.puber* were grouped together under *Liocarcinus* spp. during this study. Differentiation of Polybiinae species beyond subfamilial level is not an easy task (Paula, 1996), and with 5 different Polybiinae species reported for this region (Table 13) this was necessary due to time constraints. When combined, the values of *Liocarcinus* spp. and *N. puber* reported by Martin (2000) for the French coast of the Channel were similar with those presented here.

The identification of *Macropodia* spp. and *Inachus* spp. to species was also not attempted since there are at least three different species of each occurring in the area (Table 13). Martin (2000) reports similar abundances for *Macropodia* spp. of the North Coast of France, although values for *Inachus* larvae are higher, with abundances increasing towards the western end of the Channel.

Corystes cassivelaunus, *Pilumnus hirtellus* and *Pinnotheres pisum* appeared in zooplankton catches with a marked seasonal occurrence (Table 16) and Lebour (1947), Bodo *et al*., (1965) and Martin (2000) also noted this same marked seasonality of *C. cassivelaunus, P.hirtellus* and *P.pisum* off Plymouth, Roscoff and other stations in the North Coast of France, respectively. Abundance values for these species on the north coast

of France (Martin, 2000) are usually higher than those reported here, however further south on the Portuguese coast *Pilumnus hirtellus* is reported at lower maximum abundances (max of 0.8 organisms m^{-3}), but occurring through the entire year (Paula, 1987).

Lebour (1947), Bodo *et al*., (1965) and Martin (2000) observed larvae of *Ebalia* spp. throughout the entire year off Plymouth, Roscoff and North Coast of France, but, like this sudy, chiefly from July to September (Lebour, 1947; Martin, 2000). Generally, the maximum abundance values of *E.tuberosa* and *E.tumefacta* presented by Martin (2000) for the North Coast of France are 10 – 100 fold higher than those presented here.

The remaining brachyurans *Maja squinado, Hyas* sp. and *Pisa* sp. were all restricted to Calshot (Table 16). *Hyas* sp. and *Pisa* sp. could be the larvae of *Hyas coarctatus* and *Pisa tetraodon* since these are the only species reported locally (Table 13). The seasonal occurrence of *Hyas* sp. found in this work (Table 16) also agrees with that of *Hyas coarctatus* off Plymouth and Roscoff (Lebour, 1947; Bodo *et al*., 1965). The abundance values *Hyas* sp. and *Pisa* sp. off the south coast of the Channel were usually 10 fold higher than those presented here (Martin, 2000), but both studies reported the same seasonality.

Carideans are of particular interest, as most of the species are of some potential commercial value. The seasonal occurrence of *Crangon crangon* larvae is in agreement with that reported by Lebour (1947) off Plymouth, Bodo *et al*., (1965) off Roscoff, Wehrtmann (1989) for the Helgoland area and Martin (2000) for the North coast of France. Maximum abundances of *C.crangon* reported here are also comparable with a peak of 7 larvae m^{-3} reported by Wehrtmann (1989) at Helgoland, and with ~6 larvae m^{-3} reported by Martin (2000) for the Penly region. Martin (2000) also suggests that the abundance of *C.crangon* increases towards the eastern end of the English Channel.

Crangon bispinosus and C.*trispinosus* were found from March throughout October (Table 16), but always in very low numbers which agreed with the values reported by Wehrtmann (1989) and Paula (1987) off Helgoland and the Portuguese coast. Lebour (1947) and Bodo *et al*., (1965) reported similar seasonality pattern. In contrast, Martin (2000) found higher abundances of *C.trispinosus* off the french coast of the English Channel, also suggesting that the abundance of *C.trispinosus* increases towards the North Sea. *Crangon fasciatus*, in contrast with *C.bispinosus* and *C.trispinosus* was common and also had the same seasonal pattern as that reported by Lebour (1947), Bodo *et al*., (1965) and Martin (2000). The abundance data of Martin (2000) is similar to that presented here, but also indicates a gradual increase of abundance towards the Atlantic.

Palaemon elegans is recorded for the first time in Southampton Water, but was found only on three occasions, twice at Calshot and once at NW. Netley, and at very low abundances. The unidentified species of *Palaemon* spp. that were found through the estuary could be that of *P.longirostris* and/or *P.serratus* (Table 13). Martin (2000) reports *Palaemon* spp. abundances an order of magnitude greater on the north coast of France, but with the same seasonal pattern.

Processa sp. were only identified to genus level as the few larvae found presented characteristics ascribable to both *P.edulis* and *P.nouveli holthuisi* (Fincham & Williamson, 1978). Of these, only adults of *P. nouveli holthuisi* have been previously reported in the surrounding area (Table 13). *Thoralus cranchii* and *Hippolyte* spp. records are in good agreement with Martin (2000) with almost the same seasonality and abundance recorded. At least 2 different species of *Hippolyte* come under *Hippolyte* spp. with, probably *Hippolyte varians* one of these.

Larvae of *Alpheus glaber* were very rare, and found at Calshot on only two occasions in July 2001 (Table 16). In contrast, *Athanas nitescens* was relatively common and found in the plankton from June to September at all stations (Table 16). The seasonal pattern observed for *A.nitescens* in this study is in good agreement with Lebour (1947) off Plymouth, Bodo *et al*., (1965) off Roscoff, Wehrtmann (1989) for the region of Helgoland and Martin (2000) for the north coast of France. Present abundance values were, however, greater than those reported by Wehrtmann (1989) but lower than those of Paula (1987) in the Portuguese coast. Martin (2000) also suggests that the abundance of *A.nitescens* increases towards the western end of the Channel.

The Infraorder Thalassinidea included the presence of *Axius stirhynchus* and *Upogebia* sp. The first was only caught on 2 occasions, at Calshot and at abundances never exceeding 0.04 organisms m^{-3}. *Upogebia* sp, probably *Upogebia deltaura,* since this is the only species recorded in the region (Table 13) was found in abundances up to 0.23 organisms m^{-3} at Calshot, where it was relatively more frequent and abundant although it was also recorded at Cracknore and NW Netley. Both *A.stirhynchus* and *U.deltaura* are very common in the plankton off Plymouth and the North coast of France and are suggested to be much more abundant and frequent towards the western portion of the English Channel. (Lebour, 1947; Bodo *et al*., 1965; Martin, 2000).

Larvae of six different anomurans were recorded (Table 12) but the contribution of anomuran larvae to the zooplankton recorded in this study is much lower when compared with the seasonally data presented by Lebour (1947), Bodo *et al*., (1965) and Martin (2000) off Plymouth and the NW coast of France. Ryan *et al*., (1986) recorded

P.longicornis abundance values as high as 184 larvae m^{-3} at Killary harbour and Martin (2000) observed values as high as 900 larvae m^{-3} of *P.longicornis* on the north coast of France. Paula (1987) in contrast, reports abundances of anomurans on the Portuguese coast particularly *P.longicornis* and *A.hyndmani* closer to those reported here.

(The previous record for the palinuran larvae of *Scyllarum* (?) spp. by Barlow & Monteiro (1979) is probably in error, and refers to *Scyllarus* sp., probably *Scyllarus arctus,* since this is the only species of this genus that has been reported in the area (Bodo *et al*., 1965; Howson, 1987). However it could also have been mistaken for the relatively similar larvae of *Palinurus elephas* (v*ulgaris*) that occurs in the English Channel (Bodo *et al*., 1965; Martin, 2000). Mallinson (Pers. com.) confirms that *P.elephas* was found in the surrounding area of Southampton Water in the 1970's).

As a general statement the seasonal pattern of decapod larvae highlighted in Table 15 is in good agreement with the patterns presented by Lebour (1947) off Plymouth, Bodo *et al*., (1965) for the region around Roscoff, Werthman (1989) for Helgoland, and with the report of Martin (2000) for the north coast of France. Only the numbers of thalassinid and anomuran larvae in the present study are low compared to these reports, which also show them to be more important toward the western end of the English Channel and North-Atlantic.

In the present study many species were only found toward the mouth of the estuary at Calshot and NW. Netley, where consistent tidally-associated salinity variation is minimal (Figure 3 – Chapter 1). Equally, of the species that were recorded at all three sites (Table 16), many had highest densities at Calshot. The temporal distribution of some species, including three carideans, *Hippolyte* spp., *Thoralus cranchii*, *Processa* sp. (Table 16) suggested patterns of movement down the estuary with time, perhaps indicating some distributional behaviour. Unfortunately as no record of the larval stages is available, this pattern is conjecture.

The absence of larvae of any decapod listed on Table 13 does not necessarily imply that they do not occur in the plankton of the Solent - Southampton Water region since no other data, especially long-term data, is available. Further studies for the area are clearly needed as the sampling strategy of the present study was not focused primarily on the capture of decapods. This report is considered simply a starting point, where the common species and their basic spatial-temporal distributions are identified.

3.4.7. Minor meroplanktonic contributors.

This is the first record of Actinotrocha and Stomatopoda larvae within this estuary. Stomatopod larvae were found in Calshot and NW. Netley with Actinotrocha at Calshot and Cracknore (Table 17). Stomatopod larvae are commonly reported in samples from the southern portion of the North Sea, English Channel and off the west coast of Ireland during the summer (Mauchline, 1984). Adults of *Rissoides desmaresti* were recently reported within the Solent – Southampton Water region (Mallinson, Pers. com.), and probably local populations could have established. No previous record of phoronids was found, but the presence of early stages clearly indicates the presence of adults locally. Bodo *et al*., (1965) reported *Rissoides desmaresti* larvae off Roscoff during July-August. Roper *et al*.,(1983) observed maximum of 0.04 stomatopods m^{-3} in the Avon-Heathcote estuary (New Zealand). At Killary harbour Ryan *et al*., (1986) reported phoronid larvae with a maximum of 24 organisms m^{-3} in July. Lebour (1947) reports phoronid larvae from April to August off Plymouth.

About 1550 species of Siphonostomatoida have been described, with around 1050 species related to fish and nearly 500 associated with invertebrate hosts (Huys & Boxshall, 1991). In Southampton Water four species of siphonostomatoid copepod were recorded (Table 12), together with individuals pooled in an "unidentified copepodites" category. While siphonostomatoid copepodites were found throughout the estuary and all through the year, the identified taxa were less frequent and predominantly recorded in the lower estuary at Calshot (Table 17).

Previously, only the pennelid *Lernaeocera lusci* has been reported in Southampton Water (Evans *et al*., 1983) infecting *Trisopterus luscus,* the pouting, by Calshot at the mouth of Southampton Water. Pennelids are unique among parasitic copepods in having intermediate hosts in their life cycle. Hatching as nauplii, these siphonostomatoids develop into a free-swimming copepodite that requires a intermediate host, usually a fish, cephalopod or pteropod, to complete development. In the intermediate host they reproduce, and impregnated females undergo another period of free-swimming before finding the definitive host, which will be another fish, or even a marine mammal (Kabata, 1979). Based on differences in the mouth parts of the different "unidentified copepodites of siphonostomatoids" found, at least five different species are present, and it is almost certain that copepodites of *L.lusci* occur among them.

Considering the identified siphonostomatoids, Asterocheridae are reported on a wide variety of hosts, either as internal or external associates, or even as parasites.

Asterocheres sp. (Table 12) is considered as an ectoparasite of echinoderms (Isaac & Moyse, 1990), but is also reported in association with Porifera, Mollusca, Cnidaria, Urochordata and Bryozoa (Hansson, 1998; Boxshall & Halsey, 2004; Gotto, 2004). Four adults were caught free in the plankton.

Caligids are ectoparasites that are usually found on the outer surface, mouth, gills and opercular cavity of fish hosts (Boxshall & Halsey, 2004). *Caligus elongatus* is regarded as the most common parasitic copepod in British waters (Kabata, 1979) and was reported associated with more than 80 species of fish (Kabata, 1979; Isaac & Moyse, 1990) Only a single adult female of *C.elongatus* was caught in the zooplankton during this study, probably having been detached from its host. An adult female of *Caligus minimus,* usually reported on perciform fishes (Kabata, 1979), was identified in an opportunistic sample and re-analysis of the samples of Castro-Longoria (1998) highlighted an adult male of *C.elongatus*.

A single specimen of the cancerillid *Cancerilla tubulata* was found free. Cancerillids are typical ectoparasites of brittle stars, with this species reported on *Amphipholis squamata*, *Ophiocomina nigra*, *Ophiothrix fragilis* and *Ophiopsila aranea* (Isaac & Moyse, 1990; Hansson, 1998; Gotto, 2004), and at least two of these hosts are reported in the Solent – Southampton Water area (Table 13).

Little is known from the Artotrogidae, but they have been reported as possible associates of sponges, scleractinians and ascidians (Hansson, 1998; Gotto, 2004), bryozoans (Kim, 1996) and the polychaete *Pomatoceros triqueter* (Hansson, 1998). In this estuary only two specimens were caught freely in plankton samples.

Cyclopoid notodelphyids were recorded sporadically throughout the year, but only at Calshot. A single unidentified Notodelphydae taxon has been reported, possibly *Doropygus* sp, on three occasions free in the water column. Notodelphyids are usually associated with ascidians, and found inhabiting the pharynx or atrium, presumably sharing the food brought in by the host. Because of this many species of this family are considered commensals rather than parasitic (Boxshall & Halsey, 2004). Previously, *N.allmahi* has been reported by Castro-Longoria (1998) in the estuary. Both *N.allmahi* and Doropygines, like *Doropygus pulex* are reported to be associated with ascidians, including *Ascidia conchilega, Ascidiella aspersa* and *Ciona intestinalis* (Chordata: Ascidiacea) that have been reported here (Table 13) (Isaac & Moyse, 1990; Gotto, 2004).

Monstrilloids have an endoparasitic naupliar stage which burrows into the host, finally emerging in the last copepodite stage, to moult into a free-swimming, non-feeding adult (Huys & Boxshall, 1991; Boxshall & Halsey, 2004; Gotto, 2004). Of those recorded

in Southampton Water, *Cymbasoma rigidus* is reported as a parasite of the polychaetes *Salmacina dysteri*, *Polydora ciliata* and *Polydora giardi* while *Monstrilla helgolandica* is recorded in the gastropod *Brachystomia rissoides* (Hansson, 1998). Only free-living adults were caught during this survey, usually between May to October and toward the lower estuary, with only *C.thompsoni* being relatively abundant and frequent throughout the summer (Table 17). Isaac (1979) also reported the occurrence of *Monstrilla helgolandica* and *Cymbasoma rigidus* at Swansea Bay.

Unidentified epicaridean isopods were recorded frequently, usually found free or attached to the calanoid copepods *Acartia* spp, *Centropages hamatus* and *Temora longicornis,* although it is possible that they can also be found attached to other copepods. (Pictures of those epicaridean isopods attached to copepods can be seen in the zooplankton guide (Muxagata & Williams, 2004) included as a pdf file in the attached CD). Isaac (1979) also reported the occurence of epicaridean isopods in zooplankton samples of Swansea Bay.

This is the first report of "free-living" forms of parasitic/commensal species within the mesozooplankton of Southampton Water. The occurrence of the larvae and/or adults in plankton samples is a reasonable indicator of the presence of the infected/associate host in the estuary or surrounding areas. Some of the known hosts of a particular species have not been reported (Table 13), so they could either be associated with another, as yet, undescribed host, or the benthic host still have to be recorded in the Solent – Southampton Water region.

Gotto (2004) suggests that, particularly in copepod-invertebrate associations, very few ill-effects are discernible in hosts, with most species being regarded as harmless commensals. The real impact and degree of parasitism and/or association of the species reported here are ambiguous, and in many cases poorly known. Considering that the more well-known parasitic species of fish, like the Caligidae, are capable of serious damage to fisheries and aquaculture, it is reasonable to presume that a comparable impact could be expected on the individual and/or community-status of some invertebrate hosts.

3.4.8. Tycoplankton.

Of the taxa reported as tycoplankton in this study only mysids have a true tycoplanktonic way of life, and are found in significant numbers in zooplankton samples, especially during the night (Makings, 1977). In fact, Raymont & Carrie (1964) reported appreciable quantities of *Mesopodopsis slabberi* and *Neomysis integer* at night in

Southampton Water. Despite the fact that all sampling for this study was done during the day, 9 new species of Mysidacea were recorded, with *Anchialina agilis*, *Gastrosaccus sanctus*, *Mysidopsis gibbosa* and *Acanthomysis longicornis* being recorded for the first time in this region.

From the species reported during the present study *G.sanctus* and *P.arenosa* are sand-burrowing species, while *Siriella clausii*, *S.armata*, *A.agilis, Leptomysis lingura, M.gibbosa, A.longicornis* and *Schistomysis kervillei* are species usually found near the bottom in shallow waters (Makings, 1977). These species were never abundant, with only very few individuals recorded at Calshot. *Mesopodopsis slabberi*, by contrast, is usually found in the water column of estuaries (Makings, 1977) and was previously recorded by Raymont & Carrie (1964) and Castro-Longoria (1998) at Marchwood and Bury Buoy (Figure 1 - Chapter 1) in the inner estuary. In the present study *M.slabberi* was much more frequent and abundant in the brackish waters of Cracknore and NW. Netley. *M.slabberi* was found at abundances up to 78 organisms m^{-3} at the inner stations of the Ems estuary (Baretta & Malschaert, 1988).

Nothing much can be said of the remaining species/groups reported as tycoplankton. They were probably caught in samples through tidal resuspension of sediments, especially at Calshot where samples usually contained a relatively heavy layer of sand and other particules.

3.4.9. General remarks.

From the results presented here and in Chapter 2 it is clear that most of the diversity found in the mesozooplankton of Southampton Water is primarily due to the contribution of mero-tycoplanktonic species. As in the previous chapter, estuarine mero-tycoplankton can be summarized according to its origin:

- **Marine coastal species** which enter the estuary from the sea and are usually limited to regions influenced by the saltwater intrusion. They were represented by the bulk of the organisms listed in Table 12, with the exception of the species listed below.
- **Estuarine-associated species** which can live within a wide range of estuarine conditions of temperature and salinity. These are typically represented here by the cnidarian *Aurelia aurita*, the cyclopoid copepod *Cyclopinoides littoralis*, the harpacticoid copepod *Tisbe* spp, the decapod larvae of *Carcinus maenas* and *Crangon crangon,* the barnacle larvae of *Balanus improvisus, Elminius*

modestus and *Sacculina carcini*, the amphipods *Corophium* spp and *Jassa* sp. and the mysid *Mesopodopsis slabberi*.

- **Freshwater species** which extend into the brackish water regions of the upper estuary. Exemplified by the unidentified chydoridae cladocerans.

Of course this classification reflects mainly larval occurrences/preferences found in this estuary, which reflects the essentially marine nature of Southampton Water (Raymont, 1983).

On a general basis the mero-tycoplankton composition of estuaries everywhere (Bousfield *et al*., 1975; Hopkins, 1977; Montú, 1980; Turner, 1982; Baretta & Malschaert, 1988; Soetaert & Van Rijswijk, 1993; Perissinotto *et al*., 2000; Hoffmeyer, 2004) is much more diverse/variable than the holoplankton, where the bulk of the estuarine population is composed by a few copepod species/genera that are common in almost every estuary (Conover, 1956; Cronin *et al*., 1962; Jeffries, 1962; Jeffries, 1967; Haertel & Osterberg, 1967; Heinle, 1972; Frolander *et al*., 1973; Bousfield *et al*., 1975; Reeve, 1975; Hulsizer, 1976; Wooldridge & Melville-Smith, 1979; Alcaraz, 1983; Baretta & Malschaert, 1988; Buskey, 1993). This implies that mero-tycoplankton composition of an estuary is "unique" and in this sense probably more useful in describing/observing changes/patterns on a regional/smaller basis, since it usually mirrors the composition and health of the parental populations of the surrounding area and so is probably more useful to detect immediate/localized changes.

Despite the effort employed during this investigation, which tripled the number of identified species in the mero-tycoplankton, there are still "large components", like Polychaeta, Mollusca, Bryozoa and Ascidia about which almost nothing is known. With the exception of few organism of particular economical importance; these components are also not described for other estuaries. This is surprising since rates occur at species level, and knowledge of the species present in a particular area is needed before any attempt to quantify/evaluate/model specific processes (Soetaert & Van Rijswijk, 1993). This idea of producing models of aquatic systems should have promoted and supported new basic descriptive studies since models can not go beyond the limitation of the original data, and thus erroneous and/or even incomplete community analysis will certainly lead to an erroneous/dubious model.

Estuaries are also known as nurseries for several commercial species of fish and invertebrates and to improve our knowledge on the functioning of these ecosystems we clearly need more detailed information on several "unknown" components of the

zooplankton, particularly meroplanktonic larvae, and the role they play in the overall distribution of adults in these ecosystems (Stancyk & Feller, 1986). Understanding of estuarine ecology can only be achieved after knowing the basics about patterns of distribution and abundance of species, which in turn will also enable us to predict natural and/or anthropogenic effects in estuaries.

3.5. Chapter Conclusions

- 113 taxa were observed and considered within the mero-tycoplankton category, 72 meroplanktonic and 41 tycoplanktonic. 84 taxa are reported for the first time within the plankton of Southampton Water.

- Barnacles were the most abundant meroplanktonic component, followed by Polychaeta, Mollusca, Bryozoa, Ascidia, Decapoda and Cnidaria. All of them were only abundant during spring and summer.

- 10 barnacle species were identified, with five species being seasonally abundant. *Elminius modestus* larvae occurred all year long and were found on every sample. *E.modestus* larvae usually dominated the barnacle larvae composition of the mesozooplankton, except from February to May where the abundance of *Balanus crenatus* larvae clearly overwhelms any other. Some *Semibalanus balanoides* and *Verruca stroemia* also occurs during February to May. At the innermost station of Cracknore *B.improvisus* also appears in high numbers from May, and co-dominates with *E.modestus* from June to August. Usually *E.modestus* is the dominant barnacle larvae in this estuary from July to January.

- *Peltogaster paguri* and *Sacculina carcini* had been previously reported, and despite the low abundance they appeared on a regular basis in plankton catches.

- The barnacle larvae of *Chthamalus stellatus, Conchoderma* sp. and *Trypetesa* sp. are reported fot the first time within this estuary.

- A total of 31 Decapoda, belonging to 4 infraorders were observed. The brachiurans *Carcinus maenas*, *Liocarcinus* spp., *Pagurus bernhardus, Pisidia longicornis* and *Macropodia* spp. were the most common and abundant larval forms. These, together with the caridean *Crangon crangon* accounted for 98% of all decapod larvae found in Southampton Water. With the exception of *P.longicornis* that has been previously reported, all the remaining species are being recorded for the first time in plankton catches.

- In terms of numerical importance only *C.maenas* had any significance in catches at each station, accounting, on average, for 78, 66 and 53% of the decapods at Cracknore, NW Netley and Calshot, respectively. *C.maenas* larvae were found throughout the year, but were more abundant during spring, particularly in April when maximum abundances were recorded.

- Several other meroplankton species are being reported for this estuary, but most of then occurred rarely, or in very low numbers, usually during spring and summer.

- Tycoplanktonic organisms are also described, with species reported for the first time within this estuary. Mysids are the only organisms with a real tycoplanktonic way of life, and from the species reported here only *Mesopodopsis slabberi* was found on a regular basis.

- Correlations with biological and non-biological environmental variables measured reflect most of the seasonal patterns observed, with temperature being clearly the most important.

- Generally, mero and tycoplanktonic organisms were more abundant during spring-summer clearly reflecting the breeding patterns of adults present in the surrounding area. This is considered as only a start point, and continuous monitoring studies should be carried to extend this knowledge further. Polychaeta, Mollusca, Bryozoa and Ascidia species are yet to be identified, and as presented here they constitute a large fraction of the meroplankton of this estuary.

Chapter 4

The secondary production of barnacle larvae in Southampton water

4.1. Introduction.

It is widely accepted that in aquatic communities, zooplanktonic organisms play a critical role representing the main link between the phytoplankton and bacterioplankton and higher trophic levels (Buskey, 1993; Banse, 1995), and so the measurement of secondary production has been one of the primary goals of zooplankton research (Runge & Roff, 2000). This importance is attested by the numerous reviews concerning methodologies for estimation of the secondary production of zooplanktonic organisms (Yablonskaya *et al*., 1971; Winberg *et al*., 1971; Pechen *et al*., 1971; Bougis, 1976; Greze, 1978; Rigler & Downing, 1984; Kimmerer, 1987; Omori & Ikeda, 1992).

The measurement of zooplankton production is time consuming, involving the laborious task of sorting, identifying and measuring the different stages of the species present in plankton, but such population level estimations are necessary because they constitute one of the most important parameters for estimating the total community productivity (Greze, 1978; Kimmerer, 1987), being also the basis for the elaboration of general theories of biological productivity (Downing, 1984). By improving our knowledge about the production of the zooplanktonic organisms, we are not just increasing the understanding about the fate and flow of energy and matter through planktonic food webs, but also improving the estimation and management of the production of commercially species that rely on zooplankton for food (Mullin, 1969; Winberg, 1971; Greze, 1978; Williams, 1984; Downing, 1984; Huys & Boxshall, 1991). Alternatively, the measurement of zooplanktonic secondary production, can also be used as an indicator of its physiological and nutritional state (Kimmerer, 1987; Omori & Ikeda, 1992) as well as to determine the response of species to changes, such as pollution, in environmental conditions (Winberg, 1971; Downing, 1984).

Copepods generally form the largest component of zooplankton biomass of all groups present in estuarine, neritic and oceanic areas, and as such, almost all zooplankton production studies refers only to the contribution of the copepod component. (Evans, 1977;

Landry, 1978; Burkill & Kendall, 1982; Daro & van Gijsegen, 1984; Kimmerer & McKinnon, 1987; Castel & Feurtet, 1989; Chisholm & Roff, 1990a; Escaravage & Soetaert, 1993; Poulet *et al*., 1995; Peitsch, 1995; Hay, 1995; Webber & Roff, 1995; Fransz & Gonzalez, 1995; Escaravage & Soetaert, 1995; Uye & Sano, 1998; Hirst *et al*., 1999). Although organisms like polychaete larvae, cladocerans, barnacles and decapod larvae are also seasonally important, especially in neritic and estuarine waters (Raymont, 1983), it is really surprising that there is a limited amount of data on the secondary production of these components.

The zooplankton community structure of Southampton Water offers a scenario for the evaluation of a non-copepod component, as all the studies that have monitored the composition, distribution and abundance of the micro-mesozooplankton population of this estuary (Conover, 1957; Soares, 1958; Raymont & Carrie, 1964; Lance & Raymont, 1964; Bird, 1972; Zinger, 1989; Williams & Reubold, 1990; Geary, 1991; Lucas, 1993; Lucas & Williams, 1994; Lucas *et al*., 1995; Hirst, 1996; Castro-Longoria & Williams, 1996; Castro-Longoria, 1998; Hirst *et al*., 1999; Chinnery, 2002), including the present study (Chapters 1 and 3), indicate that the larvae of barnacles constitute one of the major elements within the meroplankton. Hirst *et al*. (1999) even suggested that barnacle larvae could be expected to account for at least as much secondary production as calanoid copepods.

Unfortunately, apart from a recently published work concerning the potential production of *Elminius modestus* at Cracknore, originated from data presented here (Muxagata *et al*., 2004 see attached pdf file or Appendix 1), no other data on production of barnacle larvae are available anywhere.

The content of the present chapter is designed to add to the body of information on pelagic carbon flux within Southampton Water by measuring the production and contribution of barnacle larvae to pelagic fluxes. Production will be determined by a number of methodologies including the use of ecological growth equations developed for copepods. The resulting data will be used to advance and refine the current perceptions of carbon flux in Southampton Water.

4.1.1. The Theory of Secondary Production.

In order to facilitate the understanding of the results concerning the secondary production of zooplanktonic organisms, this section introduces and explains the concepts behind the theoretical aspects of the secondary productivity of aquatic invertebrates.

Imagine a hypothetical finite population living within a closed system where there is no mortality. After a period of time (t), the number of animals in a cohort[6] in the end (N_f) of the investigation will be the same as in the beginning (N_i). Accepting this, we could say that the production (P) over this period of time will be the difference between the biomass at the end (B_f) and the beginning (B_i) of the period in question. This can be defined by the equation:

$$P = (B_f - B_i) \text{ or } P = \left(\overline{w}_f * N_f\right) - \left(\overline{w}_i * N_i\right), \quad (4)$$

where, $\overline{w}_f$ = average weight of an organism at end of the period; $\overline{w}_i$ = average weight of an organism at the beginning of the period; N = is abundance.

In this simplest case, if we also assume that the population was not food-limited, the biomass will be expected to be higher at the end of the period due to the growth of the individuals, and this growth could then be assumed to be the production[7] of those organisms for this period.

Systems like this are only theoretical. In the real world individuals die or are eliminated through disease, predation, malnutrition, environmental/physical factors, etc. Then, if in the end, we have equal biomass at the end and beginning of the period, one could say that the production of that period was equal to the amount eliminated (B_e), so, production can then be expressed as:

$$P = B_e + (B_f - B_i) \quad (5)$$

with

$$B_e = \overline{w} * (N_i - N_f) \quad (6)$$

where, $\overline{w}$ = average weight of an organism over the period, if t is short then $\overline{w} = \frac{1}{2}(\overline{w}_i + \overline{w}_f)$.

[6] The term "cohort" means an aggregate of individuals of the same species born at the same time and which live together under the same conditions (Neess & Dugdale, 1959) or according to Polishchuk (1990)"Cohort is an assemblage of individuals born exactly at the same moment and having at every instant exactly the same age".

[7] According to Winberg *et al.* (1971) production can be defined as the sum of the growth increments of all individuals from a specific population over a certain period of time. Or according to Ricker (1946) it is the biomass produced by a population in a time interval, regardless of whether it survives or not until the end of the interval.

Thus, we could rewrite equation 2 as:

$$P = (N_f + N_i)/2 * (\overline{w}_f - \overline{w}_i) \quad (7)$$

This concept, outlined in equations 4 to 7 were summarized by Winberg *et al*. (1971) and was based on the principle (eq. 7) introduced by Boysen-Jensen (1919) for the calculation of production of aquatic organisms with well defined generations. Since then, many different methods based on this principle were developed to estimate secondary production from field data, see the International Biological Programme (IBP) reviews of this subject: Pechen *et al*.,(1971); Yablonskaya *et al*., (1971); Winberg *et al*. (1971); and Rigler & Downing, (1984).

For zooplanktonic invertebrates, the problem really arises with the need to identify cohorts of species that reproduce more or less continuously. In this case, with the continuous recruitment, the cohorts will overlap and the individuals spread throughout different size classes, making it virtually impossible to follow the changes in abundance with time. Since most zooplanktonic organisms belong to this category, it is necessary to use methods that do not require proper cohort recognition.

According to the review of Rigler & Downing (1984), the two most frequently used methods for the calculation of the production of populations with continuous reproduction from field data are the "increment-summation" and "instantaneous-growth" protocols.

These methods were also derived from the Boysen-Jensen concepts and are basically the same as those used for production calculations of populations that have identifiable cohorts, but some assumptions are needed.

For "increment-summation" one must assume that all the individuals at the same size group and/or larval stage are growing at the same constant rate. By doing so the production can be calculated by:

$$P = \sum \left[N_i * (w_{i+1} - w_i) \right] / D_{i \rightarrow i+1} , \quad (8)$$

where, P = the production of a particular size class per unit of time, N_i = number of animals in the i^{th} size class, w_i = weight/mass of an individual in the i^{th} size class, w_{i+1} = weight/mass of an individual in the i+1 size class, D = time in days taken by an average animal to grow from w_i to w_{i+1}. (In the case of larval stages one can assume larval development as growth, then w_{i+1} = the average weight of the preceding stage and w_i = the average weight of that stage, remembering that you are ignoring the contribution of exuviae to total production).

The other method "instantaneous-growth or growth-rate", was recently reviewed by Kimerer (1987) and endorsed by Runge & Roff (2000) for the "ICES Zooplankton methodology manual"(Harris *et al*., 2000). By this method we have to assume that all the

individuals within a size class are growing exponentially, so the daily secondary production can be calculated as:

$$PR = \sum B_i * g_i \tag{9}$$

with,

$$B_i = N_i * w_i \tag{10}$$

where, B_i = is the mean biomass of the ith size class class over a certain time and g_i = is the instantaneous growth rate of the individuals in the ith size class class, *Ni* = number of organisms in the ith size class class and *wi* = weight/mass of organism in ith size class. The annual production of a population by either method (defined by equations 8 and 9) will be equal to the sum of weight increments of all the stages throughout the year. According to Rigler & Downing (1984), when there is no mortality and the population is in an approximately steady state, equations 8 and 9 are identical. However, Kimerer (1987) pointed out some errors with the determination of secondary production using the "increment-summation" equation, and since the data required for the "growth rate" method is basically the same, the later should be used instead.

Another very popular method for the calculation of secondary production of aquatic invertebrates, although not recommended by the IBP, is the so-called "Hynes method" (Waters & Hokenstrom, 1980) or simply the "size-frequency method". Despite not being used in this work, this method should be mentioned, since it was a matter of discussion for nearly 12 years (Hynes & Coleman, 1968; Hamilton, 1969; Fager, 1969; Gillespie & Benke, 1979; Benke, 1979; Menzie, 1980; Krueger & Martin, 1980) after it was first published by Hynes & Coleman (1968).

The method was originally developed for the calculation of secondary production of univoltine[8] animals (Hamilton, 1969), but later modifications introduced by Benke (1979) allowed its application with multivoltine[8] animals as well. This method has now been "clarified" by Menzie (1980) and Krueger & Martin (1980) as:

$$P = \left[f \sum_{j=i}^{i} \left(\overline{n}_j - \overline{n}_{j+1} \right) * \left(w_j * w_{j+1} \right)^{1/2} \right] * \frac{Pe}{Pa} * \frac{365}{CPI} \tag{11}$$

where, P = annual production, f = the number of size categories, $\overline{n}_j$ = mean number of organisms in size class *j*, w_j = is the mean weight of an organism in the j^{th} size category, *Pe* = estimated proportion of life cycle spent in a particular length class, *Pa* = actual

[8] The term voltinism is employed to indicate the numbers of generations per year, where: univoltine is usually employed with regard to organisms that have only one generation per year, and multivoltine for those with several/multiple generations per year (Downing, 1984).

proportion of life cycle spent in a particular length class, CPI = cohort production interval or average larval development time in days.

The "Hynes method" is similar to the "removal-summation" method for estimating secondary production (Menzie, 1980), and is thus a simplified version of the "increment-summation" described above (Rigler & Downing, 1984). Since the data required for the three methods are the same, the use of this simplified method should be avoided (Rigler & Downing, 1984).

So, it is clear that an estimate of the secondary productivity of continuously reproducing animals in the field will need:

1 - An accurate estimate of population size of each of the different size classes (or larval stages),

2 - The average body mass of each of the instars,

3 - The time taken for an animal to grown from the minimum to the maximum size within a size class (or larval stage) or the specific growth-rate of each organism.

Of these, probably the most difficult and laborious to obtain are accurate estimates of the population size, because it involves a good spatial coverage of the sampling site, with many samples, i.e. numerous hours counting and identifying animals from field data at the microscope, probably the most demanding task of any zooplankton investigation.

The weight of each size class can be obtained after weighing individuals from that particular age class (larval stage) from field samples. Later a length-weight relationship can be derived, and weights can be estimated straight from length measurements of animals from the field.

The development time and growth rate of each instar can be obtained in different ways:

- The most common was to try to simulate the field conditions in the laboratory and estimate the duration of each stage or even the growth rates at different temperatures. This approach is often criticized because it is very difficult to simulate all variables that affects the development rate in the field, however, it is recognized and accepted that temperature and food are the main factors that should be controlled (Landry, 1975a; 1975b; McLaren, 1978; Vidal, 1980a; 1980b; McLaren & Corkett, 1981).
- Another approach is the method elaborated by Rigler & Cooley (1974) where estimates of development times of field populations can be obtained from the mean pulse time of instar abundances from the field data.

However, due to the high degree of subjectivity needed in analysing the data, it becomes almost impossible to standardize and repeat the procedures.

- Alternatively, one can use any published specific development/growth-rates for each component/species, or use predictive generalist growth-rate equations from the literature.

4.2. Material and Methods.

The methodology employed for sampling, counting and identification of the different species/larval stages have been presented on Chapter 1.

4.2.1. Barnacle larvae weight measurements.

For Dry Weight (DW) determinations, between 25 – 4000 organisms of a particular size/stage, were sorted from the samples after at least 1 year of preservation, time necessary for the organisms to reach equilibrium volume and weight (Ahlstrom & Thrailkill, 1963; Beers, 1976; 1981b). Later, pre-counted batches of 50 – 1000 (Table 20) larvae were concentrated, and these larvae together with 200 – 400 µl, of the preserving fluid were pipetted onto 4 ml of de-ionised water for dilution of salt and preserving fluid. After repeating the dilution procedure a second time, the organisms were then pipetted into pre-weighed and ashed aluminium vessels of ± 200 µl capacity. After the animals have settled at the bottom of each container, the surrounding liquid was removed, as much as possible, with a fine pipette, taking care not to remove any animal. This material were then dried in an electric oven for 16-24 hours at 60 °C and transferred to silica gel desiccators for cooling (for at least 1 hour) before weighing (Lovegrove, 1966).

Table 20. Number (n^o) of naupliar stages utilized in each biomass determination, with rep. indicating the number of replicates made for each determination.

Stages	*E.modestus*		*B.crenatus*		*B.improvisus*		*S.balanoides*		*V.stroemia*	
	n^o	rep.	n^o	Rep.	n^o	rep.	n^o	rep.	n^o	rep.
N2	1000	4	1000	4	1000	2	700	3	1000	2
N3	800	4	500	4	800	2	265	2	356	2
N4	500	4	200	4	500	3	142	2	240	1
N5	200	4	100	4	200	4	100	4	90	1
N6	100	4	100	4	100	2	100	4	25	1
Cypris	100	2+2	50	2+2	25	1	50	4+1	-	-

Note: the + sign indicates that replicates with two different sizes where made

Blanks were made with ± 200 µl of the last dilution solution of four different batches, and they averaged ± 9.2% of the sample weights. Since the amount of surrounding liquid on each determination was variable, but always less than 200 µl, it was decided not

to apply any correction. Tests were also made to estimate the effect of preservation on weight loss so, the same procedure were also applied to freshly caught barnacles larvae of *E. modestus,* but due to the numbers needed only stages 5, 6 and Cypris were considered. The averaged weight of those stages obtained in replicate experiments indicated losses of 9 – 23 %. DW estimates for all species/stages were later corrected by the averaged weight loss value of 18.15% (±7.31).

After DW determination, samples were then placed in an electric muffle furnace and ashed at 500 °C (Beers, 1976; 1981b), for ±4 hours ((Kimmerer & McKinnon, 1987). After ashing, samples were placed on silica gel desiccators (for at least 1 hour) and then weighted (the same procedure was later repeated, with no difference being observed between ashings). The Ash Free Dry Weight (AFDW) were determined after subtracting the Ash Weight (AW) from the DW (AFDW = DW – AW). All weighing were performed on a Mettler MT 5 (±1 μg) scientific balance. The individual weights of each specie/stage in terms of Dry Weight (DW) were the averaged values of the replicates after the correction factor of 18.15% were applied. For AFDW the % of ash determined for the preserved animals was subtracted from the corrected DW. Differences between replicas varied and errors were calculated as a percentage of the mean and averaged for all determinations; during this work it was around ± 3.13 %.

4.2.2. Barnacle larvae size measurements.

When less than 10 specimens of any particular stage were present on the sub-sample, all specimens of that stage were measured, otherwise, at least 10 specimens of each species/stage present at each sub-sample from each station were measured with a micrometric scale (± 20 μm) attached to the Stereomicroscope eyepiece. The measurements taken can be seen on Figure 37, where:

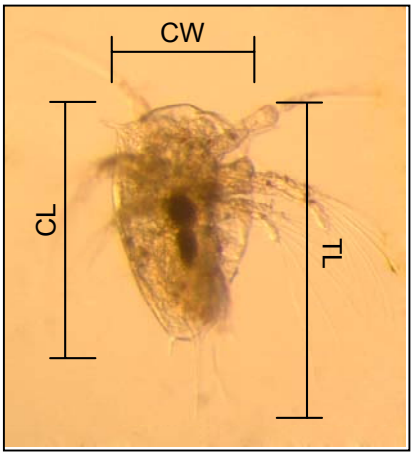


Figure 37. Nauplii 6 of *Balanus crenatus* showing the measurement axes.

TL = Total Length: measured from the anterior margin of the carapace to the end of the caudal spine.

CW = Carapace Width: or the widest section of the larvae.

CL = Carapace Length: measured from the anterior margin of the carapace to the tip of the carapace spines (carapace spines are only present after the third naupliar stage, i.e. nauplius 4 according to Lang (1979)).

4.2.3. Regression analysis.

To stabilize the variance of the data, weight and Chlorophyll *a* values were $\log_{10}$ transformed before being used in any analysis. Simple linear regressions and Backwards stepwise multiple regression analysis (F to enter = 4.0 and F to remove = 3.9) were calculated with STATISTICA for Windows. Regression graphs were drawn using SigmaPlot for Windows.

4.2.4. Development rates.

During this work, the development rates of each barnacle species were not directly measured, although the approximate duration of each larval stage in the field was estimated through the power function:

$$ln\ D = ln\ b + m\ ln\ T\ , \qquad (12)$$

Where: D = development rate in days; b and m are constant values obtained from Harms (1984; 1986) for *Elminius modestus* and *Semibalanus balanoides* and summarized in (Table 21), and T = thermal influence, i.e. field temperature in °C.

Since there is no specific data on the effect of temperature on the development rate of the other species, i.e. *Balanus crenatus*, *Balanus improvisus* and *Verruca stroemia* it was decided to use *E.modestus* values of b and m for *B.improvisus* and *S.balanoides* values of b and m for *B.crenatus* and *V.stroemia*, since those species occur at the same period (Chapter 3) and probably had similar development rates.

Table 21. Constant values needed in the power function to obtain development times of barnacles in the field (data from Harms, (1984; 1986)).

Species→	*E.modestus* and *B.improvisus*		*E.modestus* and *B.improvisus*		*S.balanoides* *B.crenatus* *V.stroemia*	
Reference	(Harms, 1986)		(Harms, 1984)		(Harms, 1984)	
Stage	b	m	b	m	b	m
II to III	158	-1.51	73.79	-1.261	16.278	-0.923
III to IV	176	-1.65	82.43	-1.489	15.185	-0.984
IV to V	147	-1.52	84.73	-1.424	8.97	-0.627
V to VI	235	-1.61	79.65	-1.249	8.687	-0.499
VI to Cypris	433	-1.63	140.55	-1.3	9.64	-0.349

4.2.5. Growth rates.

Growth rates were estimated using the general equations/methods proposed/used by Ikeda & Motoda (1978), Landry (1978), McLaren *et al*., (1989), Huntley & Boyd (1984), Huntley & Lopez (1992), Hirst & Sheader (1997), Hirst & Lampitt (1998) and Hirst *et al*. (2003). The set of equations employed are summarized on Table 22.

Table 22. Growth rate equations employed in the production estimates (Eq. a to h). Also shown are the equations used to estimate Production (Eq.8 and 9) and development (Eq. 12).

Eq.8→$\sum P = N_i*(w_{i+1} - w_i)/D_{i\rightarrow i+1}$

Eq.9→$\sum P = B*g$

Eq.12→$lnD = lnb + (m*lnT)$

	Growth Equation	taxon	Reference
a	$g=7.714*10^{[0.254*(T)-0.126]}*W_i^{(-0.0109+0.892)}*w_{ic}^{-1}$	all/copepods	(Ikeda & Motoda, 1978)
b	$g=(1/D)*\ln(w_{i+1}/w_i)$	all/copepods	(Landry, 1978)
c	$g=(w_{i+1}/w_i)^{1/D}-1$	all/copepods	(McLaren *et al*., 1989)
d	$g=0.0542*e^{0.110*(T)}$	all/copepods	(Huntley & Boyd, 1984)
e	$g=0.0445*e^{0.111*(T)}$	all/copepods	(Huntley & Lopez, 1992)
f	$Log_{10}(g)=-1.1355+[0.0246*(T)]-[0.2962*\log_{10}(w_{ic})]$	all/copepods	(Hirst & Sheader, 1997)
g	$Log_{10}(g)=-1.1408+[0.0208*(T)]-[0.3221*\log_{10}(w_{ic})]$	Br+S (adults+juveniles)	(Hirst & Lampitt, 1998)
h	$Log_{10}(g)=-1.529+[0.0345*(T)]-[0.128*\log_{10}(w_{ic})]$	Br+S (all Br+S)	(Hirst *et al*., 2003)

Where:
P = average production of a particular size class/stage in mg dry weight $m^{-3}d^{-1}$;
N_i= number of organisms m^{-3} at stage i;
w_i = the average dry weight at stage i (in µg $individual^{-1}$);
w_{i+1}= the average dry weight at stage i+1 (in µg $individual^{-1}$);
D = development rate in days;
B = biomass (i.e. N_i*w_i);
g = growth rate d^{-1};
b and m are constant values (Table 21);
W_i = the average dry weight at stage i (in mg dry weight $individual^{-1}$);
w_{ic} = the average carbon weight at stage i (in µg carbon $individual^{-1}$);
T = temperature in °C;
Br = Broadcast-spawners;
S = Sac-spawners.

4.2.6. Production.

Production of each barnacle larvae stage were calculated by the "increment-summation" and "instantaneous-growth" approaches described by equations 8 and 9 presented earlier, and also summarized in Table 22.

For the final annual production estimates, the calculated daily production and biomass of a particular larval stage for a sampling day was assumed to represent the mean over a time interval between two successive midpoints of the inter-sample period, and converted to carbon assuming the carbon: dry weight ratios obtained by Harms (1987) for each larval stage of *E.modestus*, and extrapolated for all the species found here (Table 23). Total annual production of a population will be equal to the sum of weight increments for all the stages throughout the year, excluding the non-feeding nauplius 1 (NI) and cypris.

4.3. Results.

The total composition and general contribution of each barnacle larvae in the mesozooplankton of Southampton Water has been already presented in Chapter 3. These results will now present the contribution of each larval stage of *E.modestus*, *B.crenatus*, *B.improvisus* and *V.stroemia* in terms of weight, length and total abundance necessary for the estimates of secondary production.

4.3.1. Weight-length.

The mean-weight values of the larval stages of the barnacle species found in Southampton Water are presented in Table 23, while the reported values from the literature can be seen in Appendix X.

Table 23. Mean weight values (μg) of the naupliar stages II to VI + cypris of the species considered. Also shown is the % of Ash and Carbon (C) considered for each stage, as well as the averaged body measurements of each larval stage used in the biomass analysis.

Stage	**CW** ± SD (n)	**TL** ± SD (n)	Average Weight (μg) **DW± SD (n)	Average Weight (μg) **AFDW**±SD (n)	**%Ash** ±SD	***%C** ± SD	**Species**
I	----	----	----	----	----	----	
II	156 ± 8.4 (10)	364 ± 15.8(10)	0.29 ± 0.01 (4)	0.24 ± 0.01 (4)	17.03 ± 6.25	43.31± 0.33*	
III	180 ± 0.0 (10)	390 ± 14.0(10)	0.49 ± 0.05 (4)	0.40 ± 0.04 (4)	17.88 ± 4.00	44.17± 5.24*	
IV	216 ± 8.4 (10)	428 ± 14.0(10)	0.77 ± 0.70 (4)	0.65 ± 0.06 (4)	15.25 ± 6.82	40.40± 3.42*	*Elminius modestus*
V	262 ± 6.3 (10)	478 ± 22.0(10)	1.20 ± 0.09 (4)	1.03 ± 0.08 (4)	13.61 ± 6.41	39.37± 2.22*	
VI	314 ± 9.8 (7)	537 ± 13.8 (7)	2.23 ± 0.05 (4)	1.90 ± 0.04 (4)	14.57 ± 7.74	44.69± 5.53*	
Cypris	----	530 ± 10.9 (6)	3.34 ± 0.04 (2)	3.30 ± 0.05 (2)	1.06 ± 0.74	51.94± 4.54*	
	----	666 ± 25.0(10)	7.46 ± 0.21 (2)	7.10 ± 0.20 (2)	0.05 ± 2.11	51.94± 4.54*	
I	----	----	----	----	----	----	
II	164 ± 8.4 (10)	438 ± 11.4(10)	0.46 ± 0.01 (4)	0.41 ± 0.01 (4)	11.03 ± 6.27	43.31± 0.33*	
III	196 ± 8.4 (10)	486 ± 25.0(10)	0.74 ± 0.05 (4)	0.63 ± 0.05 (4)	14.13 ± 3.68	44.17± 5.24*	
IV	250 ± 10.5 (10)	580 ± 16.3(10)	1.48 ± 0.04 (4)	1.18 ± 0.03 (4)	20.30 ± 1.97	40.40± 3.42*	*Balanus crenatus*
V	316 ± 12.6 (10)	682 ± 14.8(10)	2.70 ± 0.04 (4)	2.21 ± 0.03 (4)	18.02 ± 4.73	39.37± 2.22*	
VI	396 ± 15.8 (10)	800 ± 29.8(10)	5.47 ± 0.58 (4)	4.27 ± 0.45 (4)	21.90 ± 9.59	44.69± 5.53*	
Cypris	----	854 ± 14.0(10)	11.49±0.20 (2)	11.15 ± 0.20 (2)	3.01 ± 2.82	51.94± 4.54*	
	----	650 ± 42.4(10)	6.50 ± 0.01 (2)	6.19 ± 0.01 (2)	4.73 ± 3.61	51.94± 4.54*	
I	----	----	----	----	----	----	
II	144 ± 8.4 (10)	318 ± 14.8(10)	0.27 ± 0.03 (2)	0.20 ± 0.02 (2)	25.05 ± 3.85	43.31± 0.33*	
III	180 ± 0.0 (10)	354 ± 19.0(10)	0.46 ± 0.00 (2)	0.36 ± 0.00 (2)	20.46 ± 0.01	44.17± 5.24*	
IV	222 ± 6.7 (9)	416 ± 15.8(10)	0.76 ± 0.03 (3)	0.62 ± 0.02 (3)	18.90 ± 4.00	40.40± 3.42*	*Balanus improvisus*
V	294 ± 13.5 (10)	493 ± 10.4 (9)	1.42 ± 0.06 (4)	1.18 ± 0.05 (4)	17.12 ± 0.75	39.37± 2.22*	
VI	380 ± 0.0 (10)	600 ± 0.0 (10)	2.87 ± 0.25 (2)	2.34 ± 0.21 (2)	18.44 ± 4.34	44.69± 5.53*	
Cypris	----	530 ± 0.0 (10)	4.90 (1)	3.88 (1)	20.69	51.94± 4.54*	
I	----	----	----	----	----	----	
II	196 ± 8.4 (10)	472 ± 19.3(10)	0.69 ± 0.02 (3)	0.56 ± 0.02 (3)	18.23 ± 2.29	43.31± 0.33*	
III	230 ± 16.7 (6)	557 ± 23.4 (6)	1.11 ± 0.06 (2)	0.86 ± 0.05 (2)	22.37 ± 4.13	44.17± 5.24*	
IV	313 ± 10.4 (8)	678 ± 22.5 (8)	2.47 ± 0.15 (2)	2.01 ± 0.12 (2)	18.97 ± 1.02	40.40± 3.42*	*Semibalanus balanoides*
V	398 ± 35.8 (10)	798 ± 61.4(10)	5.56 ± 0.51 (4)	4.49 ± 0.42 (4)	19.22 ± 5.42	39.37± 2.22*	
VI	505 ± 38.2 (8)	1008 ± 42.7 (8)	10.41 ± 0.23 (4)	8.51 ± 0.18 (4)	18.31 ± 2.39	44.69± 5.53*	
Cypris	----	797 ± 29.2 (7)	9.79 ± 0.37 (4)	9.21 ± 0.35 (4)	5.93 ± 2.47	51.94± 4.54*	
	----	930 ± 49.2(10)	23.19 (1)	21.80 (1)	6.01	51.94± 4.54*	
I	----	----	----	----	----	----	
II	180 ± 0.0 (10)	408 ± 10.3(10)	0.33 ± 0.03 (2)	0.25 ± 0.03 (2)	25.17 ± 6.76	43.31± 0.33*	
III	204 ± 15.8 (10)	452 ± 27.0(10)	0.49 ± 0.02 (2)	0.37 ± 0.01 (2)	23.20 ± 2.17	44.17± 5.24*	
IV	242 ± 17.5 (10)	468 ± 23.5(10)	0.79 (1)	0.55 (1)	30.00	40.40± 3.42*	*Verruca stroemia*
V	297 ± 19.7 (6)	545 ± 25.2 (4)	1.32 (1)	1.15 (1)	12.94	39.37± 2.22*	
VI	360 ± 30.6 (3)	660 ± 30.6 (3)	3.06 (1)	2.50 (1)	18.18	44.69± 5.53*	
Cypris	----	----	----	----	----	----	

Where: DW = Dry Weight; AFDW = Ash Free Dry Weight; CW = Carapace width (μm); TL = Total length (μm); C = carbon;
SD = ±1 Standard Deviation; ---- = not available; n = number of organisms measured/ or replicates (the n° of larvae utilized for each weight replica in this work can be seen on Table 20).
* %C values used were obtained from Harms (1987) after averaging the results of different temperatures/experiments.
**Values of DW were obtained after applying a correction factor of 18.15% due to formalin preservation.

During this study a total of 15974 size measurements were taken from 3277 *E.modestus*, 1706 *B.crenatus*, 786 *B.improvisus*, 771 *S.balanoides* and 344 *V.stroemia*. The total averaged value for total length, carapace length and width of these species for each stage for the three stations can be seen on Table 24, while the reported values from the literature can be seen in Appendix IX a,b,c,d,e.

Table 24. Total length, carapace length and width of the naupliar stages I to VI + cypris of the barnacle species considered. (All measurements in μm)

Stage	Carapace						Species
	Width ± SD	(n)	Length ± SD	(n)	Total Length ± SD	(n)	
I	123 ± 7	(70)	----		242 ± 22	(70)	*Elminius modestus*
II	157 ± 13	(1033)	----		392 ± 33	(1033)	
III	187 ± 14	(732)	----		421 ± 39	(732)	
IV	222 ± 18	(538)	299 ± 22	(538)	451 ± 45	(533)	
V	271 ± 21	(440)	359 ± 27	(441)	500 ± 53	(433)	
VI	328 ± 23	(339)	436 ± 28	(341)	565 ± 54	(330)	
Cypris	----		----		553 ± 53	(122)	
I	144 ± 9	(63)	----		274 ± 21	(63)	*Balanus crenatus*
II	172 ± 12	(609)	----		433 ± 28	(609)	
III	203 ± 11	(342)	----		502 ± 25	(339)	
IV	247 ± 13	(254)	404 ± 22	(254)	575 ± 28	(249)	
V	311 ± 19	(199)	502 ± 30	(199)	679 ± 39	(198)	
VI	397 ± 29	(165)	635 ± 47	(165)	814 ± 54	(161)	
Cypris	----		----		779 ± 78	(74)	
I	139 ± 22	(16)	----		285 ± 59	(16)	*Balanus improvisus*
II	148 ± 12	(282)	----		316 ± 26	(281)	
III	181 ± 12	(188)	----		356 ± 27	(187)	
IV	227 ± 20	(144)	311 ± 27	(145)	412 ± 37	(137)	
V	289 ± 27	(77)	392 ± 33	(77)	492 ± 50	(78)	
VI	369 ± 27	(71)	502 ± 29	(71)	621 ± 48	(65)	
Cypris	----		----		523 ± 20	(6)	
I	179 ± 17	(22)	----		319 ± 28	(22)	*Semibalanus balanoides*
II	203 ± 11	(286)	----		475 ± 28	(286)	
III	238 ± 13	(157)	----		562 ± 30	(156)	
IV	298 ± 15	(89)	446 ± 22	(89)	662 ± 38	(84)	
V	385 ± 22	(96)	556 ± 31	(96)	795 ± 40	(79)	
VI	503 ± 33	(78)	725 ± 51	(79)	990 ± 66	(76)	
Cypris	----		----		835 ± 81	(42)	
I	140 ± 28	(2)	----		280	(2)	*Verruca stroemia*
II	180 ± 9	(170)	----		412 ± 36	(169)	
III	212 ± 13	(116)	----		456 ± 34	(114)	
IV	256 ± 21	(37)	297 ± 26	(37)	500 ± 37	(29)	
V	311 ± 18	(15)	371 ± 27	(15)	590 ± 44	(12)	
VI	353 ± 31	(3)	427 ± 23	(3)	653 ± 31	(3)	
Cypris	----		----		480	(1)	

Where: SD = ±1 Standard Deviation; n = number of organisms measured/ or replicas; ---- = Value/measure not available.

Considering the seasonal variation of the total length and breadth of each naupliar stage of each species, presented on Figures 38, 39, 40, 41, 42 and 43, it can be seen that the total length and carapace width of naupliar stages II to VI of *E.modestus, B.crenatus* and *B.improvisus* were usually bigger during winter and spring when compared with sizes found latter in the season or during the summer (Figures 38, 39, 40). *S.balanoides* and *V.stroemia,* in contrast, did not show any consistent change in total length and carapace width, except for some of the later stages (Figures 41, 42). With the exception of *Elminius*

modestus cyprids that also showed a decrease in size towards summer, none of the remaining species showed any seasonal trend (Figure 43).

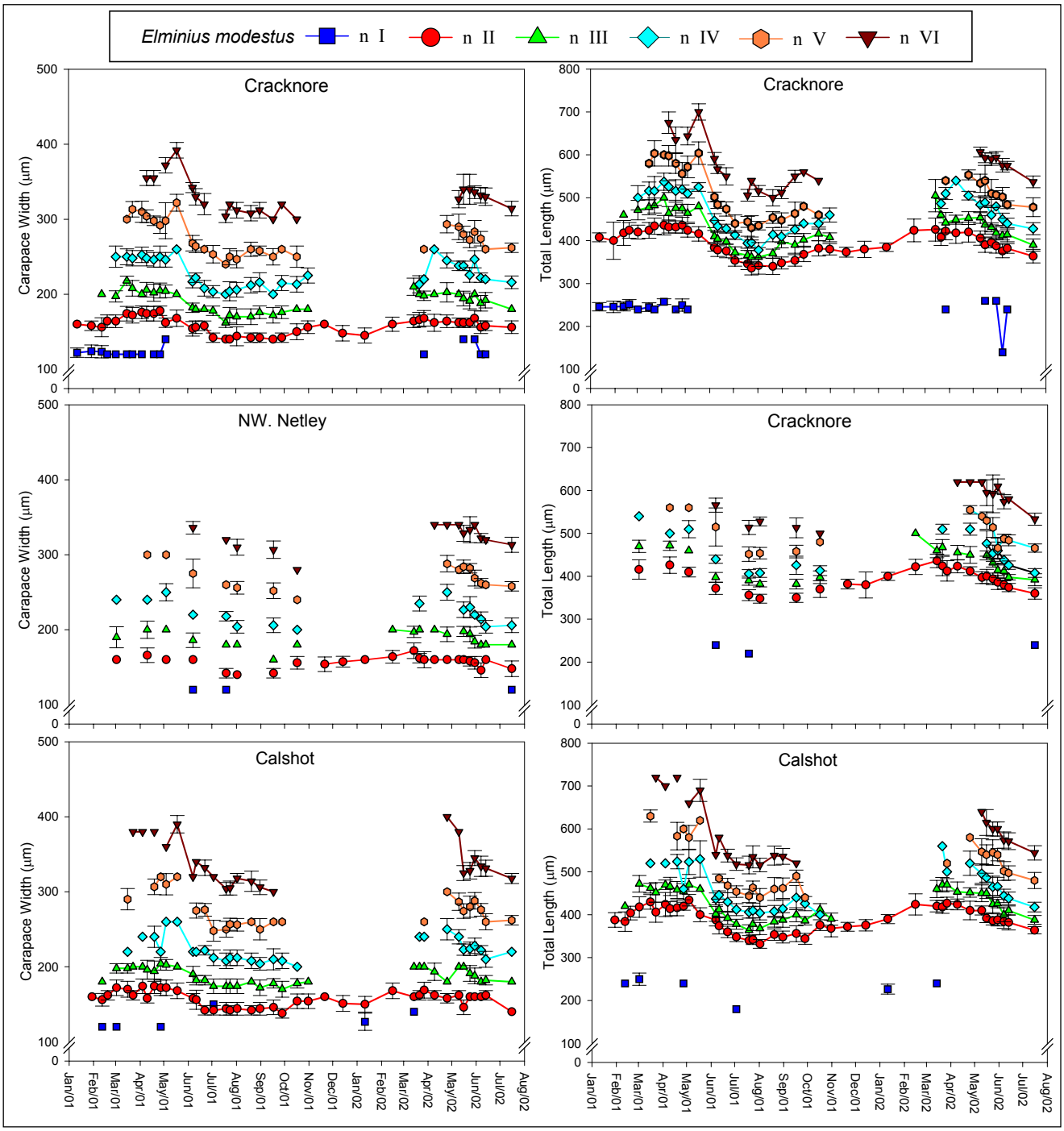


Figure 38. Seasonal changes in mean carapace width (left) and total length (right) of naupliar stages I to VI of *Elminius modestus* in Southampton Water in the three stations during 2001/02. (Error bars = ±1 Standard Deviation (SD), lines are only given when individuals were caught in consecutive samples).

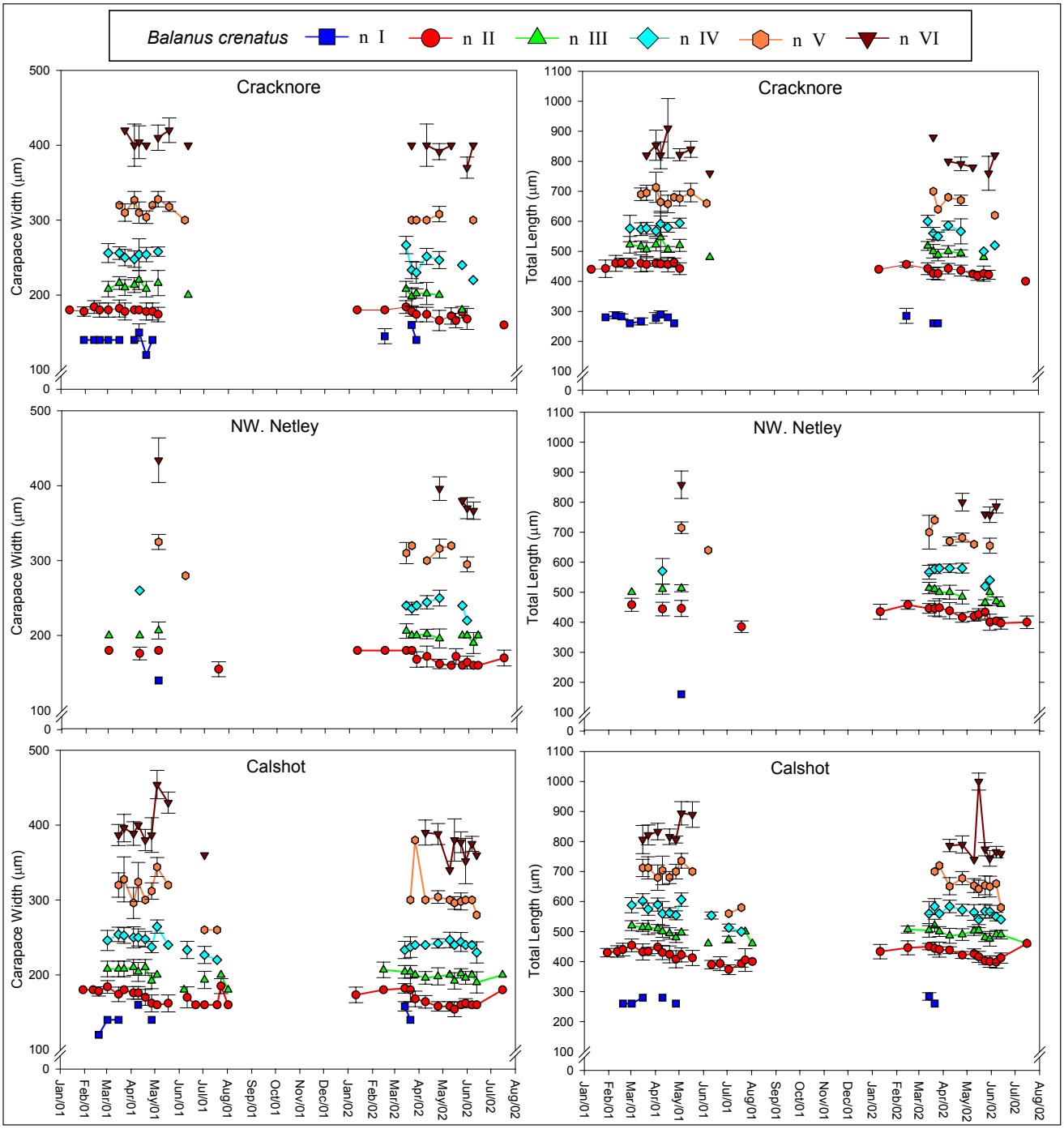


Figure 39. Seasonal changes in mean carapace width (left) and total length (right) of naupliar stages I to VI of *Balanus crenatus* in Southampton Water in the three stations during 2001/02. (Error bars = ±1 Standard Deviation (SD), lines are only given when individuals were caught in consecutive samples).

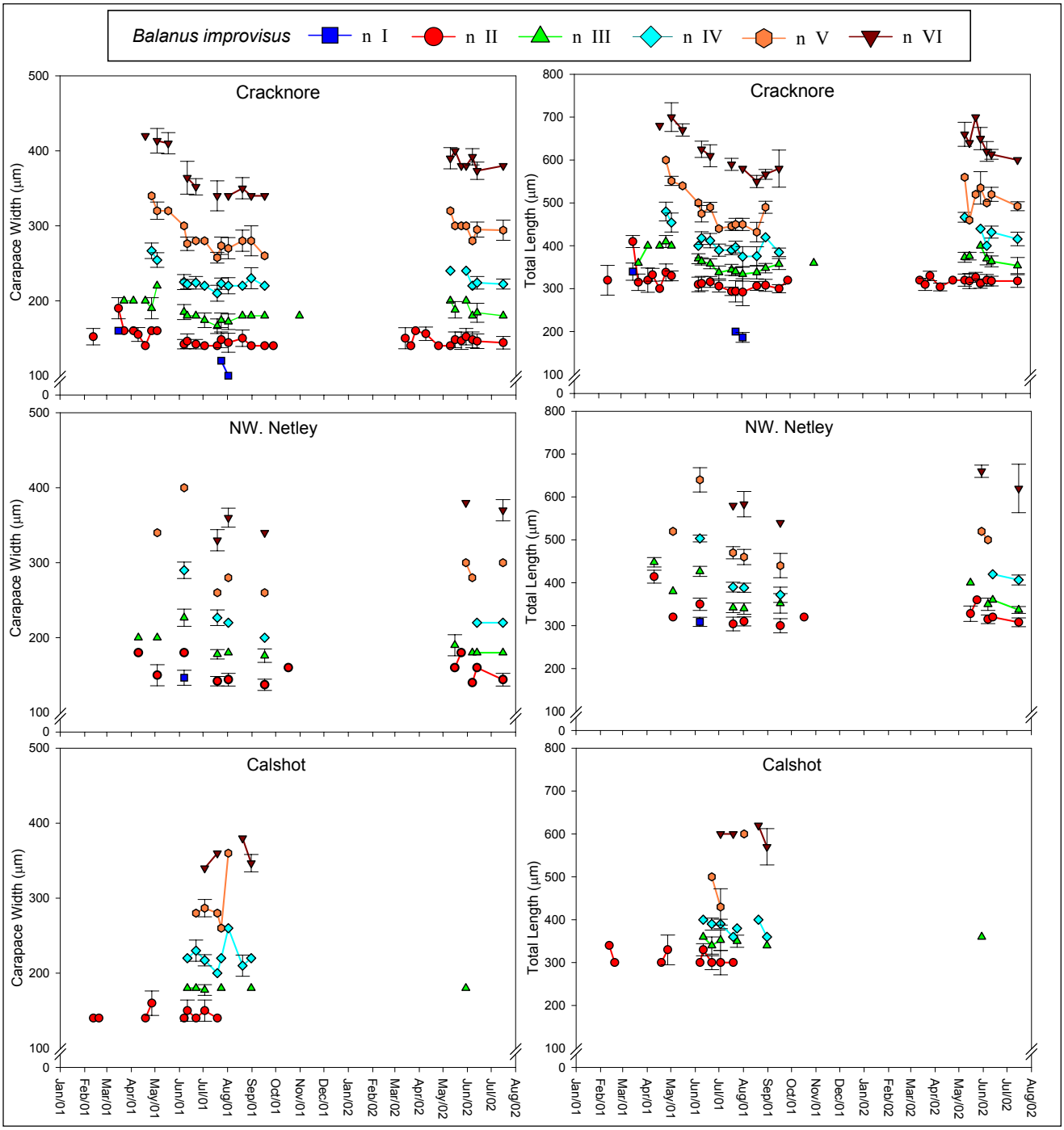


Figure 40. Seasonal changes in mean carapace width (left) and total length (right) of naupliar stages I to VI of *Balanus improvisus* in Southampton Water in the three stations during 2001/02. (Error bars = ±1 Standard Deviation (SD), lines are only given when individuals were caught in consecutive samples).

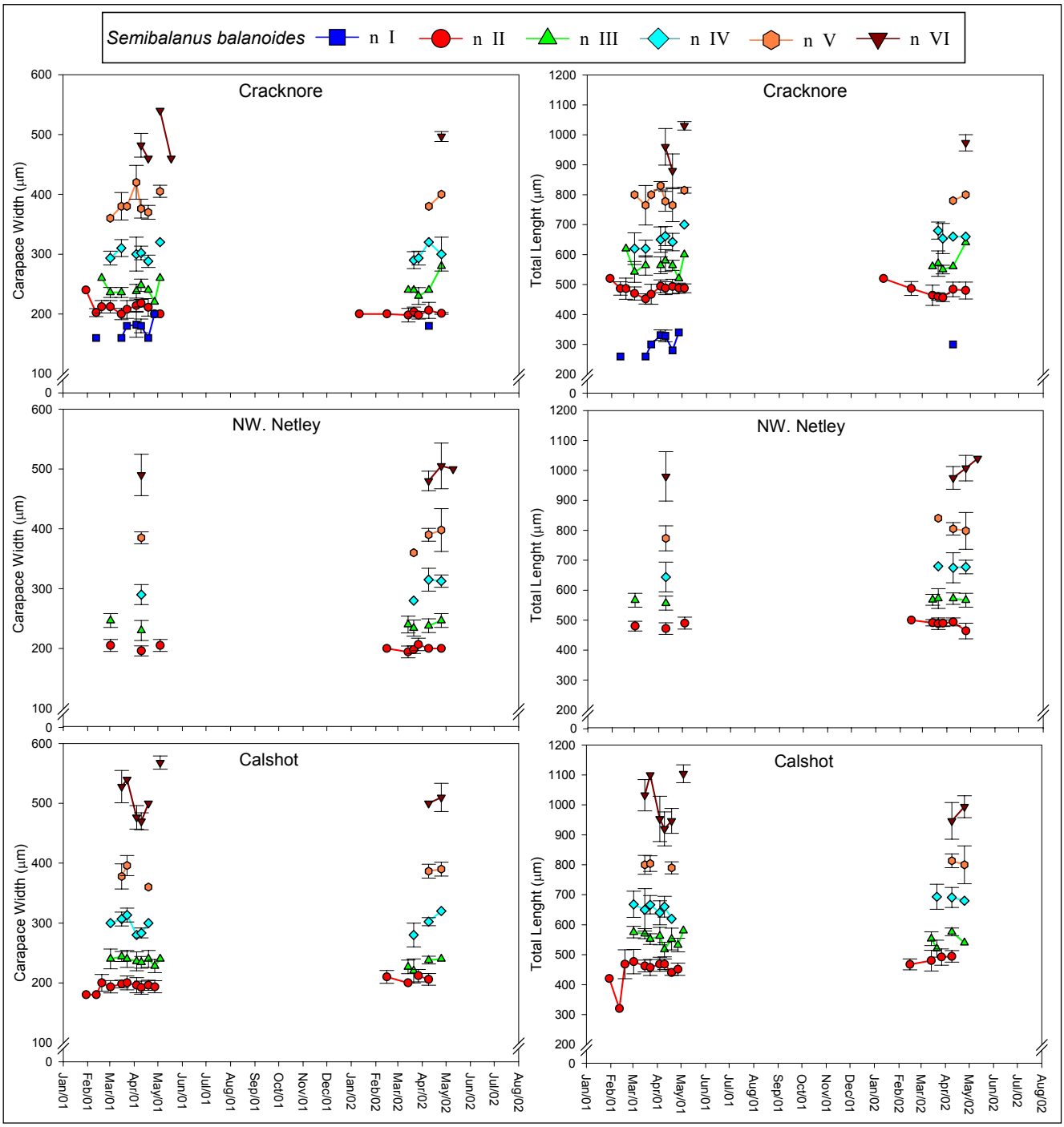


Figure 41. Seasonal changes in mean carapace width (left) and total length (right) of naupliar stages I to VI of *Semibalanus balanoides* in Southampton Water in the three stations during 2001/02. (Error bars = ±1 Standard Deviation (SD), lines are only given when individuals were caught in consecutive samples).

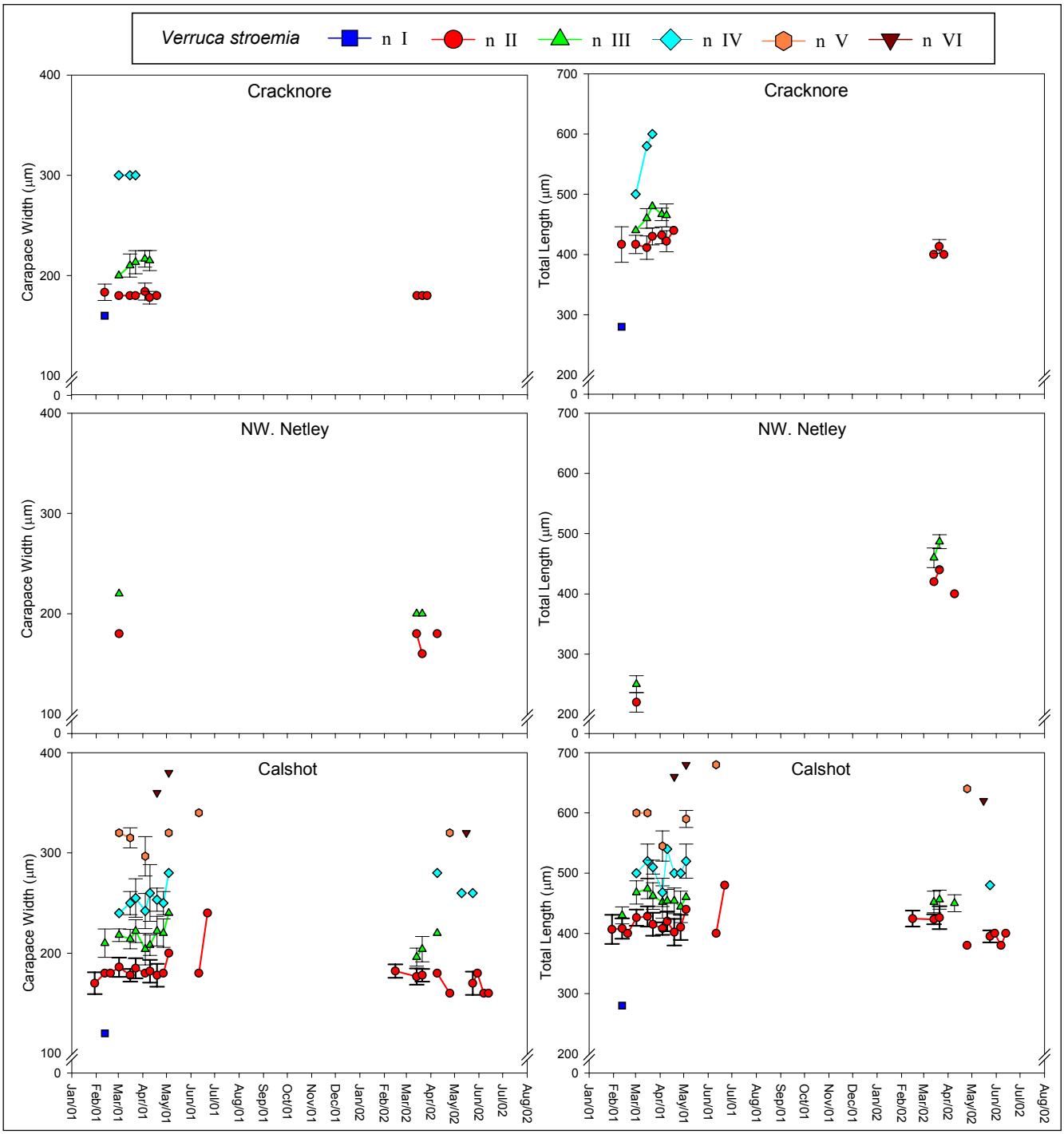


Figure 42. Seasonal changes in mean carapace width (left) and total length (right) of naupliar stages I to VI of *Verruca stroemia* in Southampton Water in the three stations during 2001/02. (Error bars = ±1 Standard Deviation (SD), lines are only given when individuals were caught in consecutive samples).

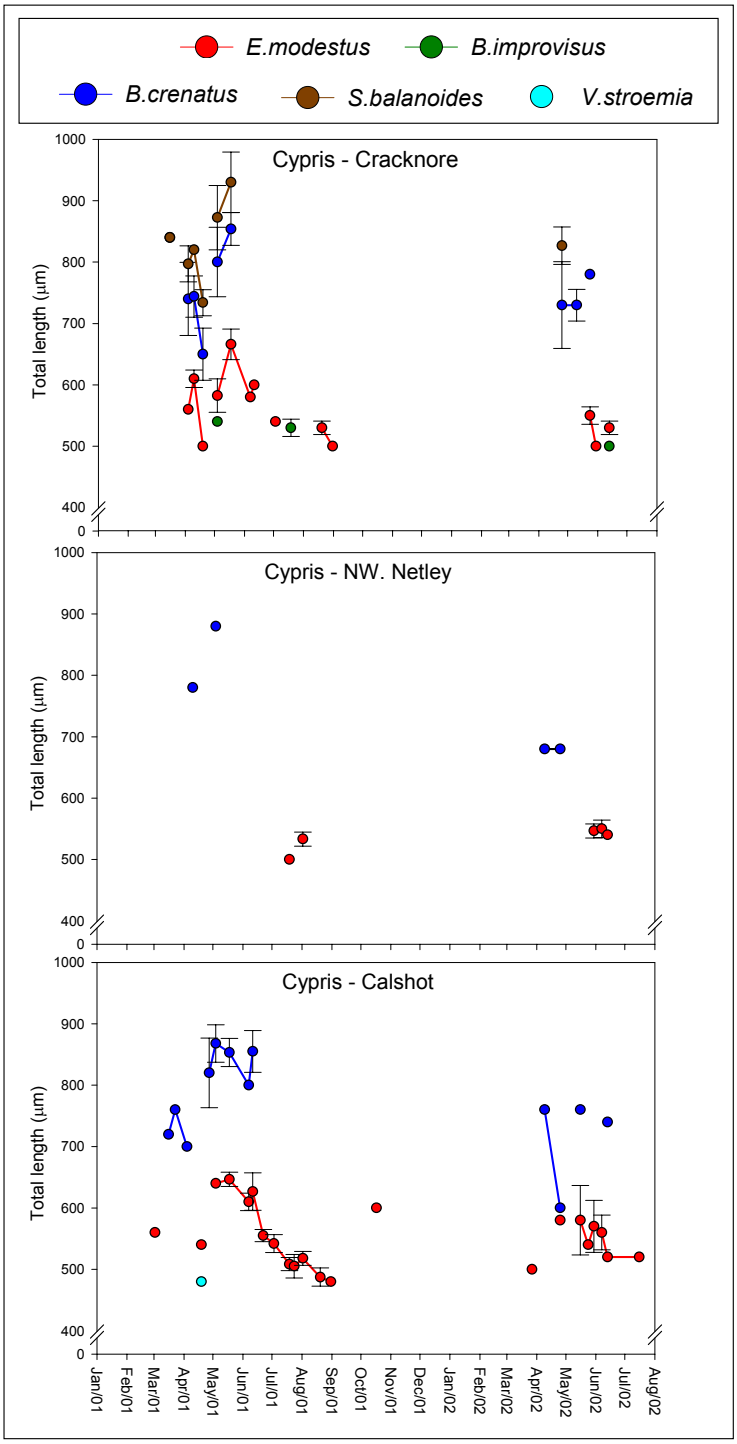


Figure 43. Seasonal changes in mean total length of the cyprids of the barnacles found in Southampton Water in the three stations during 2001/02. (Error bars = ±1 Standard Deviation (SD), lines are only given when individuals were caught in consecutive samples).

The decrease of total length and carapace width of *E.modestus*, *B.crenatus* and *B.improvisus* towards the summer suggests that an inverse relationship between these two measures, with some seasonal environmental forcing parameter, so in order to better evaluate this the average of both measures were regressed against temperature, salinity and chlorophyll a and the results presented in Table 25.

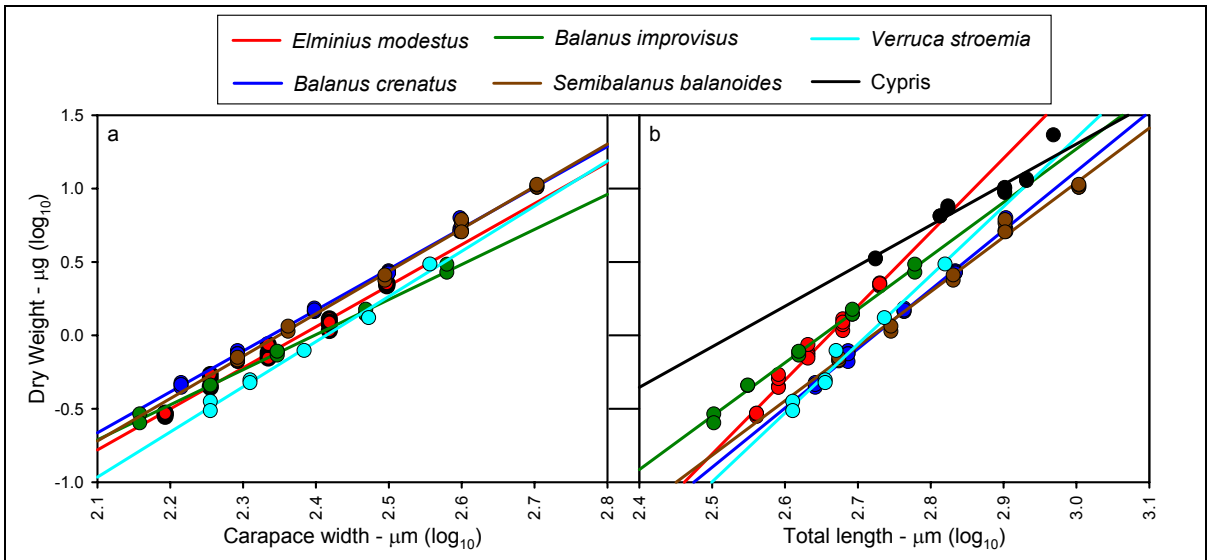
Table 25. Results of the Backwards stepwise multiple regression analysis (F to enter = 4.0 and F to remove = 3.9) between Total Length and Carapace Width of naupliar stages I to VI + cypris of each barnacle species considered with Temperature (T), Salinity (S) and Chlorophyll (C) concentration (equations in red considered all parameters, but only shows those parameters that added significantly to the prediction). Also shown are the results between the two measures with temperature (in black). All equations shown are significant at 5%.

stage	Carapace Width Equation		r^2	n	Total Length Equation		r^2	n
Elminius modestus								
n I	-	ns	-	25	r11	TL=262.0-2.39*T	0.17	25
n II	r1	CW=176.9-1.56*T	0.44	107	r12	TL=458.2-5.34*T	0.63	107
	r2	CW=181.7-2.15*T+7.76*C	0.49		r13	TL=532.6-6.47*T-2.14*S+19.35*C	0.69	
n III	r3	CW=221.0- 2.39*T	0.64	89	r14	TL=541.4- 8.46*T	0.82	89
	r4	CW=249.9-2.61*T-0.91*S+5.93*C	0.67		r15	TL=546.5-9.21*T+11.81*C	0.83	
n IV	r5	CW=273.6- 3.42*T	0.56	77	r16	TL=617.7-11.03*T	0.83	77
	r6	CW=279.1-4.25*T+13.00*C	0.61		r17	TL=624.1-12.00*T+15.08*C	0.84	
n V	r7	CW=343.3- 4.74*T	0.63	68	r18	TL=709.8-13.69*T	0.82	68
	r8	CW=349.3-5.85*T+19.61*C	0.72		r19	TL=623.9-16.26*T+3.42*S+32.36*C	0.86	
n VI	r9	CW=425.9- 6.20*T	0.59	59	r20	TL=826.4-16.28*T	0.82	58
	r10	CW=429.0-7.29*T+23.77*C	0.68		r21	TL=830.3-17.57*T+27.43*C	0.84	
cypris	-	-	-	-	r22	TL=629.1- 5.15*T	0.17	40
					r23	TL=638.4-9.01*T+80.65*C	0.57	
Balanus crenatus								
n I	-	ns	-	20	-	ns	0.11	20
n II	r24	CW=188.52- 1.513*T	0.44	74	r31	TL=477.1- 4.23*T	0.57	74
	r25	CW=207.9-0.81*T-0.83*S-7.29*C	0.51		r32	TL=553.6-3.59*T-2.70*S	0.62	
n III	r26	CW=218.6- 1.54*T	0.42	51	-	ns	0.07	51
					r33	TL=2410.4-65.94*S	0.64	
n IV	r27	CW=266.9- 2.14*T	0.37	45	r34	TL=629.7-5.92*T	0.54	44
					r35	TL=648.1-8.65*T-43.38*C	0.64	
n V	r28	CW=355.3- 4.17*T	0.37	42	r36	TL=789.0-10.21*T	0.60	42
	r29	CW=366.0-5.8*T+22.39*C	0.44		r37	TL=809.9-13.50*T+44.12*C	0.68	
n VI	-	ns	-	35	r38	TL=914.2-8.59*T	0.17	33
	r30	CW=2070.1-51.01*S	0.51					
cypris	-	-	-	-	-	ns	-	25
					r39	TL=1214.9+101.20*C	0.23	
Balanus improvisus								
n I	ns	ns	-	4	-	ns	-	4
n II	r40	CW=163.6- 0.98*T	0.11	52	r46	TL= 352.2-2.39*T	0.17	52
	r41	CW=219.1-2.17*S	0.11					
n III	r42	CW=223.6- 2.45*T	0.46	38	r47	TL= 453.8-5.60*T	0.55	38
n IV	r43	CW=281.6- 3.22*T	0.21	31	r48	TL= 556.9-8.87*T	0.48	30
n V	r44	CW=375.0- 4.94*T	0.21	33	r49	TL= 656.0-9.61*T	0.30	29
n VI	r45	CW=480.0- 6.82*T	0.63	26	r50	TL= 804.8-11.52*T	0.63	26
cypris	-	ns	-	-	-	ns	-	3
Semibalanus balanoides								
n I	-	ns	-	8	-	ns	-	8
	r51	CW=166.2+89.39*C	0.48		r55	TL=279.1+206.55*C	0.54	
n II	-	ns	-	41	-	ns	-	41
	r52	CW=261.1-1.96*S	0.16					
n III	-	ns	-	31	-	ns	-	31
	r53	CW=296.1+26.62*C	0.17					
n IV	-	ns	-	23	r56	TL=605.6+5.93*T	0.20	23
	r54	CW=377.5+35.93*C	0.20		r57	TL=449.8+5.36*S	0.29	
n V	-	ns	-	18	-	ns	-	18
n VI	-	ns	-	17	-	ns	-	16
cypris	-	ns	-	-	-	ns	-	9
					r58	TL=805.6+92.97*C	0.46	
Verruca stroemia								
n I	-	-	-	-	-	-	-	-
n II	-	ns	-	36	-	ns	-	35
n III	-	ns	-	20	-	ns	-	20
	r59	CW=210.4+20.85*C	0.20					
n IV	-	ns	-	14	-	ns	-	12
	r60	CW=466.68-6.42*S	0.43		r61	TL=921.8-13.10*S	0.58	
n V	-	ns	-	6	-	ns	-	6
n VI	-	ns	-	3	-	ns	-	3
cypris	-	-	-	-	-	-	-	-

Where: ns = not significant with temperature or any other variable (if the case); CW = carapace width (μm); TL = total length (μm); T = temperature (°C); S = Salinity; C = Chlorophyll *a* $\log_{10}$ (mg m^{-3}); r^2 = determination coefficient; p = significance level; n = number of observations; - = indicates that no data were available; r 1 to 61 indicates the number of the resulting equation

On a general basis, the regression analysis between total-length and carapace-width with the environmental variables confirmed the strong relationship of temperature in the sizes of *E.modestus*, *B.crenatus* and *B.improvisus*, but also indicated that salinity and chlorophyll *a* are also important for some stages of these species. Usually for the three species, both size measurements were negatively related with temperature and salinity and positively with chlorophyll. *S.balanoides* and *V.stroemia* did not show any relationship with temperature, but chlorophyll and salinity did have some significant influence in the sizes of some stages (Table 25).

In order to be able to predict the weight of each larval stage, at each sampling day, the average width and length of the animals used in the weight analysis were recorded (Table 23), and length-weight and width-weight relationships were established using all data available (Figure 44).



	Equation	r^2	significance	n	Species
r62	$Log_{10}(DW) = -6.655+2.797*log_{10}(CW)$	0.987	p<0.01	20	*Elminius modestus*
r63	$Log_{10}(DW) = -13.401+5.038*log_{10}(TL)$	0.985	p<0.01	20	
r64	$Log_{10}(DW) = -6.513+2.786*log_{10}(CW)$	0.996	p<0.01	20	*Balanus crenatus*
r65	$Log_{10}(DW) = -10.991+4.037*log_{10}(TL)$	0.996	p<0.01	20	
r66	$Log_{10}(DW) = -5.729+2.389*log_{10}(CW)$	0.995	p<0.01	13	*Balanus improvisus*
r67	$Log_{10}(DW) = -9.653+3.641*log_{10}(TL)$	0.995	p<0.01	13	
r68	$Log_{10}(DW) = -6.788+2.890*log_{10}(CW)$	0.997	p<0.01	15	*Semibalanus balanoides*
r69	$Log_{10}(DW) = -10.105+3.716*log_{10}(TL)$	0.988	p<0.01	15	
r70	$Log_{10}(DW) = -7.428+3.078*log_{10}(CW)$	0.989	p<0.01	7	*Verruca stroemia*
r71	$Log_{10}(DW) = -12.713+4.686*log_{10}(TL)$	0.980	p<0.01	7	
r72	$Log_{10}(DW) = -6.985+2.763*log_{10}(TL)$	0.926	p<0.01	13	Cypris

Figure 44. Regression analysis between Dry Weight values with Carapace Width (**a**) and also with Total Length (**b**) measurements. Regression equations are also shown. Where DW = Dry Weight (µg individual^{-1}); CW = Carapace Width (µm individual^{-1}); TL = Total Length (µm individual^{-1}); r^2 = coefficient of determination; n = number of data points and r 62 to 72 indicates the number of the resulting equation.

On a general basis both measures were highly positively correlated with dry weight values, with carapace width giving slightly stronger correlations. So, the seasonal overall decrease in size observed for some species also means an overall decrease in weight.

4.3.2. Abundance, biomass and production.

4.3.2.1. *Elminius modestus.*

During this investigation all stages of *Elminius modestus* were found at the three stations, with naupliar stage 2 present throughout the year and the most abundant, averaging 50 % of all *E.modestus* nauplii encountered (Figure 45).

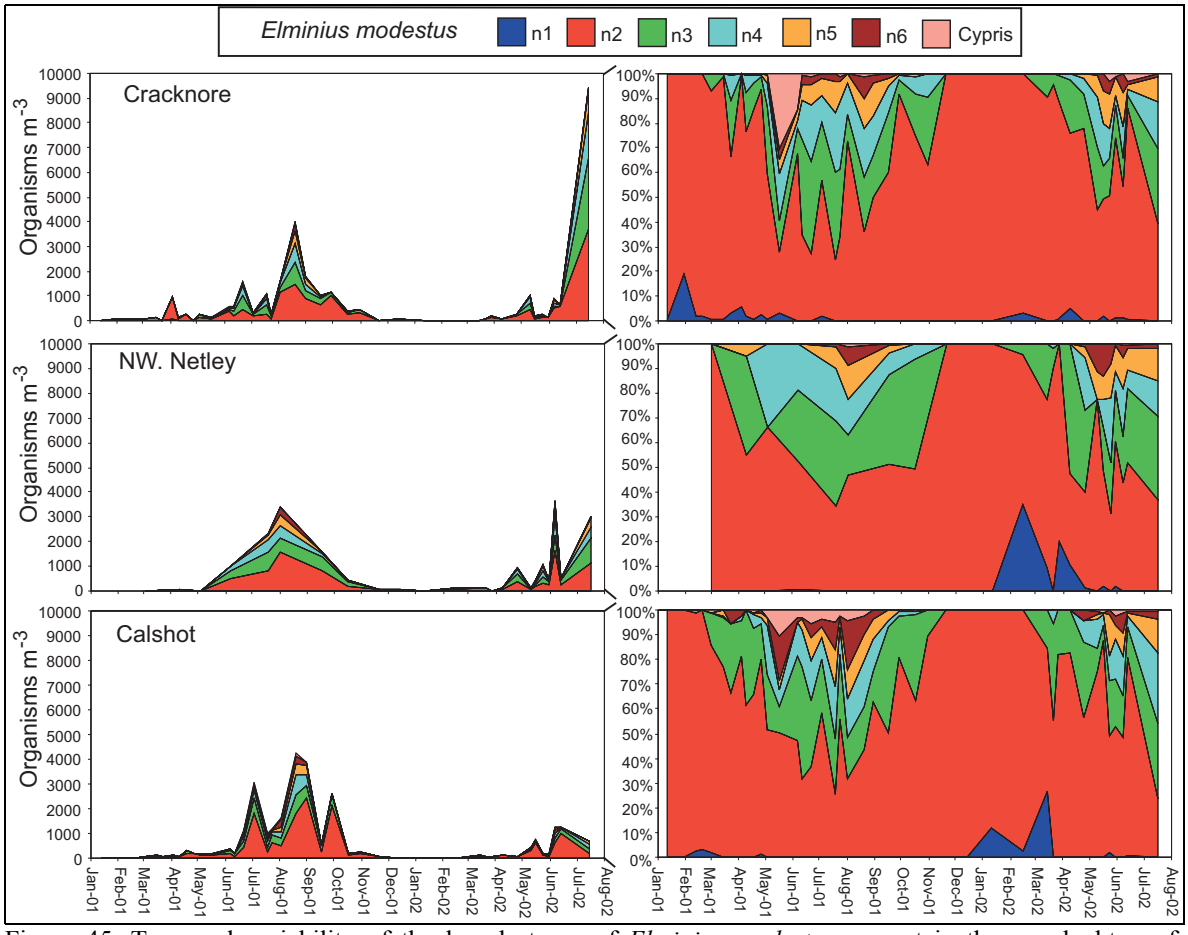


Figure 45. Temporal variability of the larval stages of *Elminius modestus* present in the zooplankton of Southampton Water during 2001/02.

Older stages were found as early as March, but they only contributed significantly in numbers from May to November (Figure 45). Apart from a massive burst in July 2002 at Cracknore, the abundance of *E.modestus* was usually quite homogeneous at the three stations.

There was a clear seasonal variation in the biomass of *E.modestus*, with highest values found during summer-autumn and lowest during winter (Figure 46). Total biomass of *E.modestus* for the period, was 99.61, 96.15 and 85.77 mg C m^{-3} at Cracknore, NW. Netley and Calshot respectively.

Based on the temporal variability of the abundance and biomass values, the production of *Elminius modestus* for the three stations over the period studied was also calculated (Table 26), and its daily variability can be seen on Figure 46. In terms of stage contribution, nauplii 2, 3 and 4 together accounted for ~72% of the production.

Table 26. Production estimates of each larval stage of *Elminius modestus* obtained using the respective equations summarized in Table 22. (all refer to total production in terms of mg C m^{-3}; and year is the annual production in terms of mg C $m^{-3}yr^{-1}$). Production using Harms (1986) data on Eq. 12 is highlighted in red.

Elminius modestus – Cracknore												
	Nauplii 2		**Nauplii 3**		**Nauplii 4**		**Nauplii 5**		**Nauplii 6**		**Total**	
Equation	all	year	all	year	all	year	all	year	all	year	all	year
Eq.8+12	7.36	4.78	11.52	7.48	10.2	6.63	5.44	3.53	2.09	1.35	36.62	23.78
Eq. 9+a	10.48	6.80	7.44	4.83	7.26	4.71	5.66	3.68	2.59	1.68	33.43	21.71
Eq.9+12+b	5.70	3.70	8.74	5.68	7.66	4.97	4.14	2.69	1.59	1.03	27.83	18.08
Eq.9+12+c	6.44	4.18	11.22	7.29	9.43	6.12	4.70	3.05	1.73	1.12	33.51	21.76
Eq.9+d	9.06	5.88	7.40	4.81	7.70	5.00	6.90	4.48	4.18	2.72	35.24	22.89
Eq.9+e	7.57	4.92	6.19	4.02	6.43	4.18	5.77	3.75	3.50	2.27	29.46	19.13
Eq.9+f	9.14	5.94	6.24	4.05	5.65	3.67	4.30	2.79	2.14	1.39	27.47	17.84
Eq.9+g	8.22	5.34	5.50	3.57	4.91	3.19	3.69	2.40	1.80	1.17	24.13	15.67
Eq.9+h	3.82	2.48	2.88	1.87	2.81	1.83	2.35	1.53	1.31	0.85	13.17	8.56
Eq.8+12	6.94	4.51	8.59	5.58	7.76	5.04	5.26	3.41	1.77	1.15	30.32	19.69
Eq.9+12+b	5.38	3.49	6.52	4.23	5.83	3.78	4.00	2.60	1.35	0.88	23.08	14.98
Eq.9+12+c	6.04	3.93	7.84	5.09	6.82	4.43	4.52	2.94	1.45	0.94	26.67	17.33
Average	7.18	4.66	7.51	4.88	6.87	4.46	4.73	3.07	2.13	1.38	28.41	18.45

Elminius modestus – NW. Netley												
	Nauplii 2		**Nauplii 3**		**Nauplii 4**		**Nauplii 5**		**Nauplii 6**		**Total**	
Equation	all	year	all	year	all	year	all	year	all	year	all	year
Eq.8+12	7.69	5.58	11.52	8.36	9.86	7.15	6.06	4.40	2.89	2.10	38.02	27.59
Eq. 9+a	9.16	6.65	8.13	5.90	6.51	4.73	6.08	4.41	3.62	2.63	33.51	24.32
Eq.9+12+b	5.63	4.09	8.83	6.41	7.26	5.27	4.55	3.30	2.20	1.59	28.47	20.66
Eq.9+12+c	6.61	4.80	10.95	7.94	9.05	6.56	5.21	3.78	2.40	1.74	34.21	24.83
Eq.9+d	7.59	5.51	8.14	5.91	6.85	4.97	7.22	5.24	5.77	4.18	35.58	25.82
Eq.9+e	6.34	4.60	6.80	4.94	5.73	4.16	6.04	4.38	4.83	3.50	29.74	21.58
Eq.9+f	7.86	5.70	7.10	5.15	5.21	3.78	4.51	3.27	2.87	2.08	27.55	19.99
Eq.9+g	7.07	5.13	6.29	4.56	4.56	3.31	3.86	2.80	2.41	1.75	24.18	17.55
Eq.9+h	3.25	2.36	3.24	2.35	2.56	1.86	2.47	1.79	1.78	1.29	13.30	9.65
Eq.8+12	7.34	5.33	8.51	6.17	7.49	5.43	5.89	4.27	2.48	1.80	31.71	23.00
Eq.9+12+b	5.36	3.89	6.53	4.74	5.51	4.00	4.42	3.21	1.88	1.37	23.70	17.21
Eq.9+12+c	6.27	4.55	7.64	5.55	6.51	4.73	5.05	3.66	2.03	1.48	27.50	19.97
Average	6.68	4.85	7.81	5.66	6.42	4.66	5.11	3.71	2.93	2.13	28.96	21.01

Elminius modestus – Calshot												
	Nauplii 2		**Nauplii 3**		**Nauplii 4**		**Nauplii 5**		**Nauplii 6**		**Total**	
Equation	all	year	all	year	all	year	all	year	all	year	all	year
Eq.8+12	7.49	4.87	6.98	4.53	6.46	4.20	4.00	2.60	2.36	1.53	27.29	17.72
Eq. 9+a	9.32	6.05	4.72	3.06	4.53	2.94	3.84	2.49	4.20	2.73	26.60	17.28
Eq.9+12+b	5.58	3.62	5.34	3.47	4.79	3.11	2.97	1.93	1.92	1.24	20.60	13.38
Eq.9+12+c	6.44	4.18	6.73	4.37	5.97	3.88	3.42	2.22	2.04	1.33	24.60	15.98
Eq.9+d	7.84	5.09	4.71	3.06	4.72	3.07	4.61	2.99	6.86	4.46	28.73	18.66
Eq.9+e	6.55	4.25	3.93	2.55	3.95	2.56	3.85	2.50	5.74	3.73	24.02	15.60
Eq.9+f	8.13	5.28	4.04	2.62	3.47	2.25	2.86	1.86	3.42	2.22	21.92	14.24
Eq.9+g	7.33	4.76	3.57	2.32	3.02	1.96	2.45	1.59	2.87	1.86	19.24	12.49
Eq.9+h	3.35	2.18	1.85	1.20	1.73	1.12	1.56	1.01	2.11	1.37	10.60	6.88
Eq.8+12	7.10	4.61	5.18	3.36	4.92	3.20	3.89	2.53	2.00	1.30	23.09	15.00
Eq.9+12+b	5.30	3.44	4.00	2.60	3.71	2.41	2.91	1.89	2.31	1.50	18.23	11.84
Eq.9+12+c	6.07	3.94	4.71	3.06	4.31	2.80	3.32	2.15	1.72	1.12	20.13	13.07
Average	6.71	4.36	4.65	3.02	4.30	2.79	3.31	2.15	3.13	2.03	22.09	14.34

The overall average production of *Elminius modestus* was 26.49 mg C m^{-3}, which represented an annual production of 17.93 mg C m^{-3} yr^{-1} for the three stations. (The production equation used to illustrate the daily contribution of each barnacle stage in Figure 46 was the equation that gave the closest value to the average of all equations used in Table 26).

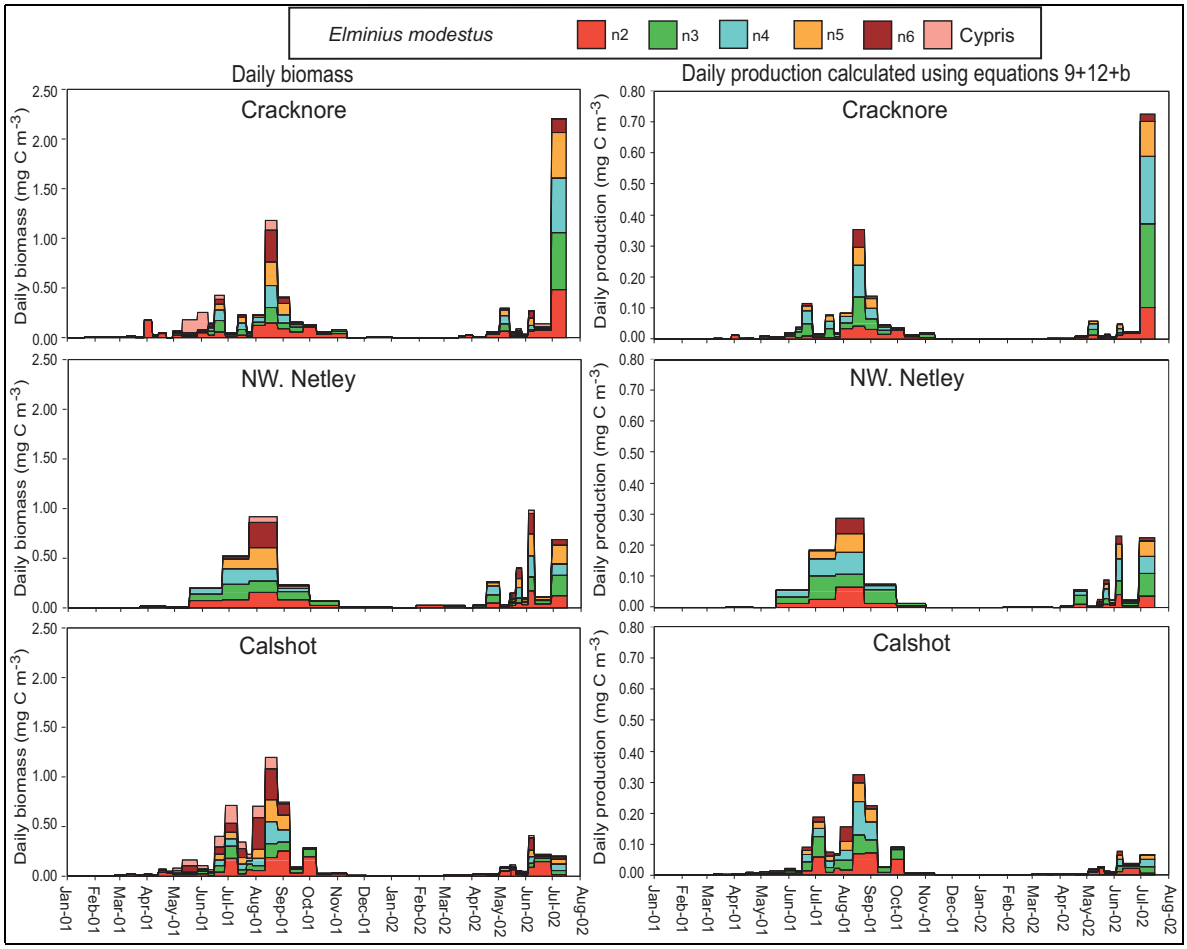


Figure 46. Seasonal production and biomass of the larval stages of *Elminius modestus* present in the zooplankton of Southampton Water during 2001/02.

4.3.2.2. *Balanus crenatus*.

Balanus crenatus nauplii occurred from December/January to July and like *E.modestus,* all naupliar stages were found at the three stations (Figure 47). Nauplii 2 accounted, on average, for 83% of all stages of *B.crenatus* found in Southampton Water. Older stages were only observed after March and were much more abundant towards Calshot. Despite a very similar composition in 2001, major abundances of nauplii 2 were only observed at NW. Netley and Calshot in 2002 (Figure 47).

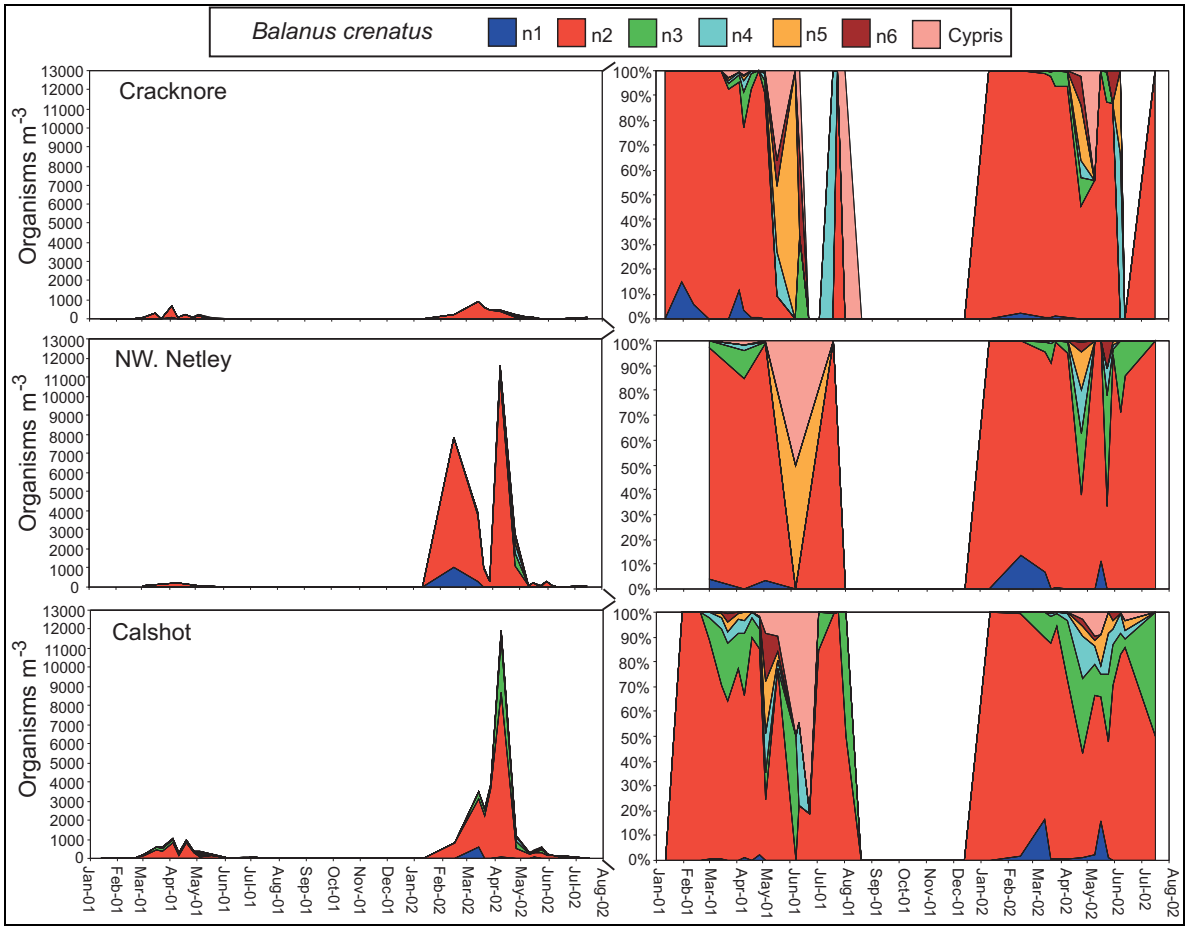


Figure 47. Temporal variability of the larval stages of *Balanus crenatus* present in the zooplankton of Southampton Water during 2001/02.

Total biomass of *B.crenatus* for the sampling period, was 48.35, 148.86 and 119.74 mg C m^{-3} at Cracknore, NW. Netley and Calshot respectively, and its daily variation can be seen in Figure 48.

The calculated production of *Balanus crenatus,* based on the temporal variability of biomass and abundance, is summarized on Table 27. The calculated productions at the three sites were unequal, with Cracknore presenting production approximately an order of magnitude lower than the other two sites.

Table 27. Production estimates of each larval stage of *Balanus crenatus* obtained using the respective equations summarized in Table 22. (all refer to total production in terms of mg C m^{-3}; and year is the annual production in terms of mg C $m^{-3}yr^{-1}$)

Balanus crenatus – Cracknore												
	Nauplii 2		**Nauplii 3**		**Nauplii 4**		**Nauplii 5**		**Nauplii 6**		**Total**	
Equation	all	year	All	year	all	year	all	year	all	year	all	year
Eq.8+12	3.17	2.06	0.30	0.20	0.20	0.13	0.49	0.32	0.23	0.15	4.40	2.86
Eq. 9+a	1.51	0.98	0.08	0.05	0.06	0.04	0.14	0.09	0.12	0.08	1.90	1.23
Eq.9+b+12	2.56	1.66	0.23	0.15	0.14	0.09	0.33	0.21	0.17	0.11	3.42	2.22
Eq.9+c+12	2.84	1.85	0.28	0.18	0.17	0.11	0.38	0.25	0.18	0.12	3.85	2.51
Eq.9+d	2.05	1.33	0.11	0.07	0.08	0.05	0.23	0.15	0.28	0.18	2.74	1.78
Eq.9+e	1.70	1.10	0.09	0.06	0.07	0.04	0.19	0.12	0.23	0.15	2.27	1.48
Eq.9+f	2.52	1.64	0.11	0.07	0.07	0.04	0.16	0.10	0.15	0.09	3.01	1.95
Eq.9+g	2.38	1.55	0.11	0.07	0.06	0.04	0.14	0.09	0.13	0.08	2.81	1.83
Eq.9+h	1.00	0.65	0.05	0.03	0.03	0.02	0.08	0.05	0.09	0.06	1.26	0.82
Average	2.19	1.42	0.15	0.10	0.10	0.06	0.24	0.15	0.18	0.11	2.85	1.85
Balanus crenatus – NW. Netley												
	Nauplii 2		**Nauplii 3**		**Nauplii 4**		**Nauplii 5**		**Nauplii 6**		**Total**	
Equation	all	year	All	year	all	year	all	year	all	year	all	year
Eq.8+12	29.96	21.74	4.63	3.36	2.57	1.86	2.62	1.90	0.38	0.27	40.16	29.14
Eq. 9+a	14.33	10.40	1.07	0.78	0.75	0.54	0.94	0.68	0.42	0.31	17.51	12.71
Eq.9+b+12	24.27	17.61	3.36	2.44	1.83	1.32	1.88	1.37	0.32	0.23	31.65	22.97
Eq.9+c+12	26.98	19.58	4.26	3.09	2.18	1.58	2.14	1.56	0.33	0.24	35.90	26.05
Eq.9+d	19.28	13.99	1.51	1.09	1.10	0.80	1.58	1.15	0.94	0.68	24.41	17.71
Eq.9+e	15.98	11.60	1.25	0.91	0.92	0.66	1.31	0.95	0.78	0.57	20.25	14.69
Eq.9+f	23.72	17.21	1.52	1.10	0.91	0.66	1.06	0.77	0.50	0.36	27.70	20.10
Eq.9+g	22.35	16.22	1.40	1.01	0.82	0.59	0.94	0.68	0.43	0.31	25.93	18.82
Eq.9+h	9.40	6.82	0.66	0.48	0.44	0.32	0.58	0.42	0.31	0.23	11.40	8.27
Average	20.70	15.02	2.18	1.59	1.28	0.93	1.45	1.05	0.49	0.36	26.10	18.94
Balanus crenatus – Calshot												
	Nauplii 2		**Nauplii 3**		**Nauplii 4**		**Nauplii 5**		**Nauplii 6**		**Total**	
Equation	all	year	All	year	all	year	all	year	all	year	all	year
Eq.8+12	19.40	12.60	10.88	7.07	3.15	2.05	1.73	1.13	0.90	0.58	36.07	23.43
Eq. 9+a	8.22	5.35	2.64	1.72	0.86	0.56	0.49	0.32	0.45	0.29	12.65	8.23
Eq.9+b+12	15.19	9.86	8.13	5.28	2.22	1.44	1.19	0.77	0.65	0.42	27.38	17.78
Eq.9+c+12	17.22	11.21	9.83	6.39	2.62	1.71	1.37	0.89	0.70	0.46	31.74	20.65
Eq.9+d	10.76	7.00	3.81	2.48	1.26	0.82	0.83	0.54	1.04	0.68	17.70	11.52
Eq.9+e	8.92	5.79	3.16	2.05	1.05	0.68	0.69	0.45	0.86	0.56	14.68	9.54
Eq.9+f	13.52	8.78	4.08	2.65	1.13	0.74	0.60	0.39	0.58	0.38	19.91	12.93
Eq.9+g	14.56	9.46	4.25	2.76	1.14	0.74	0.62	0.40	0.62	0.40	21.20	13.77
Eq.9+h	5.28	3.43	1.74	1.13	0.53	0.35	0.32	0.21	0.36	0.23	8.23	5.34
Average	12.56	8.16	5.39	3.50	1.55	1.01	0.87	0.57	0.68	0.45	21.06	13.69

In terms of developmental stage contributions, nauplii 2 alone accounted for ~72% of the production (Table 27). The daily contribution of each barnacle stage can be seen in Figure 48, and the production value chosen to illustrate the daily contribution of each barnacle stage were those produced by the equation that gave the closest value to the average.

Total averaged production of *Balanus crenatus* for the three stations over the period studied was 16.67 mg C m^{-3}, which represented an average annual production of 11.49 mg C m^{-3} yr^{-1}.

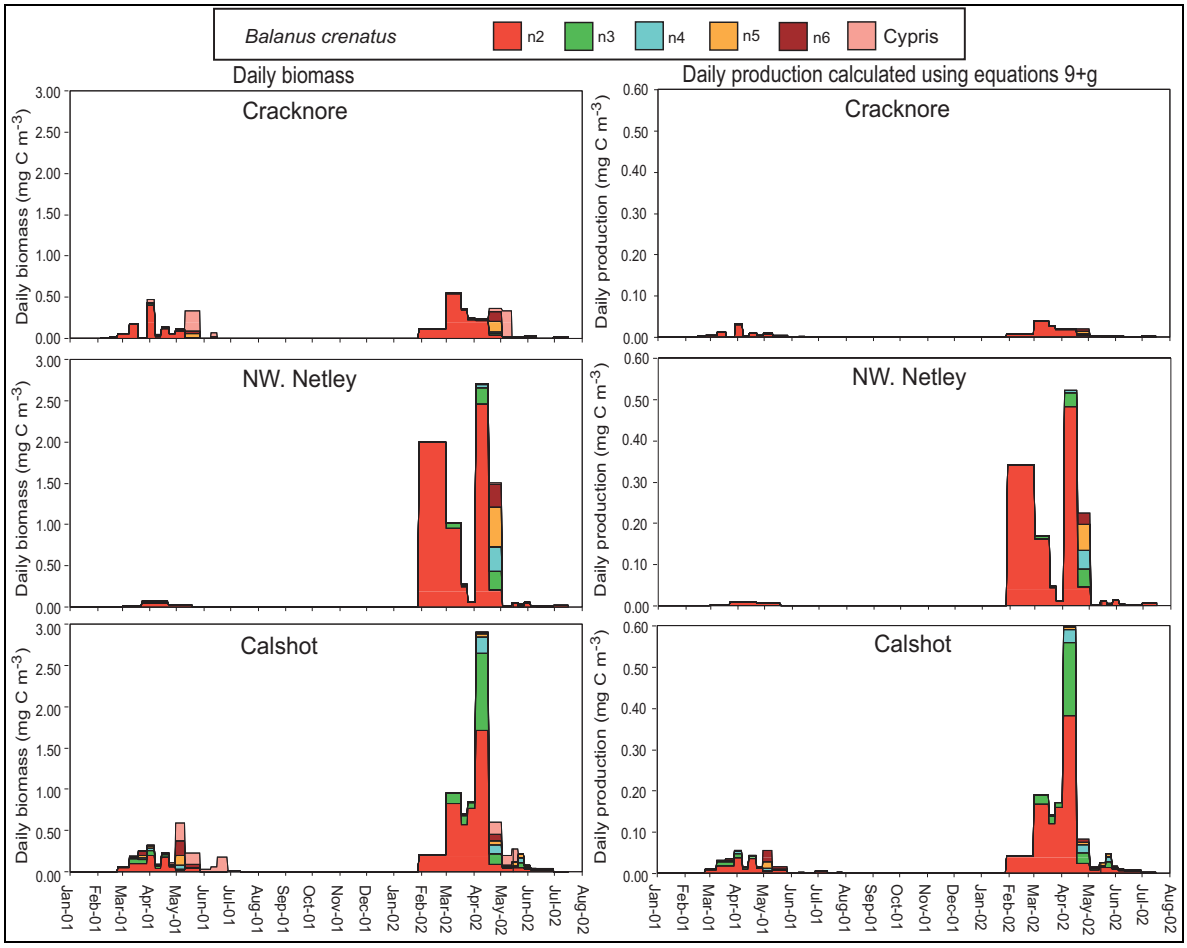


Figure 48. Seasonal production and biomass of the larval stages of *Balanus crenatus* present in the zooplankton of Southampton Water during 2001/02.

4.3.2.3. *Balanus improvisus.*

Balanus improvisus nauplii were found at all three stations from January/February until November, and 'somehow' confined to the inner reaches of Southampton Water where it was much more abundant. Naupliar stage 2 was the most abundant, averaging 45 % of the stages found (Figure 49). Older stages were found as early as March, but they only contributed significantly in numbers from June to September (Figure 49).

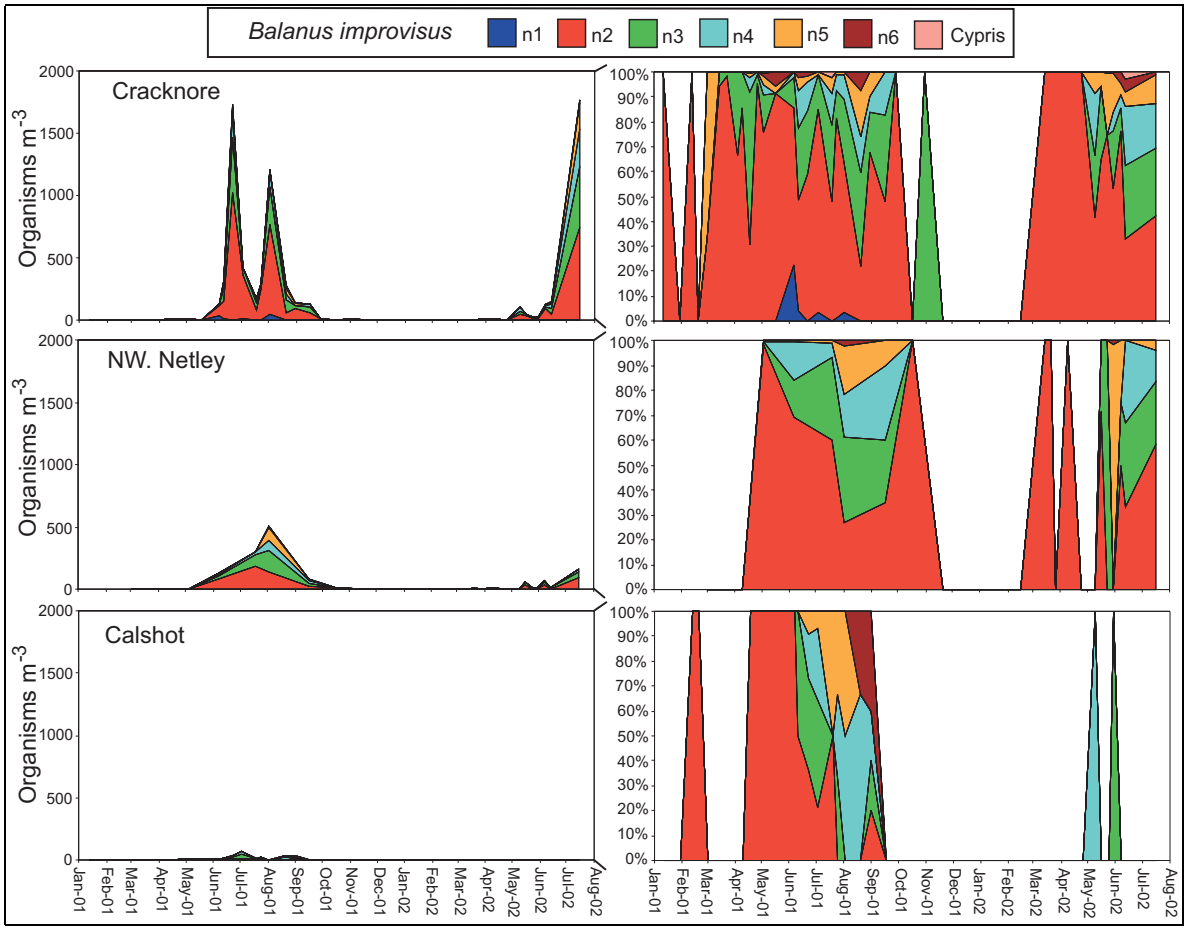


Figure 49. Temporal variability of the larval stages of *Balanus improvisus* present in the zooplankton of Southampton Water during 2001/02.

Total biomass of *B.improvisus* for the period was 19.38, 8.59 and 1.03 mg C m^{-3} at Cracknore, NW. Netley and Calshot respectively, and its daily variation can be seen in Figure 50.

The production of *Balanus improvisus* calculated, based on the temporal variability of biomass and abundance, is summarized in Table 28. Contrasting with *B.crenatus,* the production at Cracknore was approximately an order of magnitude higher than at NW.Netley and 20 times higher that at Calshot (Table 28).

Table 28. Production estimates of each larval stage of *Balanus improvisus* obtained using the respective equations summarized in Table 22. (all refer to total production in terms of mg C m^{-3}; and year is the annual production in terms of mg C $m^{-3}yr^{-1}$). Production using Harms (1986) data on Eq. 12 is highlighted in red.

Balanus improvisus – Cracknore												
	Nauplii 2		**Nauplii 3**		**Nauplii 4**		**Nauplii 5**		**Nauplii 6**		**Total**	
Equation	all	year	all	year	All	year	all	year	all	year	all	year
Eq.8+12	2.11	1.37	2.99	1.94	2.18	1.42	1.24	0.80	0.28	0.18	8.79	5.71
Eq. 9+a	2.95	1.92	1.93	1.25	1.37	0.89	1.04	0.68	0.31	0.20	7.60	4.94
Eq.9+b+12	1.60	1.04	2.27	1.47	1.59	1.03	0.90	0.59	0.21	0.14	6.57	4.27
Eq.9+c+12	1.84	1.20	2.93	1.90	2.00	1.30	1.04	0.68	0.23	0.15	8.04	5.22
Eq.9+d	2.43	1.58	1.91	1.24	1.47	0.95	1.32	0.85	0.52	0.34	7.65	4.97
Eq.9+e	2.03	1.32	1.60	1.04	1.23	0.80	1.10	0.71	0.44	0.28	6.40	4.15
Eq.9+f	2.34	1.52	1.58	1.02	1.07	0.70	0.80	0.52	0.27	0.17	6.05	3.93
Eq.9+g	2.08	1.35	1.39	0.90	0.93	0.60	0.68	0.44	0.22	0.15	5.30	3.44
Eq.9+h	1.00	0.65	0.73	0.48	0.54	0.35	0.44	0.29	0.16	0.11	2.87	1.87
Eq.8+12	2.02	1.31	2.23	1.45	1.66	1.08	1.19	0.77	0.24	0.15	7.34	4.76
Eq.9+12+b	1.54	1.00	1.69	1.10	1.21	0.78	0.87	0.57	0.18	0.12	5.49	3.57
Eq.9+12+c	1.76	1.14	2.05	1.33	1.44	0.93	1.00	0.65	0.19	0.12	6.44	4.17
Average	1.97	1.28	1.94	1.26	1.39	0.90	0.97	0.63	0.27	0.18	6.54	4.25

Balanus improvisus – NW. Netley												
	Nauplii 2		**Nauplii 3**		**Nauplii 4**		**Nauplii 5**		**Nauplii 6**		**Total**	
Equation	all	year	all	year	all	year	all	year	all	year	all	year
Eq.8+12	0.78	0.57	1.44	1.05	0.82	0.59	0.84	0.61	0.11	0.08	3.99	2.90
Eq. 9+a	0.96	0.70	1.00	0.73	0.67	0.48	0.79	0.57	0.13	0.10	3.55	2.57
Eq.9+b+12	0.59	0.43	1.10	0.80	0.61	0.44	0.61	0.44	0.08	0.06	2.99	2.17
Eq.9+c+12	0.68	0.49	1.42	1.03	0.77	0.56	0.72	0.52	0.09	0.07	3.68	2.67
Eq.9+d	0.83	0.60	0.99	0.72	0.71	0.52	0.94	0.68	0.22	0.16	3.69	2.67
Eq.9+e	0.69	0.50	0.83	0.60	0.60	0.43	0.79	0.57	0.18	0.13	3.08	2.24
Eq.9+f	0.79	0.57	0.78	0.56	0.48	0.35	0.53	0.39	0.10	0.07	2.68	1.95
Eq.9+g	0.70	0.51	0.67	0.49	0.43	0.31	0.45	0.33	0.08	0.06	2.34	1.70
Eq.9+h	0.34	0.25	0.37	0.27	0.25	0.18	0.30	0.22	0.06	0.05	1.33	0.96
Eq.8+12	0.74	0.48	1.08	0.70	0.63	0.41	0.84	0.54	0.10	0.06	3.39	2.19
Eq.9+12+b	0.56	0.36	0.83	0.54	0.46	0.30	0.61	0.40	0.07	0.05	2.53	1.65
Eq.9+12+c	0.64	0.42	1.00	0.65	0.56	0.36	0.72	0.47	0.08	0.05	3.00	1.95
Average	0.69	0.49	0.96	0.68	0.58	0.41	0.68	0.48	0.11	0.08	3.02	2.14

Balanus improvisus – Calshot												
	Nauplii 2		**Nauplii 3**		**Nauplii 4**		**Nauplii 5**		**Nauplii 6**		**Total**	
Equation	all	year	all	year	all	year	all	year	all	year	all	year
Eq.8+12	0.04	0.03	0.09	0.06	0.16	0.11	0.04	0.03	0.08	0.05	0.43	0.28
Eq. 9+a	0.05	0.03	0.07	0.04	0.10	0.07	0.04	0.03	0.10	0.06	0.35	0.23
Eq.9+b+12	0.03	0.02	0.07	0.05	0.12	0.08	0.03	0.02	0.06	0.04	0.32	0.21
Eq.9+c+12	0.04	0.02	0.09	0.06	0.15	0.10	0.04	0.02	0.07	0.04	0.39	0.25
Eq.9+d	0.04	0.03	0.06	0.04	0.10	0.07	0.05	0.03	0.16	0.11	0.43	0.28
Eq.9+e	0.04	0.02	0.05	0.04	0.09	0.06	0.04	0.03	0.14	0.09	0.36	0.23
Eq.9+f	0.05	0.03	0.05	0.03	0.07	0.05	0.03	0.02	0.08	0.05	0.28	0.18
Eq.9+g	0.04	0.03	0.05	0.03	0.06	0.04	0.03	0.02	0.06	0.04	0.24	0.16
Eq.9+h	0.02	0.01	0.02	0.02	0.04	0.02	0.02	0.01	0.05	0.03	0.15	0.10
Eq.8+12	0.04	0.03	0.07	0.05	0.13	0.08	0.04	0.03	0.07	0.05	0.35	0.24
Eq.9+12+b	0.03	0.02	0.05	0.04	0.09	0.06	0.03	0.02	0.05	0.03	0.25	0.17
Eq.9+12+c	0.03	0.02	0.07	0.04	0.11	0.07	0.03	0.02	0.06	0.04	0.30	0.19
Average	0.04	0.02	0.06	0.04	0.10	0.07	0.03	0.02	0.08	0.05	0.32	0.21

The averaged production of *B.improvisus* for the three stations over the period studied was 3.32 mg C m^{-3}, which represented an average annual production of 2.23 mg C m^{-3} yr^{-1}. In terms of stage contribution, nauplii 2, 3 and 4 together accounted for ~72% of the production (Table 28). Based on the values presented in Table 28, the equation that

gave the closest value to the average was chosen to illustrate the contribution of each barnacle stage on a daily basis (Figure 50).

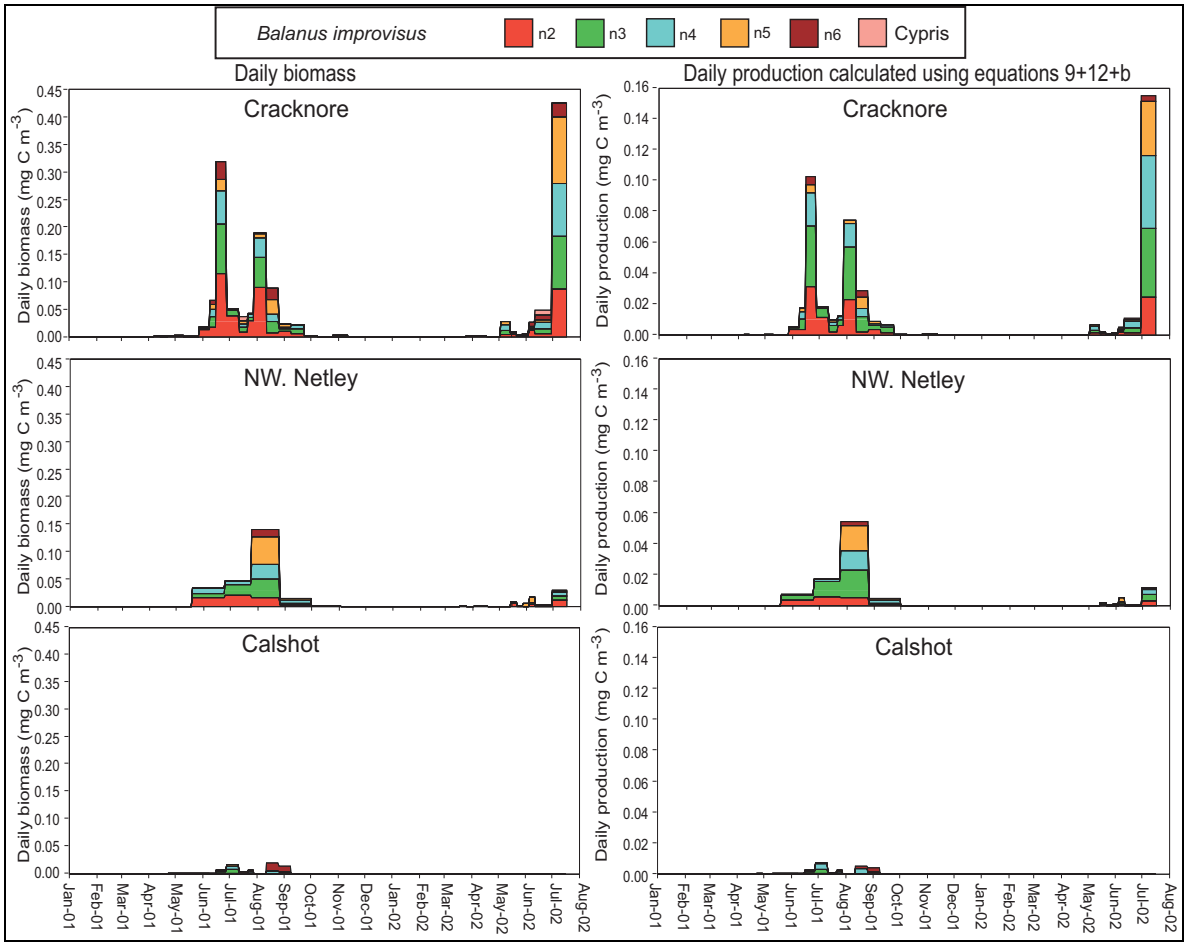


Figure 50. Seasonal production and biomass of the larval stages of *Balanus improvisus* present in the zooplankton of Southampton Water during 2001/02.

4.3.2.4. *Semibalanus balanoides*.

Semibalanus balanoides nauplii were found at all three stations from January/February until June/July, with naupliar stage 2 the most abundant and averaging 63 % of all stages found at the three stations (Figure 51). Older stages were usually found from February to July, particularly at NW.Netley and Calshot (Figure 51). The abundance of *S.balanoides* was generally quite similar at each of the three stations in 2001, with higher abundances found at NW.Netley and Calshot in 2002.

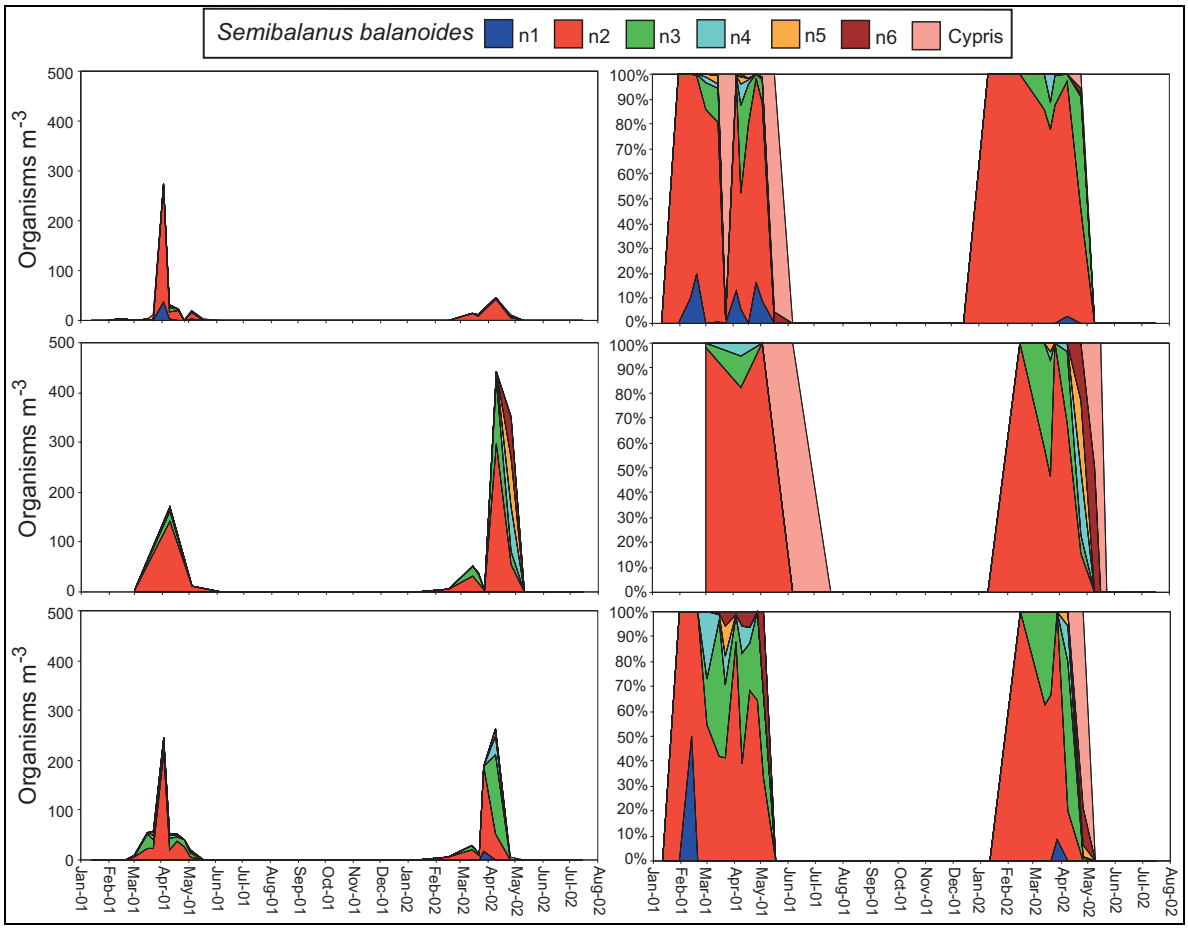


Figure 51. Temporal variability of the larval stages of *Semibalanus balanoides* present in the zooplankton of Southampton Water during 2001/02.

Total biomass of *S.balanoides* for the period was 3.01, 16.00 and 6.79 mg C m^{-3} at Cracknore, NW. Netley and Calshot respectively, with the daily variation illustrated in Figure 52.

The production of *S.balanoides,* averaged for the three stations, over the period studied was 1.46 mg C m^{-3}. This represented an average annual production of 1.02 mg C m^{-3} yr^{-1}. Like *B.crenatus,* the production of *S.balanoides* at Cracknore was 4 to 10 times lower when compared with Calshot and NW.Netley values respectively (Table 29).

Table 29 Production estimates of each larval stage of *Semibalanus balanoides* obtained using the respective equations summarized in Table 22. (all refer to total production in terms of mg C m^{-3}; and year is the annual production in terms of mg C $m^{-3}yr^{-1}$)

Semibalanus balanoides – Cracknore												
	Nauplii 2		**Nauplii 3**		**Nauplii 4**		**Nauplii 5**		**Nauplii 6**		**Total**	
Equation	All	year	all	year	all	Year	all	year	all	year	all	year
Eq.8+12	0.35	0.23	0.09	0.06	0.02	0.01	0.01	0.01	0.00	0.00	0.47	0.31
Eq. 9+a	0.15	0.10	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.18	0.12
Eq.9+b+12	0.28	0.18	0.07	0.04	0.01	0.01	0.01	0.00	0.00	0.00	0.37	0.24
Eq.9+c+12	0.31	0.20	0.08	0.05	0.01	0.01	0.01	0.00	0.00	0.00	0.42	0.27
Eq.9+d	0.23	0.15	0.04	0.02	0.01	0.00	0.00	0.00	0.01	0.00	0.28	0.18
Eq.9+e	0.19	0.12	0.03	0.02	0.00	0.00	0.00	0.00	0.01	0.00	0.23	0.15
Eq.9+f	0.32	0.21	0.04	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.37	0.24
Eq.9+g	0.24	0.15	0.03	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.28	0.18
Eq.9+h	0.11	0.07	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.13	0.08
Average	0.24	0.16	0.05	0.03	0.01	0.00	0.00	0.00	0.00	0.00	0.30	0.20
Semibalanus balanoides – NW. Netley												
	Nauplii 2		**Nauplii 3**		**Nauplii 4**		**Nauplii 5**		**Nauplii 6**		**Total**	
Equation	All	year	all	year	all	Year	all	year	all	year	all	year
Eq.8+12	1.13	0.82	1.34	0.97	1.03	0.75	1.26	0.92	0.21	0.15	4.98	3.61
Eq. 9+a	0.40	0.29	0.20	0.14	0.23	0.17	0.34	0.25	0.47	0.34	1.64	1.19
Eq.9+b+12	0.87	0.63	0.90	0.65	0.71	0.52	0.88	0.64	0.19	0.14	3.55	2.58
Eq.9+c+12	1.00	0.73	1.17	0.85	0.86	0.63	1.01	0.74	0.20	0.14	4.24	3.08
Eq.9+d	0.56	0.40	0.31	0.23	0.39	0.28	0.67	0.49	1.24	0.90	3.18	2.31
Eq.9+e	0.46	0.34	0.26	0.19	0.33	0.24	0.56	0.41	1.03	0.75	2.64	1.92
Eq.9+f	0.77	0.56	0.36	0.26	0.36	0.26	0.53	0.39	0.82	0.60	2.84	2.06
Eq.9+g	0.57	0.41	0.27	0.19	0.24	0.18	0.33	0.24	0.46	0.33	1.87	1.36
Eq.9+h	0.26	0.19	0.13	0.10	0.15	0.11	0.23	0.17	0.38	0.28	1.15	0.83
Average	0.67	0.49	0.55	0.40	0.48	0.35	0.65	0.47	0.56	0.40	2.90	2.10
Semibalanus balanoides – Calshot												
	Nauplii 2		**Nauplii 3**		**Nauplii 4**		**Nauplii 5**		**Nauplii 6**		**Total**	
Equation	All	year	all	year	all	Year	all	year	all	year	all	year
Eq.8+12	0.49	0.32	1.18	0.76	0.36	0.23	0.25	0.16	0.03	0.02	2.30	1.49
Eq. 9+a	0.21	0.13	0.19	0.12	0.07	0.04	0.05	0.03	0.06	0.04	0.57	0.37
Eq.9+b+12	0.39	0.25	0.82	0.53	0.24	0.16	0.16	0.11	0.02	0.01	1.63	1.06
Eq.9+c+12	0.43	0.28	1.02	0.66	0.29	0.19	0.19	0.12	0.02	0.02	1.95	1.27
Eq.9+d	0.30	0.20	0.31	0.20	0.12	0.08	0.09	0.06	0.16	0.11	0.99	0.64
Eq.9+e	0.25	0.16	0.26	0.17	0.10	0.06	0.08	0.05	0.14	0.09	0.82	0.53
Eq.9+f	0.43	0.28	0.38	0.25	0.12	0.08	0.08	0.05	0.12	0.08	1.14	0.74
Eq.9+g	0.33	0.21	0.28	0.18	0.09	0.06	0.05	0.04	0.07	0.05	0.82	0.53
Eq.9+h	0.14	0.09	0.14	0.09	0.05	0.03	0.03	0.02	0.05	0.04	0.42	0.27
Average	0.33	0.21	0.51	0.33	0.16	0.10	0.11	0.07	0.08	0.05	1.18	0.77

In terms of stage contribution, nauplii 2 and 3 together accounted for ~69% of the production (Table 29). The daily contribution of each barnacle stage can be seen on Figure 52 (The production value chosen to illustrate the daily contribution of each barnacle stage were those produced by the equation that gave the closest value to the average of all equations summarized on Table 29).

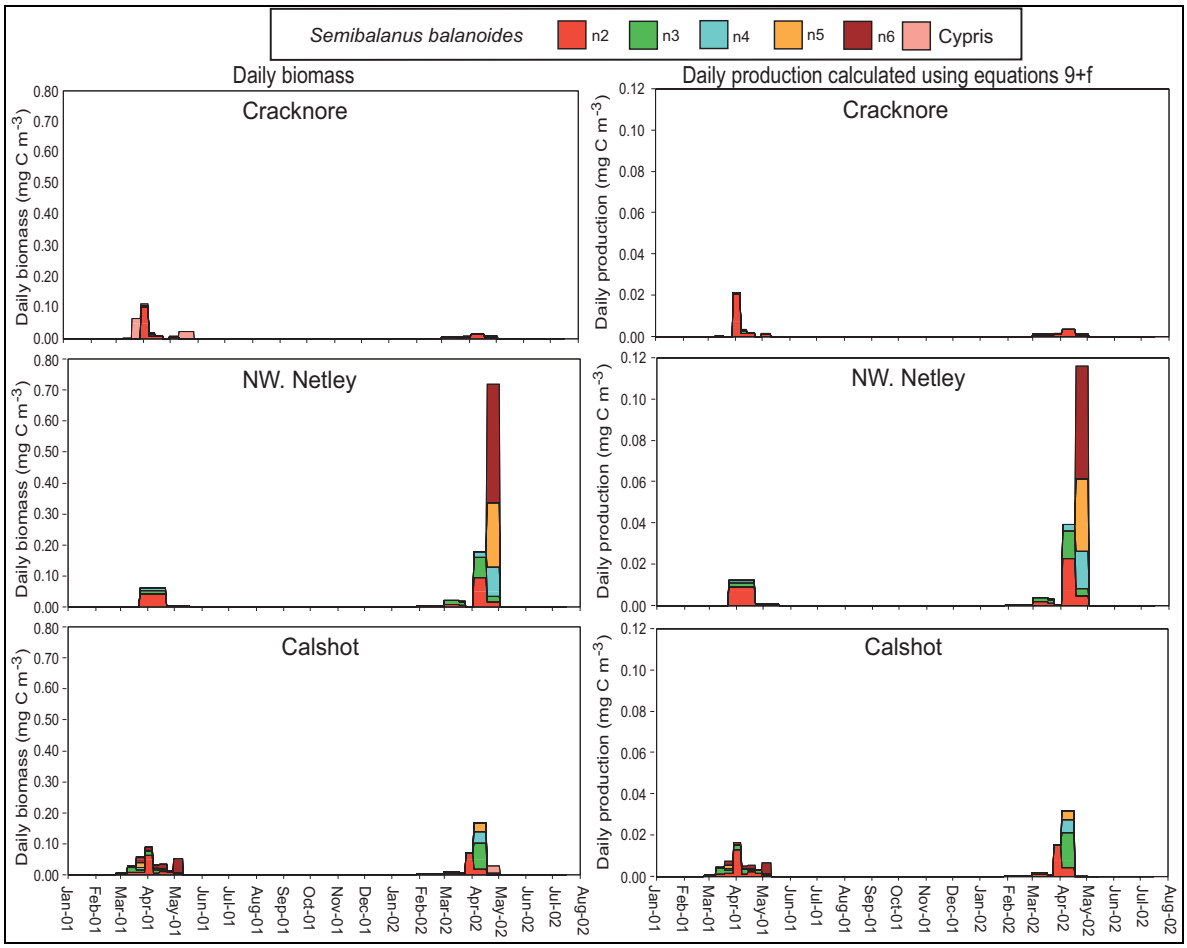


Figure 52. Seasonal production and biomass of the larval stages of *Semibalanus balanoides* present in the zooplankton of Southampton Water during 2001/02.

4.3.2.5. *Verruca stroemia.*

Verruca stroemia nauplii were found at each of the three stations from January until July, with naupliar stage 2 the most abundant, and averaging 69 % of al the stages found at the three stations (Figure 53). Older stages were usually found at Calshot, with nauplii 3 and 4 sometimes found at the inner stations (Figure 53).

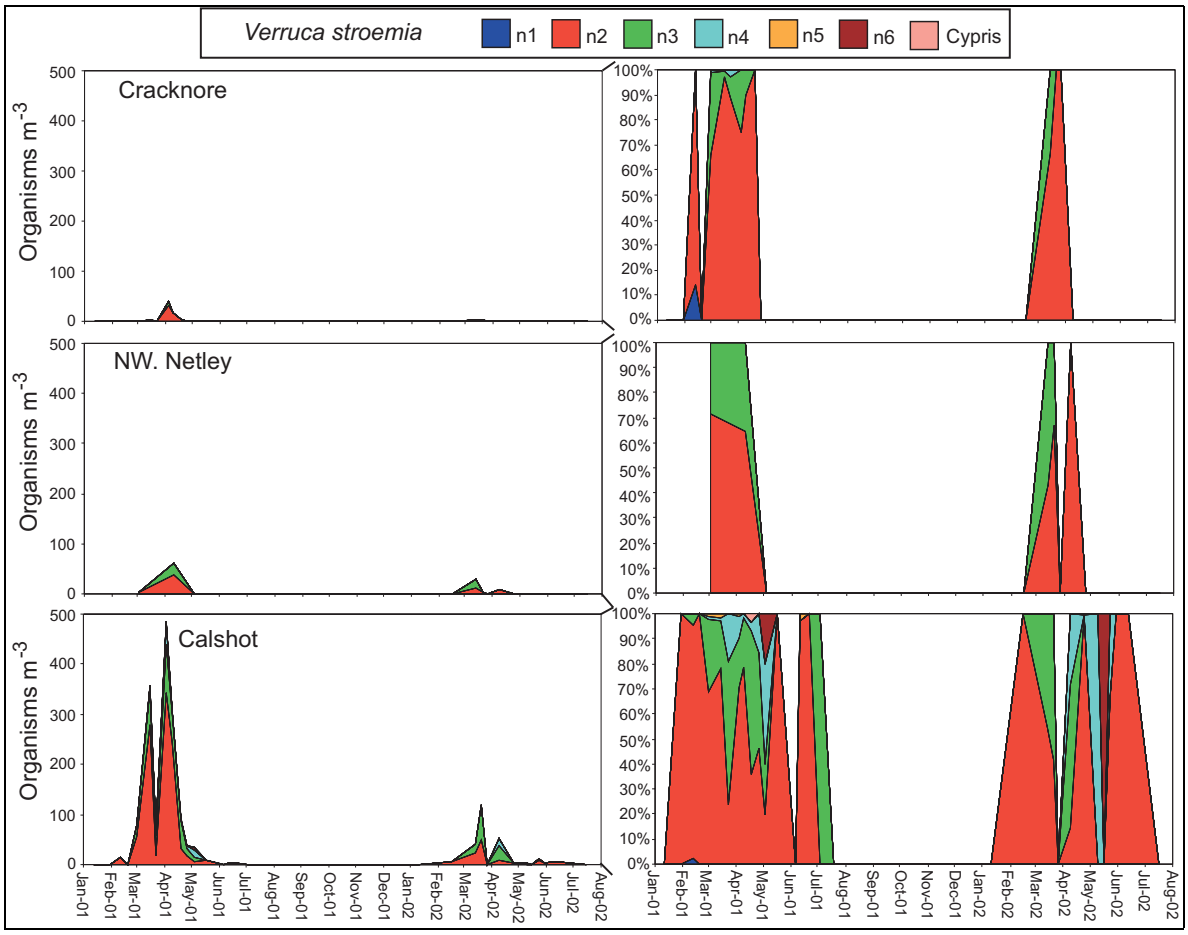


Figure 53. Temporal variability of the larval stages of *Verruca stroemia* present in the zooplankton of Southampton Water during 2001/02.

Total biomass of *V.stroemia* for the period was 0.11, 0.46 and 3.27 mg C m^{-3} at Cracknore, NW. Netley and Calshot respectively, with the daily variation illustrated in Figure 54.

V.stroemia production averaged for the three stations over the period studied was 0.09 mg C m^{-3}, which represented an average annual production of 0.06 mg C m^{-3} yr^{-1}. Like *B.crenatus,* the production of *V.stroemia* at Cracknore was lower when compared with Netley and Calshot, where productions values between 5 to 30 times higher were found respectively. In terms of developmental stage contribution, nauplii 2 and 3 together accounted for ~94% of the estimated production (Table 30).

Table 30. Production estimates of each larval stage of *Verruca stroemia* obtained using the respective equations summarized in Table 22. (all refer to total production in terms of mg C m^{-3}; and year is the annual production in terms of mg C $m^{-3}yr^{-1}$)

Verruca stroemia – Cracknore												
	Nauplii 2		**Nauplii 3**		**Nauplii 4**		**Nauplii 5**		**Nauplii 6**		**Total**	
Equation	All	year	all	year	all	year	all	year	all	year	all	year
Eq.8+12	0.02	0.02	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.02
Eq. 9+a	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01
Eq.9+b+12	0.02	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.02
Eq.9+c+12	0.02	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.02
Eq.9+d	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01
Eq.9+e	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01
Eq.9+f	0.02	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01
Eq.9+g	0.02	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01
Eq.9+h	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01
Average	0.01	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.01
Verruca stroemia – NW. Netley												
	Nauplii 2		**Nauplii 3**		**Nauplii 4**		**Nauplii 5**		**Nauplii 6**		**Total**	
Equation	All	year	all	year	all	year	all	year	all	year	all	year
Eq.8+12	0.08	0.06	0.10	0.08	0.00	0.00	0.00	0.00	0.00	0.00	0.19	0.13
Eq. 9+a	0.03	0.02	0.03	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.04
Eq.9+b+12	0.06	0.04	0.08	0.06	0.00	0.00	0.00	0.00	0.00	0.00	0.14	0.10
Eq.9+c+12	0.07	0.05	0.09	0.07	0.00	0.00	0.00	0.00	0.00	0.00	0.16	0.12
Eq.9+d	0.03	0.02	0.04	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.07	0.05
Eq.9+e	0.03	0.02	0.03	0.02	0.00	0.00	0.00	0.00	0.00	0.00	0.06	0.04
Eq.9+f	0.05	0.03	0.04	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.06
Eq.9+g	0.05	0.04	0.04	0.03	0.00	0.00	0.00	0.00	0.00	0.00	0.09	0.07
Eq.9+h	0.02	0.01	0.02	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.03
Average	0.05	0.03	0.05	0.04	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.07
Verruca stroemia – Calshot												
	Nauplii 2		**Nauplii 3**		**Nauplii 4**		**Nauplii 5**		**Nauplii 6**		**Total**	
Equation	All	year	all	year	all	year	all	year	all	year	all	year
Eq.8+12	0.40	0.26	0.45	0.30	0.15	0.10	0.01	0.01	0.00	0.00	1.03	0.67
Eq. 9+a	0.16	0.11	0.11	0.07	0.05	0.03	0.01	0.00	0.01	0.01	0.34	0.22
Eq.9+b+12	0.31	0.20	0.33	0.21	0.11	0.07	0.01	0.01	0.00	0.00	0.76	0.50
Eq.9+c+12	0.35	0.23	0.39	0.26	0.13	0.08	0.01	0.01	0.00	0.00	0.88	0.57
Eq.9+d	0.21	0.13	0.15	0.10	0.07	0.05	0.01	0.01	0.01	0.01	0.46	0.30
Eq.9+e	0.17	0.11	0.13	0.08	0.06	0.04	0.01	0.01	0.01	0.01	0.38	0.25
Eq.9+f	0.30	0.20	0.19	0.12	0.07	0.05	0.01	0.01	0.01	0.01	0.58	0.38
Eq.9+g	0.31	0.20	0.20	0.13	0.07	0.05	0.01	0.01	0.01	0.01	0.60	0.39
Eq.9+h	0.11	0.07	0.08	0.05	0.03	0.02	0.00	0.00	0.01	0.00	0.23	0.15
Average	0.26	0.17	0.23	0.15	0.08	0.05	0.01	0.01	0.01	0.00	0.58	0.38

Based on the values presented in Table 30, the equation that gave the closest production value to the averaged values was chosen to illustrate the daily contribution of each barnacle stage (Figure 54).

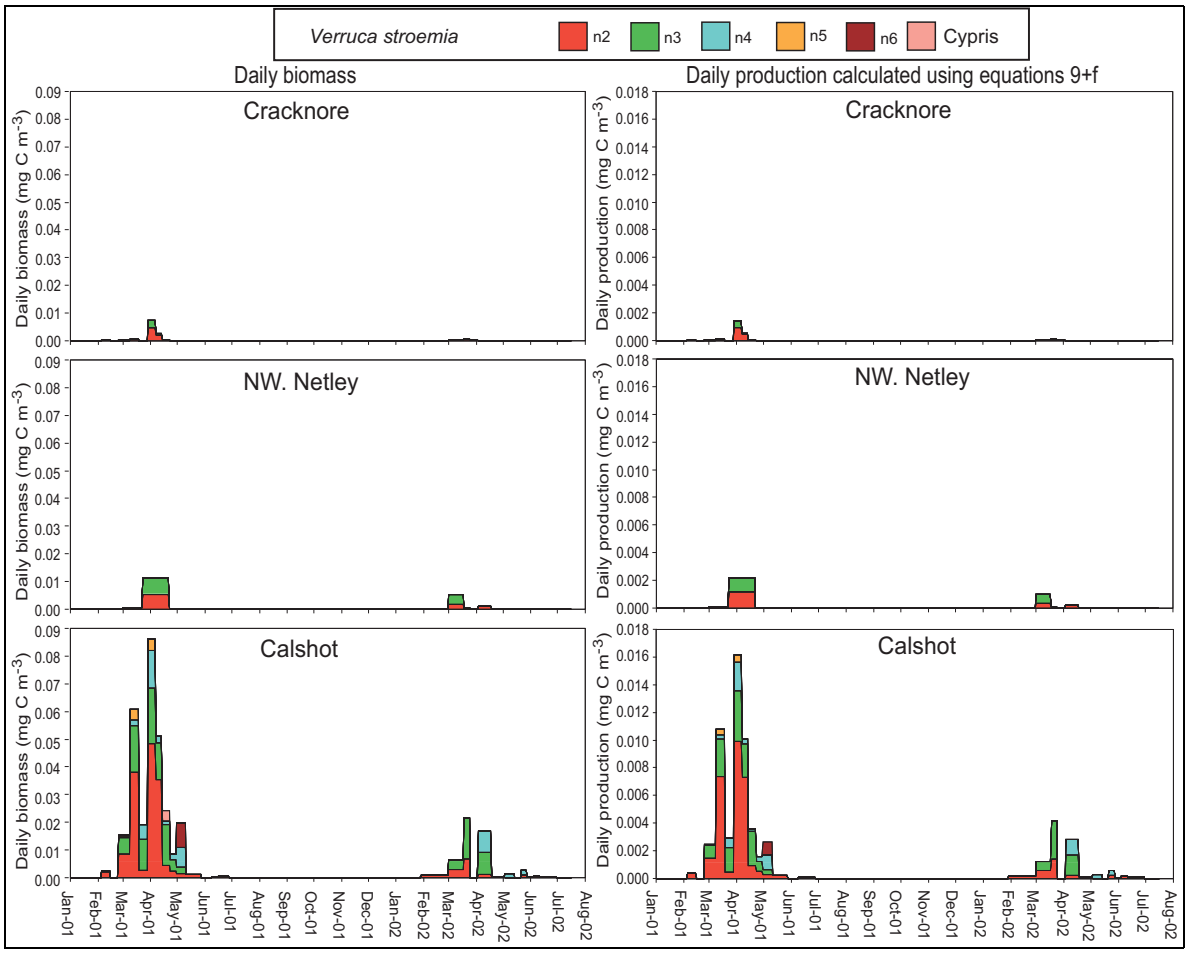


Figure 54. Seasonal production and biomass of the larval stages of *Verruca stroemia* present in the zooplankton of Southampton Water during 2001/02.

4.4. Discussion.

4.4.1. Considerations about the methodology employed.

Despite being aware of changes in weight due to formalin preservation the use of freshly caught material for weight analysis during this work was impractical. The counting and identification of the individuals required for replicate weight measurements from preserved samples often took more than a single day to obtain (i.e. more than 8 continuous hours of microscope usage), and for some stages even weeks were required until the numbers necessary for a single replicate were obtained.

There is a huge body of literature concerning the effects of formalin preservation on zooplanktonic organisms, suggesting that weight losses are most likely to occur depending on the fixative fluid, rinsing method, species composition and even stage of development (Beers, 1976; Omori, 1978; Böttger & Schnack, 1986; Giguère *et al*., 1989; Postel *et al*., 2000). Among some selected literature, Omori (1970) reported changes of 30 to 35% for *Calanus cristatus* (Copepoda), with Landry (1978) reporting losses of 37% for *Acartia clausi*. Williams & Robins (1982) reported changes between 29 to 49% for *Calanus helgolandicus,* while Böttger & Schnack (1986) found losses of 30 to 35% for *Eurytemora affinis*. Giguère *et al.* (1989) in an extensive compilation reported changes around 37 to 43% for total zooplankton, while Buskey (1993) applied a correction factor of 25%. Contrasting with them, Dumont *et al*. (1975) reported smaller losses of 5 to 10% for a selection of Copepoda, Cladocera and Rotifera, while Chisholm & Roff (1990b) did not observe any loss for a selection of tropical copepods. Omori (1978) attributes these weight changes primarily to the loss of stored lipids, and also suggests that the utilization of Hexamethylene-tetramine as a buffer in formaldehyde will minimize losses by 10% when compared with Borax buffered fixative. Based on those works one could assume that an overall loss of ~25% seems likely to occur when using formalin preserved sample.

Despite the fact that during the present work there was no evidence of lipid leakage or accumulation in sample bottles a correction factor of 18.15% was obtained after employing the same methodology for freshly caught *E.modestus* larvae of the same size employed in the analysis. This 18.15% correction factor is within the lower limits of the reported values from literature shown above and closed to that hypothetical 25% loss. When the averaged corrected weight value of each barnacle stage of *E.modestus* presented in this study were compared with the averaged values of laboratory-cultured larvae of Harms (1987), weights 27 to 52% lower were still observed (see Appendix X). This could suggest that preservation losses were much greater and an underestimation still occurred

after the correction factor of 18.15% was applied. However, comparing Harms (1987) data with the present data it is possible to observe that differences found in larval weights from specimens obtained from natural populations of Helgoland (North Sea) and cultured at 12, 18 and 24 °C under excess food were much smaller than the present study. The same occurred with data on carapace width (Harms, 1986) for specimens obtained and cultured in similar conditions (see Table 31). The difference is mainly due to the fact that usually smaller organisms of each stage were found on this study (see section 4.4.2. below). When the weight-width and/or length equations derived in the present study (equations r62 and r72) were applied to Harms data (Table 31), differences ranging from +15 to -35% were found when it was assumed that the width data of each stage presented in Harms (1986) is linked with the weight data published in Harms (1987). Therefore an overall averaged difference of -10% could be assumed between the present weight values and the relatively higher values of Harms (1987).

Table 31. Mean carapace width (µm) and weight values (µg) of the naupliar stages II to VI + cypris of *Elminius modestus* cultured in laboratory at given temperatures by Harms (1986; 1987). Also shown are the predicted DW values using equations r62 and r72 on Harms data, the % of difference and the average and range of DW predicted from Carapace Widths (CW) or Total Length (TL) in this investigation for comparison.

Elminius modestus							
Stage	T (°C)	(Harms, 1986) CW (µm) ± SD(n)	(Harms, 1987) DW(µg)±SD(n)	(Harms, 1986) Predicted DW (µg)	Difference %	**Present study CW (µm) Average(range)**	**Present study Predicted DW (µg) Average (range)**
I	----	----	----	----	----		----
II	6	175 ± 1 ***	----	0.42*	----	**157 (120-180)**	**0.31 (0.15 - 0.45)***
	9	175 ± 4 ***	----	0.42*	----		
	12	174 ± 2 ***	0.39 ± 0.03 (27)	0.41*	+5.89%		
	18	174 ± 3 ***	0.41 ± 0.03 (27)	0.41*	+0.72%		
	24	172 ± 2 ***	0.39 ± 0.03 (26)	0.40*	+2.28%		
III	6	208 ± 3 ***	----	0.67*	----	**187 (160-220)**	**0.50 (0.32 - 0.79)***
	9	200 ± 10 ***	----	0.61*	----		
	12	208 ± 6 ***	0.71 ± 0.04 (19)	0.68*	-4.78%		
	18	203 ± 10 ***	0.75 ± 0.07 (13)	0.63*	-16.26%		
	24	210 ± 7 ***	0.70 ± 0.14 (8)	0.69*	-1.46%		
IV	6	252 ± 1 ***	----	1.16*	----	**222 (180-260)**	**0.81 (0.45 – 1.26)***
	9	244 ± 4 ***	----	1.05*	----		
	12	254 ± 9 ***	1.20 ± 0.08 (20)	1.18*	-1.70%		
	18	261 ± 20 ***	1.47 ± 0.15 (13)	1.28*	-13.22%		
	24	257 ± 7 ***	1.06 ± 0.10 (15)	1.22*	+15.26%		
V	6	312 ± 6 ***	----	2.10*	----	**271 (240-340)**	**1.42 (1.01 - 2.67)***
	9	307 ± 5 ***	----	2.01*	----		
	12	315 ± 7 ***	2.45 ± 0.16 (23)	2.16*	-7.18%		
	18	311 ± 5 ***	2.62 ± 0.18 (20)	2.09*	-20.35%		
	24	311 ± 4 ***	2.33 ± 0.17 (19)	2.08*	-14.98%		
VI	6	390 ± 12 ***	----	3.92*	----	**328 (280-400)**	**2.52 (1.55 - 4.21)***
	9	388 ± 4 ***	----	3.88*	----		
	12	384 ± 10 ***	4.27 ± 0.17 (60)	3.75*	-12.27%		
	18	379 ± 9 ***	5.19 ± 0.18 (39)	3.63*	-30.11%		
	24	362 ± 5 ***	4.39 ± 0.75 (10)	3.19*	-27.44%		
Cypris	6	559 ± 10 ***	----	4.04**	----	**553 (460-700)**	**4.04 (2.36 - 7.52)****
	9	568 ± 26 ***	----	4.21**	----		
	12	573 ± 8 ***	4.56 ± 0.48 (20)	4.33**	-5.10%		
	18	545 ± 38 ***	5.81 ± 0.27 (22)	3.76**	-35.27%		
	24	528 ± 14 ***	4.38 ± 0.28 (28)	3.44**	-21.46%		

Where CW = Carapace Width; DW = Dry Weight; SD = ± 1 Standard Deviation; n = number of replicas; * predicted using equation r62; ** predicted using equation r72; *** n not given. Cypris values are Total Length

4.4.2. Weight x Size measurement.

Width-weight and length-weight regressions accounted for more than 98% of the variability for naupliar stages, and length-weight for 92% for cyprids. The predicted weights of all barnacle species/stages considered from width equations shown on Figure 44, differed from measured weights by +15 to -10%, while the equations of length differed by +13 to -29%, with an overall average of -0.3% for all stages/species on this study, and by an average of -10% against a independent data (Table 31) and can, therefore, be considered accurate and reproducible.

Unfortunately, apart from some weight determinations on some stages of *S.balanoides* from colder regions (i.e. larger animals), no other weight data exists on the species investigated here. The data on *Balanus eburneus* of Jorgensen & Vernberg (1982) is one, if not the only one, on other barnacle larvae (Appendix X a,b). Geary (1991) also provides some weight data for *E.modestus* for this estuary (Appendix X a), but these values were usually 3 to 10 greater than the ones presented by Harms (1987), and even higher when compared with the values measured here. There is no way to explain why Geary's (1991) values were so high, only that maybe an insufficient number of animals for each replicate (5 – 50 depending of stage) were used. The present study followed the numbers employed by Harms (1987) i.e. between 100 – 1000 depending of the stage being considered, and since both results are comparable to the values of Jorgensen & Vernberg (1982) for *Balanus eburneus* that has a similar sized larvae (West & Costlow, 1987), it was decided not to consider Geary (1991) data any further.

The seasonal, overall decrease in size observed for some species was expected, since body size of marine crustaceans is usually inversely related to temperature (McLaren, 1969; Landry, 1978; Mauchline, 1998). *V.stroemia* and *S.balanoides* nauplii did not show this relationship with temperature because the larvae were only present during a short period of time, when very little temperature variation occurred. An interesting factor was the overall positive effect of chlorophyll *a* concentration for some species/stages (Table 25), suggesting that sizes in the field are also affected, in some smaller degree, by food concentration. This food influence could also be inferred from Harms (1986; 1987) data, where an overall lack of variation in size and weight (Table 31) were observed from laboratory cultured barnacles larvae with excess of food (10^5 cells ml^{-1} of *Skeletonema costatum* or ~ 46 mg m^{-3} Chl *a,* according to Anil & Kurian (1996)). This indicates that some mechanism, probably related to the utilization or quality of food or even a combination of biotic and abiotic factors, limited size and consequently the weight of

E.modestus within Southampton Water for most of the year, since developmental sizes of this species, even at similar field levels of chlorophyll (~ 41 mg m^{-3}) were usually lower than the ones reported from laboratory cultures Harms (1986; 1987) (Appendix XI).

About the remaining species nothing can be said, since no published data is available for comparison. However, by similarity, it is possible to infer that the same limitation could occur with the nauplii of other species recorded here presenting an overall mean-size smaller than those obtained from laboratory cultures (Appendix XI). A contrast might be *B.improvisus,* which is apparently influenced by temperature alone (Table 25), explaining why sizes reported from laboratory and field samples are comparable (Appendix XI d).

4.4.3. Abundance, biomass and production.

In terms of stage composition, apart from the recent work of Muxagata *et al*, (2004) on the potential production of *E.modestus* at Cracknore, estimated with data presented here, only the unpublished M.Sc. dissertations of Soares (1958) and Geary (1991) give some information on barnacle larval stages. Geary's (1991) results must be ignored, as only summer-autumn samples were available and all barnacle larvae were assumed to be those of *E.modestus*. In Soares (1958) study the same species and seasonal pattern to the present study was found (Figure 55), although total abundances of *B.crenatus* and *S.balanoides* at Calshot Pier (Figure 1 – Chapter 1) were higher than the values shown here for Calshot. This was mostly due to a higher contribution of older stages (Figure 55). In contrast, *E.modestus* occurred in higher abundances in this survey, where values 74% higher were recorded, on average, for each stage (Figure 45). Soares (1958) did not differentiate *B.improvisus* and *V.stroemia* to stages, but the present total values were 18% lower for the first and 74% higher for the later species. Those differences could probably be due the sampling method used i.e. pump filtration into a '109 meshes to the inch' net (i.e. № 10 ~158 μm according to Boltovskoy (1981b) and Omori & Ikeda (1992)), which would be expected to retain fewer animals but more of the larger forms. Anyway, the shallow and more protected location of Calshot Pier (Figure 1 – Chapter 1) could also be a factor.

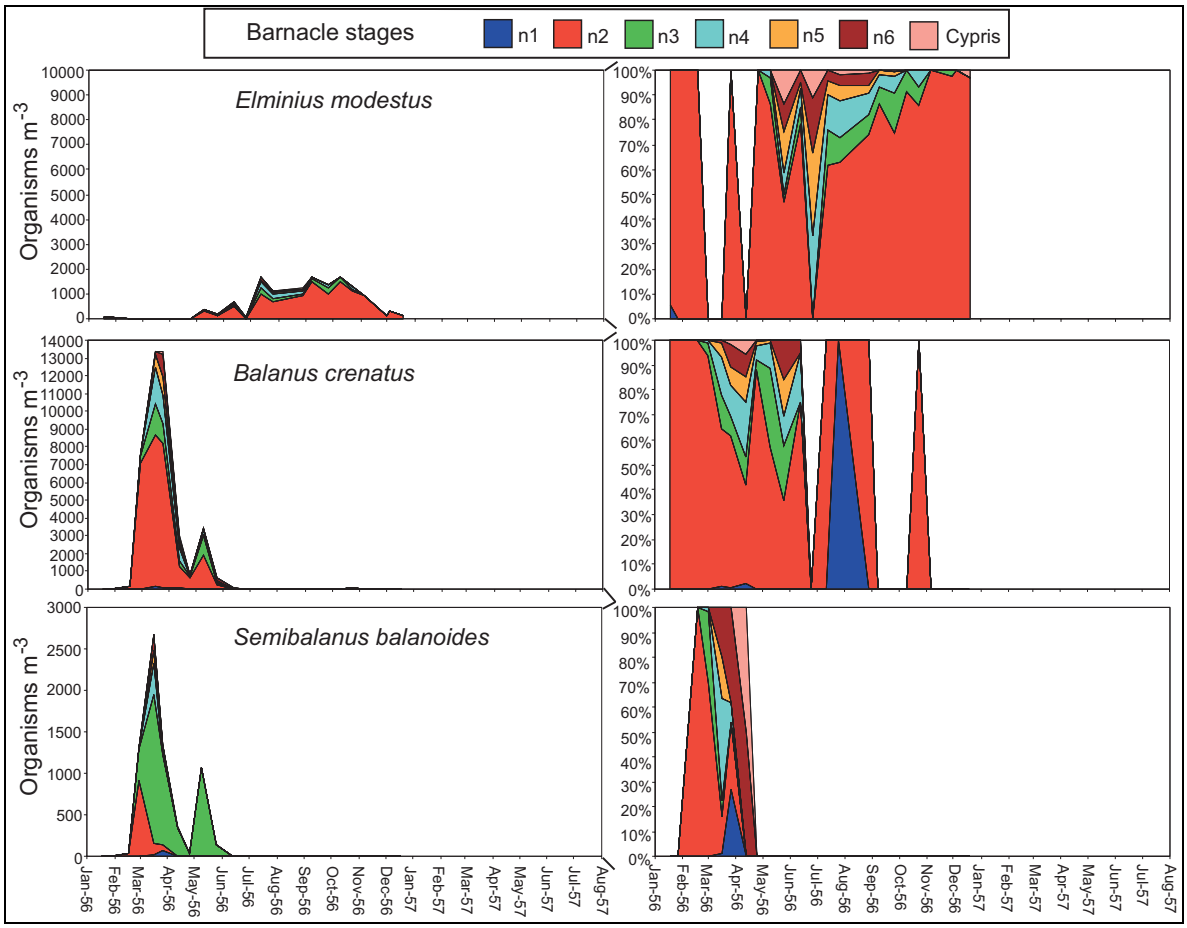


Figure 55. Temporal variability of the larval stages of *Elminius modestus*, *Balanus crenatus* and *Semibalanus balanoides* present in the zooplankton of Calshot during 1956, from the raw data of Soares (1958) (temporal scale were extended from January 1957 to August 1957 for a better comparison with the 2001-2002 results).

During this study the development/growth-rate of barnacles was not measured directly, mainly because of experimental and logistic issues. Short incubations to detect growth of each stage/species considered would require hundreds/thousands of replicates to detect any significant variations in weight (Hirst & McKinnon, 2001), and usually involve live sorting of several hundreds of specimens for each replicate. As pointed out earlier, sorting of some stages from preserved samples, usually took days, and even weeks, to be completed. Even if this task were possible to accomplish there are still several factors that affect the development/growth of specimens in the field that are very difficult to account for in simulated conditions.

Laboratory experiments usually measure the affect of a single parameter, sometimes two and rarely three or more, since the 'addition' of parameters greatly increases the number of replicate experiments to discriminate effects. This again raises the problems of sorting and counting the several hundreds/thousands of animals needed for

each replicate experiment, not including the possible effects of handling on final results. Since inclusion of all variables that affect the development/growth-rate of a particular species in the field is virtually impossible to reproduce in laboratory conditions, greater weight was given to those identified as being more important to the larval development and/or growth, such as temperature and food (Landry, 1975a; Landry, 1975b; McLaren, 1978; Vidal, 1980a; 1980b; McLaren & Corkett, 1981).

Based mainly on the effects of these two parameters, several models have been elaborated for growth-rate estimations of zooplanktonic animals with continuous reproduction, particularly copepods. The model proposed by Ikeda & Motoda (1978) relates growth-rate to respiration, and so requires body-weight and temperature data. The models proposed by Huntley & Boyd (1984) and Huntley & Lopez (1992) are temperature-dependant models, where temperature is the forcing function and animals are not considered food-limited. The models of Landry (1978) and McLaren *et al*., (1989) assume exponential growth and were usually employed to estimate growth rate from preserved samples using demographic information (Runge & Roff, 2000), requiring information on development and weight. Recent growth-rate models (Hirst & Sheader, 1997; Hirst & Lampitt, 1998; Hirst *et al*., 2003) developed with copepod data are based on weight and temperature. With the exception of the models of Huntley & Boyd (1984) and Huntley & Lopez (1992) the remaining models need inputs of temperature and weights found in the field, and this should imply that the growth-rates calculated by these equations already account any variability caused by other factors (e.g. food) and so possibly reflecting actual growth-rates.

When the potential-production of 28.08 mg C $m^{-3}y^{-1}$ for *E.modestus* calculated at Cracknore, using the weight data of Harms (1987) for animals cultured on a food-saturated environment (Muxagata *et al*., 2004), is compared with the values obtained using field-weight values and employing the same equation (i.e. equation 9+12+b in red on Table 26), values ~47% lower were found. This again suggests that some limitation, at least for *E.modestus,* occurred.

The estimates of secondary production presented here are subject to several potential biases. Growth rates are very difficult to measure *in situ* conditions, and so one must rely on the empirical approaches. Since there is no "ideal" method covering all the variability, and also no standard method widely accepted, the averaged value using all the methods possible could be considered a better approximation of the "real" production.

Based on this assumption, the total production of barnacle larvae in Southampton Water from data presented on Tables 26 through 30, could then be assumed to be 24.77,

44.26 and 29.39 mg C m^{-3} yr^{-1} at Cracknore, NW.Netley and Calshot respectively, or 32.80 mg C m^{-3} yr^{-1} (0.09 mg C m^{-3} d^{-1}) on average for the three stations. With *E.modestus* alone accounting for 54.7% of the production followed by *B.crenatus* (35%), *B.improvisus* (6.7%), *S.balanoides* (3.1%) and *V.stroemia* (0.5%). Unfortunately, apart from the results of Muxagata *et al*.,(2004) derived from data presented here, no other data concerning the secondary production of barnacle larvae were found in the literature.

Previous zooplankton production studies within Southampton Water have suggested that barnacle larvae could contribute as much secondary production as calanoid copepods (Hirst, 1996; Hirst *et al*., 1999). The results found here could be taken to corroborate this assumption. The published value of 32.2 mg C m^{-3} yr^{-1} for calanoids at Calshot for the 1993/ 94 period by Hirst *et al*. (1999) is very close to the 29.39 mg C m^{-3} yr^{-1} calculated for barnacles, at Calshot, in the present study. However, as seen in previous chapters, the current zooplankton composition and abundance values of barnacles (Chapter 3) and calanoids (Chapter 2) found during this investigation is significantly higher than the ones presented by Hirst (1996), from which the production values presented on Hirst *et al*. (1999) are derived. Current abundance values approaches those recorded by Zinger (1989) (Chapter 1). If the 1985/86 production values of 345.9, 526.65 and 263.85mg C m^{-3} yr^{-1} for calanoids at Cracknore, NW Netley and Calshot, respectively, estimated from the data of Zinger (1989) by Hirst (1996), are accepted then barnacle larvae production is lower than that of calanoids for these stations, representing 7, 8 and 11% of calanoids production at Cracknore, NW. Netley and Calshot, respectively. Copepod production was also estimated in this investigation, and production values based on copepod abundance derived in this study will be discussed on the following chapters. The production of barnacle larvae estimated during this investigation represented 20 to 31% of *Acartia* spp production, assuming only the production of copepodite stages and adult females.

Looking at values of cirripede production within Southampton Water, the overall value of 32.80 mg C m^{-3} yr^{-1} calculated in the current study is low compared with some selected literature for calanoids in other European estuaries. Escaravage & Soetaert (1993; 1995) reported production rates around 724 mg C m^{-3} yr^{-1} for *Eurytemora affinis* and 556 mg C m^{-3} yr^{-1} for *Acartia tonsa* in the Westerschelde, The Netherlands (assuming C as 40% of DW). Similarly, Guerrero & Rodriguez (1994; 1997) reported values between 768-1304 mg C m^{-3} yr^{-1} for three different species of *Acartia* in Malaga harbour, Spain (assuming C as 40% of DW, and that no production occurred after the study period).

In conclusion, within the main body of Southampton Water meroplankton production, exemplified by the production of barnacle larvae, is lower than that of calanoid copepods.

4.5. Chapter Conclusions.

- Weights for each developmental larval stage of *E.modestus, B.crenatus, B.improvisus*, *S.balanoides* and *V.stroemia* are measured for the first time within Southampton Water, and represent the only field data on these species available anywhere.

- For each barnacle species, regression equations relating carapace-width and total-length with weights for easy biomass assessments are presented.

- Carapace-width and total-length of the stages of *E.modestus, B.crenatus* and *B.improvisus* were negatively correlated with temperature and in some cases also with salinity and positively correlated with chlorophyll concentration. *S.balanoides* and *V.stroemia* did not show any relationship with temperature, but chlorophyll and salinity did have some significant influence on the sizes of some stages.

- Multiple regression equations relating carapace-width and total-length with temperature, salinity and chlorophyll concentration are also presented.

- Comparing production of field and laboratory incubated specimens, production of *E.modestus* was assumed to be limited within Southampton Water, with the same assumption being possible for the other species occurring here.

- Production values of each stage of each barnacle species are being presented for the first time within this estuary as a whole and, an overall production of 32.80 mg C m^{-3} yr^{-1} or 0.09 mg C m^{-3} d^{-1}, was estimated. *E.modestus* alone accounts for 54.7 % of the production, followed by *B.crenatus* (35%), *B.improvisus* (6.7%), *S.balanoides* (3.1%) and *V.stroemia* (0.5%).

- Overall, production of barnacle larvae within Southampton Water is lower than that of calanoid copepods.

Chapter 5

The secondary production of copepods in Southampton Water

5.1. Introduction.

The study of an ecosystem is not complete without knowledge of all of its parts, and even knowing that this will be practically impossible to accomplish, one must try to gather as much information as possible from a single survey in order to make generalizations more credible, without the bias introduced by inter-annual variability, sampling effort and different methodologies. In line with this, and since barnacle larvae accounted on average for 18% of the overall zooplankton community in this study (Chapter 1), the assessment of secondary production of barnacles presented in the previous chapter would be more useful with the assessment of a previously studied major component for comparison.

The copepods are an obvious choice, since they are the largest component of all groups present in the zooplankton of estuarine, neritic and oceanic areas (Raymont, 1983; Mauchline, 1998; Boxshall & Halsey, 2004), and the most reported zooplankton component (Evans, 1977; Durbin & Durbin, 1978; Landry, 1978; Burkill & Kendall, 1982; Uye, 1982; Daro & van Gijsegen, 1984; Kimmerer & McKinnon, 1987; Castel & Feurtet, 1989; Chisholm & Roff, 1990a; Escaravage & Soetaert, 1993; Escaravage & Soetaert, 1995; Peitsch, 1995; Hay, 1995; Poulet *et al*., 1995; Webber & Roff, 1995; Fransz & Gonzalez, 1995; Mauchline, 1998; Uye & Sano, 1998; Hirst *et al*., 1999). Also, copepods and their larval stages form the single largest food resource for several important pelagic predators.

During this study copepods contributed on average 66%, by abundance, of the zooplankton community of this estuary, and were identified in Chapter 1, as the largest and the most important component to be investigated. Despite the number of investigations on the zooplanktonic community of Southampton Water (Conover, 1957; Soares, 1958; Raymont & Carrie, 1964; Lance & Raymont, 1964; Reubold, 1988; Zinger, 1989; Williams & Reubold, 1990; Geary, 1991; Lucas, 1993; Lucas & Williams, 1994; Frid *et al*., 1994; Lucas *et al*., 1995; Hirst, 1996; Castro-Longoria & Williams, 1996; Lucas *et al*.,

1997; Castro-Longoria, 1998; Hirst *et al*., 1999; Chinnery, 2002; Muxagata *et al*., 2004) only Hirst (1996) and Hirst *et al*. (1999) have presented results on the secondary production of copepods within this estuary. From Hirst *et al*. (1999) total calanoid production at Calshot was estimated to be only 32.2 mg C $m^{-3}yr^{-1}$, which was considered to be very low; however, in retrospect, it only reflected the low abundance values found. As indicated in previous chapters, the abundance values of Hirst (1996) (from which Hirst *et al*. (1999) production values are derived) were atypically low for ~118μm mesh collections, contrasting with the results of this study and with other studies at the same station (Zinger, 1989) or neighbouring areas (Raymont & Carrie, 1964) employing similar-sized meshes.

Based on that, the present chapter is designed to expand the previous information on pelagic carbon flux within Southampton Water presented by Hirst (1996) and Hirst *et al*. (1999) by reassessing the production and contribution of calanoids to pelagic fluxes, as well as by assessing the contribution of copepod nauplii, harpacticoids and cyclopoids. Production will be determined by a number of methodologies including some already employed for barnacle larvae on Chapter 4.

5.2. Material and Methods.

The methodology employed for counting and identification of the different species has been already presented in Chapter 1.

5.2.1. Weight measurements.

The same methodology utilized for barnacle larvae dry weight determination was employed for copepods. The difference was in the numbers used, and in the fact that for *Euterpina acutifrons*, *Oithona nana* and copepod nauplii no distinction of size/stage were made, and the weights for these three groups were based on an average of all determinations, irrespective of stages (see Table 32). For copepod Dry Weight (DW) determinations, between 25 – 7288 organisms of a particular species were sorted from the preserved samples and pre-counted batches of 25 – 2500 organisms (Table 32) were then submitted to the same procedures employed for barnacle larvae, and fully described in Chapter 4.

The individual weights of each species/stage, in terms of Dry Weight (DW), were the averaged values of the replicates after the correction factor of 18.15% established for barnacles were applied. Differences between replicates varied, and errors were calculated as a percentage of the mean averaged for all determinations. During this work the error was around ± 4 %.

Table 32. Number (n°) of copepods utilized in each biomass determination.

Stages	*Acartia spp.*			*Euterpina acutifrons*		*Oithona nana*		*Nauplii*	
	PL	n°	rep.	n°	rep.	n°	rep.	n°	rep.
nauplii	-	-	-	-	-	-	-	300	2
adults+copepodites	-	-	-	100	2	100	2	-	-
adults+copepodites	-	-	-	150	1	200	2	-	-
adults+copepodites	-	-	-	200	1	344	2	-	-
adults+copepodites	-	-	-	300	1	500	2	-	-
adults+copepodites	-	-	-	400	1	1000	1	-	-
adults+copepodites	-	-	-	-	-	1500	1	-	-
adults+copepodites	-	-	-	-	-	2500	1	-	-
Acartia spp. C1	288	50	2	-	-	-	-	-	-
A. margalefi adult ♀	504	100	2	-	-	-	-	-	-
A. margalefi adult ♀	576	100	1	-	-	-	-	-	-
A.discaudata adult ♀	684	80	2	-	-	-	-	-	-
A.discaudata adult ♂	648	60	2	-	-	-	-	-	-
A.bifilosa adult ♀	828	50/60	2/1	-	-	-	-	-	-
A.bifilosa adult ♂	828	50	2	-	-	-	-	-	-
A.clausi adult ♀	792	50	2	-	-	-	-	-	-
A.clausi adult ♂	792	25	1	-	-	-	-	-	-
A.tonsa adult ♀	900	30/60	1/2	-	-	-	-	-	-

Where: rep. = the number of replicates made for each determination; PL= the average prosome length in µm individual^{-1} of the *Acartia* utilized; - = indicates no data.

5.2.2. Size measurements.

During this investigation only *Acartia* spp. were measured, with prosome length measurements being taken for all *Acartia* copepodites present in the sub-samples using a micrometric scale (± 36 μm) attached to the Stereomicroscope eyepiece. Since 5 different species were recorded during the present investigation (Chapter 2), the differentiation of the congeneric copepodites stages was difficult. Because of that, it was decided to group *Acartia* into 11 size categories, 5 for copepodites and another 6 reflecting the different adult species (Table 33). Only copepodites I to V were measured on a regular basis, with copepodite VI, i.e. adults, identified, sexed and sometimes measured for consistency. The division of copepodites into 5 size categories alluded the five pre-adult copepodite stages, but it is clear that different stages are present on each one of the defined size-intervals. That was not the best option, but was dictated by time constraints.

Table 33. Prosome-Length (PL) size categories considered for *Acartia* spp. copepodites and observed range of sizes of adults.

Category	PL - Interval	(average)	Species	PL - Interval	(average)
C1	288 – 360 μm	(324 μm)	*A. margalefi* adults ♀+♂	432 – 576 μm	(504 μm)
C2	361 – 432 μm	(396 μm)	*A.discaudata* adult ♂	576 – 720 μm	(648 μm)
C3	433 – 504 μm	(468 μm)	*A.discaudata* adult ♀	612 – 756 μm	(684 μm)
C4	505 – 576 μm	(540 μm)	*A.clausi* adults ♀+♂	756 – 828 μm	(792 μm)
C5	577 – 648 μm	(612 μm)	*A.bifilosa* adults ♀+♂	720 – 936 μm	(828 μm)
-	-		*A.tonsa* adult ♀	864 – 936 μm	(900 μm)

5.2.3. Regression analysis.

To stabilize the variance of the data, weight and prosome length were $\log_{10}$ transformed before being used in any analysis. Simple linear regressions were calculated with STATISTICA for Windows. Regression graphs were drawn using SigmaPlot for Windows.

5.2.4. Growth rates.

Growth rates were estimated using the general equations/methods proposed/used by Ikeda & Motoda (1978), Huntley & Boyd (1984), Huntley & Lopez (1992), Hirst & Sheader (1997), Hirst & Lampitt (1998), Hirst & Bunker (2003) and Hirst *et al*. (2003). The set of equations employed are summarized on Table 34. Since no distinction between stages or even between males and females were made for *O.nana* and *E.acutifrons*, both were assumed to grow at the same rate as copepodites. *Acartia* were differentiated in

copepodites and adults (males and females) and, in this case, production was calculated for each component assuming that males grow[9] as much as females, or that both grow as much as copepodites (when growth of females were not defined individually).

Table 34. Production equation employed with the equations used to estimate copepod growth.

Eq.9→$\sum P = B*g$

	Growth Equation	taxon applied	Reference
a	$g=7.714*10^{[0.254*(T)-0.126]}*W_i^{(-0.0109(T)+0.892)}* w_{ic}^{-1}$	all	(Ikeda & Motoda, 1978)
d	$g=0.0542*e^{0.111*(T)}$	all	(Huntley & Boyd, 1984)
e	$g=0.0445*e^{0.111*(T)}$	all	(Huntley & Lopez, 1992)
f	$Log_{10}(g)=-1.1355+[0.0246*(T)]-[0.2962*\log_{10}(w_{ic})]$	all	(Hirst & Sheader, 1997)
g	$Log_{10}(g)=-1.1408+[0.0208*(T)]-[0.3221*\log_{10}(w_{ic})]$	Br+S (adults+juv.)	(Hirst & Lampitt, 1998)
h	$Log_{10}(g)=-1.529+[0.0345*(T)]-[0.128*\log_{10}(w_{ic})]$	Br+S (all Br+S)	(Hirst *et al*., 2003)
i	$Log_{10}(g)=-0.6447+[0.0111*(T)]-[0.2917*\log_{10}(w_{ic})]$	Br (juveniles)	(Hirst & Lampitt, 1998)
j	$Log_{10}(g)=-0.6516-[0.5244*\log_{10}(w_{ic})]$	Br (adults)	(Hirst & Lampitt, 1998)
k	$Log_{10}(g)=-0.7568+[0.0087*(T)]-[0.4902*\log_{10}(w_{ic})]$	Br (adults+juveniles)	(Hirst & Lampitt, 1998)
l	$Log_{10}(g)=-1.7255+[0.0464*(T)]$	S (adults+juveniles)	(Hirst & Lampitt, 1998)
m	$Log_{10}(g)=-0.418-[0.141*\log_{10}(w_{ic})]$	Br (nauplii)	(Hirst *et al*., 2003)
n	$Log_{10}(g)=-1.230+[0.0352*(T)]-[0.233*\log_{10}(w_{ic})]$	Br (copepodite)	(Hirst *et al*., 2003)
o	$Log_{10}(g)=-1.196+[0.0232*(T)]-[0.285*\log_{10}(w_{ic})]$	Br (adults)	(Hirst *et al*., 2003)
p	$Log_{10}(g)=-1.222+[0.0271*(T)]-[0.287*\log_{10}(w_{ic})]$	Br (all Br)	(Hirst *et al*., 2003)
q	$Log_{10}(g)=-1.185+[0.0138*(T)]-[0.252*\log_{10}(w_{ic})]$	S (nauplii)	(Hirst *et al*., 2003)
r	$Log_{10}(g)=-1.647+[0.0324*(T)]+[0.0657*\log_{10}(w_{ic})]$	S (all S)	(Hirst *et al*., 2003)
s	$Log_{10}(g)=-0.105+[-0.0143*(T)]+[-0.363*\log_{10}(w_{ic})]+[0.135*\log_{10}(Chl\textit{a})]$	Br (juveniles)	(Hirst & Bunker, 2003)
t	$Log_{10}(g)=-1.348+[0.0125*(T)]+[-0.230*\log_{10}(w_{ic})]+[0.729*\log_{10}(Chl\textit{a})]$	Br (adults)	(Hirst & Bunker, 2003)

Where:
P = average production of a particular size class/stage in mg dry weight $m^{-3}d^{-1}$;
B = biomass (i.e. N_i*w_i);
N_i= number of organisms m^{-3} at stage i;
w_i = the average dry weight at stage i (in µg $individual^{-1}$);
g = growth rate d^{-1} (for adults it is considered as the specific egg/spermatophores production rate d^{-1});
W_i = the average dry weight at stage i (in mg $individual^{-1}$);
w_{ic} = the average carbon weight at stage i (in µg $individual^{-1}$);
Chl*a* = Chlorophyll *a* concentration (µg Chl *a* L^{-1});
T = temperature in °C;
Br = Broadcast-spawners;
S = Sac-spawners.

5.2.5. Production.

Production of each copepod species was calculated by the "instantaneous-growth" approach as described by equation 9 presented in Chapter 4 and also summarized in Table 34. For the annual production estimates, the calculated daily production and biomass of a particular stage/species for a sampling day was assumed to represent the mean over a time

[9] Growth had been defined on previous chapter as the increase in mass from one stage to another, in this sense adult male and female does not grows, but when they reach maturity their growth can be expressed as the output of eggs and spermatophores as well as changes in body weight (Hirst & McKinnon, 2001). Since most growth and production of males are usually considered negligible, the results will present those values of males and females separately.

interval between two successive midpoints of the inter-sample period, and converted to carbon assuming carbon as 40% of dry-weight (Omori & Ikeda, 1992; Postel *et al*., 2000). Total annual production of *Acartia* will be equal to the sum of weight increments for all the stages throughout the year.

5.3. Results.

The total composition and general contribution of each copepod species in the mesozooplankton of Southampton Water have been already presented in Chapters 2 and 3. The results presented here illustrate the contribution of each size category of *Acartia* spp, as well as such details necessary for the estimates of secondary production of *Acartia* spp., *E.acutifrons*, *O.nana* and copepod nauplii.

5.3.1. Weight-length.

The mean weight values of copepod nauplii, *O.nana*, *E.acutifrons* and *Acartia* (size-stages and adults) measured from organisms found in Southampton Water are presented in Table 35.

Table 35. Mean weight values (µg) of the copepods/stages considered. Also shown are the prosome lengths (PL) of the *Acartia* species/stages used in the biomass analysis

Species/stages	PL±SD (n)	**DW±SD (n)
Copepod nauplii	----	0.45±0.09 (2)
Oithona nana	----	0.54±0.07 (11)
Euterpina acutifrons	----	0.99±0.14 (6)
Acartia ┐	----	----
Acartia spp. C1	288±0.00 (100)	0.56±0.03 (2)
A. margalefi adult ♀	504±0.00 (200)	1.37±0.15 (2)
A. margalefi adult ♀	576±0.00 (100)	3.27 (1)
A.discaudata adult ♀	684±0.00 (160)	4.68±0.17 (2)
A.discaudata adult ♂	648±0.00 (120)	4.29±0.03 (2)
A.bifilosa adult ♀	828±0.00 (160)	7.79±0.20 (3)
A.bifilosa adult ♂	828±0.00 (100)	7.70±0.37 (2)
A.clausi adult ♀	792±0.00 (100)	5.85±0.22 (2)
A.clausi adult ♂	792±0.00 (25)	6.24 (1)
A.tonsa adult ♀	900±0.00 (150)	9.96±0.36 (3)

Where:
DW = Dry Weight (µg);
PL = Prosome Length (µm);
SD = Standard deviation;
---- = not available;
n = number of organisms measured/ or replicas (the n° of organisms utilized for each weight replica in this work can be seen inTable 32)

In order to estimate the biomass of each size class of *Acartia* considered, the average prosome length of the animals used in the weight analysis were recorded (Table 35), and length-weight relationship were established using all data available (Figure 56). The resulting equation (r73) can be seen on (Figure 56). *Euterpina acutifrons*, *Oithona*

nana and copepod nauplii were not measured and their biomass was based on the average values presented in Table 35.

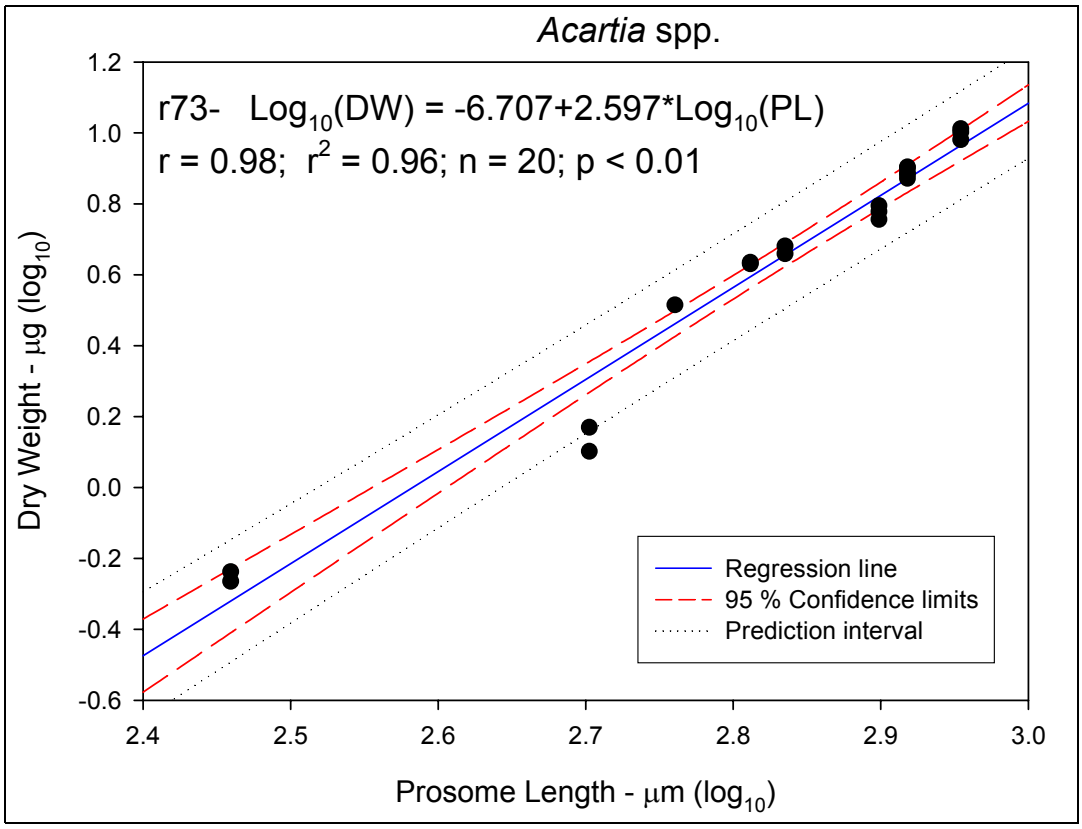


Figure 56. Regression analysis between *Acartia* Dry Weight (DW) values with prosome length (PL)

5.3.2. Abundance, biomass and production.

5.3.2.1. *Acartia* spp.

Total seasonal contributions of *Acartia* in Southampton Water have already been presented in Chapter 2, and is now presented in more detail, with the seasonal contribution of each size category. From Figure 57 it is possible to see that size class C2 is the most abundant, averaging ~29% of all *Acartia* found. Usually, trends in the abundance of each copepodite size class followed the same pattern at the three stations, with an early burst observed in spring, usually followed by a greater one during summer. At Cracknore and NW.Netley a late outburst was also detected in late autumn, i.e. November-December. A remarkable feature was the massive peak of C2 in April 2002 at NW. Netley with 9965 organisms m^{-3}, with C3, C4 and C5 also presenting peaks well in excess of 2000 organisms m^{-3} at the same time. With five congeneric species occurring together it was not possible to distinguish any obvious cohorts, with no clear relation being observed between the peaks of adults and copepodites. At Calshot and NW. Netley however, adult *Acartia discaudata* peaks were followed by peaks of copepodite stages, while at Cracknore, adults and copepodites apparently peaked at the same time.

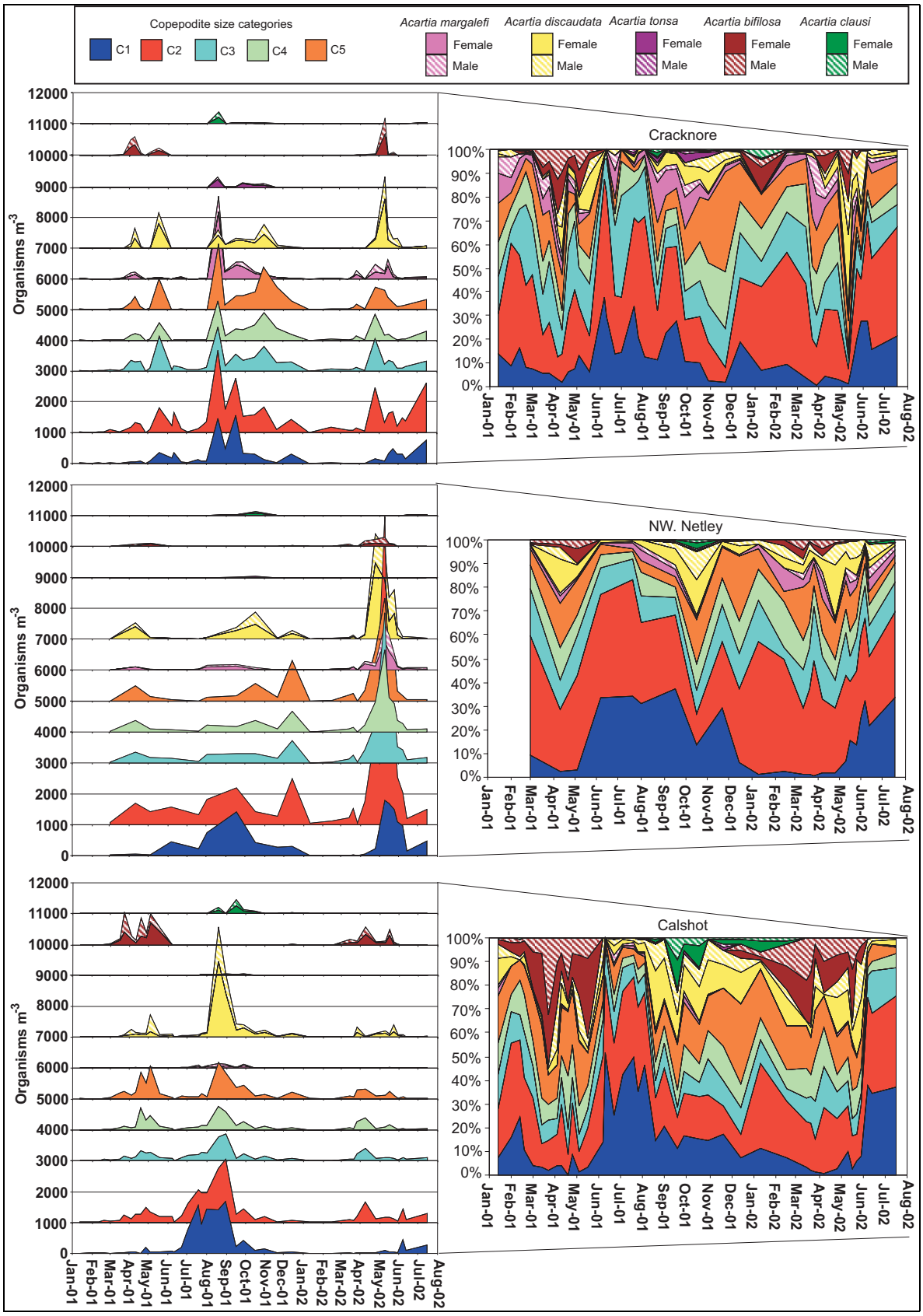


Figure 57. Temporal variability of the size stages of *Acartia* spp. present in the zooplankton of Southampton Water during 2001-2002 defined as abundance and % composition (Note that scale should be re-initiated at the base of each category).

Usually males were less abundant than females, with females averaging 75, 68 and 58% of the adult population at Cracknore, NW.Netley and Calshot respectively. Males were apparently more abundant than females earlier in the season, however.

Total biomass of *Acartia* for the period was 990.95, 1221.45 and 873.38 mg C m^{-3} at Cracknore, NW. Netley and Calshot, respectively. Its daily variation followed total *Acartia* abundances and can be seen of Figure 58. The production of *Acartia* based on its temporal abundance and biomass variability is summarized in Table 36.

Table 36. Annual production estimates (in mg C $m^{-3}yr^{-1}$) of each size category of *Acartia* spp. obtained using the respective equations summarized in Table 34. Total column also shows the production of males assuming that males and females grows at the same rate or as much as copepodites.

Cracknore											
Equation	C1	C2	C3	C4	C5	♀*Acartia margalefi*	♀*Acartia discaudata*	♀*Acartia bifilosa*	♀*Acartia clausi*	♀*Acartia tonsa*	Total +♀ /+♀♂
Eq. 9+a	6.38	17.77	12.56	13.11	23.50	9.30	11.67	2.87	1.48	3.20	101.84/110.04
Eq. 9+d	6.68	21.88	17.88	20.67	40.54	13.52	21.97	6.21	3.04	7.31	159.70/172.97
Eq. 9+e	5.58	18.26	14.91	17.23	33.81	11.30	18.30	5.16	2.54	6.10	133.21/144.25
Eq. 9+f	5.53	15.86	12.08	12.43	22.11	7.70	11.45	3.28	1.15	2.64	94.24 /102.88
Eq. 9+g	4.90	13.92	10.60	10.79	19.02	6.59	9.83	2.85	0.95	2.16	81.60 /89.18
Eq. 9+h	2.60	8.05	6.43	7.06	13.28	4.45	7.11	2.07	0.83	1.97	53.85 /58.68
Eq. 9+i+j	10.26	29.93	23.70	24.32	43.26	9.50	13.69	4.09	1.01	2.24	162.00/173.95
Eq. 9+k	9.47	25.00	18.28	17.41	29.02	10.32	14.52	4.18	1.17	2.60	131.95/144.22
Eq. 9+n+o	6.12	17.93	13.67	14.44	26.24	6.32	9.58	2.78	0.96	2.20	100.25/107.47
Eq. 9+p	4.92	14.14	10.75	11.10	19.81	6.95	10.25	2.90	1.06	2.42	84.30 /91.94
Eq. 9+s+t	18.08	52.43	43.02	41.23	71.59	2.68	7.44	16.58	4.43	2.29	259.78/274.13
Average	7.32	21.38	16.72	17.25	31.11	8.06	12.35	4.82	1.69	3.19	123.88/133.61
NW.Netley											
Equation	C1	C2	C3	C4	C5	♀*Acartia margalefi*	♀*Acartia discaudata*	♀*Acartia bifilosa*	♀*Acartia clausi*	♀*Acartia tonsa*	Total +♀ /+♀♂
Eq. 9+a	11.33	28.49	15.63	14.62	23.56	3.93	19.70	1.62	0.93	0.47	120.27/133.65
Eq. 9+d	12.10	36.71	22.83	23.56	41.70	5.96	37.36	3.49	1.93	1.07	186.71/211.17
Eq. 9+e	10.10	30.58	19.01	19.62	34.70	4.97	31.09	2.90	1.61	0.89	155.46/175.82
Eq. 9+f	10.36	29.59	16.59	15.40	25.80	3.94	20.53	1.81	0.84	0.43	125.28/139.26
Eq. 9+g	9.23	26.44	14.71	13.54	22.63	3.46	17.77	1.56	0.70	0.38	110.42/122.52
Eq. 9+h	4.80	14.35	8.57	8.44	14.69	2.14	12.46	1.15	0.57	0.31	67.49 /75.79
Eq. 9+i+j	19.58	59.37	33.81	31.55	54.09	5.69	25.81	2.20	0.83	0.40	233.34/250.99
Eq. 9+k	18.13	50.11	26.24	22.77	36.72	5.85	26.89	2.27	0.93	0.45	190.36/209.05
Eq. 9+n+o	11.29	31.89	18.17	17.22	28.93	3.27	17.22	1.53	0.70	0.36	130.57/142.05
Eq. 9+p	9.19	26.09	14.65	13.63	22.81	3.50	18.28	1.60	0.76	0.39	110.88/123.31
Eq. 9+s+t	35.40	111.9	62.49	57.06	97.36	0.59	4.00	18.39	1.69	0.28	389.22/398.85
Average	13.77	40.50	22.97	21.58	36.64	3.94	21.01	3.50	1.04	0.49	165.45/180.22
Calshot											
Equation	C1	C2	C3	C4	C5	♀*Acartia margalefi*	♀*Acartia discaudata*	♀*Acartia bifilosa*	♀*Acartia clausi*	♀*Acartia tonsa*	Total +♀ /+♀♂
Eq. 9+a	8.87	13.87	7.41	8.30	15.30	0.68	21.25	6.14	2.26	0.74	84.82 /101.01
Eq. 9+d	8.93	16.70	10.29	13.00	26.36	0.99	38.94	13.31	4.68	1.69	134.88/166.64
Eq. 9+e	7.46	13.95	8.59	10.85	21.99	0.83	32.57	11.05	3.90	1.38	112.56/137.41
Eq. 9+f	6.78	11.49	6.51	7.71	14.45	0.55	16.72	7.36	1.95	0.57	74.10 /89.28
Eq. 9+g	5.92	10.01	5.66	6.69	12.46	0.47	13.91	6.45	1.62	0.47	63.64 /76.64
Eq. 9+h	3.31	5.96	3.56	4.40	8.64	0.32	11.27	4.55	1.35	0.44	43.80 /53.31
Eq. 9+i+j	11.89	21.11	12.36	15.09	28.61	0.65	16.37	9.68	1.89	0.46	118.11/136.08
Eq. 9+k	10.87	17.54	9.48	10.81	19.25	0.72	18.60	9.71	2.12	0.54	99.64 /118.67
Eq. 9+n+o	7.81	13.31	7.58	8.99	17.06	0.45	13.82	6.27	1.62	0.48	77.40 /90.09
Eq. 9+p	6.09	10.30	5.83	6.89	12.92	0.50	15.28	6.48	1.77	0.53	66.60 /80.20
Eq. 9+s+t	18.50	34.84	20.91	26.13	49.44	4.94	0.42	13.31	11.12	0.44	180.05/197.50
Average	8.77	15.37	8.93	10.81	20.59	1.01	18.10	8.57	3.12	0.70	95.96 /113.17

Based on Table 36, the overall average annual production of *Acartia* spp. for the three stations was 128.43 mg C m^{-3} (assuming only adult female growth), with copepodite stages I to V accounting for 75% of this value, on average. Production calculated using the growth rates of Hirst & Lampitt (1998) gave the closest production estimate to the overall mean, and because of this it was chosen to illustrate the daily contribution of each size category in Figure 58 (note that production of males were not included) .

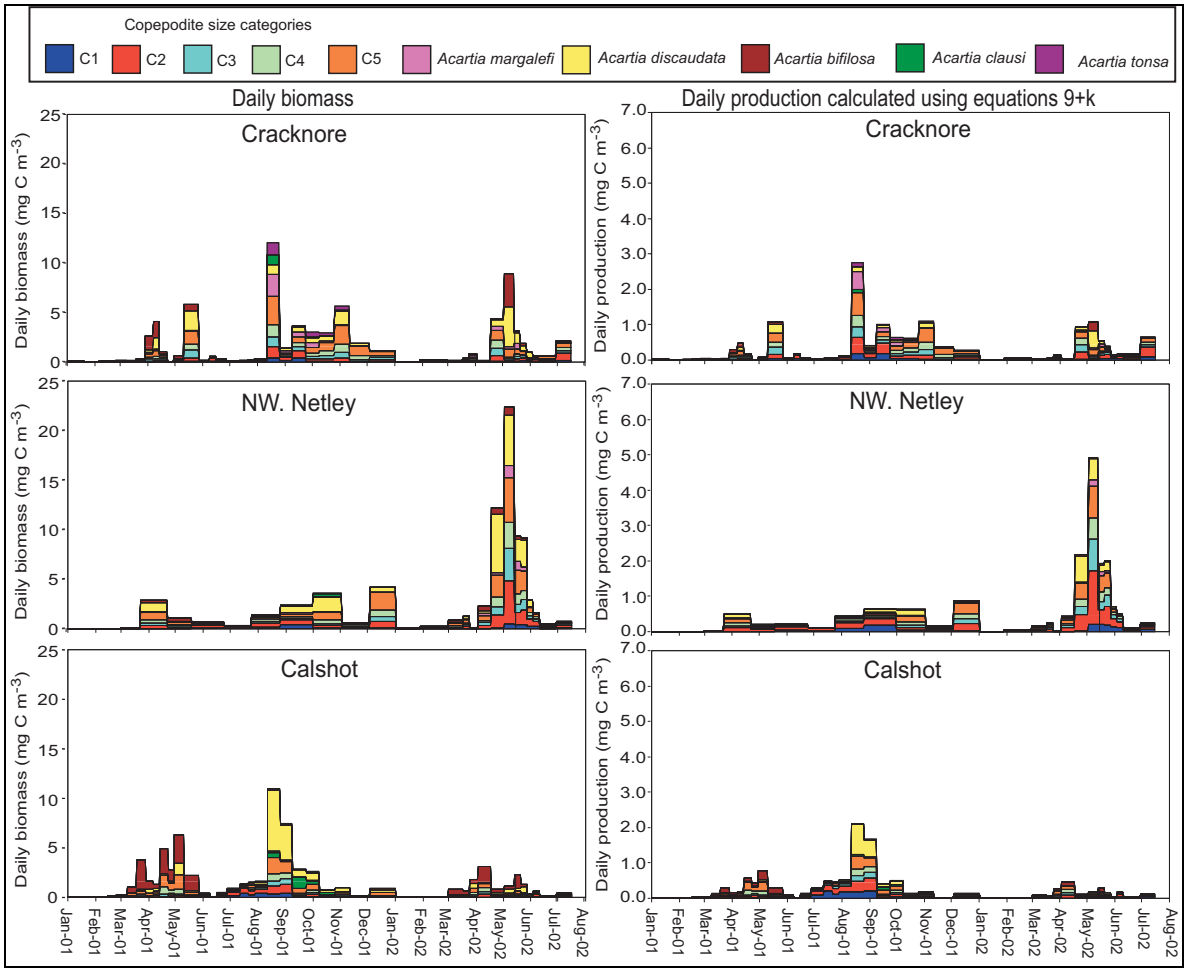


Figure 58. Seasonal production and biomass of the size stages of *Acartia* spp. present in the zooplankton of Southampton Water during 2001-2002. Adult biomass reflects the biomass of males and females while production only includes females.

Overall biomass and production followed the seasonality of abundance, being low during winter and having two productive seasons, a short one during spring and an extended one during summer-autumn.

5.3.2.2. Copepod nauplii, *Oithona nana* and *Euterpina acutifrons*.

The total seasonal contribution of copepod nauplii, *O.nana* and *E.acutifrons* have been presented in Chapter 2. Total biomass of copepod nauplii for the period was 198.21, 251.76, 116.46 mg C m^{-3}, while for *E.acutifrons* it was 252.22, 190.03 and 256.58 mg C m^{-3} and for *O.nana* 757.22, 76.34 and 8.64 mg C m^{-3} at Cracknore, NW. Netley and Calshot respectively. Daily biomass variation of those three groups/species can be seen in Figure 59.

Table 37. Total and annual production estimates (in mg C $m^{-3}yr^{-1}$) of copepod nauplii, *Oithona nana* and *Euterpina acutifrons* obtained using the respective equations summarized in Table 34. Production values assume that both male and female grow at the same rate or as much as copepodites.

Cracknore								
	Nauplii		*O. nana*		*E. acutifrons*		Total	
Equation	all	year	all	year	all	year	all	year
Eq. 9+a	71.10	46.17	261.40	169.77	89.90	58.39	422.40	274.33
Eq. 9+d	65.67	42.65	258.06	167.60	102.63	66.77	426.36	277.03
Eq. 9+e	54.86	35.63	215.53	139.98	85.84	55.75	356.22	231.36
Eq. 9+f	60.04	38.99	222.51	144.51	68.18	44.28	350.72	227.78
Eq. 9+g	53.71	34.89	197.61	128.34	58.77	38.17	310.09	201.39
Eq. 9+h	64.26	41.73	101.95	66.21	35.85	23.28	202.06	131.23
Eq. 9+l	-	-	84.88	55.12	33.60	21.82	215.04	139.66
Eq. 9+m	96.56	62.72	-	-	-	-	added above	
Eq. 9+q	33.09	21.49	-	-	-	-	added below	
Eq. 9+r	-	-	53.21	34.56	20.89	13.56	107.19	69.61
Average	62.41	40.53	174.39	113.26	61.96	40.25	298.76	194.07
NW.Netley								
	Nauplii		*O. nana*		*E. acutifrons*		Total	
Equation	all	year	all	year	all	year	all	year
Eq. 9+a	75.28	54.63	21.58	15.66	68.05	49.38	164.92	119.67
Eq. 9+d	72.49	52.60	22.30	16.18	77.51	56.24	172.30	125.03
Eq. 9+e	60.48	43.88	18.60	13.50	64.83	47.05	143.91	104.43
Eq. 9+f	71.04	51.55	20.77	15.07	51.34	37.25	143.15	103.87
Eq. 9+g	64.27	46.64	18.67	13.55	44.25	32.11	127.19	92.30
Eq. 9+h	73.81	53.56	9.21	6.69	27.02	19.60	110.04	79.85
Eq. 9+l	-	-	7.37	5.35	25.37	18.41	155.39	112.76
Eq. 9+m	122.65	89.00	-	-	-	-	added above	
Eq. 9+q	40.41	29.33	-	-	-	-	added below	
Eq. 9+r	-	-	4.84	3.51	15.74	11.42	60.99	44.26
Average	72.55	52.65	15.42	11.19	46.76	33.93	134.74	97.77
Calshot								
	Nauplii		*O. nana*		*E. acutifrons*		Total	
Equation	all	year	all	year	all	year	all	year
Eq. 9+a	37.42	24.31	3.13	2.03	87.05	56.54	127.60	82.87
Eq. 9+d	35.51	23.06	3.03	1.97	100.29	65.25	138.83	90.28
Eq. 9+e	29.64	19.25	2.53	1.65	83.85	54.46	116.02	75.35
Eq. 9+f	33.85	21.99	2.55	1.66	67.96	44.14	104.37	67.78
Eq. 9+g	30.49	19.80	2.26	1.47	58.77	38.17	91.52	59.44
Eq. 9+h	35.60	23.12	1.18	0.77	35.44	23.01	72.22	46.90
Eq. 9+l	-	-	1.00	0.65	32.87	21.35	90.61	58.85
Eq. 9+m	56.74	36.85	-	-	-	-	added above	
Eq. 9+q	19.00	12.34	-	-	-	-	added below	
Eq. 9+r	-	-	0.73	0.48	20.68	13.43	40.42	26.25
Average	34.78	22.59	2.05	1.33	60.87	39.54	97.70	63.46

The production of copepod nauplii, *O.nana* and *E.acutifrons* based on their temporal abundance and biomass variability is summarized in Table 37. The overall, averaged annual production of copepod nauplii for the three stations was 38.59 mg C $m^{-3}yr^{-1}$, while for *O.nana* and *E.acutifrons* it was 41.93 and 37.91 mg C $m^{-3}yr^{-1}$, respectively. Since production calculated using the growth equation (g on Table 34) of Hirst & Lampitt (1998) gave a close value to the overall average (Table 37), this estimate was chosen to illustrate the daily contribution of each at each station (Figure 59).

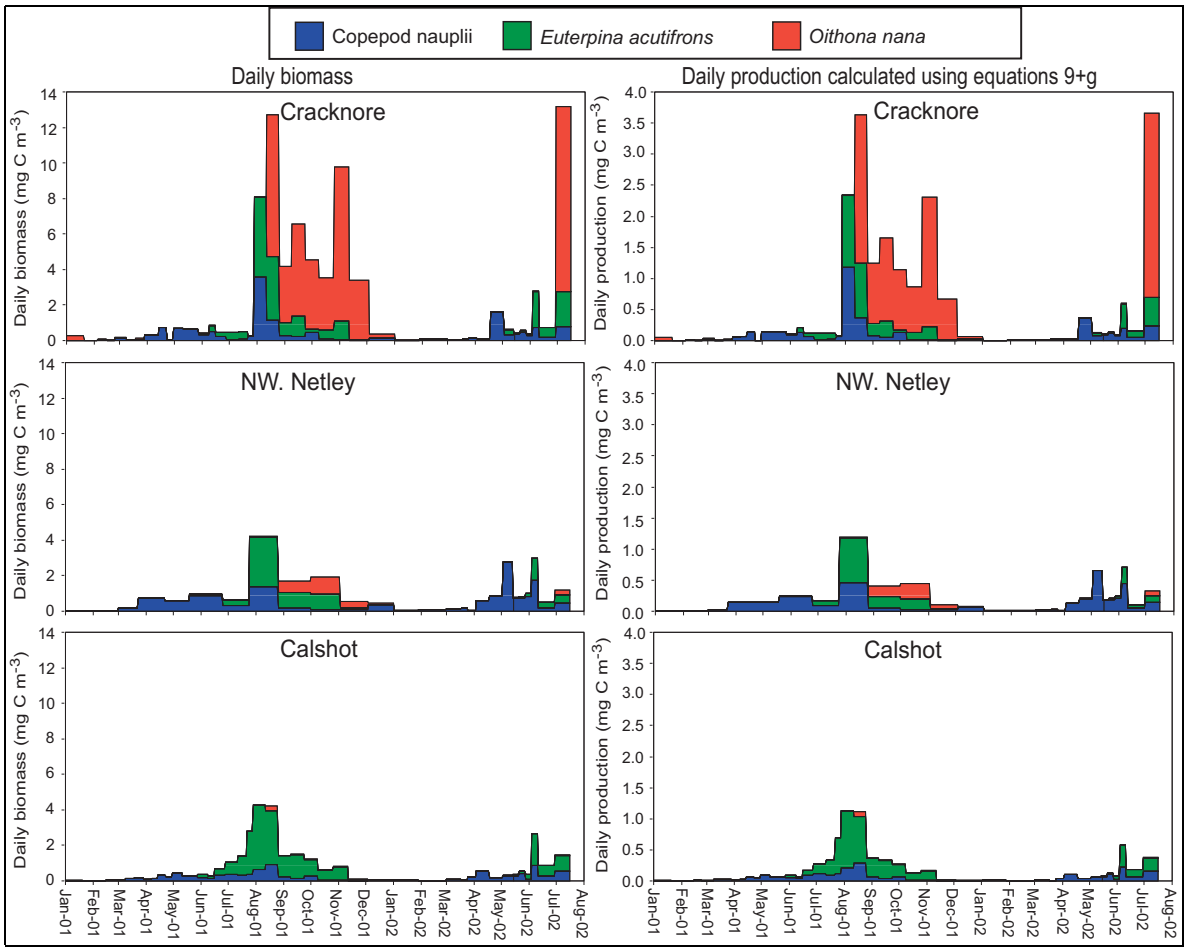


Figure 59. Seasonal production and biomass of copepod nauplii, *Oithona nana* and *Euterpina acutifrons* present in the zooplankton of Southampton Water during 2001-2002.

5.4. Discussion.

The effects of formalin preservation on marine micro-crustaceans have been discussed (Chapter 4), however it is useful to stress that the correction factor of 18.15% used during this investigation seems appropriate here, since the corrected weight of the different species of *Acartia* in this study falls in the range reported for this genus (Durbin & Durbin, 1978; Landry, 1978; Hirst & Lampitt, 1998; Hirst *et al*., 2003). This is also confirmed when the prosome length-weight relationship established for *A.bifilosa* and *A.clausi* (Durbin & Durbin, 1978; Landry, 1978; Uye, 1982; Tanskanen, 1994; Mauchline, 1998) predicts weights, on average -12% lower in terms of dry weight and -15% for Carbon, than the ones employed here. The length-weight equation established during this investigation (r73 on Figure 56) accounted for more than 96% of the variability encountered, with predicted weights of any *Acartia* species/categories differing from measured weights by only +1.4% on average.

As stated in the methods section, size measurements were only done regularly for copepodite stages of *Acartia* primarily to enable them to be grouped in size intervals, with adults only being measured occasionally, and with the average size-range of each class being used for biomass assessments (Table 33). However, differences in size were noted between adults of the same species, possibly reflecting the negative relationship with temperature that has been reported for some calanoid species in this estuary (Hirst *et al*., 1999), and observed for other species of *Acartia* (Durbin & Durbin, 1978; Landry, 1978; Uye, 1982; Mauchline, 1998) and for barnacle larvae (Chapter 4). As time constraints prevented a more detailed analysis of this variability, adults from different sampling days were picked randomly to establish, at least, the range of sizes for each adult species considered. It was also noted that in any given sample, males of *Acartia* were usually smaller than females, but the same prosome-length range was recorded for both sexes. The exception was *A.discaudata,* where the range of prosome-length of males and female was different (Table 33), resulting in different weights being attributed for each sex.

Considering that the size classification employed for *Acartia* copepodites (CI to CV) reflects the stage classification of Hirst (1996) and Hirst *et al*., (1999), abundance values for each copepodite in this study were, on average, 4 times higher than reported by Hirst (1996) from which Hirst *et al*., (1999) is derived. This difference could, in part, be explained by the temporal coverage employed. Hirst (1996) sampling effort occurring at ~26 days intervals (i.e. 16 samples covering a time interval of 416 days), while in the present study the interval was ~ 13 days (i.e. 42 samples covering 562 days). This

argument is supported, in part, by the NW. Netley data presented here, where it is clear that the longer sampling interval (~30 days) carried out at this station in 2001 clearly missed some peak abundances when compared with the other two sites where sampling occurred on ~13 days intervals. Even if the lowest values of any month from the Calshot data presented in this study is compared with Hirst's (1996) data for an equivalent period, total abundance values are still 2-3 times higher in this study, suggesting that the 1993/94 season studied (Hirst, 1996; Hirst *et al*., 1999) had lower zooplankton abundances or were underestimated on some way.

The growth rates of copepods were not measured directly, again for the same reasons explained in the previous chapter. However, several global predictive equations have been developed with copepod data, and have been widely used to predict growth rates, usually needing inputs of field temperature and weights (Ikeda & Motoda, 1978; Huntley & Boyd, 1984; Huntley & Lopez, 1992; Hirst & Sheader, 1997; Hirst & Lampitt, 1998; Hirst *et al*., 2003) and even Chlorophyll *a* as an indicator of environmental food (Hirst & Bunker, 2003). The use of those empirical models listed above usually wielded growth rates below 0.7 d^{-1} for any particular stage, decreasing with size and increasing with temperature. The only exception was the model of Hirst & Bunker (2003) where rates as high as 1.2 d^{-1} were calculated for periods of high chlorophyll concentrations, possibly overestimating production. Again, since there is no "ideal" method covering all the variability, and also no standard method widely accepted, the averaged value using all the methods possible could be considered a better approximation of the "real" production.

The estimates of secondary production presented here from the current study are subject to several potential biases, from the method employed for collection, changes in numerical abundance during sampling intervals, presence/absence of predators and including the estimations of growth rates. However, when the biomass data of each size class of *Acartia* derived in this study was applied to the raw abundance data of each *Acartia* stage of Hirst (1996), an estimated production of 18.61 mg C m^{-3} yr^{-1} for copepodites + females of *Acartia* was determined (using equation 9+f). This value is only 5% higher than the published value of 17.62 mg C m^{-3} yr^{-1} (Hirst *et al*., 1999) using the same equation (Table 38), and suggests that the values obtained in this study are comparable. However, the annual production of 95.96 mg C m^{-3} yr^{-1} estimated for *Acartia* at Calshot, using abundance data obtained during this investigation is ~4-5 times higher than the previous estimate, and again confirms the low zooplankton abundance values of Hirst in 1993/94 (Hirst, 1996; Hirst *et al*., 1999).

When yearly production values of *Acartia* predicted here are compared with *Acartia* production reported elsewhere (Table 38) the values were only directly comparable with those of Uye (1982) and Kimmerer & McKinnon (1987) for *A.omorii* (*A.clausi* ?) and *A.tranteri,* the dominant copepods at Onagawa Bay (Japan) and Westernport Bay (Australia), respectively. Like these two investigations, yearly production in the range of 96-165 mg C m^{-3} yr^{-1} reported here were considered low, because production of *Acartia* elsewhere (Table 38) is usually 3 to 20 times higher than the values reported here.

Table 38. Yearly production estimates of estuarine/marine copepods.

Species (groups),region	Daily production	Interval	~depth	(Source) Method of collection
Acartia clausi,(nauplii to adults) Jakles Lagoon, Washington, USA.	2677-3285 mg C m^{-3} yr^{-1}	~518	3	(Landry, 1978) sampled with a core-tube fitted with a 53 µm mesh
Acartia tonsa,(nauplii to adults) Narragansett Bay, Rhode Island, USA	1663-2009 mg C m^{-3} yr^{-1}	103	7.5	(Durbin & Durbin, 1981) sampled pumping into a 60 µm mesh
Acartia hudsonica,(nauplii to adults) Narragansett Bay, Rhode Island, USA	768-1304 mg C m^{-3} yr^{-1}	120	7.5	(Durbin & Durbin, 1981) sampled pumping into a 60 µm mesh
Acartia spp, (nauplii to adults of 3 sp.), Malaga Harbour, Spain	773-1618 mg C m^{-3} yr^{-1}	139	7	(Guerrero & Rodriguez, 1994; 1997) sampled using nets with 100µm mesh
Acartia tonsa,(nauplii to adults) Westerschelde, The Netherlands	556 mg C m^{-3} yr^{-1}	365	-	(Escaravage & Soetaert, 1995) sampled pumping into a 55 µm mesh
Acartia tranteri,(nauplii to adults) Westernport Bay, Australia	130 mg C m^{-3} yr^{-1}	~700	5	(Kimmerer & McKinnon, 1987) sampled using nets with 50µm mesh
Acartia omorii,(nauplii to adults) Onagawa Bay, Japan	180 mg C m^{-3} yr^{-1}	558	15	(Uye, 1982) sampled using nets with 94µm mesh
Acartia omorii,(nauplii to adults) Fukuyama harbour, Japan	749 mg C m^{-3} yr^{-1}	257	8	(Liang & Uye, 1996a a) sampled using nets with 62µm mesh
Acartia lilljeborgi,(nauplii to adults) Praia do Segredo, São Sebastião, Brazil	230 mg C m^{-3} yr^{-1}	399	4	(de La Rocha, 1998) sampled using nets with 10 and 100µm mesh
Cetropages abdominalis,(nauplii to adults) Fukuyama harbour, Japan	355 mg C m^{-3} yr^{-1}	204	8	(Liang *et al*., 1996) sampled using nets with 62µm mesh
Paracalanus sp.(nauplii to adults) Fukuyama harbour, Japan	734 mg C m^{-3} yr^{-1}	365	8	(Liang & Uye, 1996b b) sampled using nets with 62µm mesh
Pseudodiaptomus marinus,(nauplii to adults) Tomo harbour, Japan	20.7 mg C m^{-3} yr^{-1}	365	7	(Uye *et al*., 1983) sampled using nets with 94µm mesh
Pseudodiaptomus marinus,(nauplii to adults) Fukuyama harbour, Japan	51 mg C m^{-3} yr^{-1}	365	8	(Liang & Uye, 1997) sampled using nets with 62µm mesh
Eurytemora affinis,(nauplii to adults) Westerschelde, The Netherlands	724 mg C m^{-3} yr^{-1}	365	-	(Escaravage & Soetaert, 1993; 1995) sampled pumping into a 55 µm mesh
Eurytemora affinis,(nauplii to adults) Elbe estuary	289 mg C m^{-3} yr^{-1}	134	-	(Peitsch, 1995) sampled pumping into a 55 µm mesh
Oithona davisae, (copepodites to adults) Fukuyama harbour, Japan	650 mg C m^{-3} yr^{-1}	365	8	(Uye & Sano, 1998) sampled using nets with 62 µm mesh
Acartia spp (copepodites to adults of 4 sp.), Southampton Water, UK.	17.62 mg C m^{-3} yr^{-1}	416	13	(Hirst *et al*., 1999) sampled using nets with 118µm mesh
Centropages hamatus, (copepodites to adults) Southampton Water, UK.	8.16 mg C m^{-3} yr^{-1}	416	13	(Hirst *et al*., 1999) sampled using nets with 118µm mesh
Temora longicornis, (copepodites to adults) Southampton Water, UK.	4.77 mg C m^{-3} yr^{-1}	416	13	(Hirst *et al*., 1999) sampled using nets with 118µm mesh
Para-pseudocalanus, (copepodites to adults) Southampton Water, UK.	1.67 mg C m^{-3} yr^{-1}	416	13	(Hirst *et al*., 1999) sampled using nets with 118µm mesh
Acartia spp. (copepodites to adults of 5 sp.), Southampton Water, UK.	96-165 mg C m^{-3} yr^{-1}	562	13	**This study** sampled using nets with 120µm mesh
Oithona nana, (copepodites to adults), Southampton Water, UK.	1.33-113 mg C m^{-3} yr^{-1}	562	13	**This study** sampled using nets with 120µm mesh
Euterpina acutifrons, (copepodites to adults) Southampton Water, UK.	34-40 mg C m^{-3} yr^{-1}	562	13	**This study** sampled using nets with 120µm mesh
Copepod nauplii, Southampton Water, UK.	23-53 mg C m^{-3} yr^{-1}	562	13	**This study** sampled using nets with 120µm mesh

Original dry-weight/carbon values were converted/re-calculated using a conversion factor of 40%.
Interval represents the number of days from which yearly production was calculated/averaged.

Kimmerer & McKinnon (1987) attribute their low production to a combination of low growth-rate with low biomass, but if we indiscriminately apply the highest growth rate of 0.89 d^{-1} for *A.tonsa* of Durbin & Durbin (1981) to the data presented here, production in this extreme case will be in the range of 396 - 692 mg C m^{-3} yr^{-1} still in the lower range of the values presented on Table 38 i.e., 650 - 3285 mg C m^{-3} yr^{-1}. This indicates that differences in biomass is probably the major factor behind these differences, since growth in copepods usually does not exceed 0.9 d^{-1}, and rates higher than 0.7 d^{-1} were only reported for *Acartia* with temperature above 16°C (Hirst *et al*., 2003 and references therein). Apart from the results obtained with the model of Hirst & Bunker (2003), growth-rates in this study were usually below 0.7 d^{-1}.

Biomass reflects body weights and abundances of each stage, and since body weights considered in this study are in agreement with values reported from the literature, probably the factor behind the "low production" reported in Southampton Water, and in Onagawa and Westernport Bays (Uye, 1982; Kimmerer & McKinnon, 1987) should be credited to differences in abundance. However, looking at the sampling methods of studies where production level would be considered "normal", these usually employed pumps instead of nets, with production based on abundances estimated from volumes of water of 0.023-0.48 m^{-3}, while in this study abundances were based on volumes, on average, of 39 m^{-3} which is 80-1700 times higher. This clearly suggests that direct, simplistic comparisons between the different methods should not be considered/attempted.

Differences in abundances between samples collected by pumps and nets were briefly commented on Chapter 1. Anyway, when the abundance results of calanoids presented here were compared with those carried at Southampton Water where samples were collected with pumps instead of nets (Raymont & Carrie, 1964), abundances estimated from 0.5 m^{-3} samples retained on ~158 μm meshes would be expected to be lower when compared with the values presented here. However, abundance values of calanoids and barnacle larvae in the present investigation were usually 22 – 85% lower when compared with those recorded by Raymont & Carrie (1964). The exception being the abundance of calanoids at Calshot, where the averaged values presented here, for a similar time interval, were ~4 times higher than those of Raymont & Carrie (1964). This was completely unexpected, since coarser meshes should retain fewer organisms, unless pump sampling is more efficient or the lower volume sampled gave a huge overestimation of organisms. When Raymont & Carrie (1964) used a finer net mesh with '200 meshes to the inch' (i.e. № 25 or ~64 μm according to Boltovskoy (1981b) and Omori & Ikeda (1992)) in conjunction with the № 10 mesh (i.e. ~158 μm), for a more detailed analysis of *Acartia* in

the same study, they reported abundances ~ 5 times higher than the ones presented in the current study. In the classical work of Bousfield *et al*., (1975) an 8 fold increase in abundances collected with a pump strained with № 10 meshes (~158 μm) is reported when compared with catches with a towed № 10 net. If a 5 fold increase in abundance, reported above for Raymont & Carrie (1964) using finer meshes, is applied indiscriminately to all *Acartia* stages in the abundance data of this study, yearly production in the range of 588 to 1165 mg C m^{-3} yr^{-1}, using equation 9k is derived for *Acartia*, approaching of those collected with smaller meshes (Table 38). So, instead of our production values being considered low it is possible that those derived from pump collected samples were abnormally high, probably due to an overestimation in abundance due the small amount of water sampled.

Discussion concerning the use of pump and net samplers is well documented, and will not be discussed here, but advantages/disadvantages of the use of pumps in relation of nets are detailed on Beers (1981a), Boltovskoy (1981c), de Bernardi (1984), Omori & Ikeda (1992) and Sameoto *et al*.,(2000). All that can be said, based on these studies in Table 38, is that, pumps gave values of production usually an order of magnitude greater than ones collected with nets.

It is now suggested, that the low-high rates of secondary production should be revised, since most of the studies where "high" values of secondary production were reported are based on collections with pumps and sampling less than a cubic metre of water. Since collection with nets is more widespread, and volumes collected are higher, relative 'low-high' secondary production values for copepods should be set to values obtained with net samples. So, in light of this it is possible to say that the production of *Acartia* within Southampton Water is in agreement with the reported production of *Acartia* in other regions, collected in a similar fashion from regions under similar seasonal variations in temperature and similar rates of primary production i.e. 100 – 200 g C m^{-2} yr^{-1}.

Production of the other calanoid species were not measured directly, but estimates of their production will be given in Chapter 6, together with equations proposed for the estimation of production of several components.

No previous estimates of copepod nauplii, *E.acutifrons* and *O.nana* production are available for Southampton Water, and the values presented here are the first attempt to quantify it. Since this study was primarily focused on barnacle larvae production (Chapter 4), and later expanded to predict production of *Acartia*, the optimal way of predicting production of copepods was not followed. If time allowed the same method employed for barnacles would have been used, where each stage of each component is systematically

measured, and length-weight relationships established. However the measurement of prosome lengths of *Acartia* to fit it in size intervals was already a major time consumer, and to repeat this for the other species was impractical, if not impossible. So, due to time constraints, only *Acartia* copepodite size-classes could be measured, with the production of the other components estimated using other methods. Because of this, the production values of these components should be considered with caution since they include males, and were based on single averaged weight for all organisms of a particular group/species (Table 35). Another factor is that due to the small size of copepod nauplii and earlier copepodite stages, the mesh size used probably under-sampled most of those earlier stages. This is supported by the overall "heavy weight" measured for copepod nauplii, clearly indicating that it is dominated by later naupliar stages.

However, the consistency of production calculated for copepod nauplii and *E.acutifrons* is remarkable, with similar values being reported for all three stations. *O.nana* in contrast had much higher production inside the estuary at Cracknore where 113.26 mg C m^{-3} yr^{-1} was calculated. Even allowing for the low relative importance of *O.nana* in the lower estuary where the production of this species were calculated as only 1.33 C m^{-3} yr^{-1} i.e. 1.18% of the total production of *Acartia* spp (113.17 mg C m^{-3} yr^{-1}), this previously unconsidered production, together with that of copepod nauplii and *E.acutifrons,* can go some way to explain the relatively low copepod secondary production estimate of 32.2 mg C $m^{-3}yr^{-1}$ within Southampton Water (Hirst *et al*., 1999), which was exclusively based on calanoid copepods.

It is important to stress that the production of *O.nana* at Cracknore, and in Southampton Water as a whole, is expected to be much higher when abundance is more rigorously assessed and sampled i.e., with 62 μm meshes. Comparing the width of *O.nana* copepodites (~88 - 142 μm for copepodites 1 to 6) with *Acartia* copepodites of the same stage (~93 - 342 μm for copepodite 1 to 6 of the different *Acartia* species), the earlier copepodites stages of *O.nana* will be much more under-sampled by the 120 μm mesh than *Acartia* copepodites. The production of *O.nana* at Cracknore alone could be higher than that of total calanoids, since the production of *O.nana,* at Cracknore*,* amounted to 85% of that calculated for *Acartia* at the same station in the present study. If a factor of five, derived from the work of Raymont & Carrie (1964) discussed earlier, is also applied to *O.nana* in a attempt to correct values to finer meshes, the potential production of this species over the estuary is expected to range from 7 mg C m^{-3} yr^{-1} at Calshot to 565 mg C m^{-3} yr^{-1} at Cracknore, approaching the value of 650 mg C m^{-3} yr^{-1} reported by Uye & Sano (1998) for *O.davisae* in Fukuyama Harbour (Table 38).

As one of the aims of this study was to give as good an estimate of secondary production as possible, it is believed that the averaged value presented in Tables 36 and 37 based on all the conventional equations described, is a 'best approximation' of production. Altogether, copepod nauplii, *Acartia* spp., *E.acutifrons* and *O.nana* represent 99, 98 and 91% of the copepod fraction collected with a 120 μm mesh at Cracknore, NW.Netley and Calshot, respectively. Based on the averaged values presented in Tables 36 and 37 the total production of those copepods in Southampton Water can be assumed to be 327.68, 256.13 and 176.63 mg C m^{-3} yr^{-1} at Cracknore, NW.Netley and Calshot respectively, or 253.48 mg C m^{-3} yr^{-1} (including the production of *Acartia* males) as an average for the three stations. Simplisticaly this value could therefore be considered representative of 96% of the copepods in Southampton Water, when 120 μm mesh nets are being used. As a best case view, production values presented here are clearly underestimations since a considerable number of earlier stages were not properly sampled.

In conclusion, copepod production within Southampton Water is in agreement with production values elsewhere, when similar sampling methodologies were employed.

5.5. Chapter Conclusions.

- Weights for size classes of *Acartia,* as well as an averaged weight for copepod nauplii, *O.nana* and *E.acutifrons* were measured and presented for the first time within Southampton Water.

- Regression equations relating prosome-length to weight for easy biomass assessments of all *Acartia* species are presented.

- Seasonal differences in prosome-length of the adults of the different species of *Acartia* were noted, but not investigated.

- Production of *Acartia* presented here is in line with other production estimates in temperate regions where similar sampling devices were employed.

- Production values of several copepod components/species are presented for the first time within this estuary as a whole, and an overall averaged production of 253.48 mg C m^{-3} yr^{-1} was estimated, with *Acartia* accounting for 55.6 % of the production followed by *E.acutifrons* (16.0%), copepod nauplii (15.2%) and *O.nana* (13.2%).

- *O.nana* production at the inner estuary was comparable to that of calanoid copepods, and with proper sampling and detailed production measurements it is expected to be greater than that of calanoids. As said in previous Chapters the assessment of the importance of oithonids and other small species is a current 'hot topic' on pelagic ecology and the results presented here clearly indicates the potential importance of this species within this estuary.

- The production of *O.nana* together with copepod nauplii and *E.acutifrons* can go some way to explain the low copepod secondary production estimate within Southampton Water, which was exclusively based on calanoid copepods.

Chapter 6

Zooplankton production within the overall carbon flux of Southampton Water

(A simpler way of estimating zooplankton production?)

6.1. Introduction.

Secondary production has long being defined as the growth of biomass, whether or not that biomass is retained by the organisms (Ricker, 1946; McLaren *et al*., 1989). Despite the mathematics being simple in principle (Chapters 4 section 4.1.1.) zooplankton production estimates are often laborious, requiring sorting, identifying, counting, measuring, weighing and estimating the growth rates of each stage of the animals considered. Sorting, identifying and counting zooplanktonic organisms at species level is a daunting task but essential if measuring community fluxes, since rates on zooplanktonic organisms occurs at species level (Soetaert & Van Rijswijk, 1993).

Direct measurements of growth of small animals are also very difficult, and to do it properly involves the procedures listed above. These procedures is usually done under controlled situations in laboratories, with the inherent assumptions and methodological constraints already discussed in previous chapters, and with reference only to those parameters presumed to be important for the animal development/growth, such as temperature and food (Landry, 1975a; 1975b; McLaren, 1978; Vidal, 1980a; 1980b; McLaren & Corkett, 1981).

Despite the fact that *in situ* experiments would be preferable as they might accommodate all variables, carrying out these experiments and including all ranges of temperature/food conditions necessary for generalizations is impractical. Live handling of animals, even in laboratory conditions, is already a challenge and, as pointed out recently by Hirst & Mckinnon (2001), the number of replicates for detection of 1-10% changes in body weights by standard destructive methods is generally prohibitive. In addition, handling procedures and even removal of predators could also bias the results. Based on that, one must take the decision of trying to measure growth rates (lab/*in situ*) or rely on published growth-rates models like the ones provided by Ikeda & Motoda (1978), Huntley & Boyd (1984), Huntley & Lopez (1992), Hirst & Sheader (1997), Hirst & Lampitt (1998), Hirst & Bunker (2003) and Hirst *et al*. (2003). Either way, several assumptions will still be

included, making the use of empirically derived models much more appealing since they allow simple and repeatable estimations without the need for incubations, usually requiring only data on temperature, body-weights and development (Landry, 1975b; Ikeda & Motoda, 1978; McLaren *et al*., 1989; Hirst & Sheader, 1997; Hirst & Lampitt, 1998; Hirst *et al*., 2003).

During the present study, the production of different mesozooplankton components was estimated (Chapters 4 and 5) using several growth rate and production equations, with the averaged value being arbitrarily considered as a best estimate of the secondary production of those components. One of the aims of the present chapter is to determine if there is an easier way of predicting this production, without the need for sorting, measuring, weighing and estimating the growth rates of each stage of the animals considered. With the calculation of production of different mesozooplankton components, like barnacle larvae (Chapter 4) and copepods (Chapter 5), the simple pelagic carbon box flux model proposed by Hirst *et al*., (1999), was re-analysed. This model is based in the Southampton Water – Solent site at Calshot, and represented the carbon flux of the main components of the pelagic food web which had been investigated, albeit independently, during a series of studies in the 1990's. Discrimination within the individual 'box' components was only possible as far as data allowed, and so no description of significant resource parameters such as detritus was made. Several mesozooplankton parameters are added and/or modified to accommodate the new figures and/or findings.

6.2. Methods.

As described in Chapter 4 and 5, production of different components was estimated by equations 8 and 9 (Chapter 4 section 4.1.1.) and growth rate with equations a to r which are fully described on Tables 22 and 34 in Chapters 4 and 5. Due to the high growth rates observed when using equations s and t (Table 34 – Chapter 5), the production values calculated with those equations were not considered in the following analysis.

In order to investigate the relationship of production with specific environmental parameters, multiple regression analyses were carried out using the number of organisms m^{-3} (n), Temperature (°C), Salinity (S) and Chlorophyll *a* (Chl *a*) as independent variables. Production was also regressed against the total number of organisms and simple linear regressions derived.

6.2.1. Statistical analysis.

In order to stabilize the variance of data the number of organisms m^{-3} (n), production values (mg C $m^{-3}d^{-1}$) and Chlorophyll *a* (mg m^{-3}) were $\log_{10}$ transformed before being used in the analysis.

Both simple linear and backwards step-wise multiple regression analyses were completed separately for each species individually, as well as for groups and the combination of them, with the production of all methods described in Chapters 4 and 5 being considered together on a single equation. For multiple regressions, F to enter was set to 4.0, and F to remove at 3.9. Where no independent variable were removed, a multiple linear regression was produced on the form $\text{Log}_{10}\, P = a(T°C)+b(S)+c(\log_{10} \text{Chl } a)+d(\log_{10} n)+e$. If any of the independent variables did not add significantly to the prediction it was excluded, and the regression completed using the remaining variables. Zero values were not included in the analyses. Simple and multiple regressions were calculated with STATISTICA for Windows, while simple regression graphs were drawn using Sigma-Plot for Windows.

6.3. Results and Discussion.

Backwards step-wise regression analyses were performed between the production of a particular species/group of organisms and the number of organisms m^{-3} (n), temperature (°C), salinity and chlorophyll *a* as independent variables. The results are shown on Table 39.

Table 39. Results of the backwards stepwise multiple regression analyses between production, with temperature, salinity, chlorophyll *a* concentration and total number of organisms of a particular species/stage. Also shown is the linear regression between production and the total number of organisms of a particular species/stage.

eq	**Copepod Nauplii (n = all copepod nauplii)**	r^2	N	range	sig.
r74	$Log_{10}(P) = -4.833+0.031*(T)+1.002*log_{10}(n)$	0.919	864		p<0.01
r75	$Log_{10}(P) = -4.808+1.123*log_{10}(n)$	0.894	864	30 - 20025	p<0.01
	***Acartia* spp. (n = all adults)**				
r76	$Log_{10}(P) = -4.721+0.010*(T)+0.028*(S)+0.041*log_{10}(Chl\ a)+1.031*log_{10}(n)$	0.969	1070		p<0.01
r77	$Log_{10}(P) = -3.794+1.065*log_{10}(n)$	0.960	1070	1 - 4725	p<0.01
	***Acartia* spp. (n = adult females)**				
r78	$Log_{10}(P) =-4.811+0.002*(T)+0.030*(S)+0.046*log_{10}(Chl\ a)+1.033*log_{10}(n)$	0.968	1070		p<0.01
r79	$Log_{10}(P) =-3.794+1.073*log_{10}(n)$	0.957	1070	1 - 3031	p<0.01
	***Acartia* spp. (n = copepodites + adult females)**				
r80	$Log_{10}(P) =-4.653+0.012*(T)+0.014*(S)+1.064*log_{10}(n)$	0.943	1080		p<0.01
r81	$Log_{10}(P) =-4.215+1.115*log_{10}(n)$	0.938	1080	6 - 25517	p<0.01
	***Acartia* spp. (n = copepodites)**				
r82	$Log_{10}(P) =-4.293+0.017*(T)+1.049*log_{10}(n)$	0.942	1080		p<0.01
r83	$Log_{10}(P) =-4.248+1.109*log_{10}(n)$	0.935	1080	6 - 22605	p<0.01
	***Acartia* spp. (n = copepodites + adults males and females)**				
r84	$Log_{10}(P) =-4.682+0.010*(T)+0.015*(S)+1.073*log_{10}(n)$	0.943	1080		p<0.01
r85	$Log_{10}(P) =-4.206+1.118*log_{10}(n)$	0.939	1080	7 - 27330	p<0.01
	***Oithona nana* (n = copepodites + adults males and females)**				
r86	$Log_{10}(P) =-5.019+0.039*(T)+0.999*log_{10}(n)$	0.962	664		p<0.01
r87	$Log_{10}(P) =-4.639+1.054*log_{10}(n)$	0.944	664	1 - 48199	p<0.01
	***Euterpina acutifrons* (n = copepodites + adults males and females)**				
r88	$Log_{10}(P) =-4.388+0.041*(T)-0.014*(S)+1.004*log_{10}(n)$	0.980	656		p<0.01
r89	$Log_{10}(P) =-4.456+1.093*log_{10}(n)$	0.977	656	1 - 11346	p<0.01
	Copepoda (n = *Acartia* spp.+*O. nana*+*E. acutifrons*)				
r90	$Log_{10}(P) =-5.214+0.034*(S)+0.177*log_{10}(Chl\ a)+1.028*log_{10}(n)$	0.936	648		p<0.01
r91	$Log_{10}(P) =-4.302+1.092*log_{10}(n)$	0.920	648	20 - 58873	p<0.01
	Copepoda (n = all nauplii + all *Acartia* spp.+ all *O. nana*+ all *E. acutifrons*)				
r92	$Log_{10}(P) =-5.674+0.011(T)+0.034*(S)+0.065*log_{10}(Chl\ a)+1.088*log_{10}(n)$	0.938	648		p<0.01
r93	$Log_{10}(P) =-4.790+1.182*log_{10}(n)$	0.924	648	80 - 65428	p<0.01
	***Elminius modestus* (n = all nauplii stages)**				
r94	$Log_{10}(P) =-5.049+0.040*(T)+0.146*log_{10}(Chl\ a)+1.024*log_{10}(n)$	0.974	1296		p<0.01
r95	$Log_{10}(P) =-5.065+1.263*log_{10}(n)$	0.956	1296	2 - 9440	p<0.01
	***Balanus crenatus* (n = all nauplii stages)**				
r96	$Log_{10}(P) =-4.465+0.014*(T)+0.357*log_{10}(Chl\ a)+0.973*log_{10}(n)$	0.960	738		p<0.01
r97	$Log_{10}(P) =-4.156+0.950*log_{10}(n)$	0.929	738	1 - 11963	p<0.01
	***Balanus improvisus* (n = all nauplii stages)**				
r98	$Log_{10}(P) =-5.312+0.078*(T)-0.069*log_{10}(Chl\ a)+0.915*log_{10}(n)$	0.976	804		p<0.01
r99	$Log_{10}(P) =-4.509+1.111*log_{10}(n)$	0.942	804	1 - 1767	p<0.01
	***Semibalanus balanoides* (n = all nauplii stages)**				
r100	$Log_{10}(P) =-5.493+0.065*(T)+0.026*(S)+0.360*log_{10}(Chl\ a)+0.951*log_{10}(n)$	0.949	414		p<0.01
r101	$Log_{10}(P) =-4.157+1.022*log_{10}(n)$	0.912	414	1 - 441	p<0.01
	***Verruca stroemia* (n = all nauplii stages)**				
r102	$Log_{10}(P) =-5.374+0.039*(T)+0.017*(S)+0.999*log_{10}(n)$	0.929	369		p<0.01
r103	$Log_{10}(P) =-4.434+0.957*log_{10}(n)$	0.908	369	1 - 486	p<0.01
	Cirripedia (n = all nauplii)				
r104	$Log_{10}(P) =-4.866+0.014*(T)+0.174*log_{10}(Chl\ a)+1.102*log_{10}(n)$	0.959	972		p<0.01
r105	$Log_{10}(P) =-4.897+1.199*log_{10}(n)$	0.945	972	2 - 12407	p<0.01
	Cirripedia (n = all nauplii + cypris)				
r106	$Log_{10}(P) =-4.907+0.016*(T)+0.142*log_{10}(Chl\ a)+1.113*log_{10}(n)$	0.960	972		p<0.01
r107	$Log_{10}(P) =-4.921+1.205*log_{10}(n)$	0.948	972	2 - 12407	p<0.01
	Total (n = all copepod and cirripedia nauplii + *Acartia* spp. + *O.nana* + *E.acutifrons*)				
r108	$Log_{10}(P)=-5.561+0.021*(T)+0.024(S)+1.095*log_{10}(n)$	0.937	648		p<0.01
r109	$Log_{10}(P)=-4.982+1.215*log_{10}(n)$	0.922	648	151-72279	p<0.01

Where P = average production of a particular size class/stage in mg C $m^{-3}d^{-1}$; T = temperature in °C; S = Salinity; Chl a = Chlorophyll a in mg m^{-3}; n = total number of organisms m^{-3} of particular type. N = number of data points; range = range of organisms m^{-3} employed; sig. = significance level and eq. = refers to the number of the resulting equation.

As expected, production was positively related with the number of organisms and, in most cases, also with temperature. Salinity and chlorophyll were also significant in some analysis (Table 39). With a determination coefficient (r^2) ranging from 0.91-0.98 these equations can be considered/employed for estimations of production in this estuary, since most of the variability is explained by those parameters.

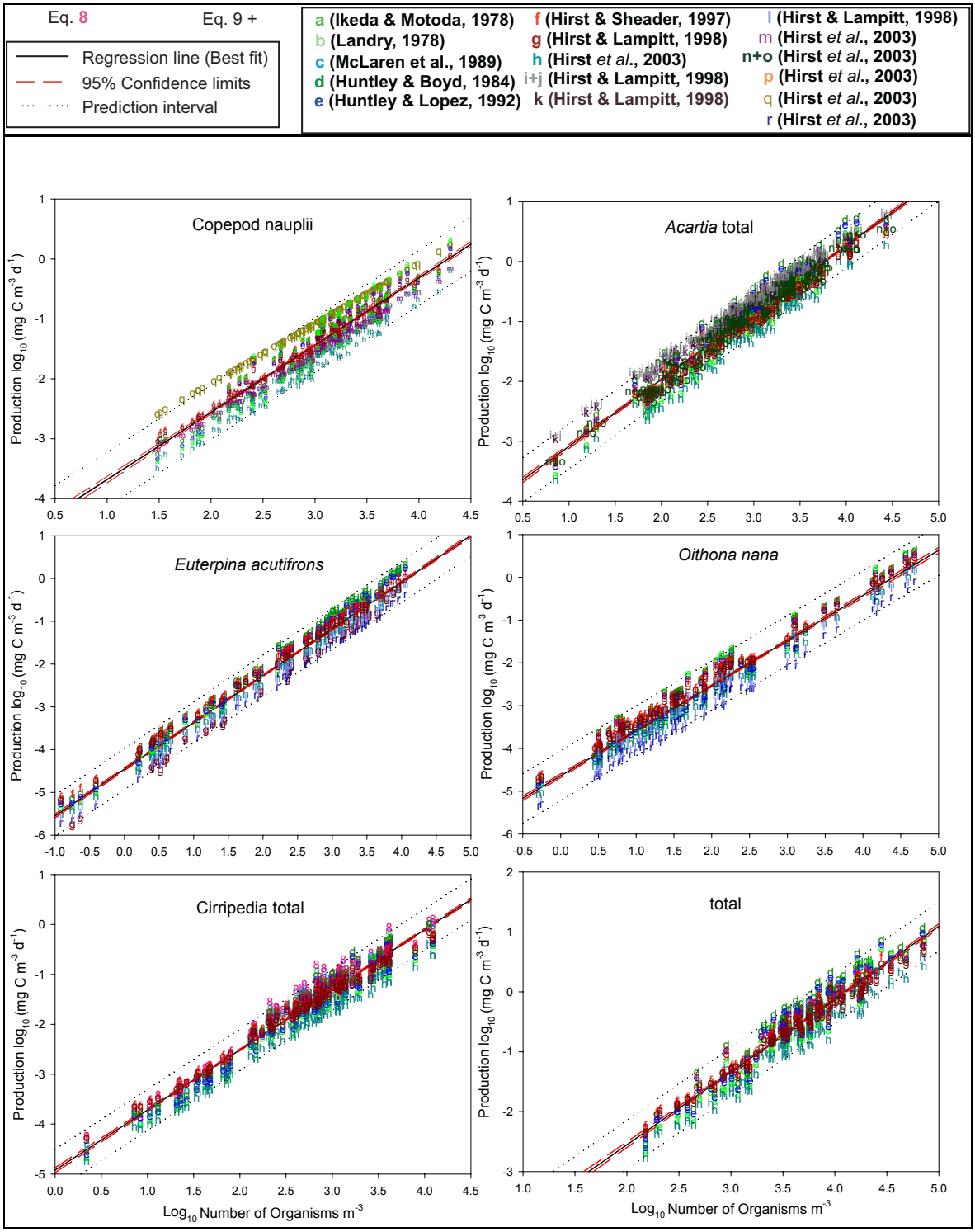


Figure 60. Regression analysis between Production values with total number of organisms. Different coloured letters indicates a production value calculated with a particular growth-equation (Tables 22 and 34) using equation 9. Cirripedia also shows the production values calculated with equation 8. For the regression equation see Table 39.

Despite a greater variability being accounted for multiple regression analyses, the objective of an easy way of predicting production is not fully accomplished, because parallel measurements of chlorophyll, temperature and salinity are still required. However, when production was regressed with only the total abundance values of specific components, significant relationships were still found (Figure 60). Overall, total abundance numbers still accounted for more than 89% of the variability of the production estimates (Table 39) and it is assumed that it could be used to predict the production of these groups, based on total numbers alone, when temperature, salinity and chlorophyll values are not available. Since this would be the simplest way of predicting production, the values needed to estimate the standard error of any value predicted by the simple linear regressions can be calculated by the equations:

$$\left(s_{\hat{Y}_i}\right)_1 = \sqrt{s^2_{Y.X}\left[1 + \frac{1}{n} + \frac{\left(X_i - \overline{X}\right)^2}{\sum x^2}\right]} \tag{12}$$

$$95 \text{ or } 99\% \text{ confidence interval} = \hat{Y}_i \pm t * \left(s_{\hat{Y}_i}\right) \tag{13}$$

The definitions can be seen in Zar (1999) and on Table 40. The set of values needed to complete equations 12 and 13 can be seen on Table 40.

Table 40. Values needed to calculate the standard errors of predicted values of the linear regression between production and the total number of organisms of a particular species/stage shown on Table 39.

Equation	$s^2_{Y.X}$	n	$\overline{X}$	$\sum x^2$	$t_{0.05(2)}$	$t_{0.01(2)}$
r75	0.0538	864	2.9800	309.2964	1.963	2.582
r77	0.0345	1070	2.1260	782.7556	1.962	2.581
r79	0.0373	1070	1.9178	765.6055	1.962	2.581
r81	0.0365	1080	2.8921	477.3982	1.962	2.581
r83	0.0368	1080	2.8188	463.2485	1.962	2.581
r85	0.0365	1080	2.9324	484.8741	1.962	2.581
r87	0.0873	664	1.8471	872.4360	1.963	2.583
r89	0.0596	656	2.1021	1377.192	1.963	2.583
r91	0.0534	648	3.2141	332.7414	1.963	2.583
r93	0.0454	648	3.4825	254.3036	1.963	2.583
r95	0.0422	1296	2.3074	741.9449	1.962	2.581
r97	0.0868	738	1.8945	920.9226	1.963	2.582
r99	0.0830	804	1.1904	871.3439	1.963	2.582
r101	0.1271	414	0.8948	519.2434	1.966	2.588
r103	0.0813	369	0.8928	320.3416	1.967	2.590
r105	0.0467	972	2.6992	543.5680	1.962	2.581
r107	0.0442	972	2.7065	540.6889	1.962	2.581
r109	0.0427	648	3.6181	221.9984	1.963	2.583

Where: $s^2_{Y.X}$ = the sample residual mean square of the population, n = number of observations, $\overline{X}$ = mean abundance value, $\sum x^2$ = sum of squares and t = critical values of the *t* distribution.

In order to observe the difference of total production calculated by the use of multiple and simple linear regressions, the production of each component was calculated

with some of the equations presented in Table 39. These results can be seen in Table 41, together with the difference observed by the use of these equations when compared with the averaged production value presented for each organism in Chapters 4 and 5.

Table 41. Annual production estimates (in mg C $m^{-3}yr^{-1}$) of each component obtained using the respective equations summarized in Table 39 (equation number in parentheses). The % difference from the production values presented on Tables 26 to 30 in Chapter 4 and Tables 36 and 37 in Chapter 5 are also shown.

Cracknore						
n	Averaged production	Multiple regression		% difference	Single regression	% difference
Copepoda Nauplii	40.53	34.54	(r74)	-14.78	32.25 (r75)	-20.43
Acartia (females)	29.77	24.48	(r78)	-17.76	25.76 (r79)	-13.46
Acartia (copepodites)	80.52	61.11	(r82)	-24.11	59.81 (r83)	-25.72
Acartia (all)	119.56	93.87	(r84)	-21.49	96.57 (r85)	-19.23
O.nana	113.26	98.85	(r86)	-12.72	90.57 (r87)	-20.03
E.acutifrons	40.25	36.21	(r88)	-10.04	31.69 (r89)	-21.27
E.modestus	18.45	18.85	(r94)	2.17	19.51 (r95)	5.75
B.crenatus	1.85	1.61	(r96)	-12.97	1.96 (r97)	5.95
B.improvisus	4.25	3.80	(r98)	-10.59	4.08 (r99)	-4.00
S.balanoides	0.20	0.19	(r100)	-5.00	0.23 (r101)	15.00
V.stroemia	0.01	0.004	(r102)	-60.00	0.01 (r103)	0.00
Cirripedia (Total)	24.76	27.22	(r104)	9.94	23.70 (r105)	-4.28
Total	342.02	405.12	(r108)	18.45	431.21 (r109)	26.08
Average	----	----		-12.22	----	-5.82
NW.Netley						
n	Averaged production	Multiple regression		% difference	Single regression	% difference
Copepoda Nauplii	52.65	44.76	(r74)	-14.99	45.10 (r75)	-14.34
Acartia (females)	30.49	24.50	(r78)	-19.65	41.47 (r79)	36.01
Acartia (copepodites)	112.59	87.84	(r82)	-21.98	94.44 (r83)	-16.12
Acartia (all)	158.36	134.54	(r84)	-15.04	141.06 (r85)	-10.92
O.nana	11.19	9.87	(r86)	-11.80	9.10 (r87)	-18.68
E.acutifrons	33.93	29.17	(r88)	-14.03	25.90 (r89)	-23.67
E.modestus	21.01	21.31	(r94)	1.43	19.23 (r95)	-8.47
B.crenatus	18.94	17.60	(r96)	-7.07	18.05 (r97)	-4.70
B.improvisus	2.14	1.97	(r98)	-7.94	1.55 (r99)	-27.57
S.balanoides	2.10	1.53	(r100)	-27.14	1.07 (r100)	-49.05
V.stroemia	0.07	0.02	(r102)	-71.43	0.06 (r103)	-14.29
Cirripedia (Total)	44.26	45.43	(r104)	2.64	50.75 (r105)	14.66
Total	300.98	245.49	(r108)	-18.44	247.07 (r109)	-17.90
Average	----	----		-17.34	----	-11.93
Calshot						
n	Averaged production	Multiple regression		% difference	Single regression	% difference
Copepoda Nauplii	22.59	19.21	(r74)	-14.96	16.87 (r75)	-25.32
Acartia (females)	31.63	23.10	(r78)	-26.97	20.26 (r79)	-35.95
Acartia (copepodites)	55.92	44.05	(r82)	-21.22	40.79 (r83)	-27.06
Acartia (all)	104.73	76.80	(r84)	-26.67	70.63 (r85)	-32.56
O.nana	1.33	1.15	(r86)	-13.53	0.81 (r87)	-39.10
E.acutifrons	39.54	32.76	(r88)	-17.15	31.63 (r89)	-20.01
E.modestus	14.34	14.13	(r94)	-1.46	14.02 (r95)	-2.23
B.crenatus	13.69	12.34	(r96)	-9.86	11.90 (r97)	-13.08
B.improvisus	0.21	0.17	(r98)	-19.05	0.10 (r99)	-52.38
S.balanoides	0.77	0.60	(r100)	-22.08	0.57 (r100)	-25.97
V.stroemia	0.38	0.09	(r102)	-76.32	0.32 (r103)	-15.79
Cirripedia (Total)	29.39	28.29	(r104)	-3.74	31.99 (r105)	8.85
Total	198.16	167.74	(r108)	-15.35	141.82 (r109)	-28.43
Average	----	----		-20.64	----	-23.77

Predicting production of zooplanktonic components using the equations presented in Table 39 gave values on average ~14 - 17% lower than the averaged value presented in Chapters 4 and 5. The highest differences were noted when multiple regression equation r102 (Table 39) was employed to predict the production of *V.stroemia* nauplii. This was more a contrasting exception than the rule, since multiple regression equations usually gave the closest results, when compared with the averaged value presented on Chapters 4 and 5. The differences presented in Table 41 appears to be high, but it should be considered that the averaged values established in previous chapters, were arbitrarily chosen as the best representation of production estimated by the different methods, considering only the end production result. Production calculated by the equations presented in Table 39 consider the best fit for all measurements using all equations, and probably reflects better the variation found within methods than a simple average.

There is no single way of saying that these are high or low differences, but predicted production with equations presented on Table 39 will clearly be within the range of values obtained with different equations (Chapters 4 and 5). However, when the multiple regression equations r78/r82 (Table 39) and the simple linear regressions r79/r83 (Table 39) were applied to a different data set where production was calculated independently i.e. the raw data of *Acartia* from Hirst (1996), a combined production of copepodites + females of 18.17 were calculated with the multiple regression and 15.91 mg C m^{-3} yr^{-1} for the simple liner regressions. These two values are, respectively, +3% and -10% different from the 17.62 mg C m^{-3} yr^{-1} published for *Acartia* by Hirst *et al*., (1999) (if equations r80 and r81 (Table 39) are used, values of 17.66 and 15.21 mg C m^{-3} yr^{-1} are obtained, with each one differing +1% and -14% respectively).

Since production values of other calanoid species were not measured during this investigation, equations r84 and r85 (Table 39) derived for *Acartia* (copepodites + males and females) was also applied to the raw total calanoid data of Hirst (1996), resulting in values of 33.94 and 29.81 mg C m^{-3} yr^{-1}, respectively. Again these values are only +5% and -7% different to the 32.22 mg C m^{-3} yr^{-1} presented in Hirst *et al*., (1999), and confirming again that the use of such equations could indeed be used for rapid estimations of the secondary production of zooplanktonic components within this estuary, predicting values within ±20% or lower from the standard methods.

Application of these equations (Table 39) needs to be assessed using more independent data collected with similar sampling devices and tested for accuracy when applied for other regions. However, it is believed that these methods could be used for quick estimations of the production of those components found in the Solent-Southampton

Water estuarine system and neighbouring regions, if similar sampling devices were employed.

To be able to make comparisons with previous zooplanktonic investigations, data presented here and in previous investigations (Soares, 1958; Zinger, 1989; Geary, 1991; Lucas, 1993; Hirst, 1996; Castro-Longoria, 1998) were 'scaled' to a common unit where all calanoids were assumed to be *Acartia,* harpacticoids to be *E.acutifrons* and cyclopoids to be *O.nana.*

Table 42. Yearly/daily production estimates using equation r85 for calanoids, r89 for harpacticoids, r87 for cyclopoids, r75 for copepod nauplii and r107 for barnacle larvae on data from the present study and previous zooplankton investigations in Southampton Water. Details of equations can be seen on Table 39. All values as mg C m^{-3} d^{-1}/yr^{-1}

Ref	Calanoids (r85)		Harpacticoids (r89)		Cyclopoids (r87)		Cirripedia (r107)		C.nauplii (r75)		
	day	year	day	year	day	year	day	year	day	year	o/i
Cracknore Buoy											
2	0.73	267.2	0.02	6.9	----	----	0.08	28.7	----	----	37/723
3	0.25	92.9	<0.01	0.1	----	----	0.02	9.0	----	----	34/622
4	0.31	111.8	----	----	----	----	0.03	9.4	----	----	25/350
7	**0.32**	**117.3**	**0.09**	**33.1**	**0.25**	**90.6**	**0.07**	**24.1**	**0.09**	**32.2**	**42/562**
NW.Netley Buoy											
2	1.22	444.1	0.03	12.6	----	----	0.14	50.9	----	----	39/736
3	0.30	110.7	<0.01	0.1	----	----	0.02	8.5	----	----	19/267
7	**0.54**	**195.4**	**0.08**	**27.8**	**0.02**	**9.1**	**0.14**	**50.8**	**0.12**	**45.1**	**24/503**
Calshot Buoy/Pier											
1	----	----	----	----	----	----	0.10	38.3	----	----	39/851
2	0.49	178.3	0.04	15.7	----	----	0.38	139.8	----	----	30/736
5	0.08	29.8	0.05	16.6	<0.01	0.03	0.02	7.1	0.01	3.9	16/416
7	**0.26**	**96.1**	**0.10**	**34.9**	**<0.01**	**0.8**	**0.09**	**32.3**	**0.05**	**16.9**	**42/562**
Bourne Gap											
6	0.18	66.2	<0.01	0.3	----	----	0.01	5.3	----	----	14/383
Bury Buoy											
6	0.40	144.7	<0.01	0.5	0.01	3.0	0.04	16.4	----	----	13/395
PAD											
2	0.79	289.5	0.02	7.2	----	----	0.12	44.9	----	----	38/736
Greenland Buoy											
3	0.12	44.7	----	----	----	----	0.02	8.5	----	----	33/594
Hamble Buoy											
2	0.39	140.6	0.04	15.0	----	----	0.22	80.2	----	----	35/723

o/i = number of observations (o)/ interval days considered (i); ---- = indicates no data
Ref = references employed (see below).
1 – 01/1955 – 04/1957 (Soares, 1958) collected with pump and filtered onto ~ 158 μm mesh ;
2 – 04/1985 – 04/1987 (Zinger, 1989) collected with 100 μm net;
3 – 03/1990 – 12/1991 (Lucas, 1993) collected with 212 μm net;
4 – 08/1990 – 08/1991 (Geary, 1991), collected with 150 and 212 μm nets and all copepods = calanoids;
5 – 12/1992 – 01/1994 (Hirst, 1996) collected with 118 μm net;
6 – 10/1994 – 04/1996 (Castro-Longoria, 1998) collected with 212 μm net;
7 – 01/2001 – 07/2002 Present investigation collected with 120 μm net;
Assuming all calanoids as *Acartia* spp; all harpacticoids as *Euterpina acutifrons* and all cyclopoids as *Oithona nana* . Sample sites can be seen on Figure 1 – Chapter 1.

Since some environmental data were not complete /available for all studies, production for the three copepod categories/ species were predicted using the simple linear

regression equations r85, r89 and r87, respectively. Similarly, copepod nauplii and barnacle larvae were predicted with equations r75 and r107, respectively (see Table 39). Their use implies that the results generated will be probably underestimations, as the calanoid data of Hirst (1999) predicted values usually 7% lower when using the same simple linear equation derived for *Acartia* (i.e. r85 on Table 39). Assuming the composition found in this work is representative of other investigations, *Acartia*, *Euterpina*, *Oithona* + copepod nauplii together will represent ~96% of the copepod component found at this estuary, and thus, the inclusion of abundance of other species as one of those genera mentioned above, indicates that some of the production of the remaining ~4% are being accounted for.

From Table 42 only the results of Zinger (1989) and Hirst (1996) can be directly compared with those presented in this study because of the same methodologies employed, with differences usually attributed to inter annual variation. From the data of Zinger (1989) and the present investigation, it is clear that production of calanoids in the inner estuary, was greater than that calculated around the mouth, i.e. Calshot, Hamble and Bourne Gap (Figure 1 – Chapter 1). This agrees with the concentration of chlorophyll observed during the present study (Chapter 1), and with most of the data on chlorophyll concentrations available for this estuary (Leakey *et al*., 1992; Iriarte & Purdie, 1994; Howard *et al*., 1995), where chlorophyll concentrations at the inner estuary stations were usually higher than at the mouth region, and so, able to support higher productions.

Also from the data of Zinger (1989) it is clear that production, and consequently the abundance of calanoids, was much higher during 1985-1987 than in subsequent years (Figures 61, 62 and 63 - Table 42). However, it is believed that Zinger (1989) counted all copepod nauplii as calanoids, since the finer 100 μm mesh employed by Zinger (1989) was anticipated to collect much more copepod nauplii than any other study at this estuary, however, no copepod nauplii were presented by her. Supporting this argument is the fact that if the copepod nauplii abundances of the present study are added to calanoids, the production of calanoids will be predicted to be 255.2, 394.5 and 172.7 mg C m^{-3} yr^{-1} for Cracknore, NW. Netley and Calshot respectively, which are similar to the values calculated from the data of Zinger (1989) presented on Table 42. If we argue the other way, i.e. that a similar proportion of copepod nauplii to the present study i.e. 46 – 56% were included into Zinger's (1989) calanoid data, and if this proportion is excluded form the raw calanoids data of Zinger (1989), calanoid production in 1985-1987 would now be 42 – 52 % lower, or 112.19, 195.52, and 93.3 mg C m^{-3} yr^{-1} for Cracknore, NW. Netley and Calshot respectively. Either way, these results are remarkably close to the ones

presented here, i.e. 117.3, 195.4 and 96.1 mg C m^{-3} yr^{-1} for Cracknore, NW. Netley and Calshot respectively, suggesting that this was probably the case.

The production of harpacticoids presented here is double that calculated from Zinger (1989) and Hirst (1996) data. Barnacle larvae presented similar production values only with Zinger's (1989) data (Table 42). It is clear that a major contribution by barnacles was recorded at Calshot in 1985-1987, since production was 72 % higher than that calculated in the present investigation using the same equations (Figure 63).

Generally, when comparing studies conducted in this estuary (Table 42) where coarser mesh sizes was used, production values were usually higher in investigations that employed finer mesh sizes, with the exception of Hirst (1996) where the lowest calanoid production values were derived (Figure 63, Table 42), clearly reflecting the low abundances found. It should be stressed however, that these low values presented could, in part, be a reflection of a low sampling effort represented by the bigger sampling interval (Table 42). Calculation of production with the equations presented on Table 39 are not recommended for data collected with different sampling devices (Soares, 1958; Geary, 1991; Lucas, 1993; Castro-Longoria, 1998), since different methodologies collect different proportions of the community giving different results and clearly different interpretations. It is possible to generalize that overall, calanoids are the greatest contributors to copepod biomass with barnacle larvae, harpacticoids, copepod nauplii and cyclopoids altogether potentially equalling that production, when finer meshes are employed. However, examined on an individual basis, cyclopoids had comparable production to calanoids towards the inner reaches of this estuary in 2001-2002, probably contributing to more production alone than all calanoids together at Cracknore if properly sampled and assessed, i.e. with nets of 64 μm mesh or smaller. This sudden occurrence/detection of *O.nana* in the inner estuary has been discussed in Chapters 2 and 5, but it is good to point out again that the sudden occurrence of this small species in higher abundances, positively detected only after the 1994-1996 investigation carried out by Castro-Longoria (1998), could be the first indication of major changes in the copepod community of this estuary. This may be associated with increasing eutrophication since this species is recognized as a biological indicator of anthropogenic perturbed systems (Richard & Jamet, 2001). Certainly, such changes in copepod communities, where smaller, more numerous species start to occur where only large species have been previously detected, has been associated with increasing eutrophication in other planktonic communities (Zaitsev, 1992; Uye, 1994).

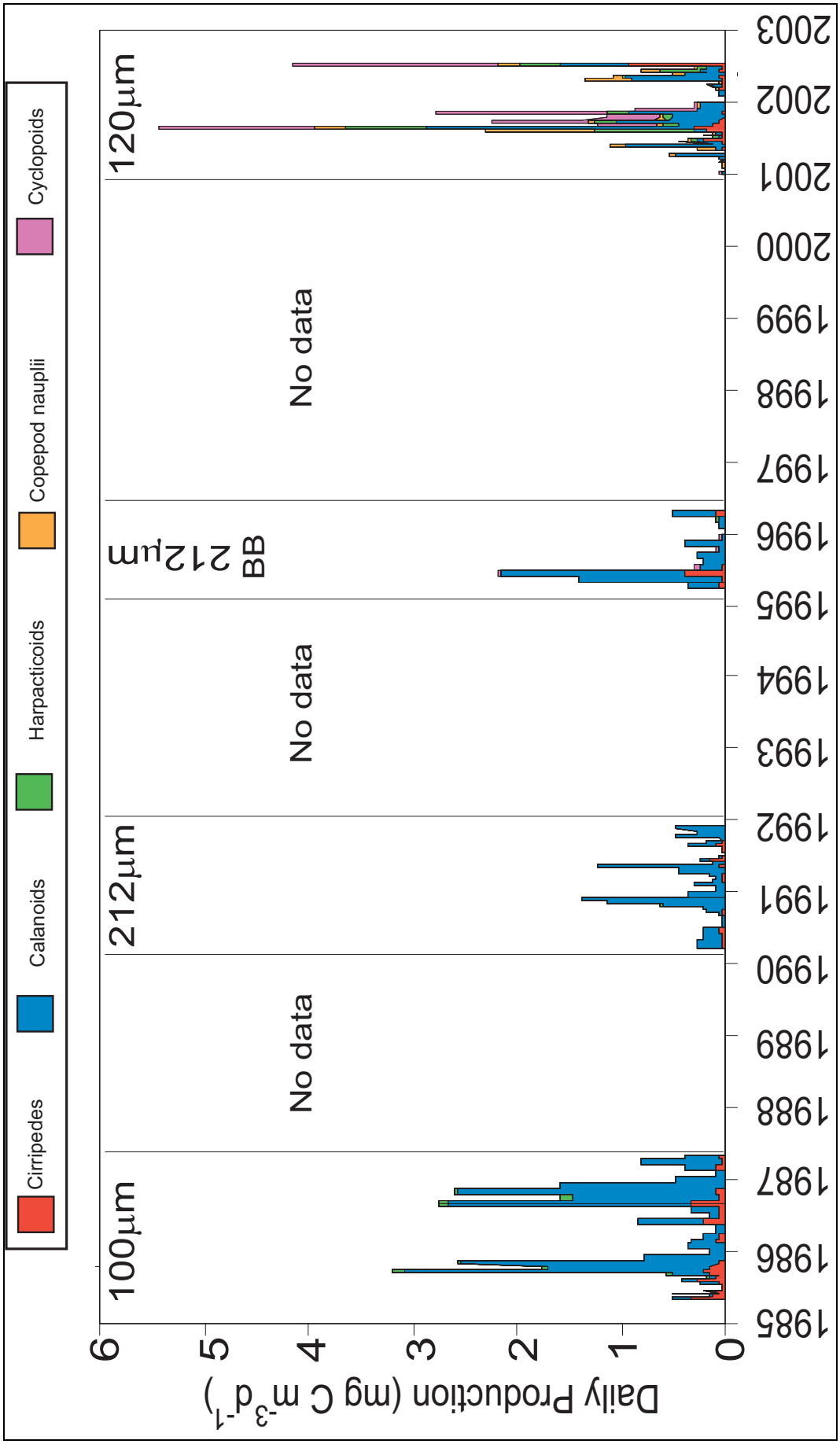


Figure 61. Integrated production of cirripedes, calanoids, harpacticoids, copepod nauplii and cyclopoids at Cracknore for the last 18 years calculated from the raw data of Zinger (1989), Lucas (1993), Castro-Longoria (1998) and the present investigation. Castro-Longoria (1998) data presented for Cracknore are from Bury Buoy (BB).

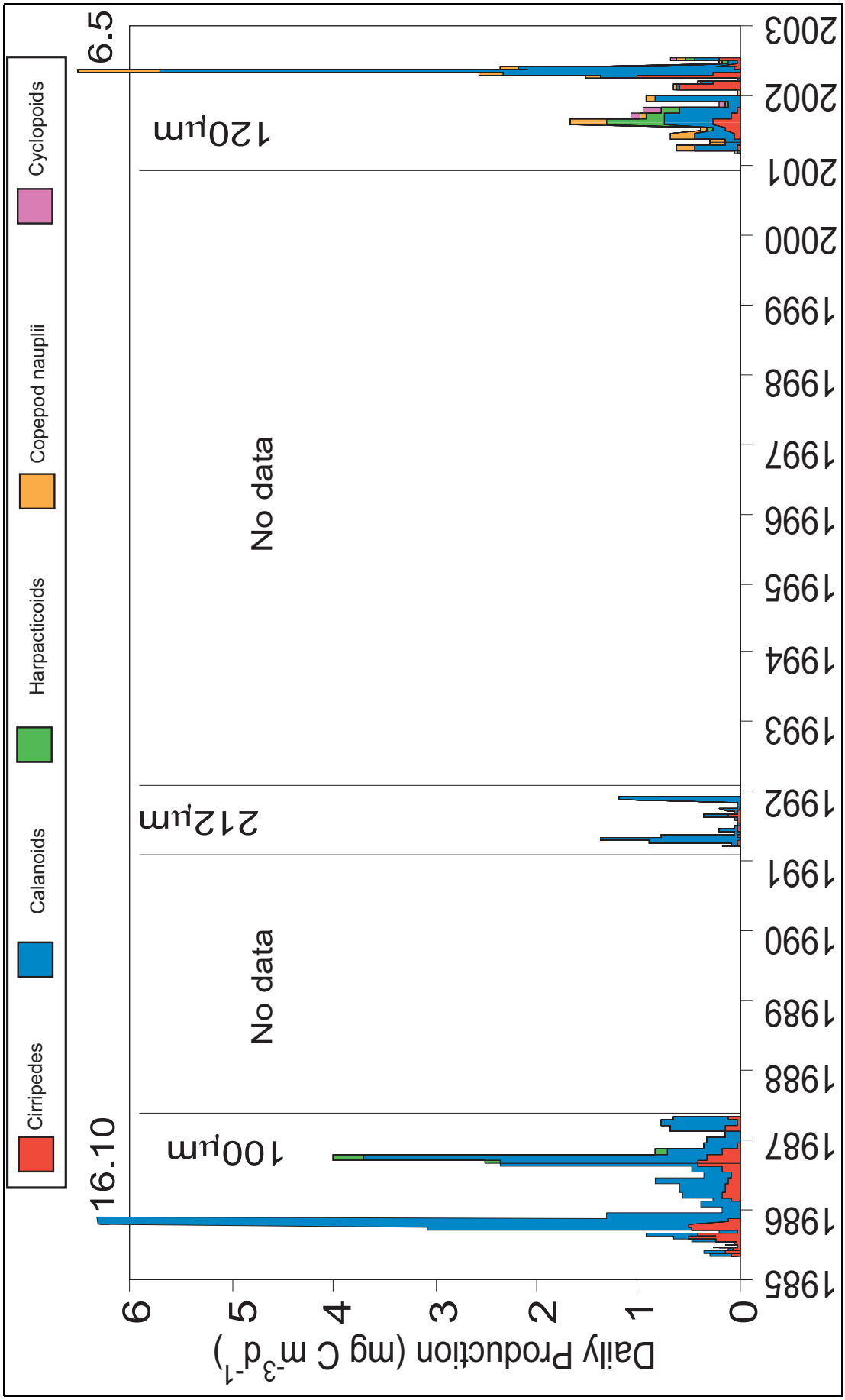


Figure 62. Integrated production of cirripedes, calanoids, harpacticoids, copepod nauplii and cyclopoids at NW.Netley for the last 18 years calculated from the raw data of Zinger (1989), Lucas (1993) and the present investigation.

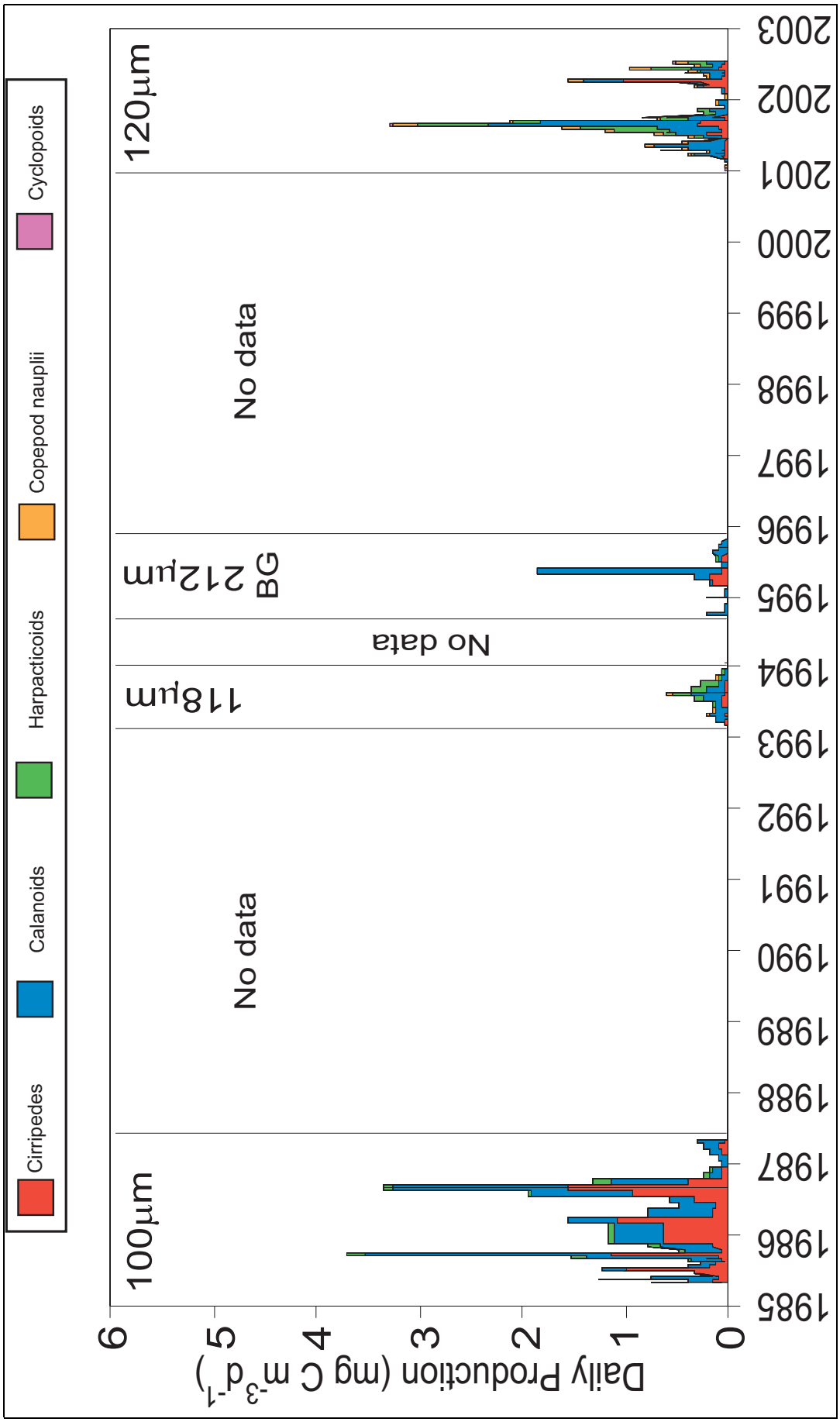


Figure 63. Integrated production of cirripedes, calanoids, harpacticoids, copepod nauplii and cyclopoids at Calshot for the last 18 years calculated from the raw data of Zinger (1989), Hirst (1996), Castro-Longoria (1998) and the present investigation. Castro-Longoria (1998) data presented for Calshot are from Bourne Gap (BG).

Previous assumptions that suggested that, within Southampton Water, barnacle larvae could contribute as much secondary production as calanoid copepods (Hirst, 1996; Hirst *et al*., 1999) were not observed during the present study, nor in calculations of data from previous investigations, with barnacle larvae production generally being 8 to 34% of total calanoid production (Table 42). The exception was Zinger's (1989) Calshot and Hamble data, where barnacle larvae represented the equivalent of 57 – 78 % of calanoid production. If calanoid production of Zinger (1989) is corrected for the inclusion of copepod nauplii, as discussed above, production of barnacle larvae during the season 1985 - 1987 will be 2 to 40 % higher than calanoids at Calshot and Hamble. Therefore within Southampton Water overall barnacle production is usually lower than that of calanoids, but in exceptional year's /circumstances it can match it or even exceed calanoid production, at particular points/ regions of this estuary.

Since abundance of animals of a particular species/stage at a particular point within an estuary is the result of a combination of several factors such as temperature, salinity, degree of tidal mixing, flushing rates, type of estuary, input of freshwater, concentration of dissolved gases, turbidity, light, nutrients, predators, advection and even a reflection of the sampling devices, the equations employed to predict production are clearly subjected to bias. However, if we consider that the equations derived in the present study were based on common production methods that require the same abundance data and are thus subjected to the same problems, we could consider them as an alternative, as good as any other, to provide easy and repeatable production estimates for this estuary based only on the total numbers of particular groups/species. Care must be taken to only compare production estimates based on catches with a 100-120 μm plankton mesh, which will be expected to sample the same proportion of the community.

In light of the results presented here, the model of pelagic carbon flux proposed by Hirst *et al*., (1999) for Calshot were modified, with some parameters added. As with the earlier model, previous production estimates of bacteria (Antai, 1989), ciliate (Leakey *et al*., 1992) and size-fractioned primary production (Iriarte & Purdie, 1994) for the estuary are included. A hypothetical station is now proposed, where the averaged values of each component measured at this estuary will represent this hypothetical station which, in turn, represents Southampton Water as a whole. In this example, the primary production was 13040 and 17650 mg C m^{-3} yr^{-1} for Calshot and NW.Netley respectively, resulting in an averaged value of 15345 mg C m^{-3} yr^{-1} (assuming an averaged depth of ~10 metres), with 81.7% of this production in the >3μm fraction, 12.1% at the 1-3μm fraction and 6.2% at the <1μm fraction (Iriarte & Purdie, 1994). Annual bacterial production, based on the

median hourly rates calculated from January 1987 to January 1988 by Antai (1989) was 26105 and 83746 mg C m^{-3} yr^{-1} at Calshot and NW.Netley respectively, giving an overall average of 54925 mg C m^{-3} yr^{-1}. Leakey *et al*., (1992) estimated the total potential production of heterotrophic ciliates at Calshot and NW.Netley as 2200 and 9200 mg C m^{-3} yr^{-1} from June 1986 to June 1987 giving an overall average of 5700 mg C m^{-3} yr^{-1}. Zooplanktonic production was presented earlier and will be based on the average of each group estimated from the results obtained only from the 2001 – 2002 data presented in Table 42.

To estimate the trophic importance of zooplanktonic components and the potential flow of carbon between the different compartments it is necessary to determine the amount of carbon required by the different consumers to support their estimated annual production. This can be determined from the ratio of ingested material that is incorporated into growth divided by the annual production. The gross growth efficiency (GGE) of ciliates ranges from 30 – 50 %, while for marine crustaceans it can range from 5 – 76 % with average around 33% for copepods (Parsons *et al*., 1984; Harms, 1987; Omori & Ikeda, 1992; Båmstedt *et al*., 2000 and references therein). Following Nielsen & Kiørboe (1994) and Leakey *et al*., (1992), a value of 40 % GGE was employed for ciliates while a value of 33% was considered for copepods and barnacles, with the exception of calanoids where a value of 29% was determined from the Scope for Growth (SfG) data of Chinnery (2002) for *Acartia bifilosa* and *A.discaudata* from this estuary. Based on these growth efficiencies, the averaged carbon requirements of ciliates and zooplanktonic organisms was estimated to be 14.3 g C m^{-3} yr^{-1} and 0.88 g C m^{-3} yr^{-1} or 99% of the total primary production (Figure 64 a).

Differences from the previous model Hirst *et al*., (1999) are evident (Figure 64 b), with the values of production of phytoplankton and bacteria much lower in the earlier model. Unfortunately Hirst *et al*., (1999) did not specify how those figures were reached, but on a re-evaluation of those values, total primary production should be 13040 mg C m^{-3} yr^{-1} assuming an averaged depth of ~10 metres, with 10810 mg C m^{-3} yr^{-1} in the >3µm fraction, 1410 mg C m^{-3} yr^{-1} at the 1-3µm fraction and 820 mg C m^{-3} yr^{-1} at the <1µm fraction (Iriarte & Purdie, 1994). Bacteria production derived from the data of Antai (1989) at Calshot ranged from 0.06 to 5.9 mg C m^{-3} hr^{-1}, resulting in an averaged value of 26105 mg C m^{-3} yr^{-1}. Corrections apart are also clear that production of calanoids were much lower during that particular year.

From Figure 64 (a) it is clear that averaged annual bacterial production exceeds the averaged primary production. While this could indeed occur if unaccounted allochthonous inputs are being supplied or even if some material is being recycled, one must bear in mind

that these values were obtained during different investigations, by different investigators, and in different years. Inter-annual variability will play a major role, and that is why as much information as possible should be collected in a single investigation to eliminate the bias introduced from data obtained for a variety of purposes. Unless studies of several components are carried out at the same time and with the same goals, generalizations based on data collected by different methods and for different purposes should be interpreted carefully. Also from Figure 64 (a) it is possible to infer that, if the rates are typical for this estuary, almost all algae production will be grazed by ciliates and metazoan zooplankton, with ciliates the major grazers of primary production of this estuary, grazing ~93% of all phytoplankton production if only microalgae is being considered as food resource. It is reported, however, that both ciliates and copepods do not graze only on phytoplankton. The smaller oligotrich ciliates (10-15 μm) are bacterivorous, while ciliates, bacteria and detritus, among several other resources are considered important food resources for copepods (Raymont, 1983; Leakey *et al*., 1992; Kiørboe & Nielsen, 1994; Nielsen & Kiørboe, 1994; Mauchline, 1998). Based on that, the question that naturally arises as to why mesozooplankton grazing accounts for relatively so little of the pelagic carbon of Southampton Water?

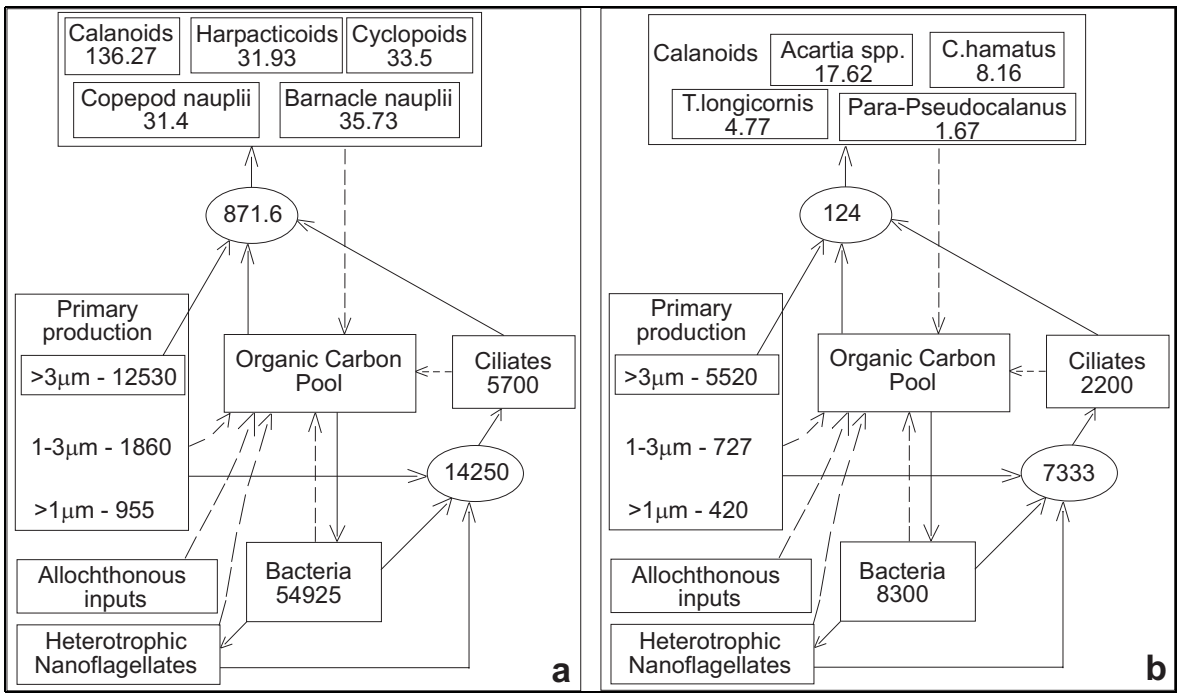


Figure 64. Diagram of hypothetical carbon flux through the pelagic community of Southampton Water (a) determined from the present study compared with (b) showing the pelagic carbon flux at Calshot redraw from Hirst *et al*., (1999). All values in boxes are production estimates; those in ellipses are estimated ingestion demands for the production (all values in mg C m^{-3} yr^{-1}). Solid arrows represent ingestion of carbon; dashed arrows represent movement to a non-living organic carbon 'pool'. Modified from Hirst *et al*., (1999).

From the values presented in Figure 64 (a), mesozooplankton averaged production is only 1.6% of primary production, while ciliates accounted for more than 45%, if only the production of >3μm algae is being considered. However, the production of ciliates determined by Leakey *et al*., (1992) was predicted using the multiple-regression equation of Montagnes *et al.* (1988), which was later observed by the same authors (Leakey *et al*., 1994), in study at Plymouth Sound – UK, to predict near maximal food saturated rates, giving values usually 32 – 56 % higher than the *in situ* rates measured by Leakey *et al.* (1994). The four dominant taxa in this later study by Leakey *et al.* (1994) grew at an averaged rate of 53.4% of those predicted by the Montagnes *et al.* (1988) equation, so, following Hirst (1996) a correction factor of 0.534 were applied to the production rates of Leakey *et al*., (1992), in an attempt to correct for sub-optimal growth. The averaged production of ciliates on Southampton Water, after this correction, falls to an average of 3044 mg C m^{-3} yr^{-1} which represents 20% of the total primary production and requiring about 61% of total primary production for growth, if only algae are considered as a food source.

This alone, only reduces the gap between the two, however, the production of copepods were clearly under-evaluated by the 120 μm mesh, when compared with a 64 μm (see previous chapters), and if we assume that mesozooplankton abundances is being underestimated by a factor of 5 (as shown on Chapter 5 from the data of (Raymont & Carrie, 1964)) due to the use of coarser meshes, mesozooplankton production, represented by those components, is expected to be at least 1344 mg C m^{-3} yr^{-1} or ~11% of primary production of the >3μm algae and requiring ~35% for growth, again if only algae >3μm are being considered as food.

The contribution of detritus as a supply, possibly a major source of nutrition, for micro and macrozooplankton is not possible to assess within the present structure of the model. While references (Raymont, 1983; Leakey *et al*., 1992; Kiørboe & Nielsen, 1994; Nielsen & Kiørboe, 1994; Mauchline, 1998) identify the potential role of particulate detritus as a food resource, particularly in times of low phytoplankton supply, no data was available for Southampton Water. The original model presented in Figure 64 (b) (Hirst *et al*., 1999) was not, therefore, able to accommodate this component and the present study is not able to introduce the resource into the model.

If both assumptions are correct, i.e. the production of ciliates were overestimated while production of zooplankton were underestimated, this correction increase the importance of copepods and barnacle larvae in relation to ciliates as major grazers of phytoplankton production. In either case, even allowing for this change between the

importance of ciliates and zooplankton, almost all phytoplankton primary production is consumed. In this sense, assuming only phytoplankton grazing, and ignoring the contribution of other known food sources like detritus and bacteria (Raymont, 1983; Leakey *et al*., 1992; Kiørboe & Nielsen, 1994; Nielsen & Kiørboe, 1994; Mauchline, 1998), mesozooplankton production in Southampton Water is potentially limited by the amount of available phytoplankton.

Those later values seems more appealing, but are only assumptions, the real measured averaged production of mesozooplanktonic organisms during this investigation amounted only 1.6% of the primary production and despite of being low, it apparently reflects the amount of available phytoplankton. Anyway, this value is also in the lower range reported elsewhere (Uye, 1982; Uye *et al*., 1983; Kimmerer & McKinnon, 1987; Kiørboe & Nielsen, 1994; Liang *et al*., 1996; Liang & Uye, 1996a; 1996b; Liang & Uye, 1997) when allowing for mesh corrections.

6.4. Chapter Conclusions.

- A new set of regression equations are being proposed for the quick estimation of production for copepod nauplii, *Acartia* spp., *Euterpina acutifrons*, *Oithona nana*, *Elminius modestus*, *Balanus crenatus*, *Semibalanus balanoides*, *Balanus improvisus*, *Verruca stroemia* and the combination of them, based primarily on the total number of organisms as well as in conjunction with temperature, salinity and chlorophyll *a*.

- Production values calculated by this new method were usually ±20% of the averaged value presented in previous chapters, however, when applied to an independent data set, differences of only ±7% were observed.

- When the set of equations was applied to earlier zooplanktonic studies in this estuary, the production values obtained from samples collected with similar methodologies gave comparable results.

- Of the groups investigated, calanoids were identified as the greatest contributor to total production. However, cyclopoids were also identified as a major contributor within the inner reaches of this estuary.

- The earlier assumption that barnacle larvae could provide as much secondary production as calanoids were not observed during the present investigation, however data of one previous investigation indicates that this is possible on a localized basis.

- Production of the mesozooplankton components investigated during the present study amounted to 1.6% of phytoplankton primary production, but it is estimated that this could be as high as 11% if samples are obtained with a finer mesh net, so collecting all life stages of the zooplankters.

Chapter 7

General Conclusions and Future Suggestions

This study was initiated with the primary objective of investigating the contribution of meroplankton, exemplified by barnacle larvae, to the pelagic carbon flux of Southampton Water, and was later extended to accommodate copepods, especially calanoids, for comparison. In order to do this, both elements had to be identified to species since rates in zooplankton populations are performed at species level, and any study considering fluxes in zooplanktonic communities requires detailed information about the spatial-temporal importance of species, abundances and biomasses before any attempt to quantify and model any specific processes (Soetaert & Van Rijswijk, 1993). During the identification of barnacles and calanoids it became clear that other components were relatively abundant and, despite the numerous studies reported in the estuary, several mesozooplankton components were completely undescribed. Effort was therefore made to identify as many as possible of the other zooplankton species found in zooplankton catches. In this respect, the present study identified a total of 144 different taxa within the zooplankton of Southampton Water, with 90 taxa being recorded for the first time. This doubled the number of recorded taxa creating the beginnings of a database to enable changes within the estuary resulting from long-term environmental change or even human impact to be detected through zooplankton diversity analysis.

Most of the new records were among the mero and tycoplanktonic fraction that was, compared with the holoplankton, clearly understudied in the estuary. Effort was focused on the identification of crustaceans in general, and other important groups of the meroplankton, the Polychaeta, Pelecypoda, Gastropoda, Ascidia and Bryozoa remain to be described in detail. (Given the relative abundance of these groups they should, logically, have been investigated in preference to some of the less abundant crustacean groups, however the time required to identify them together with the crustaceans was considered to great for completion. Identification of soft-bodied organisms is a task in itself since for some, like gastropods, identification is only possible on live and/or unpreserved individuals (Fretter & Pilkington, 1970). In an attempt to aid future taxonomic studies on those groups, a list of the benthic adults reported in the Solent – Southampton Water estuarine system that could be supplying larvae to the water column is provided (Table 13

– Chapter 3). This list is probably incomplete, since it was based on the very few benthic surveys carried out in this area (Barnes *et al*., 1973; Thorp, 1980; Collins & Mallinson, 2000) and on personal communications).

In terms of individual species, *Oithona nana* and *Euterpina acutifrons* were recognized as major components of the copepod fraction of this estuary, with both usually outnumbering *Acartia* during the summer-autumn months in parts of the estuary. This is a major observation as recent studies (Zinger, 1989; Lucas, 1993; Castro-Longoria, 1998) considered the mesozooplankton of Southampton Water to be dominated only by calanoid copepods, primarily from the genus *Acartia.* The occurrence of these two species in high numbers was essentially attributed to the use of finer mesh-size nets (120 μm), since the coarser nets, mesh ~220 μm, employed by Lucas (1993) and Castro-Longoria (1998) clearly under-sampled these two components. The occurrence of *Oithona nana* is definitely a "new feature" of this estuary that should be investigated further, as it might be related with major environmental and/or biological changes in this estuary. Oithonids have been proposed at the Marine Zooplankton Colloquium 2 (MZC2) as a potential group for future studies (Paffenhöfer *et al*., 2001) since underestimation by coarser meshes employed in earlier studies clearly minimized the important role that this group could have in the functioning of ecosystems. In line with this, *O.nana* production in this estuary was comparable to that of *Acartia* in the inner estuary, and if this species is reassessed with nets of 62 μm or smaller, production estimates would be expected to be greater than for *Acartia*. This previously unaccounted production of *O.nana* together with that of *Acartia*, copepod nauplii and *E.acutifrons,* when considered with the previously low copepod secondary production estimate which was exclusively based on calanoid copepods re-establishes in Southampton Water the "accepted" role of copepods in pelagic communities (Williams, 1984; Huys & Boxshall, 1991; Buskey, 1993; Williams *et al*., 1994; Banse, 1995). Future studies at this estuary should clearly re-investigate the seasonal and spatial occurrence of both *O.nana* and *E.acutifrons* employing meshes of ~62 μm or lower, and compare the results with those obtained at this study. Production of both species should also be reassessed, ideally measuring *in situ* growth rates and also establishing/ measuring the weight of each stage. Egg production of both species under natural diet conditions/concentrations could also provide an alternate way of establishing growth rates. Since oithonids have been reported in estuaries where eutrophication and/or a shift in food resources has occurred (Uye, 1994) the diet together with other biological/nonbiological

parameters should also be investigated to try to explain its "sudden occurence" in this estuary.

Acartia were only observed to numerically dominate zooplankton samples throughout the estuary during spring, and contrary to previous studies no simplistic species succession among the different *Acartia* species was observed. All species co-existed and peaked almost at the same period. Five *Acartia* species are identified, with *A.margalefi* and *A.discaudata* found throughout the year while *A.tonsa* and *A.clausi* are found during summer-autumn and *A.bifilosa* in winter-spring. *A.margalefi* and *A.tonsa* are more abundant in the inner reaches, with *A.clausi* and *A.bifilosa* at the mouth. *A.discaudata* is found at high abundances throughout the estuary, with no apparent spatial preferences. *Acartia* production has been reassessed and values 5 to 10 times higher than the previous estimate (Hirst *et al*., 1999) were obtained. Studies of *Acartia* should be continued in order to establish which factors, apart from temperature and salinity, control the seasonal/spatial distribution of *Acartia* species in this estuary. Like *O.nana* and *E.acutifrons in situ* growth rates should be measured for the different *Acartia* species in order to better evaluate the production of this component.

Attention should also be drawn to the occurrence of *Oncaea* sp*.,* which, like *Oithona* sp*.,* is a small species that has been consistently under-sampled by coarser mesh-size nets. The genus *Oncaea* has also been identified by the MZC2 as a potential species for future studies (Paffenhöfer *et al*., 2001) since it has also been reported in massive abundances, especially in the Antartic (Metz, 1998). Despite the fact that *Oncaea* is ubiquitous, except in estuaries (Paffenhöfer *et al*., 2001), the occurrence of this genera in Southampton Water should be closely monitored since, like *O.nana,* this genera were only observed recently at Southampton Water by Castro-Longoria (1998).

Due to the larger mesh size employed in previous studies (Lucas, 1993; Castro-Longoria, 1998), the numerical importance of *Oikopleura* sp. was missed. With the finer mesh size employed in this investigation, it is clear that it can account for ~5% of the total holoplankton. With rapid growth rates and short generation times (Deibel, 1998), appendicularians can attain massive number in short periods (Raymont, 1983) and this, coupled with the fact that they are efficient grazers (Fenaux, 1976), could suggest a huge feeding impact. Because of that, this species should be considered for future studies in Southampton Water. Due to their small size and the fact that they have very short generation time, probably an investigation with a finer mesh ~64 μm and relatively short

sampling interval ~2 to 3 days during April to June would give a clearer picture of the status of this species. Short incubations can also be conducted to investigate clearance rates in natural food concentrations, since *O.dioica* at densities of 4578 m^{-3} were reported to have filtered ~37.7% of the water available in the California current (Alldredge, 1981). *Oikopleura* sp. has also been identified at the MZC2 as a potential species for future studies (Paffenhöfer *et al*., 2001), since its high growth rates and massive abundances clearly indicate that a potential for a key role in marine ecosystems function.

Ten barnacle species were identified during this study, with five of them being seasonally abundant. *Elminius modestus* larvae occurred all year long and were found in every sample, and usually dominated the barnacle larvae composition of the mesozooplankton except from February to May, when *Balanus crenatus* larvae clearly exceeded other barnacle larvae. *Semibalanus balanoides* and *Verruca stroemia* only occured from February to May. At the innermost station (Cracknore) *B.improvisus* also appeared in high numbers from May, and co-dominated with *E.modestus* from June to August. Overall, production of barnacle larvae for this estuary was estimated to be 32.80 mg C m^{-3} yr^{-1}, with *E.modestus* alone accounting for 54.7% of this production, followed by *B.crenatus* (35%), *B.improvisus* (6.7%), *S.balanoides* (3.1%) and *V.stroemia* (0.5%). This production value was substantially lower than that of calanoid copepods. *In situ* growth rates should be measured to enable a better estimation of production values. Length and width of larval stages of barnacle larvae from this estuary cultured on excess food (~10^5 cells ml^{-1} of *Skeletonema costatum* or ~ 46 mg m^{-3} Chl *a*) should be obtained and compared with the values presented here for wild animals on natural diets, as well as to those of Harms (1986; 1987) in order to investigate if the species are food limited in the field.

In the present study a total of 31 Decapoda taxa belonging to 4 infraorders were identified. The brachiurans *Carcinus maenas*, *Liocarcinus* spp., *Pagurus bernhardus, Pisidia longicornis* and *Macropodia* spp. together with the caridean *Crangon crangon* were the most common and abundant larval forms, accounting for 98% of all decapod larvae found. With the exception of *P.longicornis,* the other species are recorded for the first time in Southampton Water. This is the first assessment of decapod larvae in this estuary where basic temporal and spatial patterns are recognized. Future studies should evaluate this meroplankton component employing coarser meshes of ~300 – 500 μm concurrently with the 120 μm employed in this investigation, in order to assess the

importance of the older/ bigger larval stages. When critical data becomes more available for this group, together with the patterns observed during this study, this will allow more conclusive remarks about the exploitability of the adult population.

Typically, mero and tycoplanktonic species were more abundant during spring-summer clearly reflecting the breeding patterns of the adults present in the area. Continuous monitoring studies should be undertaken to extend meroplankton knowledge further. The Polychaeta, Mollusca, Bryozoa and Ascidia were not identified to species, and from the results of this study they clearly constitute a large fraction of the meroplankton (~44%) of this estuary.

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Appendix I

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Composition and temporal distribution of cirripede larvae in Southampton Water, England, with particular reference to the secondary production of *Elminius modestus*

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Muxagata, E., Williams, J. A., and Sheader, M. 2004. Composition and temporal distribution of cirripede larvae in Southampton Water, England, with particular reference to the secondary production of *Elminius modestus*. – ICES Journal of Marine Science, 61: 585–595.

Southampton Water, an estuary on the south coast of England, has been the focus of a number of studies to determine the seasonality and productivity of its pelagic community. Although recognized as important in previous studies, the meroplankton component and, in particular, the cirripedes have been largely ignored, though they rank second to the Copepoda in abundance. In order to estimate the contribution of barnacle larvae to the pelagic community, 42 quantitative zooplankton samples were collected from a fixed station within the estuary during a period of 19 months (from 12 January 2001 until 16 July 2002). As expected, barnacles were the second most abundant group averaging 13% of the total population, and accounting for up to 60% on some occasions. Eight barnacle species were identified: *Elminius modestus*, *Balanus improvisus*, *Balanus crenatus*, *Semibalanus balanoides*, *Verruca stroemia*, *Chthamalus stellatus*, *Sacculina carcini*, and *Peltogaster paguri*. Of these *E. modestus* was the most abundant and frequent, dominating the Cirripedia fraction throughout the year, but being outnumbered by *B. crenatus* from February to May. Secondary production was calculated for *E. modestus* and mean daily rates of 0.077 mg C m^{-3} d^{-1} (28.08 mg C m^{-3} yr^{-1}) were found.

Keywords: Cirripedia, *Elminius modestus*, secondary production, Southampton Water, zooplankton.

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Introduction

It is widely accepted that in aquatic communities zooplankton play a critical role representing the main link between phytoplankton and bacterioplankton and the higher trophic levels (Buskey, 1993; Banse, 1995), and so the measurement of secondary production has been one of the primary goals of zooplankton research (Runge and Roff, 2000). This importance is reflected in the numerous reviews concerning the methodologies of zooplankton secondary production (Pechen *et al.*, 1971; Winberg *et al.*, 1971; Yablonskaya *et al.*, 1971; Rigler and Downing, 1984; Kimmerer, 1987; Omori and Ikeda, 1992).

Copepods generally form the largest component of zooplankton biomass present in estuarine, neritic, and oceanic areas and, as such, almost all zooplankton production refers only to the copepod component. Although organisms such as polychaete larvae, cladocerans, barnacles, and decapod larvae are also seasonally important in estuarine and neritic waters (Raymont, 1983), it is surprising that there is a lack of data on the secondary production of these components.

The zooplankton community structure of Southampton Water offers a scenario for the evaluation of a non-copepod component, as all the studies that have monitored the composition, distribution, and abundance of the micro-mesozooplankton population of this estuary (Conover, 1957; Soares, 1958; Lance and Raymont, 1964; Raymont and Carrie, 1964; Zinger, 1989; Williams and Reubold, 1990; Geary, 1991; Lucas, 1993; Lucas and Williams, 1994; Castro-Longoria and Williams, 1996; Hirst, 1996; Lucas *et al.*, 1997; Castro-Longoria, 1998; Hirst *et al.*, 1999) have indicated that the larvae of barnacles constitute the major element within the meroplankton. Hirst *et al.* (1999) even suggested that this component could be expected to account for at least as much secondary production as calanoid copepods. Unfortunately, despite the

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number of zooplankton studies, only unpublished MSc dissertations (Soares, 1958; Geary, 1991) are available on barnacle larvae in this estuary.

Soares (1958) recorded the dominance of three species of barnacle larvae within the cirripedes at a station towards the mouth of Southampton Water. The nauplii of both *Semibalanus balanoides* and *Balanus crenatus* were most abundant during late February throughout early April, with the cypris larvae only appearing after late March. On the other hand, *Elminius modestus* were the most abundant barnacle larvae during the summer months being commonly found throughout the year, and even during the zooplankton winter minimum. The occasional appearance of *Balanus improvisus*, *Verruca stroemia*, *Sacculina carcini*, and *Peltogaster paguri* nauplii, always in very low numbers, was also noted (Soares, 1958). Geary (1991) also working in this region recorded the summer dominance of *E. modestus*.

Although the meroplankton component is undescribed in detail, a number of authors have reported the seasonal cycle of abundance, biomass, and production rates for several components of the pelagic community of the Southampton Water and Solent ecosystem on the south coast of the UK (Figure 1). Ciliates (Leakey *et al.*, 1992), bacteria (Antai, 1989), size-fractionated primary production (Iriarte and Purdie, 1994), gelatinous predators (Lucas and Williams, 1994; Lucas *et al.*, 1997), and calanoid copepods (Hirst, 1996; Hirst *et al.*, 1999) have been highlighted in particular.

The present study, by giving a first estimation of the density and secondary production of barnacle larvae, will add the contribution of this meroplanktonic component to the body of information on pelagic carbon flux within Southampton Water.

Material and methods

Southampton Water is a coastal plain estuary (Dyer, 1973) located on the south coast of England (Figure 1). It is shallow, depths usually between 1 and 8 m, and is essentially marine in character, with little salinity variation near the mouth and some stratification based on the state of the tide and the freshwater inflow at the head of the estuary (Raymont and Carrie, 1964; Webber, 1980). Water temperature varies with a winter minimum ($T < 7°C$ on December–February) and maximum during the summer ($T > 17°C$ June–August) (Raymont and Carrie, 1964; Leakey *et al.*, 1992; Howard *et al.*, 1995; Hirst, 1996). The tidal features of the Solent area are characterized by a "stand" of high water (double high water), a period of 2–3 h where little tidal water movement occurs. The consequence of this is to make the ebb currents faster than the corresponding flood.

During a 19-month period between 12 January 2001 and 16 July 2002, 42 samples were collected at a fixed site, marked by the Cracknore shipping buoy (50°53′93″N 01°25′12″W) within Southampton Water (Figure 1). This site was sampled on a time scale that was comparable to the breeding and recruitment phases of the target species and also associated with tide conditions. In barnacle larvae, moulting occurs at regular intervals and the metanauplius stage is usually reached within 3–4 weeks (Bassindale, 1936; Pyefinch, 1948, Harms, 1984), followed by the cyprid stage. Because of this, a bimonthly sampling programme was carried out during the barnacle's non-breeding season. During the breeding season, a more focused and intensive sampling programme involving a shorter sample frequency, three to four times a month, was carried out.

Samples were collected in the extended period of "slack water" during the high tide from 5-m double oblique tows using conventional cod end plankton nets of 50-cm mouth diameter and 120-μm mesh with a calibrated flowmeter (TSK). Towing times varied according to season, but sampled on average 39 m^{-3} in each tow. Samples were preserved in approximately 4% formaldehyde–seawater solution buffered with borax until processing. Temperature and salinity measurements were obtained at 1-m depth intervals. Samples of water were collected with a 5-l Niskin water bottle from surface, 2- and 8-m depth for Chl *a* analysis.

Subsamples between 0.39% and 12.1% of the original sample were taken and all individuals were counted and identified, with an average counting error of $\pm 10\%$, based on all specimens counted following a Poisson distribution (Postel *et al.*, 2000).

The Cirripedia were identified to species level based on the following: Hoek (1909); Bassindale (1936); Pyefinch (1948, 1949); Knight-Jones and Waugh (1949); Jones and Crisp (1954); Crisp (1962); Lang (1980), and Branscomb and Vedder (1982). They were also sorted to larval stage in accordance with the definitions presented by Lang (1979) for the production estimates. The results are expressed as number of organisms per cubic meter or as percentages during the period of study.

The fluorimetric technique of Welschmeyer (1994) was used to determine Chl *a* concentration. The final Chl *a* concentration (mg m^{-3}) for each stratum on each sample date was obtained by averaging the duplicate results. Replica error was calculated as a percentage of the mean averaged for all measurements; during this work replica error was around $\pm 5.7\%$.

Assuming that all the individuals of the same size group and/or larval stage are growing exponentially, the secondary production of continuously reproducing animals can be calculated by the "instantaneous growth" approach (Rigler and Downing, 1984; Kimmerer, 1987; Runge and Roff, 2000), using the equation:

$$PR = \sum B_i G_i \quad (1)$$

where PR is instantaneous rate of production by a particular size class per unit of time (day), B_i is the biomass of the particular stage, and G_i is the growth rate (d^{-1}) of stage i.

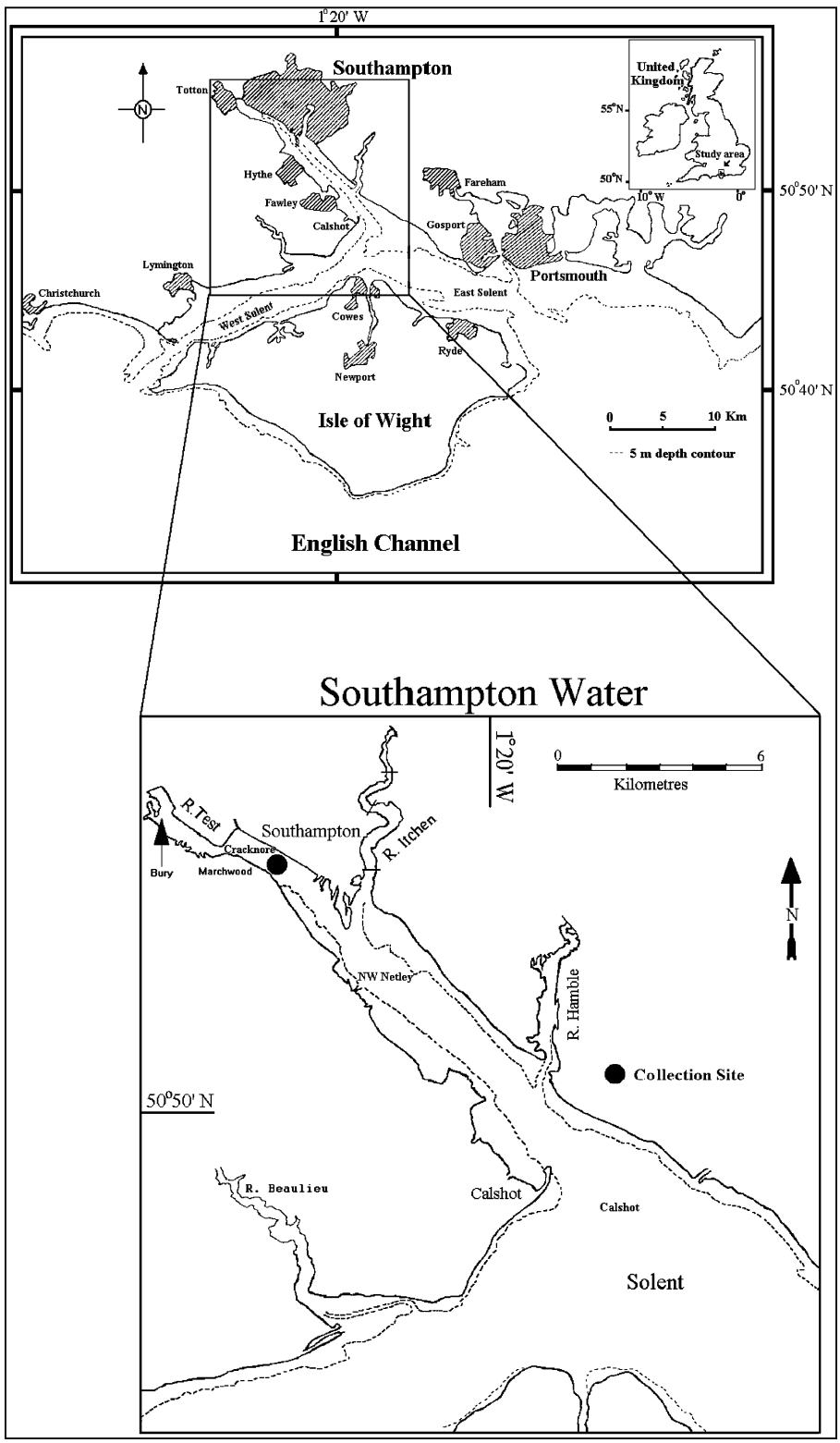

Figure 1. The study area with detail showing the position of the Cracknore sampling site and sites sampled in previous studies.

Biomass was calculated as:

$$B_i = N_i W_i \quad (2)$$

where N_i is the abundance of each developmental stage and W_i is the average weight of each stage.

Growth rate was estimated assuming that development and growth were linked; by doing so, the growth rate of a particular stage can be estimated using the duration of a particular larval stage in the equation:

$$G_i = (1/D)\ln(W_{i+1}/W_i) \quad (3)$$

where W_i is the average weight of a stage, W_{i+1} is average weight of a successive stage, and D is the larval development (d^{-1}), i.e. the time taken by an average animal to grow from one stage to another, or from W_i to W_{i+1}.

Weights of each larval stage of *E. modestus* were obtained from Harms (1987) for cultured *nauplii* at 12, 18, and 24 °C. The average weight of each larval stage (at those temperatures) was then considered in the production calculations (Table 1).

According to Harms (1984, 1986), the influence of temperature on the duration of the larval development of *E. modestus* can be expressed as a power function:

$$\ln D = \ln b + m \ln t \quad (4)$$

where t is thermal influence, D is larval development, and b and m are constants (Table 2).

Using the most recent equations of Harms (1986) it was possible to calculate the approximate duration of each larval stage for each sampling day based on field temperatures ranging from 6 °C to 24 °C and salinities around 30.

For the final annual production estimates, the calculated daily production of a particular larval stage for a sampling day was assumed to represent the mean daily production over a time interval between two successive midpoints of the inter-sample period, and converted to carbon assuming the average conversion ratio from each larval stage (Table 1). Total annual production of a population will be equal to the sum of weight increments for all the stages throughout the year, excluding the non-feeding nauplius 1 (NI) and cypris.

Table 1. *Elminius modestus* weights used in the production calculations. Also shown is the carbon:dry weight ratio for each larval stage (data from Harms, 1987).

Stage	Dry weight, µg (average)	Average C as % of dry weight
I	Not considered	Not considered
II	0.39–0.41 (0.397)	43.31
III	0.70–0.75 (0.72)	44.17
IV	1.06–1.47 (1.243)	40.40
V	2.33–2.62 (2.467)	39.37
VI	4.27–5.19 (4.617)	44.69
Cypris	4.38–5.81 (4.916)	51.94

Table 2. Constant values needed in the power function to obtain growth rates of *E. modestus* in the field with salinities around 30 (data from Harms, 1986).

Stage	b	m
II to III	158	−1.51
III to IV	176	−1.65
IV to V	147	−1.52
V to VI	235	−1.61
VI to Cypris	433	−1.63

Due to the oblique nature of the zooplankton sampling, temperature, salinity, and Chl *a* data from each stratum of each station had to be averaged before any analysis could be made. The Pearson's product-moment correlation coefficient r was used in order to measure the intensity of the association between the biotic and abiotic variables. To stabilize the variance of the data, zooplankton abundances were $\log_{10}(x + 1)$ transformed and the average Chl *a* concentrations were $\log_{10}(x)$ transformed before analysis (Prepas, 1984).

Results

The temporal variability of the water temperature, salinity, and Chl *a* at three depths at the Cracknore buoy site during the period of study can be seen in Figure 2. Temperature (Figure 2a) varied according to season with the minimum temperature recorded during this investigation being 5.4 °C in January 2002, and the maximum 20.4 °C in August 2001. No pattern of temperature difference with depth was evident, but on some occasions slight differences of temperature at the surface were observed but these never exceeded 2.3 °C. Salinity (Figure 2a) did not have any clear seasonal variation, but presented some vertical stratification with minimum values in the surface layer and gradually increasing with depth. The minimum recorded was 11.7 and the maximum 32.5.

Concentration of Chl *a* at Cracknore during the 2001–2002 season is illustrated in Figure 2b. At the beginning of 2001, Chl *a* was low, <2 mg m^{-3}, increasing to an average of 14 mg m^{-3} from May through August 2001, with successive peaks occurring in May (38 mg m^{-3}), June–July (31 mg m^{-3}), July–August (63 mg m^{-3}), and August–September (13 mg m^{-3}). During autumn the concentration returned to low values of <2 mg m^{-3} until July 2002, apart from two minor increases in April (3 mg m^{-3}) and July (5 mg m^{-3}) of 2002 (Figure 2). Chl *a* was uniform with depth during the low concentration period. During May through September the surface layer usually had higher concentrations.

After copepods, barnacles were the second most abundant mesozooplankton group at Cracknore during 2001–2002 (Figure 3). They averaged 13% of the total population and contributed up to 60% on some occasions.

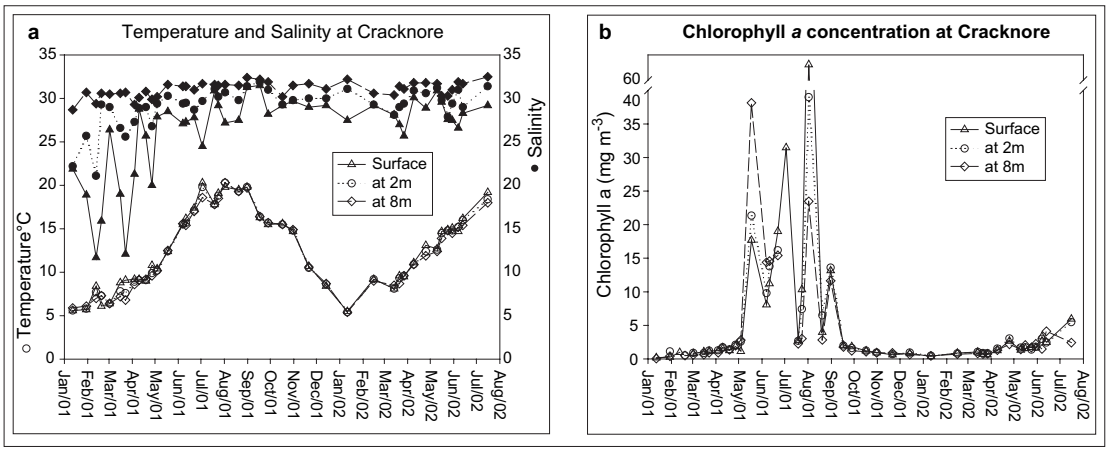

Figure 2. Temporal variability of (a) temperature, salinity, and (b) Chl *a* at three depths at Cracknore during 2001−2002.

During this investigation, eight Cirripedia species were identified, and the temporal density distribution of the most abundant ones at the Cracknore site can be seen in Figure 4. *E. modestus* was the most abundant, occurring in the plankton throughout the year with a frequency of occurrence (FO) of 100%. Generally, this species had the lowest densities in winter, with an average of 57 org. m^{-3} in 2001 and 16 org. m^{-3} in 2002. In spring, its density starts to increase with averages of 326 org. m^{-3} in 2001 and 376 org. m^{-3} in 2002. Maximum density is reached during the summer−autumn months, with an average of 1053 org. m^{-3} in 2001. From autumn its density gradually declined towards the winter values.

The second most abundant species was *B. improvisus* (FO = 83%), with a very marked seasonal pattern of abundance and with a summer−autumn average of 339 org. m^{-3} in 2001. This species was also present in very low numbers during the winter, with an average of 0.4 org. m^{-3} in 2001 and 0.5 org. m^{-3} in 2002, and spring with averages of 55 org. m^{-3} in 2001 and 49 org. m^{-3} in 2002. This species was absent from samples from mid-autumn to early winter (October−February).

Marked seasonality was also shown by *B. crenatus* (FO = 71%), which was most abundant during late winter and early spring, with winter−spring averages of 121 org. m^{-3} in 2001 and 229 org. m^{-3} in 2002. This species was very rarely found during the summer−autumn months. *S. balanoides* (FO = 45%) presents the same pattern of distribution as *B. crenatus*, but with much lower densities, and completely disappears from the plankton from June to

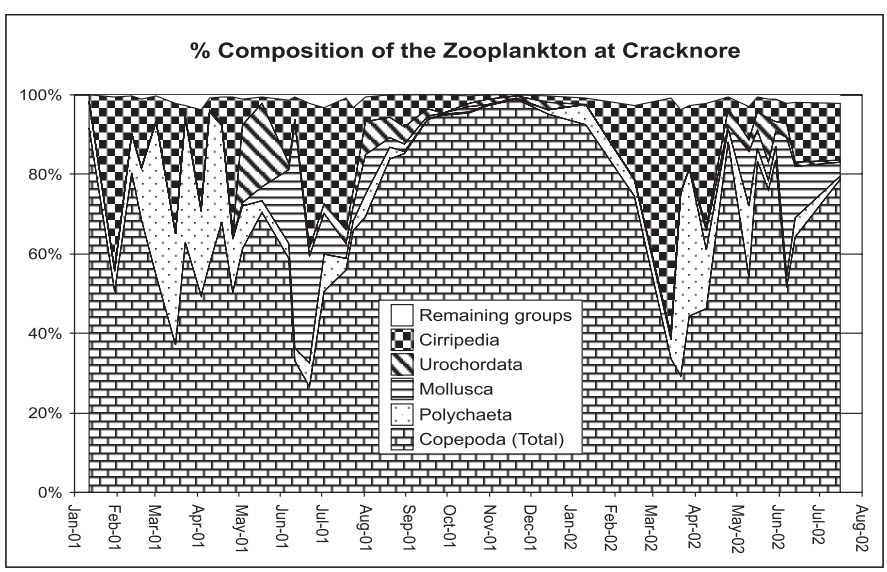

Figure 3. Total composition of the mesozooplankton at Cracknore during 2001−2002.

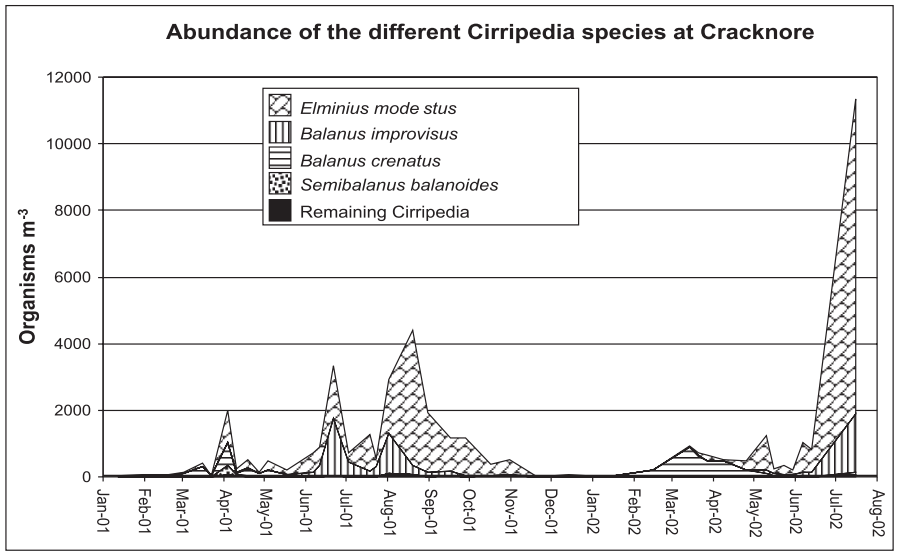

Figure 4. Density of the different Cirripedia species present in the zooplankton of Cracknore during 2001–2002.

February. *V. stroemia* (FO = 24%), *P. paguri* (FO = 26%), *S. carcini* (FO = 86%), and *Chthamalus stellatus* (FO = 2%) were present at very low densities, and in Figure 4 are pooled under the heading "remaining Cirripedia". *V. stroemia* occurred in the same winter–spring period as *S. balanoides*, and a maximum density of 41 org. m^{-3} in April 2001 and 4 org. m^{-3} in March 2002 was observed. *C. stellatus* was only present in one sample in March 2001.

The parasitic species *P. paguri* was present sporadically, with a maximum of 11 org. m^{-3} detected in October 2001, and was more frequent during the winter–early spring of 2001. *S. carcini* was present throughout the year, with a maximum density of 106 org. m^{-3} observed in August 2001.

Figure 5 shows the general seasonal pattern presented by the different Cirripedia species. At the beginning of the year, *E. modestus* generally dominates the composition of Cirripedia, and is then replaced in dominance by *B. crenatus* from February to May, with *S. balanoides* and some *V. stroemia* also occurring. From May, *B. improvisus* begins to replace *B. crenatus* and co-dominates along with *E. modestus*. From September to January *E. modestus* is again the dominant barnacle species at Cracknore. A

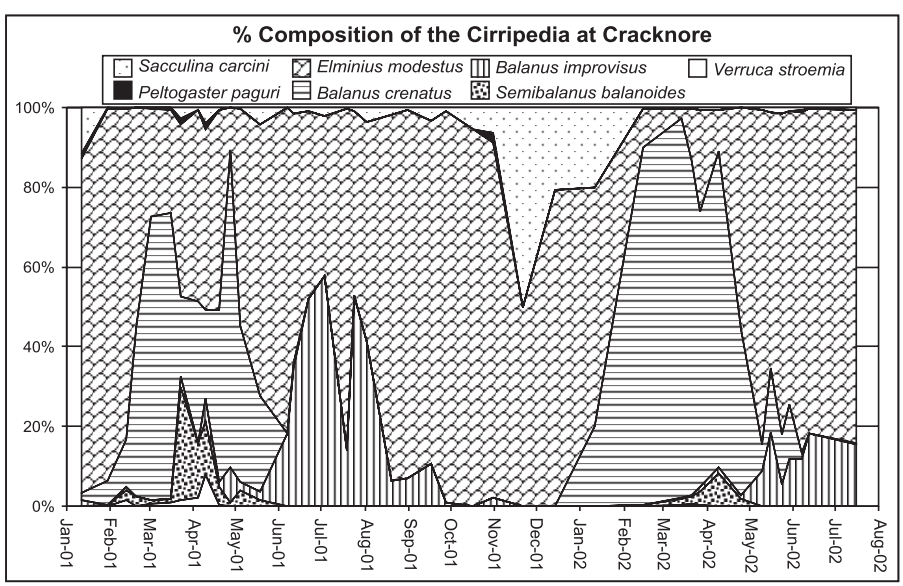

Figure 5. Temporal variability of the different Cirripedia species present in the zooplankton of Cracknore during 2001–2002.

remarkable feature is the strong peak of *S. carcini* during late autumn, but this is also a reflection of the low total numbers found.

Within the annual pattern, *E. modestus* alone contributes an average of 60% of the total barnacle population, and its larval stage composition can be seen in Figure 6a. The daily secondary production of this species was estimated (Figure 7) based on this larval density (Figure 6b). For the 2001–2002 period, production was estimated as 0.077 mg C m^{-3} d^{-1} or 43.15 mg C m^{-3} over the whole period, which represents an average annual production of 28.08 mg C m^{-3} yr^{-1}. In 2001 production was calculated as 21.21 mg C m^{-3} yr^{-1}.

Based on the seasonal distribution of the different barnacle species found, correlations with the environmental variables measured were made in order to identify any pattern (Table 3). Within the barnacle species, the correlations confirmed the seasonality of occurrence, being positive for those most abundant during summer (*E. modestus*, *B. improvisus*, and *S. carcini*) and negative for those peaking during winter–spring (*S. balanoides*, *B. crenatus*, and *V. stroemia*). Chlorophyll was positively correlated with those species, with a very marked spring–summer occurrence.

Discussion

The temperature and salinity profiles agree with the patterns reported from other studies at this station (Zinger, 1989; Lucas, 1993, Hirst, 1996) and neighbouring areas (Raymont and Carrie, 1964; Castro-Longoria, 1998). Similarly, the Chl *a* values measured at Cracknore concur with most Chl *a* data reported for this estuary (Williams, 1980; Leakey *et al.*, 1992; Kifle and Purdie, 1993; Iriarte and Purdie, 1994; Howard *et al.*, 1995), which corresponds to primary production values of 130–177 g C m^{-2} yr^{-1} (Iriarte and Purdie, 1994).

Several authors have described the basic spatial and temporal pattern of the micro-mesozooplankton populations of Southampton Water. Recently, Hirst (1996) and others (Zinger, 1989; Lucas, 1993; Castro-Longoria, 1998)

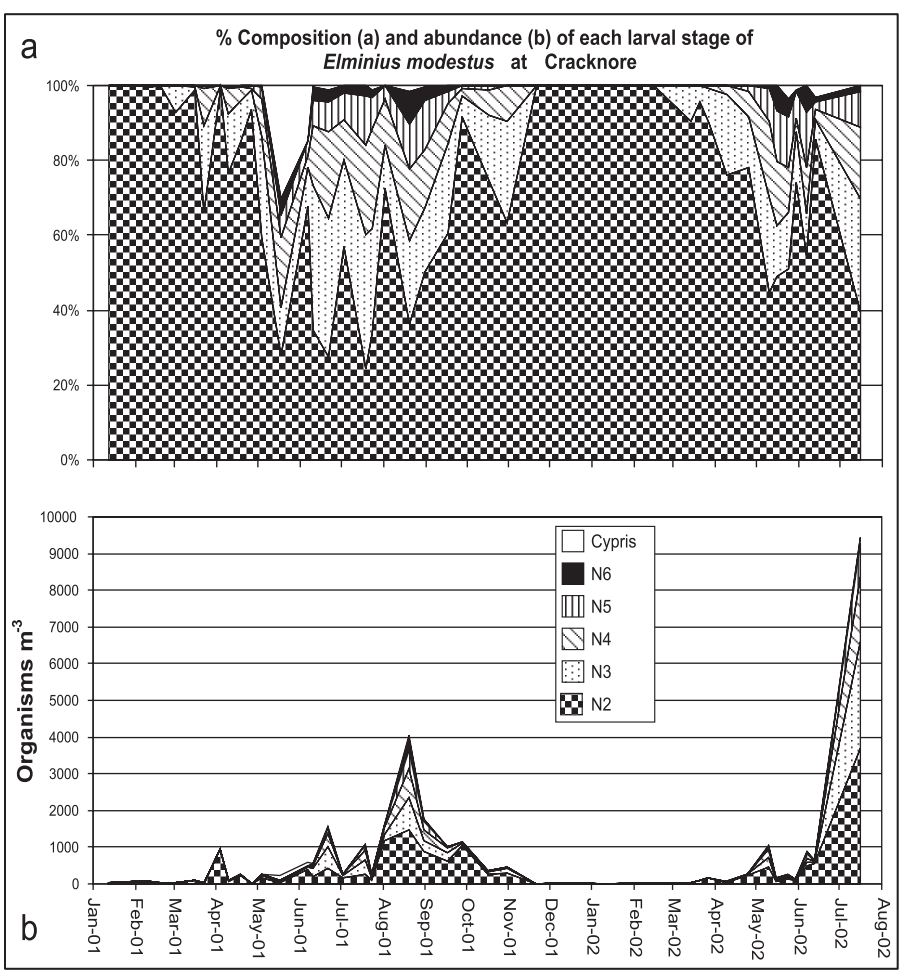

Figure 6. Temporal variability of the larval stages of *Elminius modestus* present in the zooplankton of Cracknore during 2001–2002.

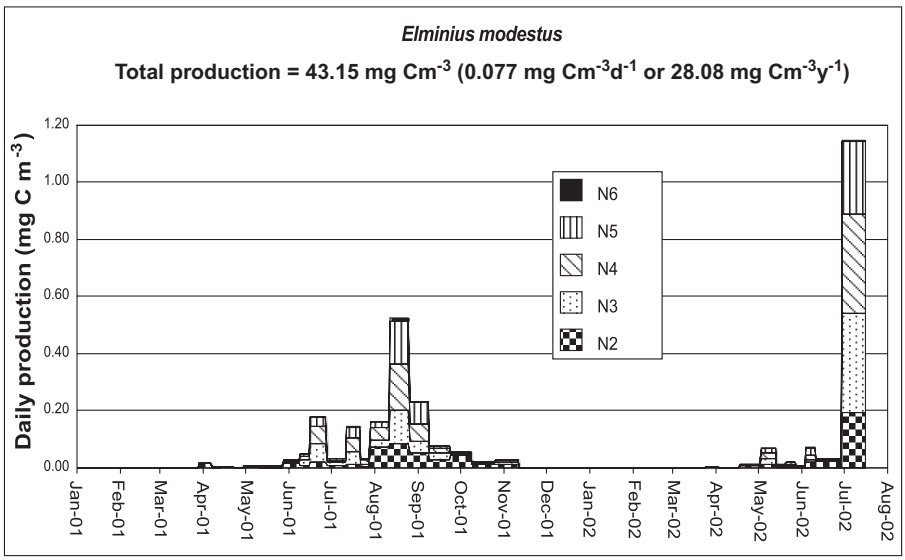

Figure 7. Seasonal production of the larval stages of *Elminius modestus* present in the zooplankton of Cracknore during 2001−2002.

have reported that the zooplankton was primarily dominated by calanoid copepods, with barnacle nauplii being more numerous mainly during early spring (February−March) and summer (June−September). This reflects the generally accepted view that, in estuaries, copepods, mainly from the genus *Acartia*, *Eurytemora*, and *Oithona*, are dominant (Jeffries, 1967; Conover, 1979; Miller, 1983; Escaravage and Soetaert, 1995; Irigoien and Castel, 1995), with meroplanktonic larvae being only seasonally abundant. In terms of general community composition the present results agree with earlier ones, identifying Copepoda as dominant followed by Cirripedia, with some seasonal contribution by other meroplankton (Zinger, 1989; Lucas, 1993; Hirst, 1996; Castro-Longoria, 1998).

As with most meroplankton, barnacle nauplii usually have a very short planktonic life, although they can represent a large proportion of the zooplankton on a seasonal time scale. In terms of species composition, only Soares (1958), Raymont and Carrie (1964), and Geary (1991) have studied cirripede larvae within Southampton Water. Soares (1958) described a station at the mouth of Southampton Water, with the nauplii of both *S. balanoides* and *B. crenatus* being the most abundant forms during spring and those of *E. modestus* during the summer; Raymont and Carrie (1964) offered a very general picture of the distribution of the dominant species over the entire estuary. Geary's (1991) results from Cracknore should be compared cautiously with the present study, since only summer−autumn samples were available, and all individuals found in the summer were assumed to be *E. modestus*.

In terms of total Cirripedia density, the values reported here concur with those presented by Zinger (1989) for the same station. However, Zinger (1989) found that barnacles and calanoids represent on average 30.2% and 35.4% of the total zooplankton composition, whereas in the present study barnacles and calanoids represented on average only 13.6% and 17.5%, respectively, of the total zooplankton. This difference is mainly because of the large number of cyclopoids recorded in the present study and due to the fact that Zinger (1989) did not include copepod nauplii in the data. The species recorded at Cracknore are the same and show the same seasonal pattern as in the study of Soares (1958), although densities of *S. balanoides* and *B. crenatus* were higher compared with the present study. In contrast, *E. modestus* and *B. improvisus* occurred in higher densities in this survey. These differences could, in part, be due to the different location. Raymont and Carrie (1964) reported that higher densities of both *S. balanoides* and *B. crenatus* were commonly found at Calshot in the spring when compared to Marchwood (Figure 1), with the opposite occurring with

Table 3. Pearson's product-moment correlation of biotic and abiotic parameters from data collected at Cracknore (marked correlations * are significant at $p < 0.05$ and ** at $p < 0.01$).

	T°C	Salinity	Chl *a*
Temperature	1.00		
Salinity	0.58**	1.00	
Chlorophyll *a*	0.77**	0.38*	1.00
E. modestus (total)	0.79**	0.41**	0.61**
B. crenatus (total)	−0.48**	−0.16	−0.27
B. improvisus (total)	0.86**	0.46**	0.78**
S. balanoides (total)	−0.48**	−0.25	−0.22
V. stroemia (total)	−0.39**	−0.32*	−0.23
P. paguri (total)	−0.09	−0.06	−0.17
S. carcini (total)	0.69**	0.48**	0.49**
C. stellatus (total)	−0.17	−0.19	−0.11

E. modestus during the summer. Supporting this is the idea that both *E. modestus* and *B. improvisus* could be more salinity tolerant than the other two, as they are common inhabitants of brackish water regions in several British estuaries (Jones and Crisp, 1954). *P. paguri* and *S. carcini* are nauplii of parasitic forms that infect hermit crabs and crabs, respectively, and their occurrence is linked with the presence of the infected benthic host organism within the estuary.

Laboratory-defined growth rates for field production estimates are commonly used for assessments of the secondary production of species with continuous reproduction (Landry, 1978; Durbin and Durbin, 1981; McLaren and Corkett, 1981; McLaren *et al.*, 1989; Huntley and Lopez, 1992; Escaravage and Soetaert, 1995; Irigoien and Castel, 1995). The power function utilized during this study takes into account variation in temperatures (Harms, 1984, 1986), but does not account for food concentration, since it was developed under optimal food conditions. The daily production value of 0.077 mg C m^{-3} d^{-1} estimated during this investigation therefore represents potential production, assuming no food limitation.

As a first figure, the averaged value of 28.08 mg C m^{-3} yr^{-1} reported here for *E. modestus* gives an indication of the lowest potential production of barnacles at Cracknore, since it does not include the production values of the remaining barnacle species present. So, accepting that *E. modestus* grossly averages 60% of the barnacles at this station, the remaining 40% could probably contribute an additional 20–30 mg C m^{-3} yr^{-1}, or more, considering that *E. modestus* has the smallest larvae.

Previous zooplankton production studies within this estuary suggested that barnacles might contribute as much secondary production as calanoid copepods (Hirst, 1996; Hirst *et al.*, 1999), and the present results could be taken to corroborate this assumption. However, the published value of 32.2 mg C m^{-3} yr^{-1} (36.2 mg C m^{-3} yr^{-1} assuming C as 45% of DW; Table 4) for calanoids at Calshot (1993–1994) (Hirst *et al.*, 1999) is not directly comparable

Table 4. Production estimates of estuarine copepods and cirripedes.

Species (groups), region	Daily production	Interval (days)	~Depth (m)	Source
Acartia clausi, Jakles Lagoon, Washington, USA	22–27 mg C m^{-2} d^{-1} 7.3–9 mg C m^{-3} d^{-1}	365 365	3 3	Landry, 1978
Acartia hudsonica, Narragansett Bay, Rhode Island, USA	7.52–12.77 mg C m^{-3} d^{-1} (2.47–4.19 mg C m^{-3} d^{-1})*	120 (365)*	6 6	Durbin and Durbin, 1981
Acartia tonsa, Narragansett Bay, Rhode Island, USA	18.98–22.91 mg C m^{-3} d^{-1} (5.35–6.46 mg C m^{-3} d^{-1})*	103 (365)*	6 6	Durbin and Durbin, 1981
Acartia tranterti, Westernport Bay, Australia	0.4 mg C m^{-3} d^{-1}	365	5	Kimmerer and McKinnon, 1987
Eurytemora affinis, Westerschelde, The Netherlands	2.23 mg C m^{-3} d^{-1}	365	—	Escaravage and Soetaert, 1993, 1995
Acartia tonsa, Westerschelde, The Netherlands	1.7 mg C m^{-3} d^{-1}	365	—	Escaravage and Soetaert, 1995
Acartia spp. (three species), Malaga Harbour, Spain	13.1 mg C m^{-3} d^{-1} (4.99 mg C m^{-3} d^{-1})*	139 (365)*	7 7	Guerrero and Rodríguez, 1997
Calanoids, Cracknore, Southampton Water, UK	1.07 mg C m^{-3} d^{-1}	365	5	Hirst, 1996
Calanoids, NW Netley, Southampton Water, UK	1.62 mg C m^{-3} d^{-1}	365	5	Hirst, 1996
Calanoids, Calshot, Southampton Water, UK	0.813 mg C m^{-3} d^{-1}	365	5	Hirst, 1996
Calanoids, Calshot, Southampton Water, UK	0.099 mg C m^{-3} d^{-1}	365	5	Hirst *et al.*, 1999
Elminius modestus, Cracknore, Southampton Water, UK	0.077 mg C m^{-3} d^{-1}	365	5	Present study

Dry weight values were converted to carbon using a conversion factor of 45% (original values obtained using a conversion value of 40% where re-calculated and standardized at 45%).
Values in parentheses ( )* are calculated daily rates assuming that there was no production after the examined period.

with the present study. This is because Calshot usually has significantly lower zooplankton densities compared with those of the inner stations (e.g. Cracknore), as well as a different community (Raymont and Carrie, 1964; Zinger, 1989). The current zooplankton composition and density values of barnacles and calanoids at Cracknore approach those recorded by Zinger (1989) for the same location (Figure 1). Comparing the averaged calanoid copepod production value of 389.1 mg C m^{-3} yr^{-1} (1985−1986) (Table 4) estimated from the data of Zinger (1989) by Hirst (1996), the current production of *E. modestus* represents only 7% of the calanoid production. However, if we add the production of the remaining barnacle species we could expect values approaching to 12−15% of the production of calanoids.

Looking at the overall value of cirripede production within Southampton Water, the values of 0.077 mg C m^{-3} d^{-1} in the current study are low compared with the published literature for calanoids in other European estuaries (Table 4). Escaravage and Soetaert (1993, 1995) reported production rates around 2.23 mg C m^{-3} d^{-1} for *Eurytemora affinis* and 1.7 mg C m^{-3} d^{-1} for *Acartia tonsa* in the Westerschelde, The Netherlands (assuming C as 45% of DW), while Guerrero and Rodríguez (1997) reported values of 4.99 mg C m^{-3} d^{-1} for three different species of *Acartia* in Malaga Harbour, Spain (assuming C as 45% of DW and that no production occurred after the study period). Hirst (1996) calculated the production of calanoids from the data of Zinger (1989) for Southampton Water and it ranged from 0.81 to 1.62 mg C m^{-3} d^{-1}. We can also speculate that the high numbers of cyclopoids found in the upper part of this estuary (Muxagata *et al.*, unpubl.) would also significantly increase estimated copepod production, and thus the zooplankton production of Southampton Water as a whole. In conclusion, within the main body of Southampton Water, meroplankton production using the production of *E. modestus* as an example is substantially lower than that of total calanoid copepods.

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Appendix II – Sampling dates, showing the data collected at each station (where, Zoo = Zooplankton samples, T-S = temperature and salinity; O_2 = Oxygen; Chl-*a* = Chlorophyll-*a*; x = data collected; - = data not collected).

	Cracknore				Calshot				NW – Netley			
Date	Zoo	T-S	O_2	Chl-a	Zoo	T-S	O_2	Chl-a	Zoo	T-S	O_2	Chl-a
12/01/01	x	x	x	x	x	x	x	x	-	-	-	-
30/01/01	x	x	x	x	x	x	x	x	-	-	-	-
12/02/01	x	x	-	x	x	x	-	x	-	-	-	-
19/02/01	x	x	x	x	x	x	x	x	-	-	-	-
02/03/01	x	x	x	x	x	x	x	x	x	x	x	x
16/03/01	x	x	x	x	x	x	x	x	-	-	-	-
23/03/01	x	x	x	x	x	x	x	x	-	-	-	-
04/04/01	x	x	x	x	x	x	x	x	-	-	-	-
10/04/01	x	x	x	x	x	x	x	x	x	x	x	x
19/04/01	x	x	x	x	x	x	x	x	-	-	-	-
27/04/01	x	x	x	x	x	x	x	x	-	-	-	-
04/05/01	x	x	x	x	x	x	x	x	x	x	x	x
18/05/01	x	x	x	x	x	x	x	x	-	x	x	x
07/06/01	x	x	x	x	x	x	x	x	x	x	x	x
11/06/01	x	x	x	x	x	x	x	x	-	-	-	-
22/06/01	x	x	x	x	x	x	x	x	-	-	-	-
03/07/01	x	x	x	x	x	x	x	x	-	-	-	-
19/07/01	x	x	x	x	x	x	x	x	x	x	x	x
24/07/01	x	x	x	x	x	x	x	x	-	-	-	-
02/08/01	x	x	x	x	x	x	x	x	x	x	x	x
20/08/01	x	x	x	x	x	x	x	x	-	-	-	-
31/08/01	x	x	x	x	x	x	x	x	-	-	-	-
17/09/01	x	x	x	x	x	x	x	x	x	x	x	x
28/09/01	x	x	x	x	x	x	x	x	-	-	-	-
17/10/01	x	x	x	x	x	x	x	x	x	x	x	x
31/10/01	x	x	x	x	x	x	x	x	-	-	-	-
21/11/01	x	x	x	x	x	x	x	x	x	x	x	x
14/12/01	x	x	x	x	x	x	x	x	x	x	x	x
11/01/02	x	x	x	x	x	x	x	x	x	x	x	x
15/02/02	x	x	x	x	x	x	x	x	x	x	x	x
14/03/02	x	x	x	x	x	x	x	x	x	x	x	x
21/03/02	x	x	x	x	x	x	x	x	x	x	x	x
28/03/02	x	x	x	x	x	x	x	x	x	x	x	x
09/04/02	x	x	x	x	x	x	x	x	x	x	x	x
25/04/02	x	x	x	x	x	x	x	x	x	x	x	x
10/05/02	x	x	x	x	x	x	x	x	x	x	-	x
16/05/02	x	x	x	x	x	x	x	x	x	x	x	x
24/05/02	x	x	x	x	x	x	x	x	x	x	x	x
30/05/02	x	x	x	x	x	x	x	x	x	x	x	x
07/06/02	x	x	x	x	x	x	x	x	x	x	x	x
13/06/02	x	x	x	x	x	x	x	x	x	x	x	x
16/0702	x	x	x	x	x	x	x	x	x	x	x	x

Appendix III a – Zooplankton data at Cracknore, showing the sampling dates, aliquot size, volume filtered, sampling time (British summer time corrected), organisms density per m^3 (only showing by species the most abundant), total density and counting errors based on total density of raw data.

Date	Aliquot size (%)	Volume Filtered	Samp. Time	*Acartia* spp.	Other Calanoida	*O.nana*	Other Cyclop	*E acutifrons*	Other harpact.	Remaining Copepoda	Copepoda Nauplii
12/01/01	3.125	82.408	13:35	126.98	4.30	1318.71	0.42	0.39	2.00	0.17	66.40
30/01/01	6.250	73.631	15:55	7.17	0.43	41.72	0.22	0.00	3.04	0.22	30.64
12/02/01	6.250	93.514	11:57	78.53	13.35	295.31	1.37	0.00	13.10	0.51	249.80
19/02/01	3.125	79.994	12:07	100.41	13.21	80.81	0.05	0.00	2.43	0.04	120.81
02/03/01	3.125	86.754	13:46	239.02	9.64	362.59	0.00	0.00	1.12	0.37	695.30
16/03/01	3.125	40.279	12:42	130.29	19.14	139.03	0.00	0.00	1.66	0.07	181.16
23/03/01	3.125	50.982	10:31	330.78	49.68	345.85	1.88	0.00	12.02	0.63	299.40
04/04/01	3.125	6.197	10:24	1791.91	249.32	113.61	10.33	0.00	72.30	10.33	1709.29
10/04/01	1.563	35.490	12:40	2757.25	128.46	61.31	0.00	0.00	23.50	1.83	1718.55
19/04/01	1.563	34.364	09:44	1147.26	39.37	20.49	0.00	0.03	1.86	0.12	4223.99
27/04/01	12.100	44.504	14:05	19.87	11.35	0.56	0.37	0.02	2.79	0.02	155.62
04/05/01	1.563	38.589	10:02	543.99	61.88	11.61	0.03	1.66	29.85	0.16	3826.19
18/05/01	3.125	6.760	10:34	5296.98	222.78	0.00	0.30	56.80	123.08	0.59	3521.85
07/06/01	1.563	23.660	12:53	454.43	97.38	0.00	2.70	197.46	32.46	0.00	1893.47
11/06/01	1.563	19.154	13:59	1236.32	290.70	6.68	0.00	842.04	30.07	3.39	2890.32
22/06/01	1.563	6.197	12:08	454.43	73.26	0.00	0.00	640.34	51.64	31.15	1218.71
03/07/01	3.125	6.197	09:32	108.77	10.49	0.00	0.00	1022.47	108.44	0.00	258.20
19/07/01	1.563	32.674	10:17	352.58	17.66	82.27	0.03	1028.35	190.00	0.06	470.10
24/07/01	1.563	23.097	15:35	415.64	8.36	5.54	0.00	169.03	22.17	0.00	1174.87
02/08/01	1.563	4.225	12:29	590.76	227.69	136.33	0.00	11345.67	196.92	15.15	20025.33
20/08/01	0.391	24.918	12:55	12925.28	609.80	36916.06	10.31	9031.23	431.57	51.97	6555.09
31/08/01	0.391	58.964	13:01	2118.86	117.62	14667.00	0.00	1940.84	47.80	4.36	1419.81
17/09/01	0.391	46.904	13:06	5638.44	16.78	23880.04	0.00	2996.60	152.85	21.90	1173.53
28/09/01	0.781	24.918	11:24	3015.40	41.30	17989.39	0.00	482.87	15.41	0.04	2645.50
17/10/01	0.391	59.803	13:23	3056.65	38.65	13635.04	4.28	1339.96	55.65	12.84	406.70
31/10/01	0.391	22.279	12:13	5125.10	231.89	40092.62	0.00	2769.37	22.98	0.04	149.38
21/11/01	0.391	35.178	15:56	1725.16	15.10	15457.89	0.00	87.33	0.00	0.00	36.39
14/12/01	0.781	66.252	12:23	1605.51	23.29	1008.51	0.00	11.59	3.86	0.02	823.04
11/01/02	3.125	58.630	12:16	15.52	1.23	80.23	0.00	0.00	0.56	0.02	52.94
15/02/02	3.125	46.025	15:06	378.32	2.24	9.73	0.00	0.00	0.72	0.02	502.69
14/03/02	3.125	43.386	13:48	182.20	5.44	5.90	0.00	0.00	0.76	1.50	325.26
21/03/02	1.563	45.145	17:05	421.11	7.13	17.01	0.00	0.00	1.42	0.02	576.98
27/03/02	1.563	47.490	09:46	901.57	18.11	6.74	0.00	0.00	5.39	0.11	882.70
09/04/02	1.563	48.956	12:30	145.11	17.18	13.07	0.00	2.61	2.61	0.04	614.43
25/04/02	0.781	27.263	12:20	5108.17	38.62	18.78	0.00	4.70	9.39	0.00	9084.84
10/05/02	0.391	28.142	12:25	5121.70	56.64	245.62	0.00	627.70	45.49	0.00	1919.50
16/05/02	0.781	46.025	15:02	3256.69	14.56	33.37	0.00	41.72	22.25	0.00	2177.62
24/05/02	0.781	28.142	10:23	2324.18	19.40	72.77	0.00	259.25	45.48	0.07	2610.72
30/05/02	1.563	34.299	16:13	1082.29	22.57	39.19	0.00	214.59	33.62	7.46	1615.93
07/06/02	0.781	21.986	11:04	1129.48	105.38	145.55	0.00	5070.80	98.97	5.87	4168.42
13/06/02	1.563	27.556	15:07	966.57	26.38	30.19	0.00	1356.36	20.90	2.32	1066.04
16/07/02	0.391	12.312	16:46	3514.10	499.37	48199.35	0.00	5032.03	166.35	62.38	4283.46

Appendix III a (cont.) – Zooplankton data of Cracknore.

Date	Polycha.	Mollusca	*Elminius modestus*	*Balanus improvisus*	*Balanus crenatus*	*Semibalan. balanoides*	Remain. Cirripedia	Urochor.	Remain. animals	Total organisms	Count.error (%) lower	higher
12/01/01	106.79	4.27	19.96	0.39	0.39	0.00	3.01	1.16	0.13	1655.47	-7.9	8.3
30/01/01	8.26	0.43	67.15	0.00	4.35	0.22	0.22	0.00	0.08	164.14	-13.8	15.2
12/02/01	79.39	2.22	62.79	0.86	8.90	1.71	1.37	0.00	2.17	811.38	-7.6	8.1
19/02/01	60.00	1.60	44.00	0.00	33.60	2.01	0.01	0.00	3.11	462.10	-11.5	12.4
02/03/01	925.46	2.97	40.97	0.03	106.53	1.29	1.49	0.00	9.49	2396.26	-6.8	7.1
16/03/01	351.95	2.38	107.58	0.84	296.36	2.98	6.50	0.00	26.32	1266.27	-10.1	10.8
23/03/01	518.45	7.53	18.95	1.27	8.83	12.38	2.59	0.63	43.78	1654.65	-8.3	8.8
04/04/01	1698.96	15.81	962.28	0.48	713.28	275.63	52.12	20.66	301.61	7997.92	-9.0	9.5
10/04/01	3139.55	9.10	103.58	12.65	51.39	30.99	30.66	27.05	74.95	8170.83	-6.9	7.3
19/04/01	1927.61	13.07	261.76	6.08	227.89	23.34	5.79	44.70	35.74	7979.08	-7.6	8.0
27/04/01	51.07	1.69	14.08	11.67	104.57	1.14	0.02	2.60	1.71	379.16	-10.0	10.7
04/05/01	786.14	51.41	264.74	10.99	189.90	18.66	1.71	1427.98	66.99	7293.88	-7.0	7.3
18/05/01	397.63	449.70	151.77	5.18	53.11	3.25	9.47	2736.06	63.90	13092.45	-8.5	9.0
07/06/01	173.12	916.98	592.85	132.63	0.04	0.00	0.00	73.03	54.90	4621.46	-9.7	10.4
11/06/01	504.55	9158.82	561.36	310.75	10.02	0.00	13.37	93.56	100.14	16052.11	-7.5	7.9
22/06/01	557.71	2478.72	1580.19	1735.11	0.00	0.00	30.98	196.23	193.00	9241.47	-12.9	14.1
03/07/01	278.86	304.68	289.51	418.61	0.00	0.00	15.49	72.30	96.02	2983.83	-14.8	16.5
19/07/01	107.73	144.95	1079.28	176.38	1.96	0.00	3.92	131.24	33.60	3820.10	-10.1	10.8
24/07/01	66.50	102.52	260.47	296.49	2.77	0.00	5.54	108.07	83.60	2721.57	-12.7	13.8
02/08/01	2696.30	4604.92	1608.03	1212.06	0.24	0.00	106.03	3862.68	237.87	46865.96	-8.7	9.3
20/08/01	2486.41	1746.65	4037.85	277.41	0.00	0.00	82.20	4171.42	59.20	79392.48	-6.4	6.7
31/08/01	117.23	447.22	1780.19	134.68	0.00	0.00	13.03	1011.67	5.72	23826.00	-7.3	7.6
17/09/01	27.29	289.29	1020.70	125.65	0.00	0.00	38.21	687.75	25.97	36095.00	-6.6	6.9
28/09/01	30.82	61.64	1145.61	10.27	0.00	0.00	10.27	749.99	1.69	26200.19	-7.5	7.8
17/10/01	68.50	222.61	368.18	0.00	0.00	0.00	21.41	166.96	23.95	19421.36	-7.4	7.8
31/10/01	68.95	68.95	471.14	11.49	0.00	0.00	45.96	632.01	28.14	49718.03	-7.8	8.2
21/11/01	43.67	14.56	7.28	0.00	0.00	0.00	7.28	116.47	22.91	17534.04	-9.4	10.1
14/12/01	32.84	0.00	44.44	0.00	0.00	0.00	11.59	69.55	13.99	3648.24	-10.2	11.0
11/01/02	8.19	0.00	1.64	0.00	0.55	0.02	0.55	0.00	1.38	162.82	-17.3	19.5
15/02/02	47.28	4.17	21.55	0.00	198.15	0.70	0.74	0.00	33.42	1199.73	-10.5	11.3
14/03/02	75.23	16.23	23.60	1.48	879.91	15.49	3.69	0.00	10.97	1547.66	-9.9	10.6
21/03/02	1611.87	9.92	95.05	2.84	616.72	12.76	5.67	1.42	129.05	3508.97	-9.4	10.0
27/03/02	1532.27	1.35	164.43	8.09	442.09	21.63	5.39	0.00	109.56	4099.42	-8.8	9.3
09/04/02	253.61	84.97	54.91	6.54	422.32	44.49	3.94	16.99	32.09	1714.92	-11.3	12.3
25/04/02	516.45	131.46	277.01	4.70	206.58	10.34	0.00	704.25	58.58	16173.86	-8.3	8.8
10/05/02	2674.56	2010.47	1037.08	109.24	81.91	0.00	9.10	454.86	405.64	14799.51	-10.0	10.7
16/05/02	205.80	303.14	164.09	47.30	41.76	0.00	2.78	305.92	33.07	6650.07	-9.4	10.0
24/05/02	168.29	318.38	268.35	18.26	36.49	0.00	4.55	773.21	64.35	6983.76	-10.6	11.4
30/05/02	123.15	138.08	151.46	24.46	28.02	0.00	1.87	87.70	39.21	3609.59	-10.0	10.7
07/06/02	558.89	7283.08	885.42	122.26	17.51	0.00	11.64	751.01	452.15	20806.42	-8.3	8.7
13/06/02	262.45	689.79	657.28	148.64	0.00	0.00	2.32	69.68	75.63	5374.55	-9.2	9.8
16/07/02	519.84	2744.74	9440.25	1767.45	41.59	0.00	83.17	374.28	1578.11	78306.48	-8.1	8.6

Appendix III b – Zooplankton data at Calshot, showing the sampling dates, aliquot size, volume filtered, sampling time (British summer time corrected), organisms density per m^3 (only showing by species the most abundant), total density and counting errors based on total density of raw data.

Date	Aliquot size (%)	Volume Filtered	Samp. Time	*Acartia* spp.	Other Calanoida	*O.nana*	Other Cyclop	*E acutifrons*	Other harpact.	Remaining Copepoda	Copepoda Nauplii
12/01/01	3.125	137.838	15:37	71.27	9.30	147.88	0.00	0.23	7.44	2.79	75.22
30/01/01	6.250	89.536	14:40	89.17	32.00	12.87	3.93	0.18	17.89	5.92	82.92
12/02/01	3.125	89.571	10:29	67.88	5.00	2.86	2.86	0.00	11.48	0.73	76.10
19/02/01	3.125	78.023	10:50	223.53	4.10	3.28	0.82	0.00	5.75	0.41	250.59
02/03/01	1.563	77.178	14:52	213.12	34.03	45.61	4.98	0.00	8.38	4.15	194.88
16/03/01	1.563	46.757	14:07	636.48	30.20	24.64	5.48	0.00	21.99	2.76	740.51
23/03/01	0.781	37.180	11:42	1886.58	123.96	34.43	0.00	0.00	20.66	0.00	919.19
04/04/01	0.781	56.334	11:36	986.12	27.44	4.54	0.00	0.00	27.27	0.00	495.33
10/04/01	0.781	45.349	13:56	1072.57	28.29	8.47	0.00	0.00	14.11	0.02	680.24
19/04/01	0.781	38.589	10:56	3137.91	56.54	3.32	0.00	0.00	16.61	6.63	1781.24
27/04/01	0.781	43.659	15:18	2275.09	26.64	0.00	0.00	2.93	23.50	0.00	1310.52
04/05/01	0.781	18.309	11:30	3908.12	174.89	0.00	0.00	27.97	62.98	0.00	2509.87
18/05/01	3.125	4.225	11:42	1234.54	1060.58	0.00	0.00	7.57	30.30	0.00	1567.79
07/06/01	3.125	5.070	14:46	549.11	637.67	0.00	0.00	429.19	157.79	0.20	1123.46
11/06/01	3.125	13.238	15:25	74.93	377.16	0.00	0.00	261.06	82.49	4.83	865.36
22/06/01	1.563	19.999	14:15	742.45	419.53	3.20	0.00	953.67	400.08	16.00	1692.92
03/07/01	0.391	48.166	11:11	1770.09	196.71	0.00	0.00	1626.49	350.81	10.67	2189.92
19/07/01	0.391	41.405	12:23	3159.61	154.68	6.18	0.00	2776.24	235.01	12.37	1681.82
24/07/01	0.391	32.110	14:18	2678.96	526.44	23.92	16.01	6171.11	470.41	71.85	2096.90
02/08/01	0.781	28.730	10:51	3114.20	494.60	49.01	8.91	9115.38	271.80	13.40	3684.47
20/08/01	0.391	21.986	14:06	9804.55	1152.97	1234.30	11.69	7685.28	931.55	104.80	5158.45
31/08/01	0.391	42.647	10:51	8236.28	486.42	114.06	0.05	3025.57	228.12	18.03	1200.62
17/09/01	0.391	41.041	11:00	1983.70	437.39	180.90	0.00	3399.74	87.33	37.48	767.28
28/09/01	0.781	30.781	10:06	2482.59	270.72	178.81	4.16	2395.26	149.70	20.86	1467.93
17/10/01	1.563	40.455	11:40	616.99	270.62	175.60	1.58	1430.14	75.94	18.98	188.26
31/10/01	3.125	31.367	10:39	1000.79	107.15	130.58	1.02	1889.37	19.38	5.10	217.30
21/11/01	3.125	34.299	14:37	142.75	81.40	33.59	0.96	224.85	29.86	7.49	32.65
14/12/01	1.563	43.973	10:30	689.88	40.84	30.56	1.46	26.20	11.64	0.00	148.46
11/01/02	3.125	38.403	10:33	81.66	34.24	15.83	0.83	3.33	4.19	0.89	256.65
15/02/02	3.125	51.301	13:06	51.77	12.65	3.12	1.89	2.50	11.23	8.77	106.66
14/03/02	0.781	34.005	11:50	500.63	1.12	0.00	0.00	3.76	11.41	0.00	485.57
21/03/02	0.391	62.148	15:23	395.47	8.75	0.00	0.00	4.12	20.68	28.85	168.90
27/03/02	0.391	31.367	11:26	1428.37	0.29	0.00	0.00	0.00	24.55	8.16	1199.80
09/04/02	0.391	34.005	10:37	2394.12	48.41	0.00	0.03	15.06	120.55	7.56	2973.83
25/04/02	0.781	33.126	10:41	606.65	144.21	0.00	0.00	19.32	11.59	0.00	1066.47
10/05/02	0.781	34.299	10:54	925.55	135.14	0.00	0.06	93.30	78.37	3.73	1477.84
16/05/02	0.781	16.710	13:31	1363.53	483.91	7.66	0.00	229.81	153.21	15.32	1447.79
24/05/02	1.563	16.416	12:15	982.49	589.10	0.00	0.00	413.24	50.86	7.92	2210.47
30/05/02	1.563	30.781	14:36	276.54	262.08	0.00	2.08	632.08	108.12	20.79	642.48
07/06/02	1.563	9.967	09:32	1200.75	745.05	6.42	19.26	4520.46	372.52	25.68	4931.42
13/06/02	0.781	29.022	13:45	317.55	264.63	4.41	0.00	1486.33	92.72	17.64	1477.50
16/07/02	0.781	22.573	14:54	754.23	374.35	158.78	0.00	2239.88	442.31	34.07	3090.47

Appendix III b (cont.) – Zooplankton data of Calshot.

Date	Polycha.	Mollusca	*Elminius modestus*	*Balanus improvisus*	*Balanus crenatus*	*Semibalan. balanoides*	Remain. Cirripedia	Urochor.	Remain. animals	Total organisms	Count.error (%) lower	higher
12/01/01	4.41	6.27	8.36	0.00	0.00	0.00	0.93	0.93	0.36	335.39	-11.7	11.4
30/01/01	10.01	7.51	21.62	0.00	0.36	0.01	4.29	1.61	1.55	291.83	-10.8	11.6
12/02/01	17.51	5.00	26.79	0.36	4.64	0.71	17.45	0.00	2.04	241.41	-14.0	15.5
19/02/01	25.02	4.92	13.53	0.41	6.56	1.23	0.47	0.00	47.02	587.66	-11.2	12.1
02/03/01	98.68	108.63	88.73	0.00	203.17	9.12	82.93	0.00	74.14	1170.53	-11.2	12.1
16/03/01	135.51	169.73	120.45	0.00	606.37	55.24	366.83	2.74	177.60	3096.51	-9.6	10.3
23/03/01	688.53	68.85	61.97	0.00	588.70	58.53	75.74	0.00	126.84	4653.98	-11.4	12.3
04/04/01	86.34	97.70	97.70	0.00	1049.74	245.39	490.79	4.54	85.12	3698.03	-10.6	11.4
10/04/01	228.63	87.50	73.39	0.00	268.17	50.81	307.68	16.94	57.25	2894.05	-12.4	13.5
19/04/01	384.78	89.56	318.46	3.32	928.97	53.18	109.46	238.83	190.60	7319.41	-9.7	10.3
27/04/01	193.50	87.95	208.16	14.66	375.27	41.05	49.84	504.27	103.51	5216.90	-10.3	11.1
04/05/01	517.35	657.18	216.78	6.99	398.50	20.97	49.10	3481.65	79.96	12112.32	-10.5	11.3
18/05/01	143.90	871.00	212.07	15.15	234.79	0.00	7.57	3953.56	342.95	9681.78	-11.6	12.6
07/06/01	88.36	1256.00	372.38	12.62	12.62	0.00	0.00	0.00	92.31	4731.70	-13.7	15.1
11/06/01	50.76	691.32	212.79	9.67	21.75	0.00	2.49	4.83	47.89	2707.33	-12.1	13.1
22/06/01	243.22	652.85	1120.08	35.20	51.20	0.00	6.40	9.60	283.27	6629.67	-9.8	10.5
03/07/01	79.73	696.31	3066.95	74.44	69.20	0.00	5.36	15.95	208.25	10360.89	-9.9	10.6
19/07/01	86.56	692.51	970.75	12.41	12.41	0.00	18.57	519.38	103.69	10442.21	-10.5	11.3
24/07/01	87.70	1897.58	1156.34	23.92	15.98	0.00	39.87	87.70	319.82	15684.50	-9.9	10.6
02/08/01	138.11	1109.35	1643.98	0.07	8.91	0.00	0.00	84.65	61.02	19797.85	-7.7	8.1
20/08/01	128.09	1548.70	4238.55	34.93	0.00	0.00	34.93	1374.03	31.84	33474.68	-8.8	9.4
31/08/01	24.01	1062.55	3872.01	30.02	0.00	0.00	12.01	846.44	5.89	19162.08	-8.5	9.0
17/09/01	18.71	455.38	536.47	0.00	0.00	0.00	0.00	542.71	134.92	8582.02	-10.9	11.8
28/09/01	20.79	1106.14	2603.18	0.00	0.00	0.00	41.58	324.36	38.43	11104.52	-9.0	9.6
17/10/01	7.91	213.57	174.05	0.00	0.00	0.00	20.57	79.10	41.43	3314.74	-9.8	10.5
31/10/01	17.34	117.32	228.52	0.00	0.00	0.00	5.10	144.87	26.43	3910.27	-8.2	8.7
21/11/01	3.73	53.18	35.45	0.00	0.00	0.00	4.66	61.58	4.40	716.56	-13.4	14.7
14/12/01	11.64	10.19	13.10	0.00	0.00	0.00	5.82	49.49	6.37	1045.65	-13.9	15.3
11/01/02	11.67	1.67	21.67	0.00	5.00	0.00	1.67	1.67	3.75	444.71	-15.0	16.6
15/02/02	26.82	11.85	23.08	0.00	819.63	4.99	10.60	0.00	5.17	1100.73	-10.4	11.2
14/03/02	120.45	63.99	97.87	0.00	3504.38	30.11	48.93	0.00	18.67	4886.89	-11.3	12.3
21/03/02	90.63	94.75	74.15	0.00	2578.79	12.36	119.46	0.00	60.57	3657.48	-12.4	13.5
27/03/02	220.37	106.11	89.85	0.00	3860.63	187.72	0.00	0.03	88.79	7214.67	-12.6	13.8
09/04/02	376.43	2747.97	127.99	0.00	11963.11	263.59	60.23	97.87	164.16	21360.90	-8.8	9.3
25/04/02	85.01	405.72	88.93	0.00	1217.17	4.92	7.76	1696.31	76.89	5430.96	-10.8	11.6
10/05/02	41.05	608.30	425.44	0.03	302.29	0.00	3.73	970.30	17.26	5082.39	-11.1	12.0
16/05/02	53.62	1578.02	727.97	0.00	429.10	0.00	7.72	1578.08	48.59	8124.32	-12.1	13.2
24/05/02	66.28	385.95	206.68	0.00	597.27	0.00	27.29	1060.40	213.44	6811.41	-9.6	10.3
30/05/02	43.66	646.64	162.18	2.08	241.19	0.00	6.24	207.92	41.65	3295.72	-10.7	11.6
07/06/02	179.79	1971.28	1264.96	0.00	154.81	0.00	32.11	1207.17	281.93	16913.61	-9.0	9.6
13/06/02	22.05	1204.06	1270.21	0.00	123.53	0.00	17.64	70.57	43.14	6411.98	-10.4	11.2
16/07/02	90.73	674.80	714.49	0.00	11.34	0.00	22.68	130.42	149.43	8887.99	-10.3	11.1

Appendix III c – Zooplankton data at NW. Netley, showing the sampling dates, aliquot size, volume filtered, sampling time (British summer time corrected), organisms density per m^3 (only showing by species the most abundant), total density and counting errors based on total density of raw data.

Date	Aliquot size (%)	Volume Filtered	Samp. Time	*Acartia* spp.	Other Calanoida	*O.nana*	Other Cyclop	*E acutifrons*	Other harpact.	Remaining Copepoda	Copepoda Nauplii
12/01/01	-	-	-	-	-	-	-	-	-	-	-
30/01/01	-	-	-	-	-	-	-	-	-	-	-
12/02/01	-	-	-	-	-	-	-	-	-	-	-
19/02/01	-	-	-	-	-	-	-	-	-	-	-
02/03/01	3.125	57.179	16:00	162.30	1.19	3.36	0.56	0.00	1.14	0.00	940.21
16/03/01	-	-	-	-	-	-	-	-	-	-	-
23/03/01	-	-	-	-	-	-	-	-	-	-	-
04/04/01	-	-	-	-	-	-	-	-	-	-	-
10/04/01	0.781	29.857	14:50	2705.19	13.20	0.00	4.29	0.00	4.59	0.00	4132.76
19/04/01	-	-	-	-	-	-	-	-	-	-	-
27/04/01	-	-	-	-	-	-	-	-	-	-	-
04/05/01	0.781	37.744	10:39	1051.30	20.77	0.00	0.00	3.39	6.81	0.05	3343.81
18/05/01	-	-	-	-	-	-	-	-	-	-	-
07/06/01	0.781	13.802	13:37	1307.65	1140.79	0.00	0.00	231.85	64.92	9.27	4924.56
11/06/01	-	-	-	-	-	-	-	-	-	-	-
22/06/01	-	-	-	-	-	-	-	-	-	-	-
03/07/01	-	-	-	-	-	-	-	-	-	-	-
19/07/01	1.563	21.689	11:13	681.69	112.13	0.00	0.00	843.95	29.51	11.90	1696.74
24/07/01	-	-	-	-	-	-	-	-	-	-	-
02/08/01	0.781	10.422	11:47	2394.98	614.39	184.23	0.00	7123.54	49.13	12.28	7737.64
20/08/01	-	-	-	-	-	-	-	-	-	-	-
31/08/01	-	-	-	-	-	-	-	-	-	-	-
17/09/01	0.391	68.011	12:09	3820.81	131.80	3060.41	0.00	2187.08	527.01	15.13	1050.25
28/09/01	-	-	-	-	-	-	-	-	-	-	-
17/10/01	0.391	48.370	12:39	3196.91	360.10	4536.01	5.29	2170.09	121.74	15.90	465.77
31/10/01	-	-	-	-	-	-	-	-	-	-	-
21/11/01	1.563	39.575	15:31	941.19	5.00	1743.31	0.00	163.33	3.23	1.64	608.06
14/12/01	0.391	59.803	11:42	4803.43	81.86	325.36	0.00	25.69	8.56	4.28	2097.70
11/01/02	3.125	60.096	11:55	70.99	1.95	21.30	0.02	1.60	1.06	0.00	336.00
15/02/02	0.391	41.041	14:18	262.07	13.06	6.24	0.00	0.12	6.26	0.10	449.14
14/03/02	0.391	58.630	13:02	838.39	8.92	30.57	4.37	0.00	21.83	4.37	751.06
21/03/02	3.125	25.211	16:31	1477.45	3.97	5.08	2.54	2.54	5.12	0.00	930.39
27/03/02	3.125	61.855	10:28	117.44	3.14	0.52	0.00	0.02	0.52	0.02	231.25
09/04/02	0.391	32.540	11:35	2368.21	17.64	0.00	0.00	0.00	7.87	0.00	3477.57
25/04/02	0.391	28.436	11:36	10993.12	108.57	0.00	9.00	18.01	18.01	0.00	4951.86
10/05/02	0.391	22.866	11:45	27330.67	146.87	11.20	0.00	44.79	33.59	11.20	15585.53
16/05/02	0.391	32.833	14:25	11072.57	33.44	15.60	0.00	77.98	31.22	7.80	4132.71
24/05/02	0.391	30.781	11:12	11070.46	242.41	33.27	8.32	216.25	8.35	16.67	4083.84
30/05/02	0.781	26.090	15:27	4390.89	84.82	34.34	0.00	421.92	73.67	9.81	4768.65
07/06/02	0.391	27.556	10:17	2991.65	269.43	37.16	0.00	3158.84	167.45	9.29	9745.96
13/06/02	0.781	36.644	14:36	702.11	66.83	0.00	0.00	744.03	48.93	3.49	1086.35
16/07/02	0.781	18.468	15:55	1393.08	243.12	1282.18	20.79	1157.43	138.61	0.05	2571.30

Appendix III c (cont.) – Zooplankton data of NW. Netley.

Date	Polycha.	Mollusca	*Elminius modestus*	*Balanus improvisus*	*Balanus crenatus*	*Semibalan. balanoides*	Remain. Cirripedia	Urochor.	Remain. animals	Total organisms	Count.error (%) lower	higher
12/01/01	-	-	-	-	-	-	-	-	-	-	-	-
30/01/01	-	-	-	-	-	-	-	-	-	-	-	-
12/02/01	-	-	-	-	-	-	-	-	-	-	-	-
19/02/01	-	-	-	-	-	-	-	-	-	-	-	-
02/03/01	198.11	25.18	19.64	0.00	40.29	2.27	4.48	0.00	16.12	1414.86	-9.2	9.8
16/03/01	-	-	-	-	-	-	-	-	-	-	-	-
23/03/01	-	-	-	-	-	-	-	-	-	-	-	-
04/04/01	-	-	-	-	-	-	-	-	-	-	-	-
10/04/01	325.82	124.33	85.78	0.00	222.93	171.79	60.02	38.58	117.06	8006.33	-10.2	10.9
19/04/01	-	-	-	-	-	-	-	-	-	-	-	-
27/04/01	-	-	-	-	-	-	-	-	-	-	-	-
04/05/01	108.52	27.13	20.43	3.44	106.03	10.20	0.00	3031.81	64.62	7798.32	-9.5	10.1
18/05/01	-	-	-	-	-	-	-	-	-	-	-	-
07/06/01	222.58	890.32	994.51	121.22	0.14	0.07	0.00	92.74	199.47	10200.10	-11.5	12.5
11/06/01	-	-	-	-	-	-	-	-	-	-	-	-
22/06/01	-	-	-	-	-	-	-	-	-	-	-	-
03/07/01	-	-	-	-	-	-	-	-	-	-	-	-
19/07/01	182.95	224.27	2304.62	301.08	11.80	0.00	23.61	153.44	89.17	6666.87	-9.7	10.4
24/07/01	-	-	-	-	-	-	-	-	-	-	-	-
02/08/01	1166.79	3574.05	3414.39	503.56	0.00	0.00	12.28	1007.12	253.22	28047.58	-8.4	8.9
20/08/01	-	-	-	-	-	-	-	-	-	-	-	-
31/08/01	-	-	-	-	-	-	-	-	-	-	-	-
17/09/01	82.82	436.66	1573.51	75.30	0.00	0.00	45.17	737.81	21.04	13764.80	-8.2	8.7
28/09/01	-	-	-	-	-	-	-	-	-	-	-	-
17/10/01	31.76	381.09	418.18	10.59	0.00	0.00	31.76	317.57	46.29	12109.04	-8.9	9.4
31/10/01	-	-	-	-	-	-	-	-	-	-	-	-
21/11/01	25.87	24.26	46.90	0.00	0.00	0.00	6.47	66.30	27.57	3663.14	-9.7	10.4
14/12/01	77.06	47.09	34.25	0.00	0.00	0.00	21.42	89.90	48.24	7664.84	-10.3	11.0
11/01/02	5.32	1.06	7.99	0.00	2.66	0.00	0.00	0.53	1.70	452.18	-13.1	14.4
15/02/02	268.24	99.81	143.48	0.00	7822.52	6.24	24.95	0.02	60.67	9162.92	-10.9	11.7
14/03/02	406.10	69.88	135.37	4.37	3916.91	52.40	34.95	0.00	35.63	6315.11	-10.7	11.5
21/03/02	316.05	67.27	142.16	7.62	1043.40	38.08	7.70	2.54	97.77	4149.67	-8.4	8.9
27/03/02	16.04	5.69	5.17	0.00	284.54	3.62	0.52	0.53	6.32	675.32	-11.0	11.9
09/04/02	1140.83	1148.70	149.52	7.87	11597.19	440.97	15.74	62.97	225.76	20660.84	-8.7	9.3
25/04/02	486.18	684.26	945.35	0.00	2818.06	351.34	0.07	1530.61	43.12	22957.55	-8.6	9.1
10/05/02	515.04	436.66	100.77	0.00	44.87	0.09	0.00	615.81	39.62	44916.70	-8.0	8.4
16/05/02	163.75	319.70	413.27	54.58	210.53	0.06	0.00	927.91	72.49	17533.62	-9.5	10.2
24/05/02	216.25	399.24	1089.61	8.32	74.92	0.00	8.32	1239.29	75.99	18791.51	-9.3	9.9
30/05/02	240.39	171.71	453.69	10.00	285.16	0.00	34.34	505.32	117.02	11601.74	-9.3	9.9
07/06/02	1644.46	4255.15	3669.83	74.33	65.14	0.00	18.58	1876.72	364.41	28348.41	-8.5	9.1
13/06/02	80.34	171.16	530.95	10.48	24.45	0.00	0.00	125.75	20.71	3615.59	-11.6	12.6
16/07/02	207.92	2439.62	3001.17	166.45	90.10	0.00	20.79	263.37	358.94	13354.91	-10.0	10.8

Appendix IV a – Temperature and Salinity data collected on each sampling date at Cracknore (- = indicates no data)

Date	Temperature °C						Salinity					
Cracknore	Surf.	2m	4m	6m	8m	average	Surf.	2m	4m	6m	8m	average
12/01/01	5.6	5.6	5.7	5.9	5.9	5.7	21.9	22.2	28	28.6	28.7	25.9
30/01/01	5.7	5.8	6.0	6.0	6.1	5.9	18.9	25.7	27.8	29.0	30.7	26.4
12/02/01	8.4	7.7	7.2	7.1	7.0	7.5	11.7	21.1	26.9	28.7	29.4	23.6
19/02/01	6.1	7.3	7.4	7.3	7.3	7.1	15.9	29.3	30.1	30.5	30.6	27.3
02/03/01	6.4	6.4	6.4	6.4	6.4	6.4	26.4	29.0	30.0	30.4	30.5	29.3
16/03/01	8.8	7.8	7.3	7.2	7.2	7.7	19.0	26.6	29.7	30.1	30.6	27.2
23/03/01	9.1	7.6	7.1	6.9	6.8	7.5	12.1	25.6	29.3	30.3	30.7	25.6
04/04/01	9.2	8.9	8.7	8.6	8.6	8.8	21.3	27.3	28.2	29.1	29.3	27.1
10/04/01	9.2	9.1	9.1	9.1	9.1	9.1	28.8	28.9	29.4	29.9	30.1	29.4
19/04/01	9.0	9.1	9.2	9.2	9.2	9.1	25.7	29.0	30.1	30.8	30.8	29.3
27/04/01	10.8	9.9	9.6	9.6	9.6	9.9	20.0	26.8	28.9	29.6	29.9	27.0
04/05/01	10.4	10.2	10.2	10.2	10.2	10.2	27.9	29.4	29.9	30.1	30.2	29.5
18/05/01	12.4	12.4	12.4	12.6	12.5	12.5	28.5	30.3	30.8	31.5	31.6	30.5
07/06/01	15.5	15.5	15.6	15.6	15.6	15.6	27.1	29.4	30.9	31.1	31.4	30.0
11/06/01	16.2	15.7	15.5	15.4	15.4	15.6	27.3	29.5	30.6	31.0	31.4	30.0
22/06/01	17.4	17.1	17.0	17.0	17.0	17.1	27.8	28.7	-	-	31.0	29.2
03/07/01	20.3	19.8	19.3	19.1	18.6	19.4	24.5	29.7	30.7	31.0	31.7	29.5
19/07/01	17.8	17.8	17.8	17.8	17.8	17.8	30.9	31.1	31.3	31.4	31.6	31.3
24/07/01	19.1	18.8	18.7	18.5	18.5	18.7	29.2	30.2	30.7	31.1	31.5	30.5
02/08/01	19.8	20.3	20.4	20.4	20.3	20.2	27.2	30.7	31.3	31.5	31.6	30.5
20/08/01	19.5	19.3	19.3	19.3	19.3	19.3	27.5	29.8	30.6	31.0	31.5	30.1
31/08/01	19.8	19.8	19.8	19.8	19.7	19.8	31.3	31.4	31.6	31.9	32.4	31.7
17/09/01	16.3	16.4	16.4	16.4	16.4	16.4	31.5	31.9	31.9	32.2	32.2	31.9
28/09/01	15.5	15.7	15.7	15.7	15.7	15.7	28.2	31.0	31.4	31.6	31.9	30.8
17/10/01	15.6	15.5	15.5	15.5	15.5	15.5	29.2	29.3	29.3	29.6	30.2	29.5
31/10/01	14.7	14.8	14.9	14.9	14.9	14.8	29.7	29.8	31.0	31.2	31.5	30.6
21/11/01	10.7	10.5	10.5	10.5	10.6	10.6	29.0	30.0	31.5	31.5	31.7	30.7
14/12/01	8.4	8.6	8.6	8.7	8.7	8.6	29.2	30.0	30.9	31.1	31.1	30.5
11/01/02	5.5	5.4	5.4	5.4	5.4	5.4	27.5	31.1	31.5	31.9	32.2	30.8
15/02/02	9.2	9.2	9.0	9.0	9.0	9.1	29.2	29.3	30.2	30.4	30.6	29.9
14/03/02	8.1	8.1	8.4	8.5	8.5	8.3	28.1	28.1	29.6	30.3	30.4	29.3
21/03/02	9.6	9.3	8.9	8.9	8.7	9.1	27.0	29.0	31.0	31.1	31.4	29.9
28/03/02	9.5	9.6	9.6	9.6	9.6	9.6	25.7	29.4	30.5	31.1	31.1	29.6
09/04/02	11.1	10.9	10.9	10.9	10.9	10.9	30.1	30.9	31.4	31.5	31.8	31.1
25/04/02	13.1	12.4	12	11.9	11.9	12.3	28.9	30.6	31.3	31.5	31.8	30.8
10/05/02	12.7	12.6	12.4	12.4	12.4	12.5	30.9	31.2	31.5	31.6	31.7	31.4
16/05/02	14.7	14.5	14.3	14	13.9	14.3	29.6	29.8	30.2	30.2	30.3	30.1
24/05/02	14.9	14.8	14.8	14.8	14.8	14.8	27.6	27.9	28.5	29.0	30.3	28.7
30/05/02	15.1	14.8	14.6	14.6	14.5	14.7	27.5	29.4	30.2	30.8	31.0	29.8
07/06/02	14.7	15.2	15.2	15.2	15.2	15.1	26.6	31.0	31.6	31.7	31.9	30.6
13/06/02	16.2	16.0	15.4	15.4	15.4	15.7	28.3	29.0	31	31.1	31.7	30.2
16/07/02	19.2	18.4	18.0	18.0	18.0	18.3	29.2	31.4	32.2	32.5	32.5	31.6

Appendix IV b – Temperature and Salinity data collected on each sampling date at Calshot (- = indicates no data)

Date	Temperature °C						Salinity					
Cracknore	Surf.	2m	4m	6m	8m	average	Surf.	2m	4m	6m	8m	average
12/01/01	5.9	6.0	6.0	6.0	6.1	6.0	32.6	32.7	32.7	32.7	32.7	32.7
30/01/01	5.8	5.8	5.8	5.8	5.8	5.8	32.1	32.1	32.1	32.2	32.4	32.2
12/02/01	7.1	7.1	7.1	7.2	7.2	7.1	31.8	31.8	31.7	31.6	31.6	31.7
19/02/01	6.7	6.9	6.8	6.9	6.9	6.8	31.0	31.0	31.1	31.1	31.3	31.1
02/03/01	5.9	6.0	6.0	6.1	6.1	6.0	32.4	32.4	32.4	32.4	32.4	32.4
16/03/01	7.3	7.3	7.2	7.2	7.2	7.2	32.4	32.5	32.5	32.5	32.6	32.5
23/03/01	7.2	7.2	7.1	7.0	7.0	7.1	31.8	31.8	31.9	31.9	32	31.9
04/04/01	8.6	8.6	8.6	8.6	8.6	8.6	30.9	30.9	30.9	30.9	30.9	30.9
10/04/01	9.1	9.0	9.0	9.0	9.0	9.0	31.5	31.6	31.6	31.6	31.6	31.6
19/04/01	9.0	9.0	8.9	8.9	8.9	8.9	31.5	31.5	31.7	31.7	31.7	31.6
27/04/01	10.2	10.1	10.1	10.1	10.0	10.1	31.5	31.6	31.6	31.6	31.7	31.6
04/05/01	10.2	10.2	10.2	10.2	10.2	10.2	31.8	31.8	31.8	31.9	31.9	31.8
18/05/01	12.6	12.5	12.1	12.1	12.1	12.3	31.3	31.4	32.0	32.1	32.1	31.8
07/06/01	15.4	15.3	15.3	15.3	15.3	15.3	32.8	32.8	32.8	32.8	32.8	32.8
11/06/01	15.5	15.4	15.4	15.3	15.3	15.4	32.5	32.5	32.5	32.6	32.6	32.5
22/06/01	17.0	17.0	17.0	17.0	17.0	17.0	-	32.5	-	-	32.5	32.5
03/07/01	19.4	19.0	19.0	19.0	19.0	19.1	32.7	32.8	32.8	32.8	32.8	32.8
19/07/01	17.9	17.7	17.7	17.7	17.7	17.7	32.5	32.5	32.7	32.7	32.7	32.6
24/07/01	18.8	18.5	18.5	18.5	18.5	18.6	32.8	33.1	33.1	33.1	33.1	33.0
02/08/01	19.9	19.9	19.9	19.9	19.9	19.9	33.0	33.0	33.0	33.1	33.1	33.0
20/08/01	19.2	19.2	19.2	19.3	19.3	19.2	32.9	32.9	32.9	33.0	33.0	32.9
31/08/01	19.3	19.3	19.3	19.3	19.3	19.3	33.3	33.3	33.3	33.3	33.4	33.3
17/09/01	16.1	16.4	16.4	16.4	16.4	16.3	33.6	33.6	33.6	33.6	33.6	33.6
28/09/01	15.8	15.8	15.8	15.7	15.7	15.8	33.5	33.6	33.6	33.7	33.7	33.6
17/10/01	15.5	15.5	15.5	15.5	15.5	15.5	33.4	33.4	33.4	33.4	33.4	33.4
31/10/01	14.8	14.8	14.8	14.8	14.8	14.8	33.2	33.2	33.2	33.2	33.2	33.2
21/11/01	10.7	10.7	10.7	10.7	10.7	10.7	33.7	33.7	33.7	33.7	33.7	33.7
14/12/01	8.6	8.6	8.6	8.6	8.6	8.6	33.3	33.3	33.3	33.3	33.3	33.3
11/01/02	5.7	5.8	5.8	5.8	5.9	5.8	33.6	33.6	33.6	33.6	33.6	33.6
15/02/02	8.9	8.9	8.9	8.9	8.9	8.9	32.1	32.2	32.3	32.3	32.4	32.3
14/03/02	8.1	8.2	8.2	8.2	8.3	8.2	33.2	33.1	33.1	33.1	33.1	33.1
21/03/02	9.2	9.1	9.1	9.1	9.0	9.1	32.8	32.9	32.9	32.9	33.0	32.9
28/03/02	9.6	9.6	9.6	9.6	9.6	9.6	32.4	32.4	32.4	32.4	32.4	32.4
09/04/02	10.4	10.4	10.4	10.4	10.4	10.4	33.2	33.3	33.4	33.4	33.4	33.3
25/04/02	12.1	11.8	11.8	11.7	11.7	11.8	33.1	33.3	33.3	33.3	33.3	33.3
10/05/02	12.7	12.5	12.4	12.4	12.4	12.5	33.2	33.2	33.2	33.3	33.3	33.2
16/05/02	13.5	13.5	13.4	13.4	13.3	13.4	33.3	33.4	33.4	33.4	33.5	33.4
24/05/02	14.4	14.4	14.4	14.4	14.4	14.4	33.4	33.4	33.4	33.4	33.4	33.4
30/05/02	14.5	14.5	14.5	14.5	14.5	14.5	33.0	33.0	33.0	33.0	33.1	33.0
07/06/02	14.7	14.9	14.9	14.9	14.9	14.9	33.1	33.1	33.2	33.2	33.2	33.2
13/06/02	15.3	15.2	15.2	15.2	15.2	15.2	32.8	33.1	33.1	33.2	33.2	33.1
16/07/02	17.9	17.8	17.8	17.8	17.8	17.8	33.7	34.1	34.1	34.1	34.1	34.0

Appendix IV c – Temperature and Salinity data collected on each sampling date at NW - Netley (- = indicates no data)

Date	Temperature °C						Salinity					
Cracknore	Surf.	2m	4m	6m	8m	average	Surf.	2m	4m	6m	8m	average
12/01/01	-	-	-	-	-	-	-	-	-	-	-	-
30/01/01	-	-	-	-	-	-	-	-	-	-	-	-
12/02/01	-	-	-	-	-	-	-	-	-	-	-	-
19/02/01	-	-	-	-	-	-	-	-	-	-	-	-
02/03/01	5.7	5.9	6.0	6.0	6.1	5.9	28.5	28.5	30.0	30.7	31.3	29.8
16/03/01	-	-	-	-	-	-	-	-	-	-	-	-
23/03/01	-	-	-	-	-	-	-	-	-	-	-	-
04/04/01	-	-	-	-	-	-	-	-	-	-	-	-
10/04/01	9.6	9.6	9.5	9.4	9.2	9.5	28.3	28.5	28.5	29.4	30.1	29.0
19/04/01	-	-	-	-	-	-	-	-	-	-	-	-
27/04/01	-	-	-	-	-	-	-	-	-	-	-	-
04/05/01	10.2	10.3	10.3	10.3	10.3	10.3	28.7	28.6	28.6	30.2	30.8	29.4
18/05/01	13.5	12.8	12.7	12.6	12.5	12.8	28.2	30.1	31.5	32.1	32.2	30.8
07/06/01	15.3	15.6	15.6	15.6	15.6	15.5	31.4	31.4	31.6	31.6	32.4	31.7
11/06/01	-	-	-	-	-	-	-	-	-	-	-	-
22/06/01	-	-	-	-	-	-	-	-	-	-	-	-
03/07/01	-	-	-	-	-	-	-	-	-	-	-	-
19/07/01	17.9	17.9	17.9	17.9	17.9	17.9	31.4	31.5	31.5	31.9	32.0	31.7
24/07/01	-	-	-	-	-	-	-	-	-	-	-	-
02/08/01	20.3	20.3	20.3	20.3	20.3	20.3	31.9	31.9	31.9	32.1	32.1	32.0
20/08/01	-	-	-	-	-	-	-	-	-	-	-	-
31/08/01	-	-	-	-	-	-	-	-	-	-	-	-
17/09/01	16.2	16.2	16.2	16.2	16.1	16.2	32.6	32.6	32.7	32.7	32.7	32.7
28/09/01	-	-	-	-	-	-	-	-	-	-	-	-
17/10/01	15.6	15.5	15.5	15.5	15.5	15.5	31.9	31.9	31.9	32.1	32.1	32.0
31/10/01	-	-	-	-	-	-	-	-	-	-	-	-
21/11/01	10.5	10.4	10.4	10.4	10.4	10.4	31.3	31.4	31.5	31.8	32.4	31.7
14/12/01	8.3	8.3	8.3	8.3	8.3	8.3	31.7	31.7	31.7	31.7	31.9	31.7
11/01/02	5.3	5.4	5.5	5.6	5.6	5.5	29.8	31.7	31.8	32.7	32.9	31.8
15/02/02	8.7	8.7	8.7	8.7	8.7	8.7	29.4	29.6	29.7	29.8	29.8	29.7
14/03/02	8.4	8.4	8.4	8.4	8.5	8.4	31.3	31.3	31.4	31.4	31.4	31.4
21/03/02	9.6	9.6	9.3	9.1	9.0	9.3	29.0	29.4	30.3	31.6	32.2	30.5
28/03/02	9.6	9.6	9.6	9.6	9.6	9.6	29.1	29.3	30.9	31.2	31.3	30.4
09/04/02	10.8	10.8	10.8	10.7	10.7	10.8	29.8	29.8	31.3	31.5	31.9	30.9
25/04/02	12.9	12.7	12.6	12.3	12.2	12.5	30.3	31.2	32.1	32.4	32.4	31.7
10/05/02	13.1	13.0	12.9	12.9	12.7	12.9	31.4	31.5	31.6	31.8	32.4	31.7
16/05/02	14.5	14.2	14	13.9	13.7	14.1	31.1	31.3	31.3	31.3	31.5	31.3
24/05/02	15.0	15.0	14.9	14.9	14.9	14.9	30.9	31.0	31.1	31.1	31.3	31.1
30/05/02	14.8	14.8	14.8	14.5	14.5	14.7	30.5	30.5	30.5	31.4	31.5	30.9
07/06/02	15	15.2	15.2	15.2	15.2	15.26	31.5	31.5	31.8	31.9	32.0	31.7
13/06/02	15.4	15.4	15.6	15.4	15.3	15.4	30.6	30.6	31.5	31.9	32.2	31.6
16/07/02	19.3	18.8	18.5	18.4	18.4	18.7	31.4	32.4	32.8	33.1	33.1	32.6

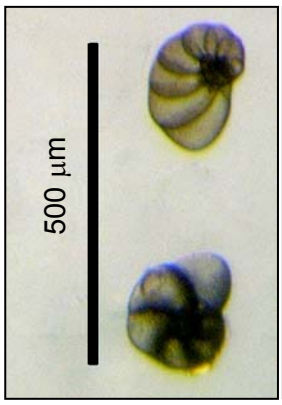
Appendix V

Zooplankton samples of any given area will contain organisms from several phyla, requiring the use of numerous taxonomic guides for the identification of the different species or group of animals present. These detailed, illustrated taxonomic references are vital, but are usually dispersed in different guides, atlases or individual papers, and usually intended for researchers with some prior knowledge in species identification. Students and 'new' researchers however, usually do not have time for searching through countless disparate references or the prior knowledge for the identification of rare species that only appear in low numbers. However, information about species and their spatio-temporal patterns is needed before attempting to quantify any planktonic processes (Soetaert & Van Rijswijk, 1993).

The primary objective of this work is to give a permanent photographic-record summary of the taxa recorded in the mesozooplankton of the Solent-Southampton Water (SW) system. In the attached pdf file (Zooplanktonguide.pdf) an extended version of the present Appendix is included, where each taxon is presented individually at an orientation to give a general overview of the whole animal, as well as highlighting features of taxonomic importance together with a suggested literature needed to identify them. This could aid future research and studies within this estuarine system and in neighbouring regions where a similar mesozooplankton composition would be expected to be found.

A total of 152 different taxa are presented here, including 62 of the 90 previously reported in the mesozooplankton of this system, together with 90 taxa reported for the first time within this system. Only 62 of the previously reported taxa in this system were identified in this study, either because the species did not occurr in the sampling period (for methods see Muxagata *et al*., 2004), or they may be included as 'unidentified' specimens. The previously reported species *Polydora ciliata* and *Polydora ligni* could, in this study, be under 'unidentified Spionidae' or, as in the case of *Necora puber* which are under *Liocarcinus* spp. Taxa were identified to the nearest level possible, with 96 identified to species, 32 to genus and 24 only identified at a lower level i.e. Family, Class, Order or Phylum.

This work is intended to be an aid to the detailed taxonomic guides, and species should ultimately be identified using the references provided. The identification of most of organisms was made by E. Muxagata. Taxa identified by the photo-numbers 23, 49, 64, 66 were in identified containers by Dr. E. Castro-Longoria, and taxa 17, 18, 96 to 107 and 109 were identified by Dr. M. Sheader.



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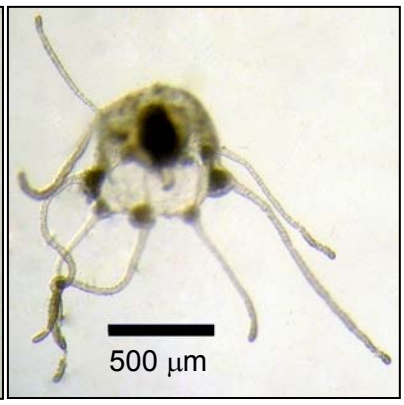

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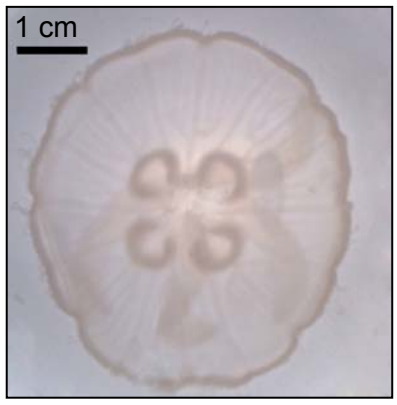

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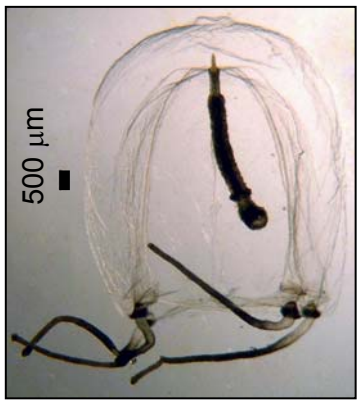

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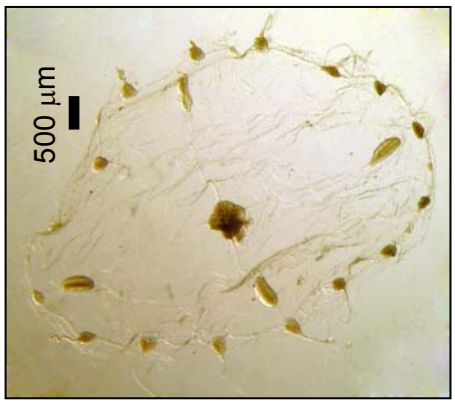

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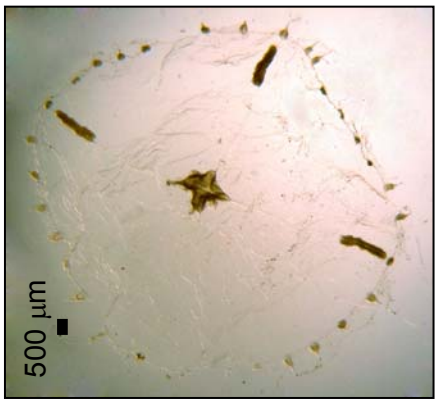

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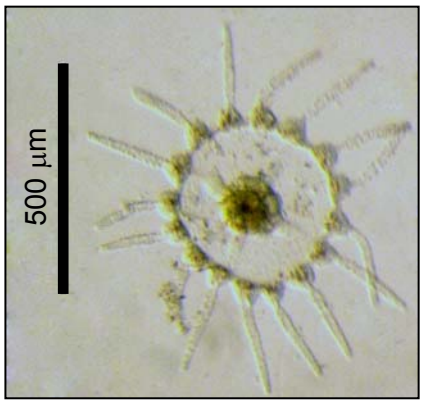

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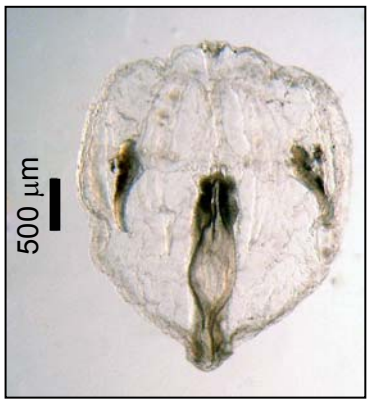

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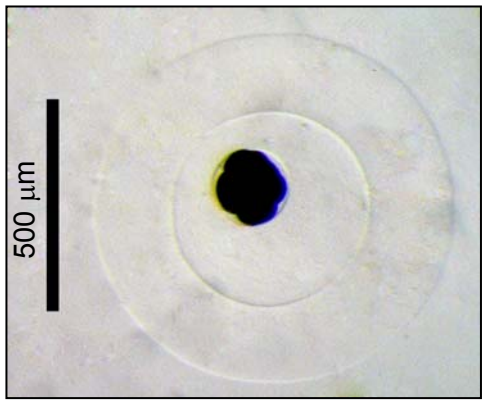

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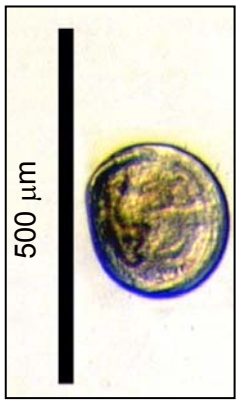

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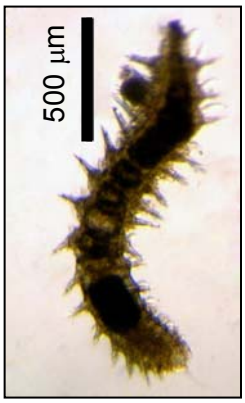

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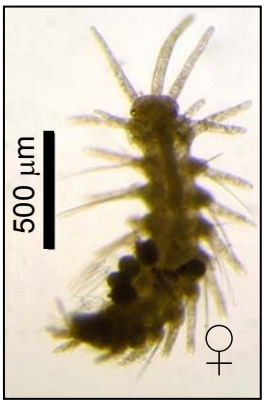

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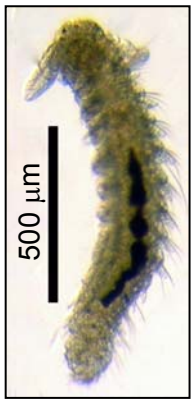

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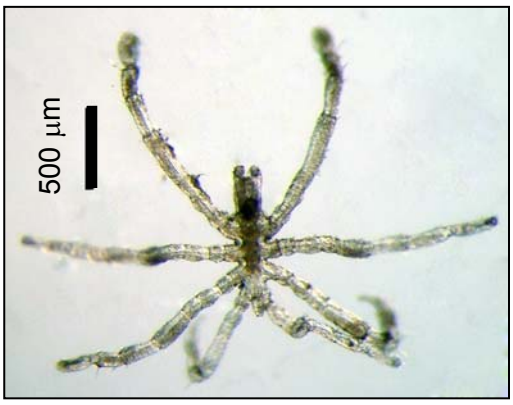

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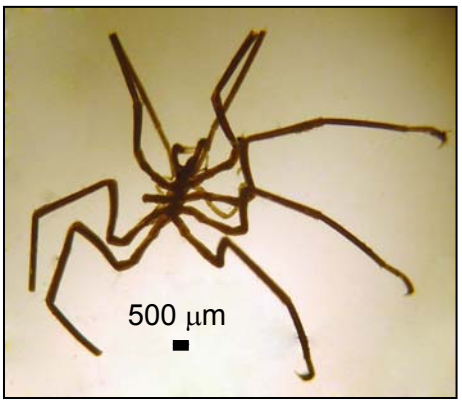

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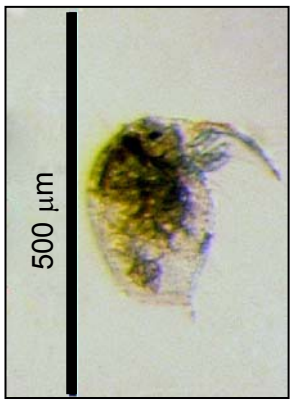

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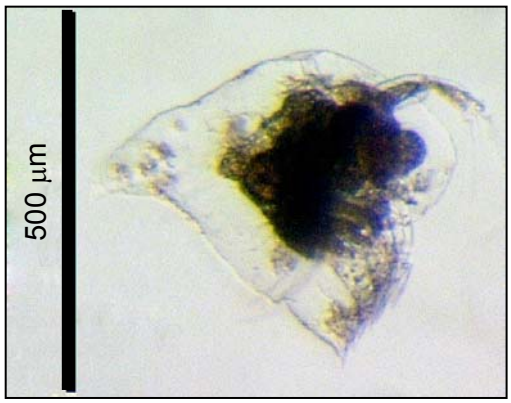

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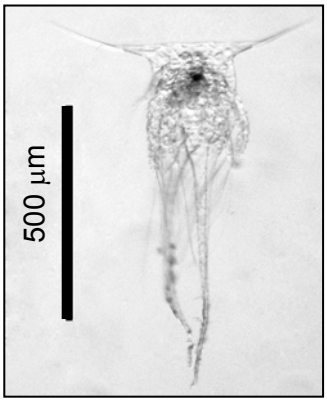

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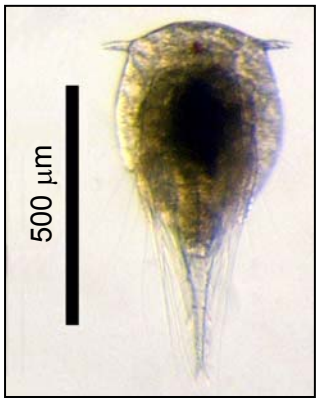

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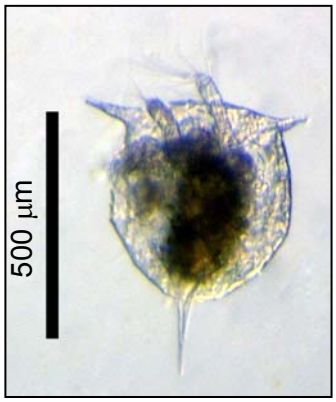

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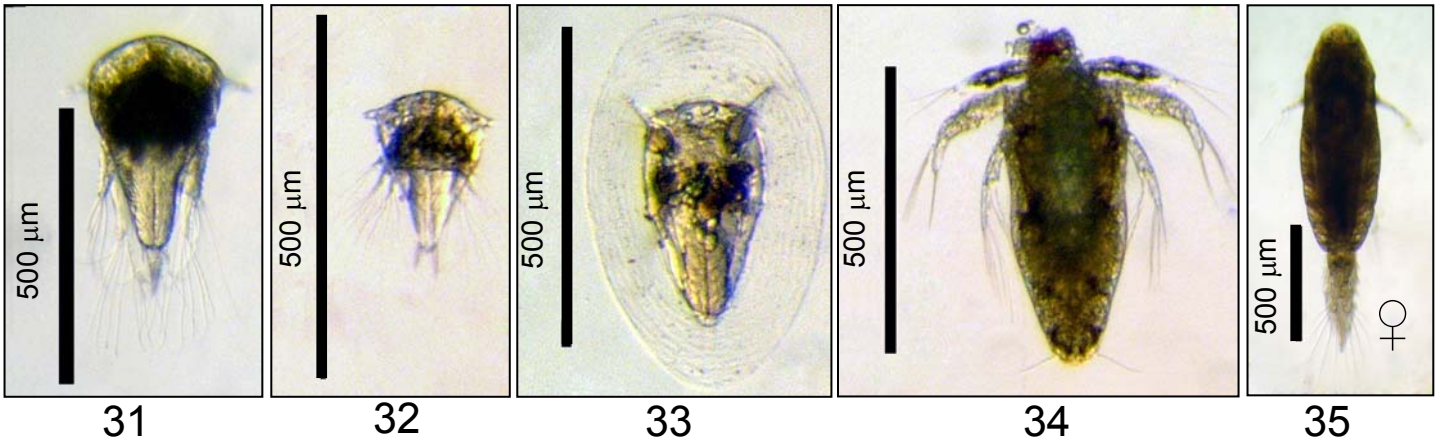
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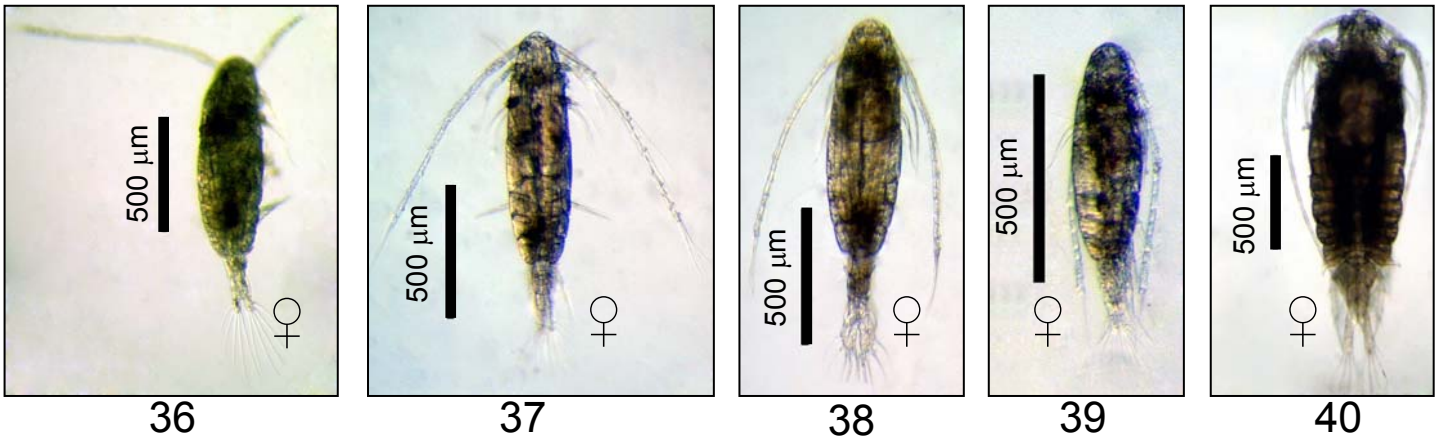
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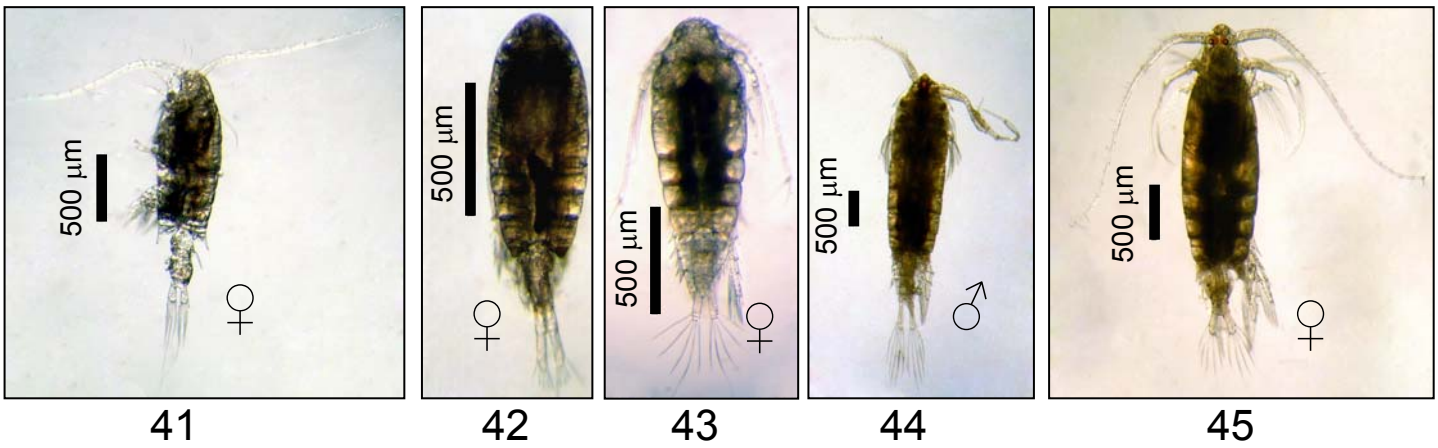
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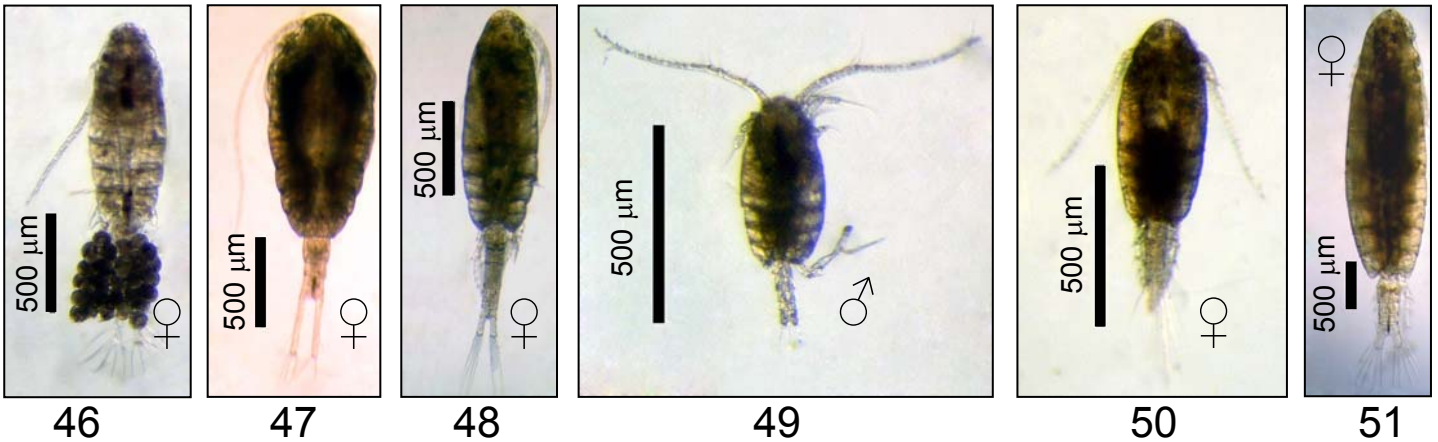
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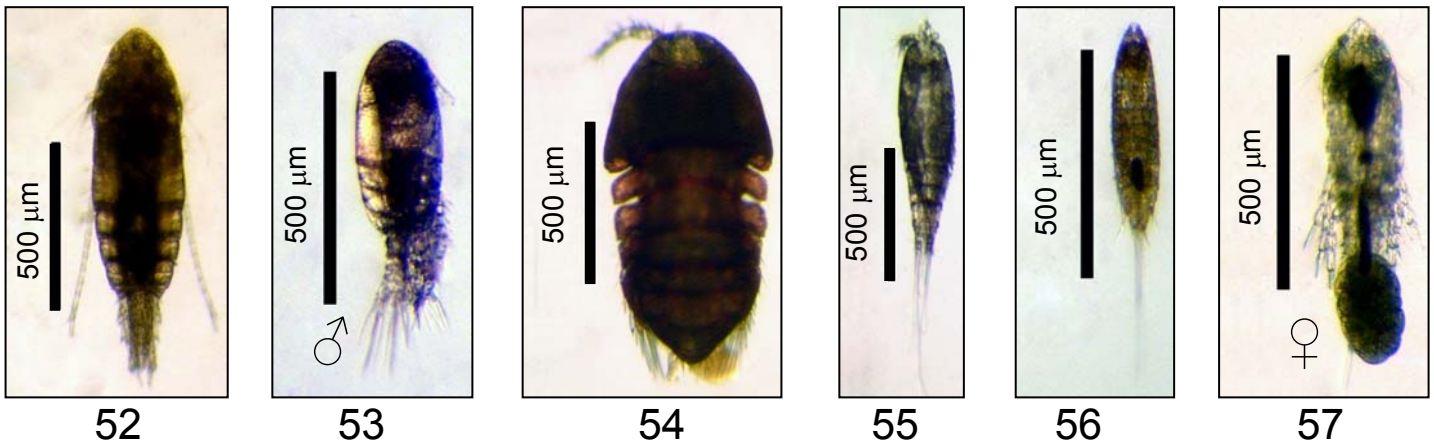

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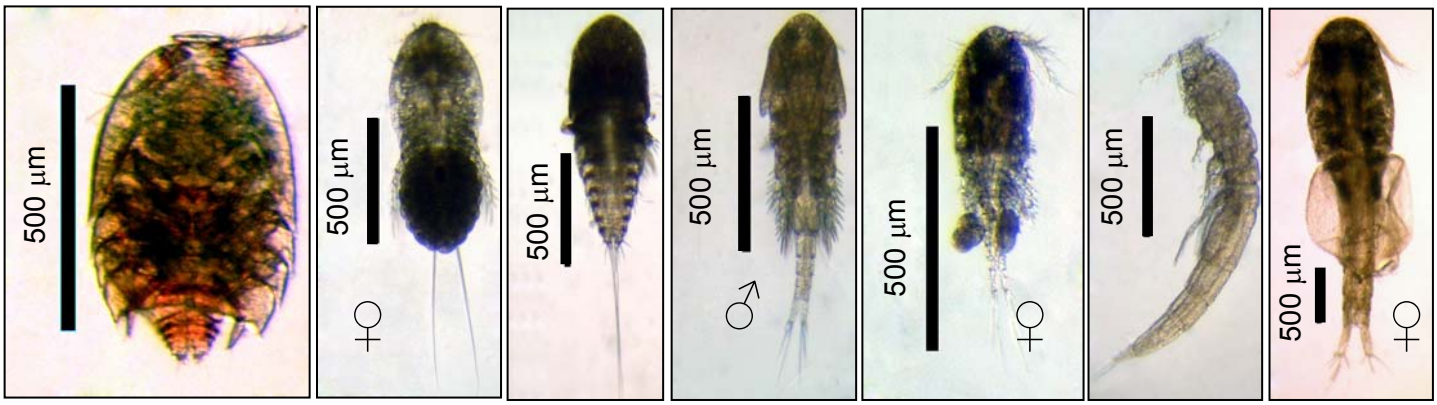

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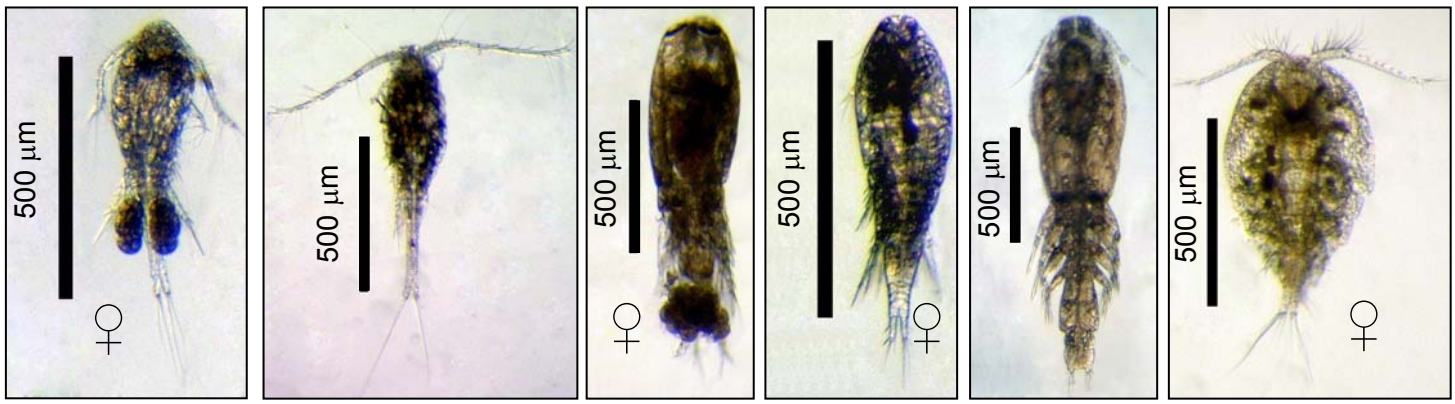

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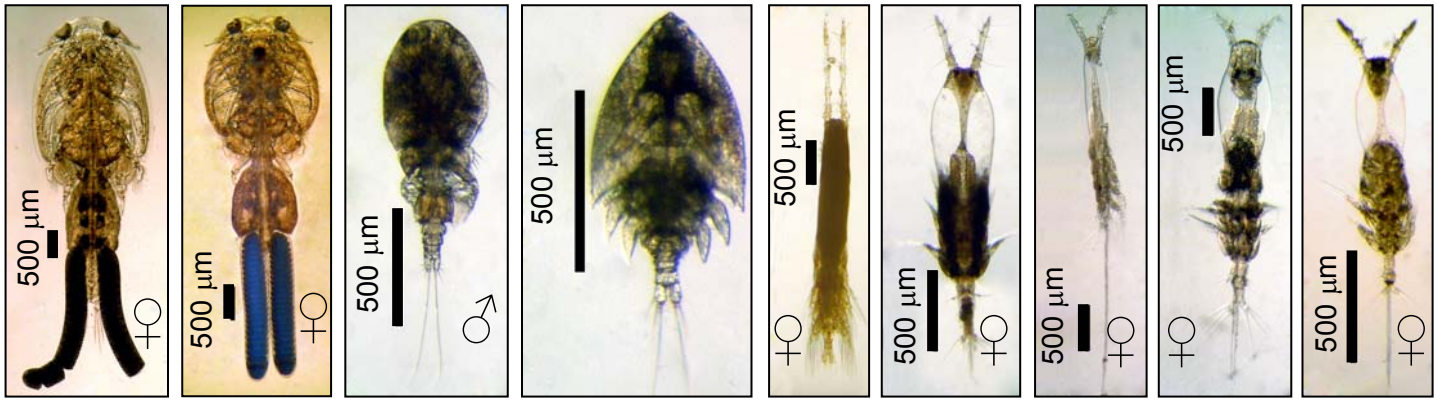

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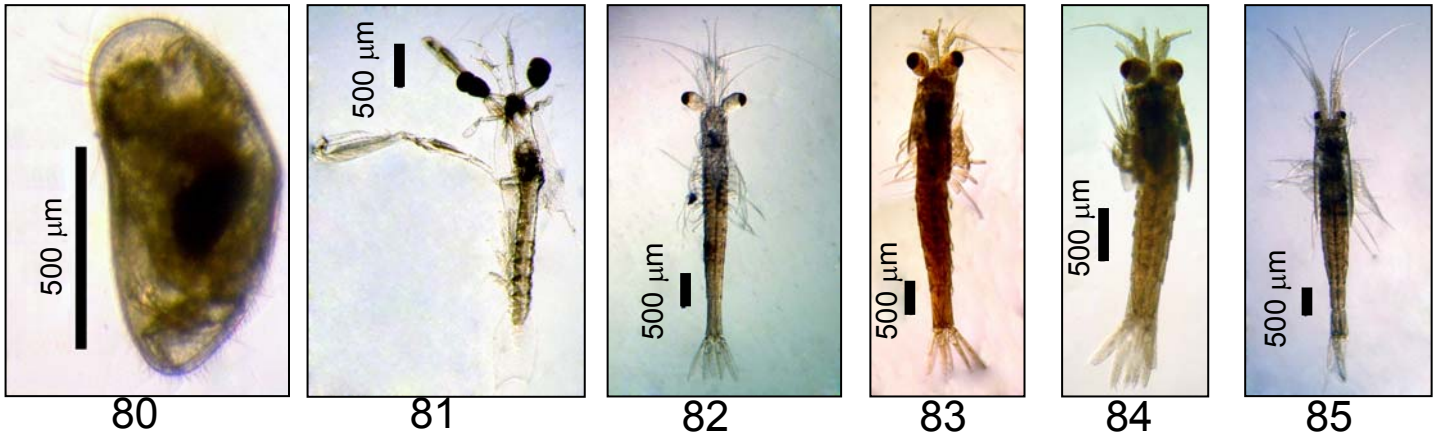
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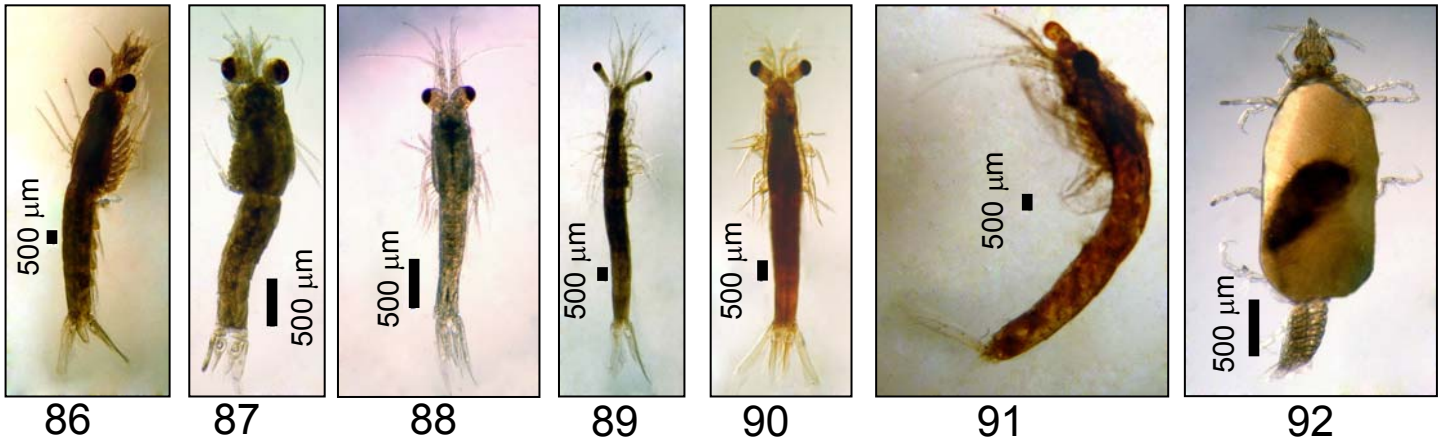
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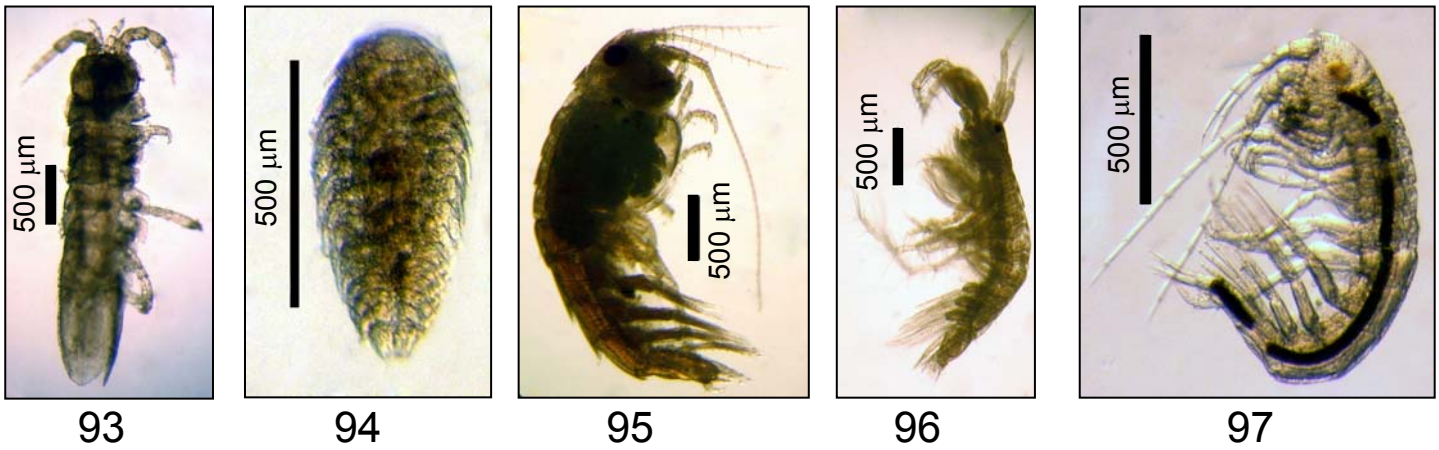
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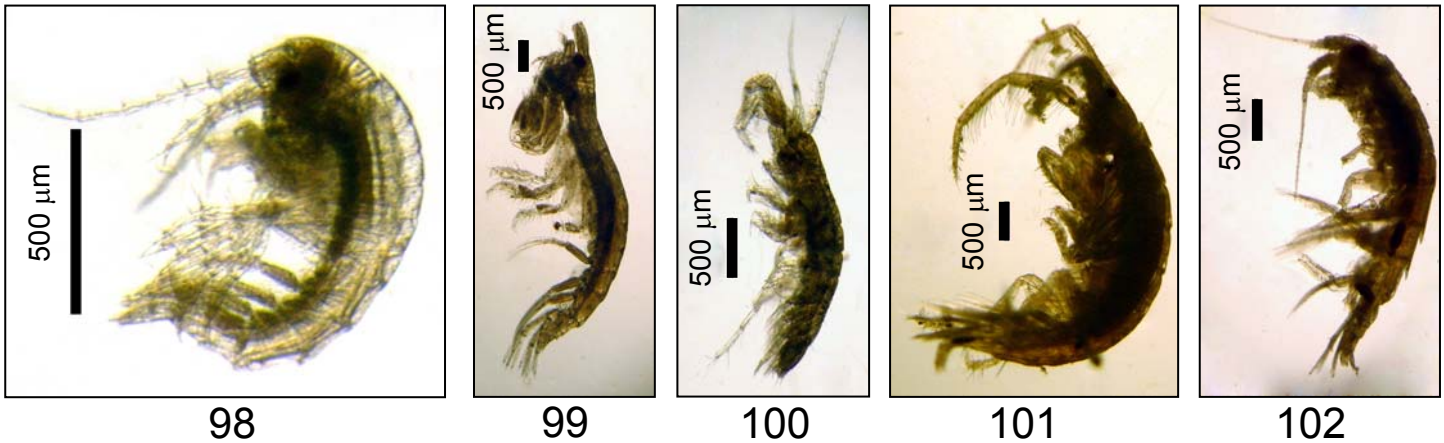
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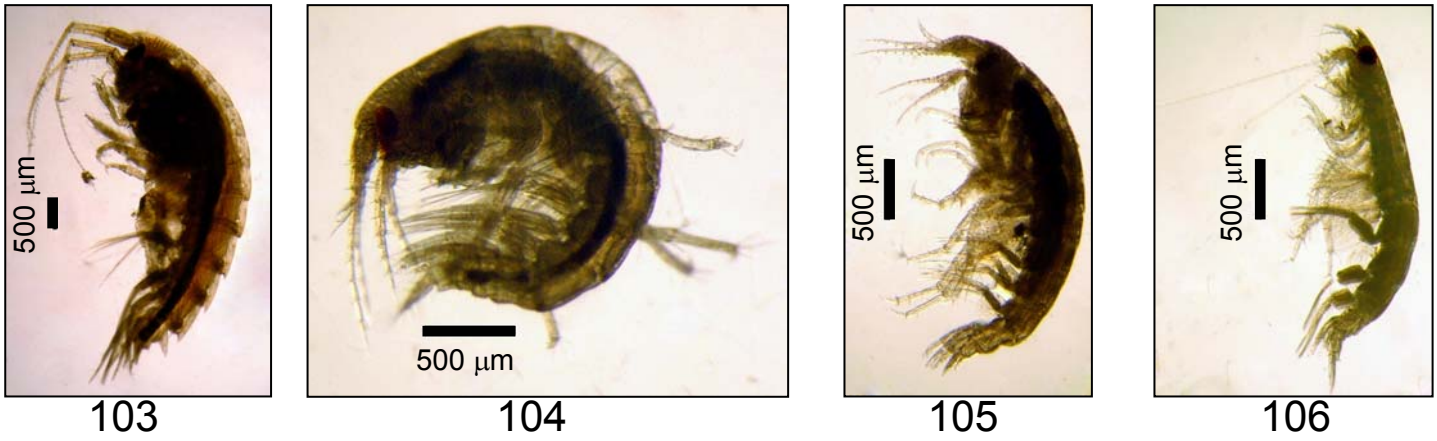

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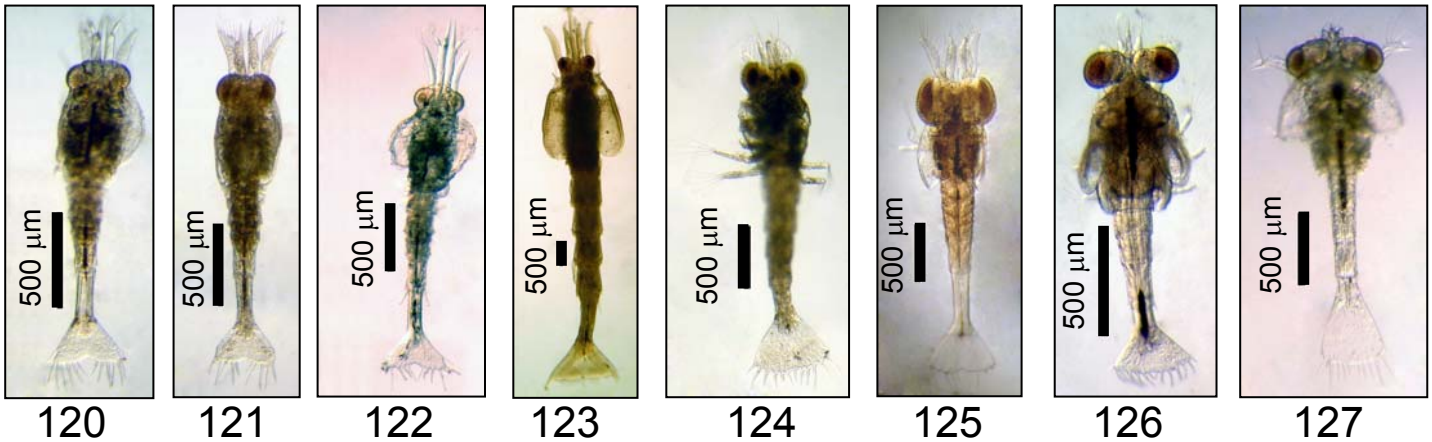

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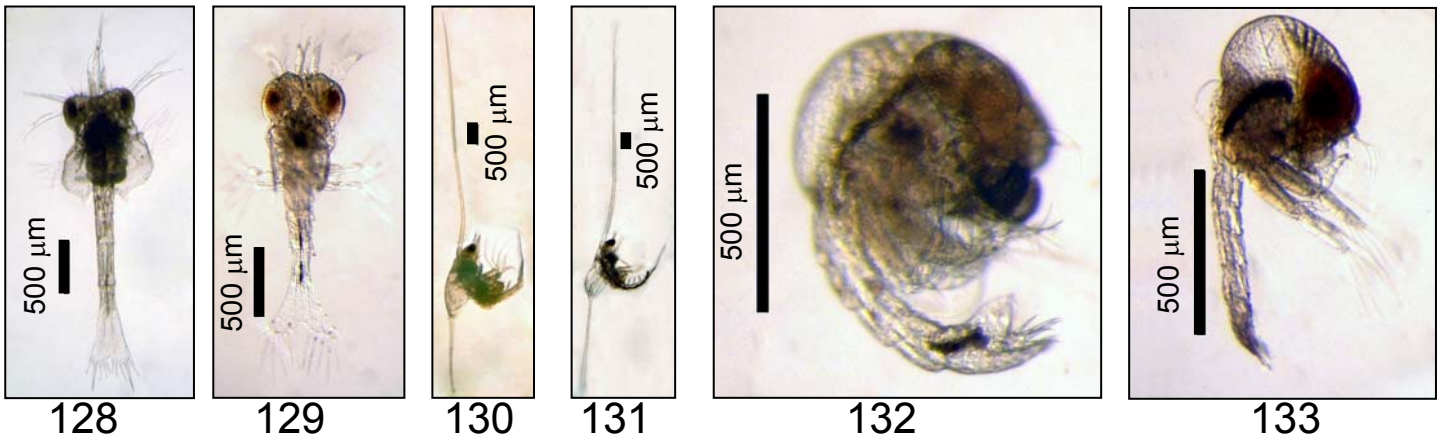

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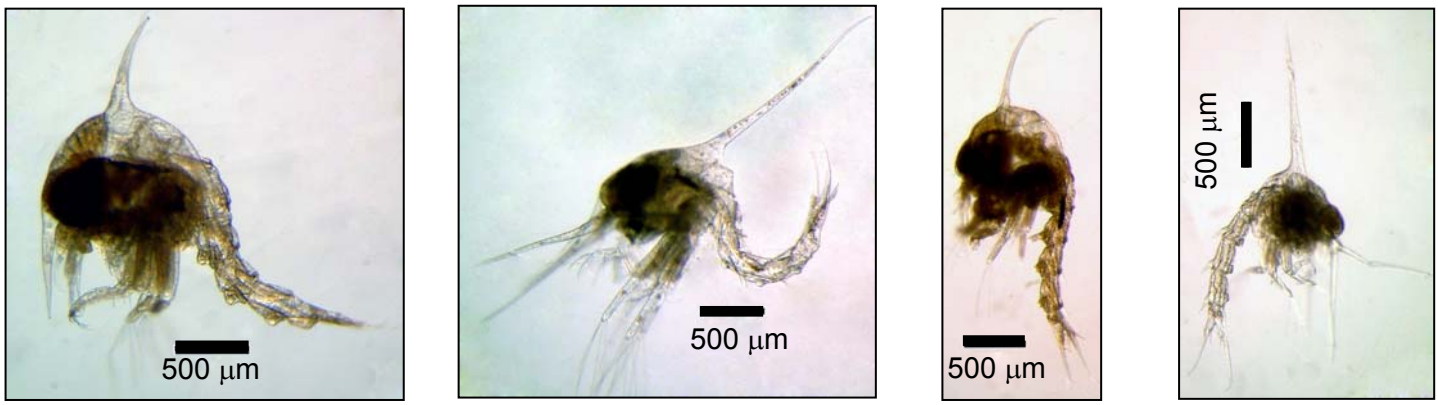

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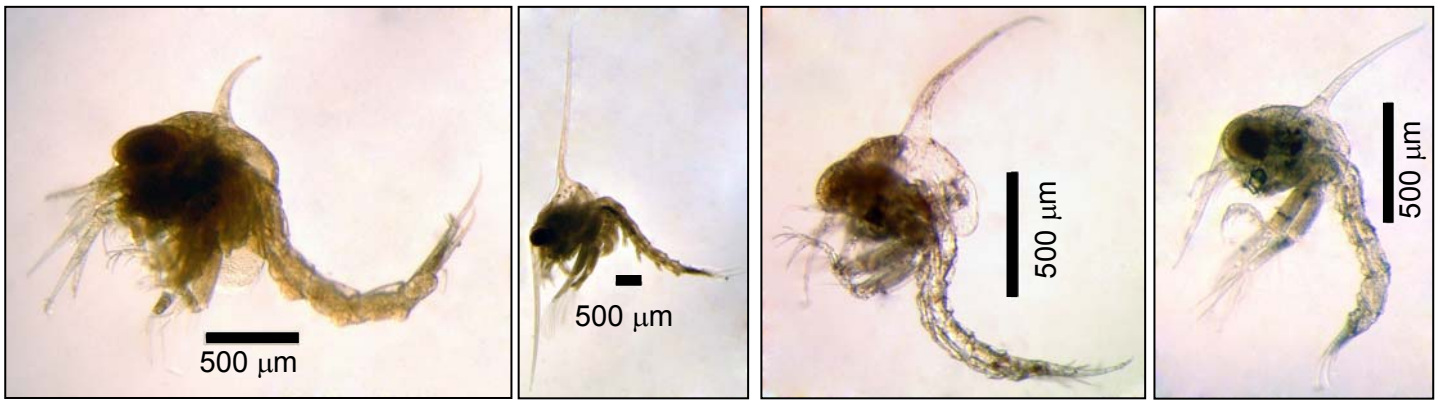

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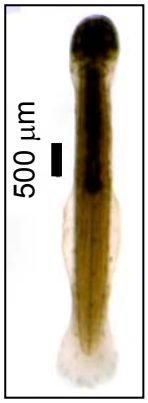

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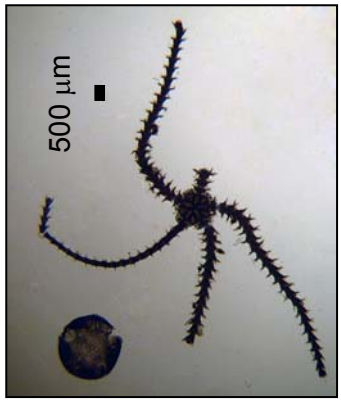
147



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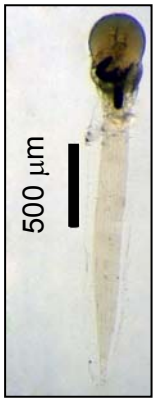

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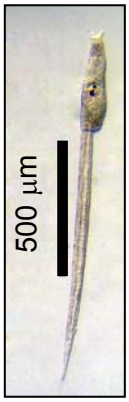

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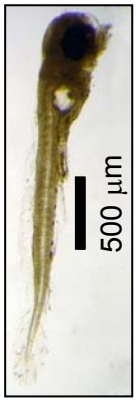

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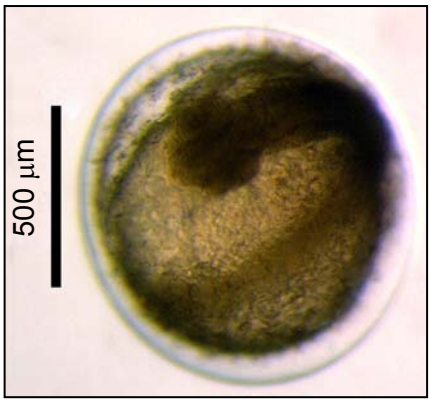

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Appendix VI a – Average final Chl. *a* concentration for each depth stratum at Cracknore. Differences between replicas were calculated as a percentage of the mean averaged for all measurements (error). (Where, * = indicates that no replicate were available; - = indicates no data).

Cracknore	Surface		2 meters		8 meters		Total
date	Chlorophyl (mg m^{-3})	error	Chlorophyl (mg m^{-3})	error	Chlorophyl (mg m^{-3})	error	average
12/01/01	0.19	*	-	-	0.05	*	0.12
30/01/01	0.26	*	1.11	*	0.41	*	0.59
12/02/01	0.98	*	-	-	-	-	0.98
19/02/01	-	-	0.52	*	0.49	*	0.51
02/03/01	0.82	6.26	0.89	10.13	0.60	13.60	0.77
16/03/01	1.08	0.92	0.88	26.08	0.63	5.32	0.86
23/03/01	1.17	22.29	1.25	2.4	0.92	4.46	1.11
04/04/01	1.22	0.38	1.27	0.99	0.93	3.58	1.14
10/04/01	1.53	8.70	1.73	3.08	1.71	0.39	1.66
19/04/01	1.27	2.79	1.40	2.86	1.35	0.60	1.34
27/04/01	1.85	2.16	2.10	0.32	1.98	4.38	1.98
04/05/01	1.15	1.05	2.57	1.54	2.81	0.0	2.18
18/05/01	17.68	2.81	21.34	1.63	38.13	5.11	25.72
07/06/01	8.06	1.79	9.79	2.58	14.40	2.14	10.75
11/06/01	11.23	0.44	13.78	0.85	14.58	3.09	13.20
22/06/01	19.00	2.46	16.18	0.27	15.40	6.49	16.86
03/07/01	31.47	2.41	-	-	-	-	31.47
19/07/01	2.72	1.18	2.67	0.5	2.26	0.29	2.55
24/07/01	10.35	1.03	7.41	0.45	3.02	15.67	6.92
02/08/01	63.07	0.21	38.98	0.97	23.47	2.27	41.84
20/08/01	3.99	2.68	6.47	2.37	2.83	1.18	4.43
31/08/01	13.17	1.14	13.60	0.98	11.63	0.23	12.80
17/09/01	2.04	3.70	1.99	3.38	1.77	1.50	1.93
28/09/01	1.84	0.72	1.60	0.74	1.21	0.17	1.55
17/10/01	1.20	3.88	1.23	0.0	1.07	0.06	1.17
31/10/01	0.94	0.21	0.95	3.58	0.91	3.07	0.93
21/11/01	0.64	0.21	0.68	0.69	0.91	2.58	0.74
14/12/01	0.81	2.91	0.94	8.35	0.65	10.50	0.80
11/01/02	0.40	5.88	0.47	4.77	0.46	10.43	0.44
15/02/02	0.87	2.15	0.82	0.57	0.70	0.28	0.80
14/03/02	1.02	3.13	1.04	1.15	0.81	9.06	0.96
21/03/02	0.72	3.26	0.87	16.78	0.73	4.75	0.77
28/03/02	0.63	0.64	0.84	0.16	0.77	1.38	0.75
09/04/02	1.26	2.43	1.53	9.57	1.31	3.97	1.37
25/04/02	2.67	1.25	3.05	2.41	2.18	3.40	2.63
10/05/02	1.33	13.51	1.69	1.19	1.41	0.94	1.48
16/05/02	1.57	1.28	1.73	0.37	2.07	2.89	1.79
24/05/02	1.72	1.55	1.39	0.96	1.69	5.14	1.60
30/05/02	1.67	0.8	1.80	2.22	2.25	1.48	1.90
07/06/02	3.33	2.8	2.99	5.36	1.49	1.35	2.60
13/06/02	2.49	2.67	2.44	4.92	4.13	9.21	3.02
16/0702	5.95	1.68	5.47	1.71	2.43	0.00	4.62

Appendix VI b – Average final Chl. *a* concentration for each depth stratum at Calshot. Differences between replicas were calculated as a percentage of the mean averaged for all measurements (error). (Where, * = indicates that no replicate were available; - = indicates no data).

Cracknore	2 meters		8 meters		Total
date	Chlorophyl (mg m^{-3})	error	Chlorophyl (mg m^{-3})	error	average
12/01/01	0.15	*	0.38	*	0.27
30/01/01	0.32	*	0.51	*	0.42
12/02/01	0.77	*	0.91	*	0.84
19/02/01	0.08	*	0.69	*	0.38
02/03/01	0.55	7.84	1.08	5.72	0.82
16/03/01	1.13	14.71	0.83	48.55	0.98
23/03/01	1.05	3.51	1.08	0.31	1.06
04/04/01	1.43	3.26	1.43	3.26	1.43
10/04/01	2.03	0.33	2.16	*	2.10
19/04/01	0.89	2.86	1.45	2.75	1.17
27/04/01	2.69	0.50	2.95	2.48	2.82
04/05/01	6.91	4.26	8.19	0.41	7.55
18/05/01	11.79	2.43	16.80	3.64	14.30
07/06/01	15.47	6.03	34.53	2.70	25.00
11/06/01	11.10	1.82	11.86	2.39	11.48
22/06/01	8.94	0.70	9.80	0.05	9.37
03/07/01	6.67	1.64	-	-	6.67
19/07/01	2.33	8.00	2.16	3.09	2.25
24/07/01	2.67	0.50	2.75	1.16	2.71
02/08/01	4.46	3.14	3.87	3.96	4.17
20/08/01	2.92	0.91	2.77	1.92	2.85
31/08/01	2.83	0.71	2.15	15.79	2.49
17/09/01	1.62	4.52	1.76	1.01	1.69
28/09/01	1.45	2.30	1.34	0.80	1.39
17/10/01	1.51	5.73	1.46	0.46	1.49
31/10/01	0.90	8.90	0.95	6.89	0.92
21/11/01	0.89	1.94	0.84	0.24	0.86
14/12/01	1.05	0.95	1.11	3.37	1.08
11/01/02	0.71	9.88	0.69	12.84	0.70
15/02/02	0.99	5.25	0.42	36.39	0.71
14/03/02	1.81	1.47	1.76	10.61	1.79
21/03/02	0.97	6.16	0.92	6.36	0.95
28/03/02	1.85	6.14	1.82	0.37	1.83
09/04/02	2.31	5.48	1.84	17.39	2.08
25/04/02	3.35	4.17	3.95	1.35	3.65
10/05/02	2.14	3.43	2.61	12.24	2.38
16/05/02	2.40	1.82	2.60	1.93	2.50
24/05/02	2.97	6.97	3.05	0.87	3.01
30/05/02	3.38	3.75	3.43	4.28	3.40
07/06/02	2.47	3.50	2.30	3.77	2.39
13/06/02	3.21	0.62	3.17	2.74	3.19
16/0702	3.20	4.58	2.82	1.35	3.01

Appendix VI c – Average final Chl. *a* concentration for each depth stratum at NW. Netley. Differences between replicas were calculated as a percentage of the mean averaged for all measurements (error). (Where, * = indicates that no replicate were available; - = indicates no data).

Cracknore	2 meters		8 meters		Total
date	Chlorophyl (mg m^{-3})	error	Chlorophyl (mg m^{-3})	error	average
12/01/01	-	-	-	-	-
30/01/01	-	-	-	-	-
12/02/01	-	-	-	-	-
19/02/01	-	-	-	-	-
02/03/01	0.55	4.88	0.67	8.32	0.61
16/03/01	-	-	-	-	-
23/03/01	-	-	-	-	-
04/04/01	-	-	-	-	-
10/04/01	1.44	3.70	1.56	0.00	1.50
19/04/01	-	-	-	-	-
27/04/01	-	-	-	-	-
04/05/01	1.85	3.60	4.80	5.28	3.33
18/05/01	17.07	3.52	19.53	0.34	18.30
07/06/01	11.23	2.40	15.53	0.43	13.38
11/06/01	-	-	-	-	-
22/06/01	-	-	-	-	-
03/07/01	-	-	-	-	-
19/07/01	3.22	1.86	2.07	0.00	2.64
24/07/01	-	-	-	-	-
02/08/01	20.93	2.55	16.60	1.20	18.77
20/08/01	-	-	-	-	-
31/08/01	-	-	-	-	-
17/09/01	1.99	2.93	2.24	0.80	2.11
28/09/01	-	-	-	-	-
17/10/01	1.45	3.67	1.74	0.38	1.60
31/10/01	-	-	-	-	-
21/11/01	0.71	2.52	0.71	3.93	0.71
14/12/01	0.85	2.26	0.80	2.00	0.83
11/01/02	0.63	3.59	0.65	1.58	0.64
15/02/02	0.65	2.07	0.63	0.11	0.64
14/03/02	1.08	3.88	1.25	3.00	1.16
21/03/02	0.66	0.30	0.96	2.79	0.81
28/03/02	0.53	8.31	1.23	1.08	0.88
09/04/02	1.28	5.04	5.52	*	3.40
25/04/02	3.19	2.19	4.20	6.98	3.70
10/05/02	1.59	0.00	1.95	3.07	1.77
16/05/02	2.41	3.31	2.66	0.25	2.54
24/05/02	1.80	3.70	2.90	3.19	2.35
30/05/02	2.87	2.79	3.11	1.07	2.99
07/06/02	2.73	4.39	1.57	5.08	2.15
13/06/02	3.05	2.41	4.13	2.26	3.59
16/0702	6.90	3.58	5.17	34.19	6.03

Appendix VII a – Average final dissolved Oxygen concentration and saturation for each depth stratum at Cracknore. Differences between replicas were calculated as a percentage of the mean averaged for all measurements (error). (Where, * = indicates that no replicate were available; - = indicates no data).

Cracknore	Surface			2m			8m			
Date	Oxygen ml l^{-1}	error	% Sat	Oxygen ml l^{-1}	error	% Sat	Oxygen ml l^{-1}	error	% Sat	Total average
12/01/01	7.03	*	92.34	-	-	-	6.75	*	93.39	6.89
30/01/01	7.61	*	98.26	6.84	*	92.59	7.25	*	102.03	7.23
12/02/01	-	-	-	-	-	-	-	-	-	-
19/02/01	-	-	-	7.21	*	103.43	7.96	*	115.28	7.59
02/03/01	6.95	*	95.89	6.92	*	96.98	6.63	*	93.92	6.83
16/03/01	6.72	*	93.51	6.81	*	97.16	6.55	*	94.60	6.69
23/03/01	6.71	*	89.88	6.61	*	93.28	6.17	*	88.26	6.49
04/04/01	7.00	2.72	99.75	5.22	5.90	76.80	5.91	1.24	87.35	6.04
10/04/01	6.66	0.05	99.49	6.55	0.06	97.79	6.59	0.25	99.10	6.60
19/04/01	5.87	4.23	85.62	5.73	0.50	85.57	5.32	3.07	80.59	5.64
27/04/01	6.77	0.32	99.22	6.62	0.05	99.27	6.50	0.09	98.77	6.63
04/05/01	6.54	0.05	99.83	6.55	0.01	100.52	6.56	0.16	101.22	6.55
18/05/01	8.78	0.54	140.50	8.91	0.96	144.12	8.24	0.21	134.78	8.64
07/06/01	5.45	0.86	92.29	5.60	0.08	96.06	6.55	8.19	114.00	5.87
11/06/01	6.26	0.00	107.60	6.59	1.22	113.59	5.45	0.43	94.56	6.10
22/06/01	6.91	0.38	121.89	7.53	10.52	132.87	6.07	0.59	108.17	6.84
03/07/01	8.99	-	164.50	-	-	-	-	-	-	8.99
19/07/01	4.87	0.27	88.20	4.88	0.28	88.50	4.87	0.18	88.67	4.87
24/07/01	5.58	3.82	102.60	6.96	11.44	127.98	5.05	3.70	93.18	5.86
02/08/01	7.47	0.19	137.66	6.96	7.09	132.16	5.75	0.23	109.78	6.73
20/08/01	6.10	18.06	111.91	5.02	0.62	92.95	4.80	0.17	89.87	5.31
31/08/01	6.02	14.48	113.64	6.16	14.27	116.24	5.19	0.14	98.40	5.79
17/09/01	5.24	0.30	92.53	5.31	0.26	94.25	5.32	1.43	94.53	5.29
28/09/01	5.36	0.44	91.27	5.34	0.95	92.88	4.95	0.31	86.59	5.22
17/10/01	5.28	0.11	90.61	5.28	0.20	90.51	5.18	0.83	89.41	5.25
31/10/01	5.35	0.19	90.54	5.38	0.06	91.32	5.39	0.03	92.54	5.38
21/11/01	6.29	0.01	97.26	6.25	0.03	96.93	6.07	0.04	95.36	6.20
14/12/01	6.51	0.24	95.72	6.33	0.16	94.12	6.30	0.13	94.44	6.38
11/01/02	7.02	0.02	95.45	6.94	0.20	96.36	6.87	0.15	96.08	6.95
15/02/02	6.54	0.18	98.03	6.49	0.09	97.34	6.40	0.01	96.33	6.48
14/03/02	6.66	0.04	96.56	6.68	0.07	96.85	6.50	0.11	96.64	6.61
21/03/02	6.50	0.03	96.97	6.47	0.24	97.04	6.38	0.02	95.90	6.45
28/03/02	6.35	0.18	93.75	6.31	0.54	95.56	6.32	0.76	96.53	6.33
09/04/02	6.37	0.11	100.18	6.35	0.53	99.85	6.38	0.15	100.96	6.37
25/04/02	7.05	2.08	114.76	6.79	0.54	110.02	6.59	0.06	106.52	6.81
10/05/02	6.09	0.08	99.55	-	-	-	-	-	-	6.09
16/05/02	6.12	0.60	103.47	6.18	0.08	104.18	6.04	0.39	100.90	6.11
24/05/02	5.83	0.25	97.78	5.85	0.05	98.02	5.76	0.07	97.93	5.81
30/05/02	5.95	0.02	100.03	5.93	0.03	100.27	5.72	0.28	97.19	5.87
07/06/02	5.85	0.06	97.15	5.81	0.02	100.15	5.65	0.01	97.77	5.77
13/06/02	5.88	1.65	101.73	6.01	0.05	104.31	5.82	0.12	101.01	5.90
16/07/02	6.10	0.12	112.45	5.87	0.02	107.92	5.40	0.38	99.17	5.80

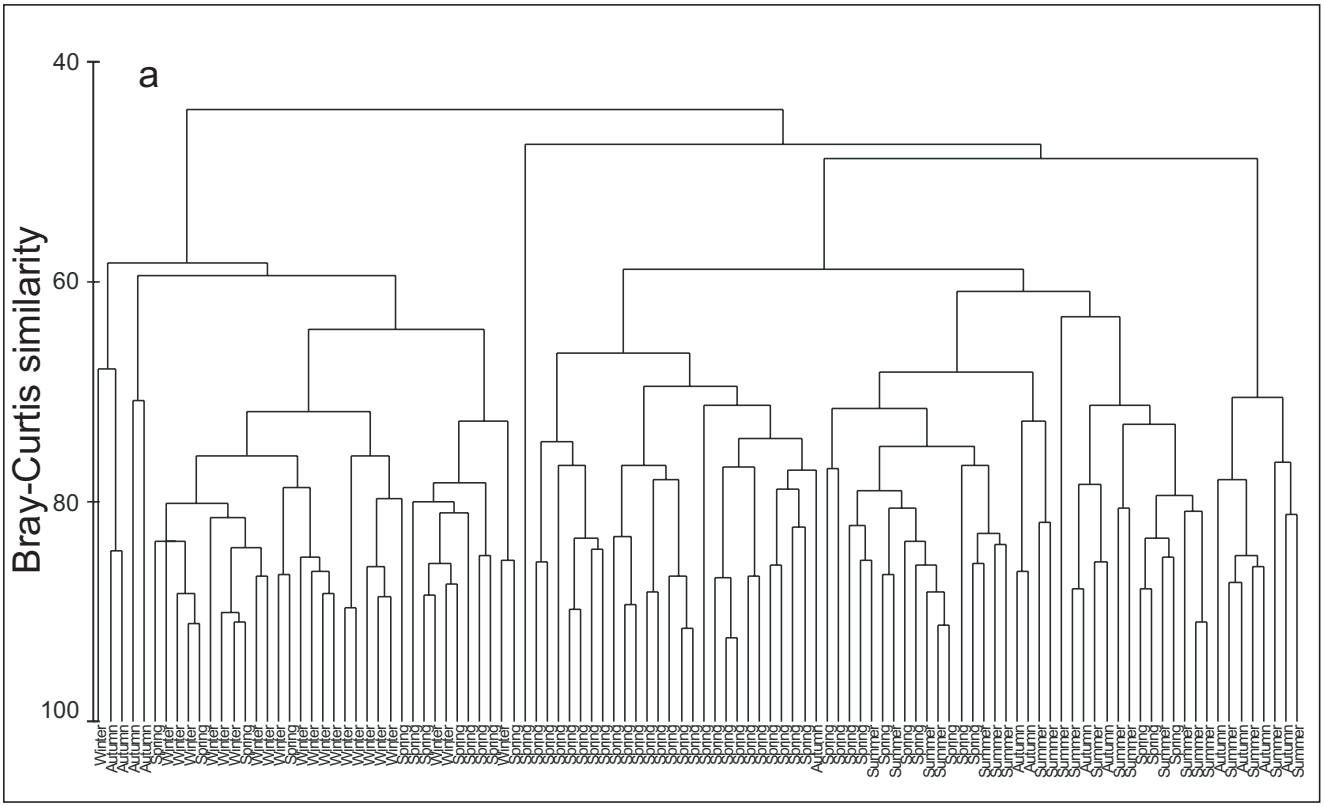
Appendix VII b – Average final dissolved Oxygen concentration and saturation for each depth stratum at Calshot. Differences between replicas were calculated as a percentage of the mean averaged for all measurements (error). (Where, * = indicates that no replicate were available; - = indicates no data; blank space = not processed).

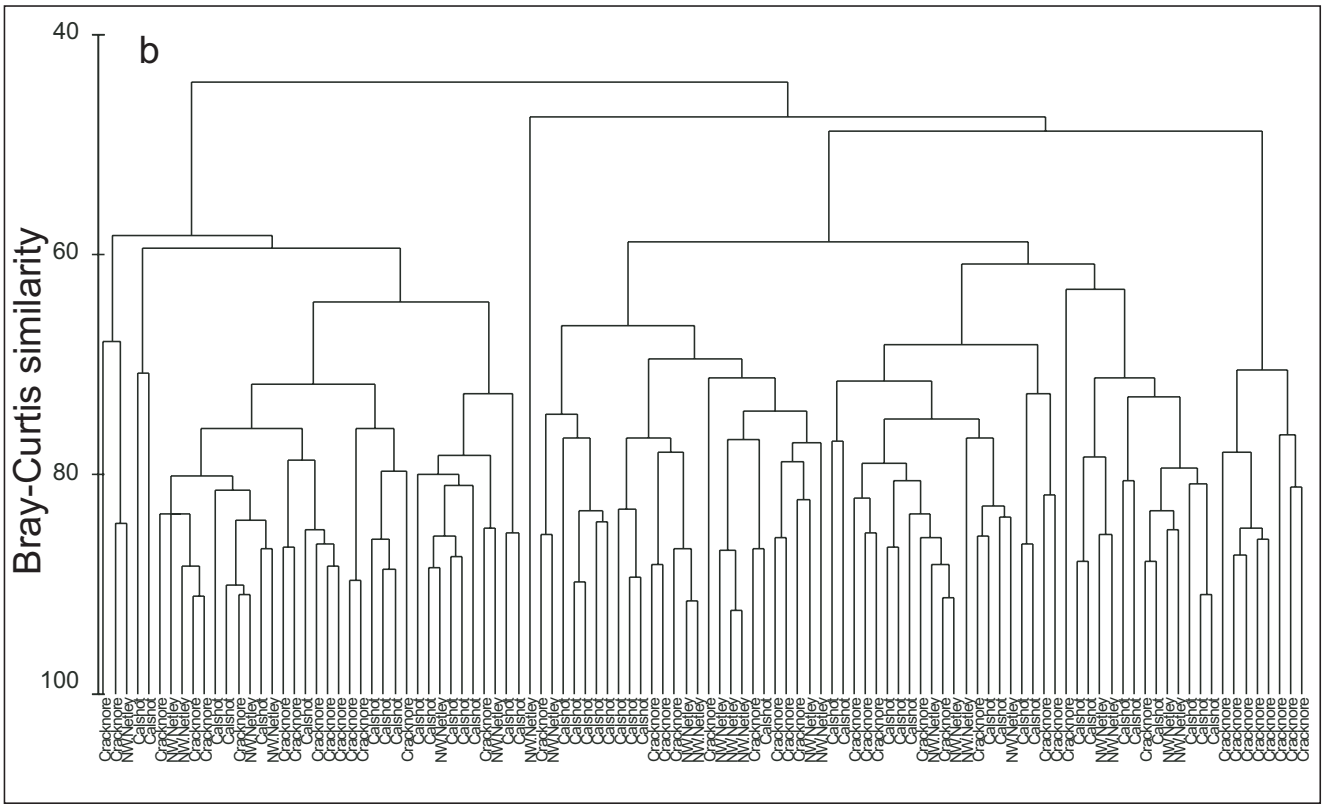
Cracknore	2m			8m			
Date	Oxygen ml l^{-1}	error	% Sat	Oxygen ml l^{-1}	error	% Sat	Total average
12/01/01	7.24	*	103.10	7.60	*	108.44	7.42
30/01/01	-	-	-	6.99	*	98.87	6.99
12/02/01	-	-	-	-	-	-	-
19/02/01	6.80	*	97.82	-	-	-	6.80
02/03/01	7.01	*	99.54	7.43	*	105.72	7.22
16/03/01	7.32	*	107.28	6.87	*	100.47	7.09
23/03/01	6.73	*	98.00	6.73	*	97.62	6.73
04/04/01	6.63	0.76	99.06	5.61	21.63	83.76	6.12
10/04/01	6.74	0.05	102.03	6.74	0.20	102.16	6.74
19/04/01	5.42	11.20	82.02	6.07	0.41	91.76	5.74
27/04/01	6.84	0.76	106.17	6.82	1.57	105.65	6.83
04/05/01	7.52	4.29	117.12	7.22	0.89	112.50	7.37
18/05/01	7.84	0.24	127.99	7.86	0.99	127.87	7.85
07/06/01	6.66	4.11	116.30	6.34	0.03	110.62	6.50
11/06/01	6.56	0.20	114.42	6.40	0.30	111.49	6.48
22/06/01	6.42	4.18	115.59	7.10	8.14	127.82	6.76
03/07/01	5.78	0.44	109.06	-	-	-	5.78
19/07/01	5.19	0.24	94.81	5.39	3.62	98.52	5.29
24/07/01	5.93	11.92	110.43	5.21	0.08	96.95	5.57
02/08/01	5.82	5.72	111.09	6.72	7.51	128.49	6.27
20/08/01	5.58	8.37	105.15	5.12	0.05	96.62	5.35
31/08/01	5.35	0.60	101.19	5.25	0.81	99.40	5.30
17/09/01	5.45	0.03	97.72	5.49	2.07	98.37	5.47
28/09/01	5.55	1.55	98.36	5.44	0.53	96.16	5.50
17/10/01	5.45	0.12	95.90	5.51	0.44	96.81	5.48
31/10/01	5.68	0.15	98.43	5.64	0.08	97.67	5.66
21/11/01	6.22	0.38	99.14	6.25	0.18	99.56	6.23
14/12/01	6.51	0.33	98.78	6.61	0.22	100.34	6.56
11/01/02	6.92	0.24	98.62	6.93	0.02	98.93	6.92
15/02/02	6.50	0.20	98.65	6.69	3.98	101.65	6.60
14/03/02	6.57	0.02	98.66	6.51	0.99	97.99	6.54
21/03/02	6.52	0.59	99.87	6.57	0.10	100.45	6.55
28/03/02	6.56	0.24	101.20	6.57	0.12	101.36	6.56
09/04/02	6.62	0.04	104.59	6.63	0.16	104.72	6.62
25/04/02	6.84	0.13	111.28	6.78	0.68	110.19	6.81
10/05/02	6.35	*	104.92	6.35	*	104.73	6.35
16/05/02	6.32	0.02	106.76	6.28	0.06	105.61	6.30
24/05/02	6.06	0.22	104.24	6.06	0.03	104.22	6.06
30/05/02	6.16	0.01	105.84	6.14	0.24	105.64	6.15
07/06/02	6.00	0.75	104.02	5.97	0.05	103.53	5.98
13/06/02	6.08	0.10	106.10	6.10	0.05	106.44	6.09
16/07/02	5.80	0.51	107.10	5.79	0.51	107.03	5.80

Appendix VII c – Average final dissolved Oxygen concentration and saturation for each depth stratum at NW. Netley. Differences between replicas were calculated as a percentage of the mean averaged for all measurements (error). (Where, * = indicates that no replicate were available; - = indicates no data; blank space = not processed).

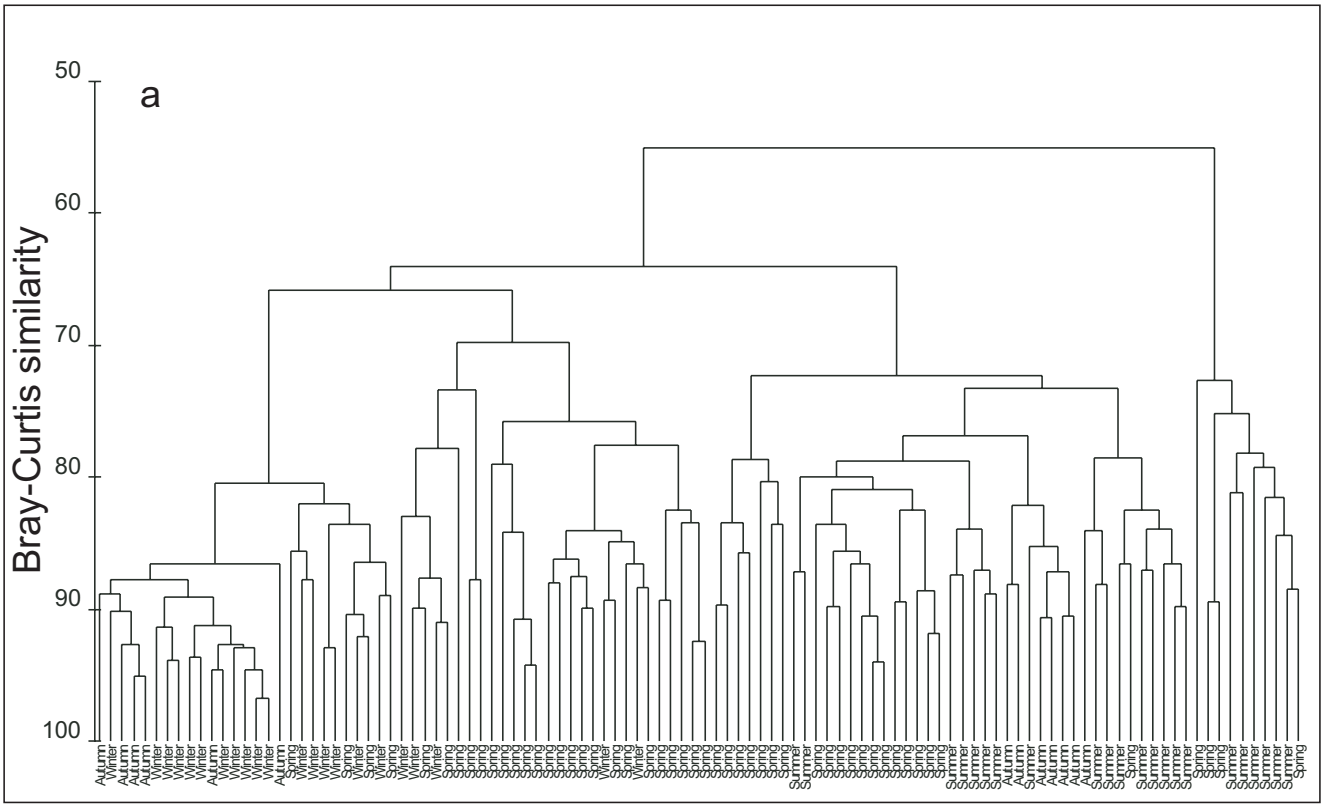
Cracknore	2m			8m			
Date	Oxygen ml l^{-1}	error	% Sat	Oxygen ml l^{-1}	error	% Sat	Total average
12/01/01	-	-	-	-	-	-	-
30/01/01	-	-	-	-	-	-	-
12/02/01	-	-	-		-	-	-
19/02/01	-	-	-	-	-	-	-
02/03/01	7.06	*	97.49	6.76	*	95.58	6.91
16/03/01	-	-	-	-	-	-	-
23/03/01	-	-	-	-	-	-	-
04/04/01	-	-	-	-	-	-	-
10/04/01	6.74	0.64	101.38	6.75	0.24	101.79	6.75
19/04/01	-	-	-	-	-	-	-
27/04/01	-	-	-	-	-	-	-
04/05/01	6.76	0.50	103.41	6.92	0.54	107.30	6.84
18/05/01	8.67	0.06	141.34	7.54	1.06	123.73	8.11
07/06/01	6.50	0.15	113.08	6.04	0.32	105.75	6.27
11/06/01	-	-	-	-	-	-	-
22/06/01	-	-	-	-	-	-	-
03/07/01	-	-	-	-	-	-	-
19/07/01	5.48	4.77	99.82	5.35	3.54	97.80	5.41
24/07/01	-	-	-	-	-	-	-
02/08/01	6.06	0.15	115.79	5.76	0.16	110.25	5.91
20/08/01	-	-	-	-	-	-	-
31/08/01	-	-	-	-	-	-	-
17/09/01	5.28	0.72	93.62	5.49	2.91	97.33	5.38
28/09/01	-	-	-	-	-	-	-
17/10/01	5.39	0.32	93.87	5.30	0.62	92.51	5.34
31/10/01	-	-	-	-	-	-	-
21/11/01	6.26	0.42	97.74	6.19	0.12	97.16	6.22
14/12/01	6.52	0.18	97.23	6.55	0.18	97.89	6.54
11/01/02	7.03	0.08	97.93	6.91	0.08	97.56	6.97
15/02/02	6.56	0.04	97.46	6.58	0.15	97.82	6.57
14/03/02	6.56	0.22	97.75	6.56	0.04	98.06	6.56
21/03/02	6.52	0.67	98.62	6.46	0.03	98.16	6.49
28/03/02	6.60	0.04	99.87	6.47	0.19	99.18	6.54
09/04/02	6.66	0.17	103.84	6.60	0.14	103.96	6.63
25/04/02	6.88	0.30	113.10	6.80	0.15	111.08	6.84
10/05/02	-	-	-	-	-	-	-
16/05/02	6.46	2.91	109.28	6.09	0.14	101.99	6.28
24/05/02	6.05	0.02	103.84	5.98	0.01	102.55	6.02
30/05/02	6.07	0.13	103.45	5.82	0.12	99.14	5.95
07/06/02	5.94	0.09	102.54	5.83	0.03	101.10	5.88
13/06/02	6.34	1.77	110.52	6.06	0.10	105.44	6.20
16/07/02	5.94	0.45	110.72	5.67	0.81	105.35	5.81

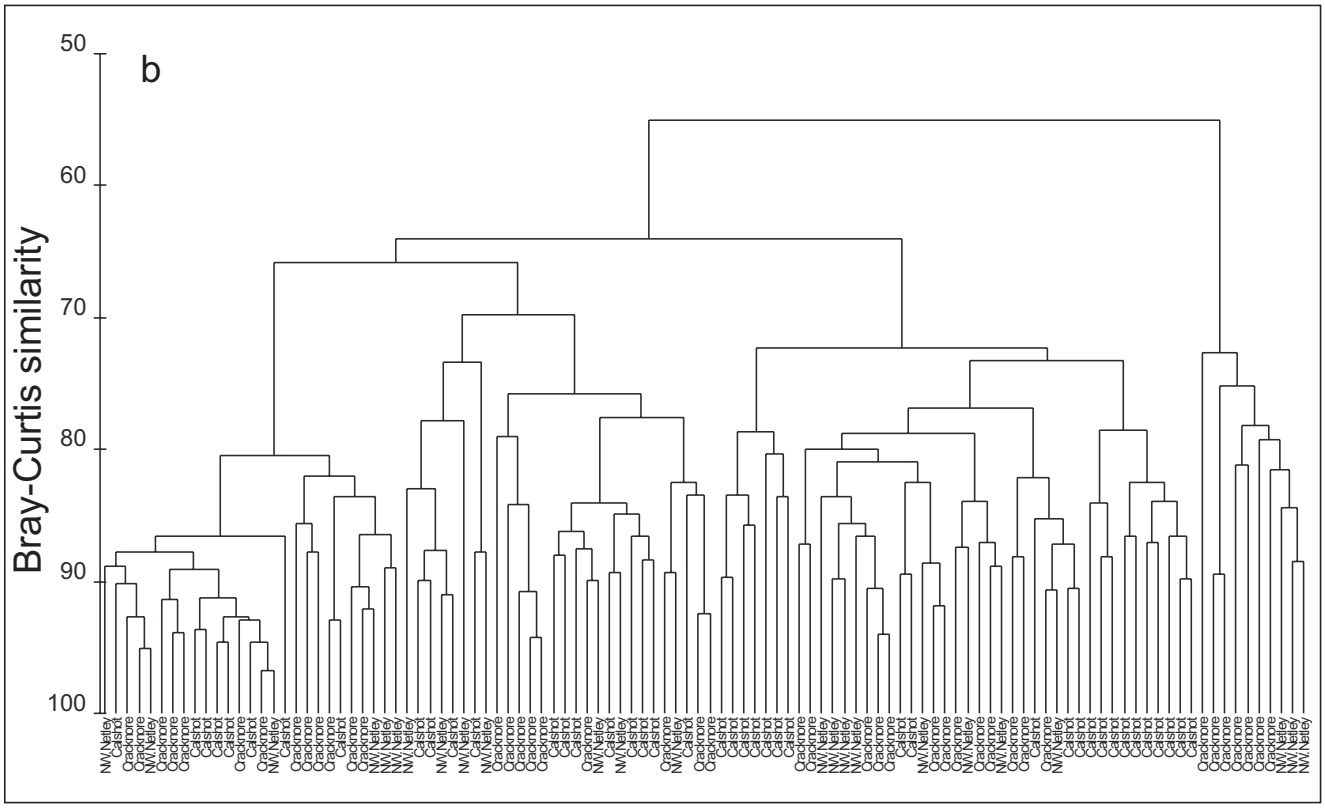
Appendix VIII. Dendrogram of the 108 samples, using group-average clustering from Bray-Curtis similarities on square root transformed abundance data of all holoplanktonic species/groups collected at the three sites during 2001/02. (a) showing seasons and (b) *Meganyctiphanes norvegica* stations



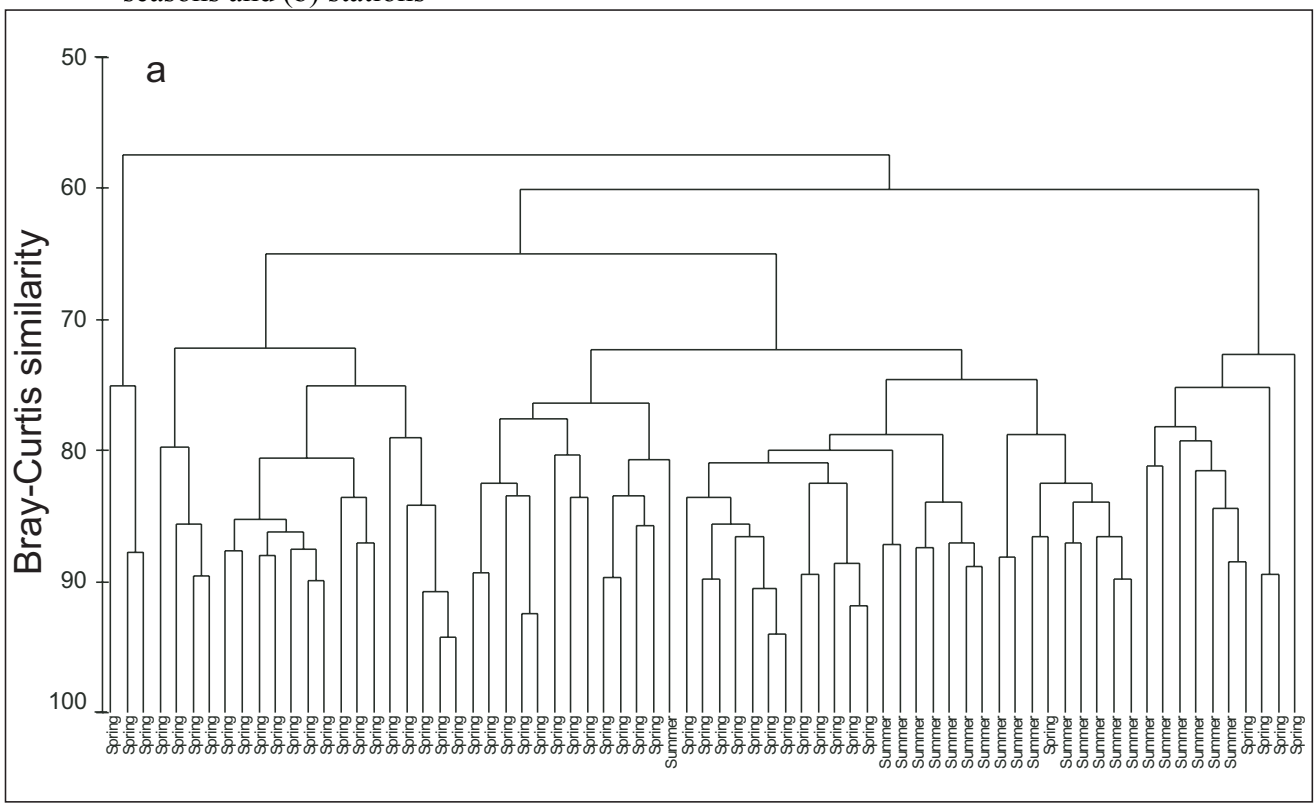


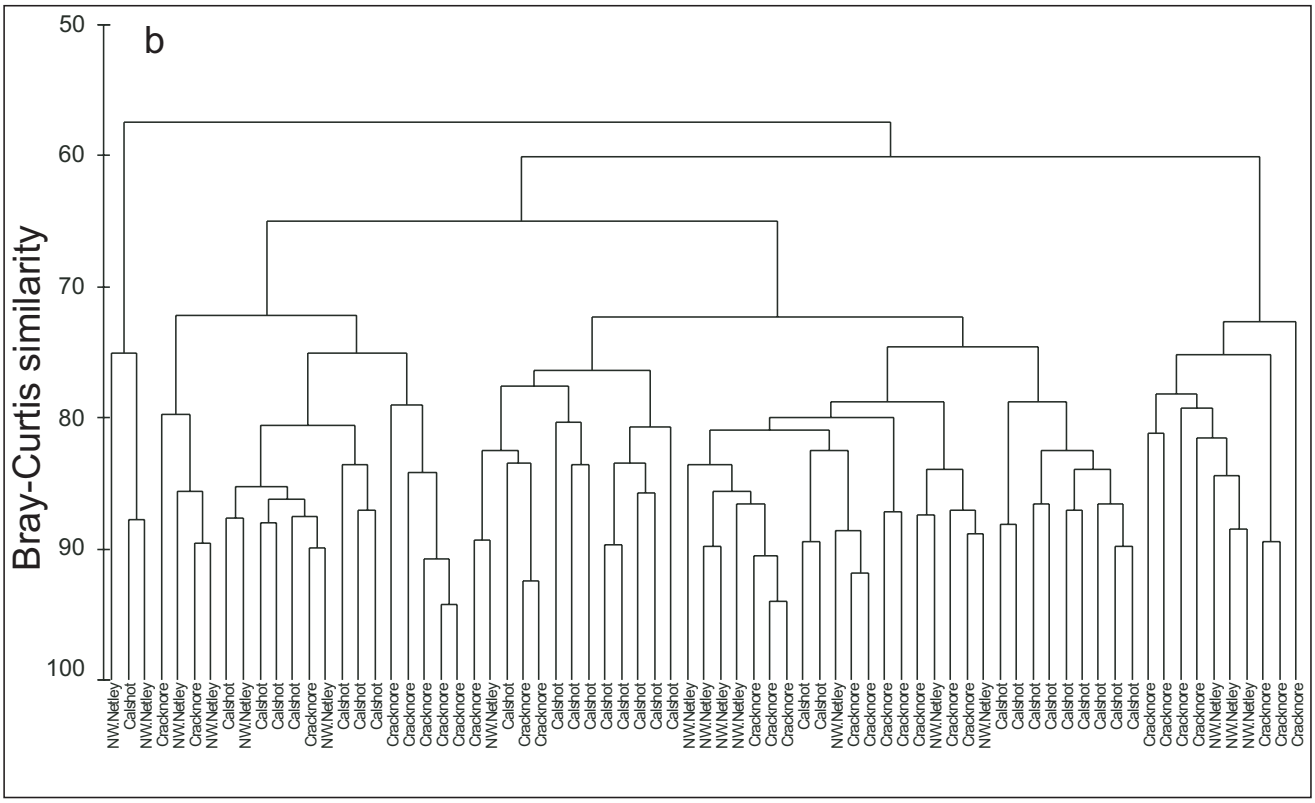
Appendix IX a. Dendrogram of the 108 samples, using group-average clustering from Bray-Curtis similarities on square root transformed abundance data of all mero – tycoplanktonic species/groups collected at the three sites during 2001/02. With (a) seasons and (b) stations



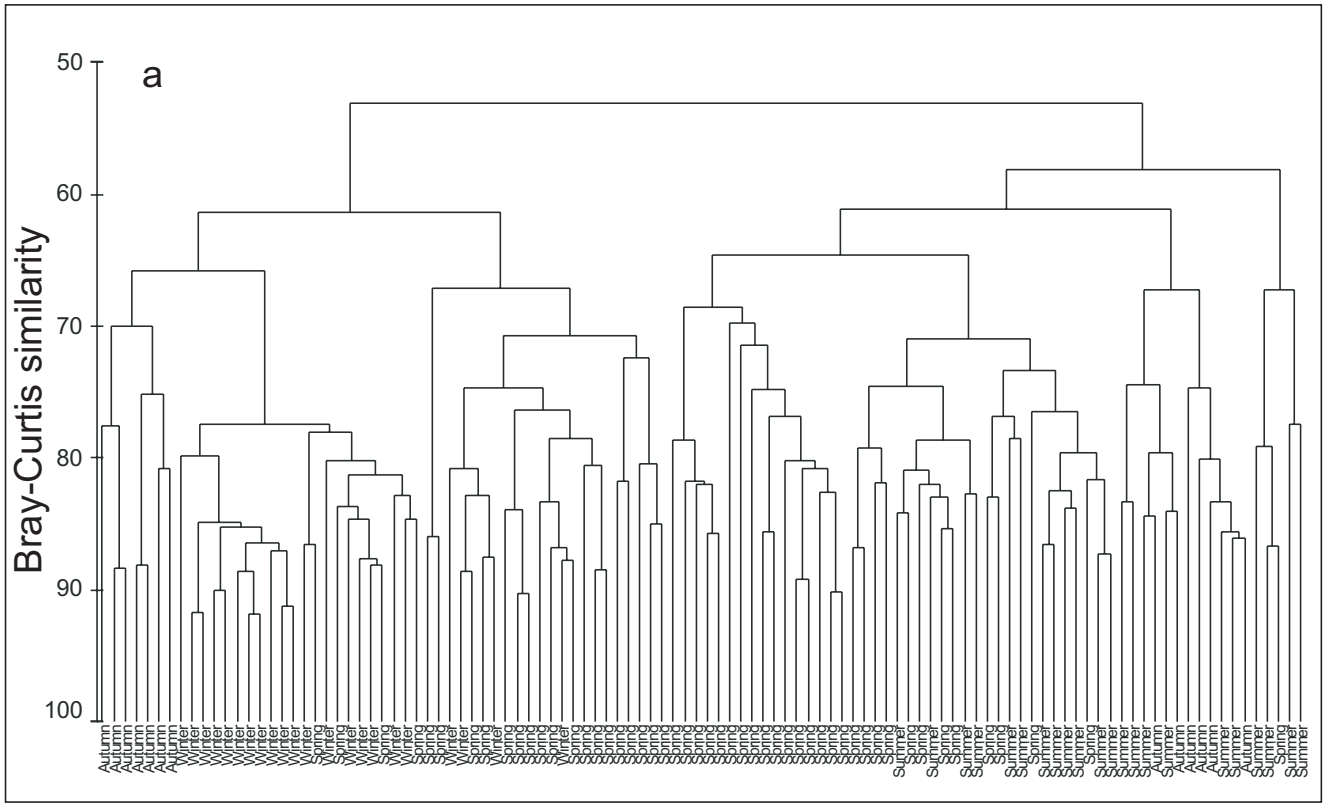


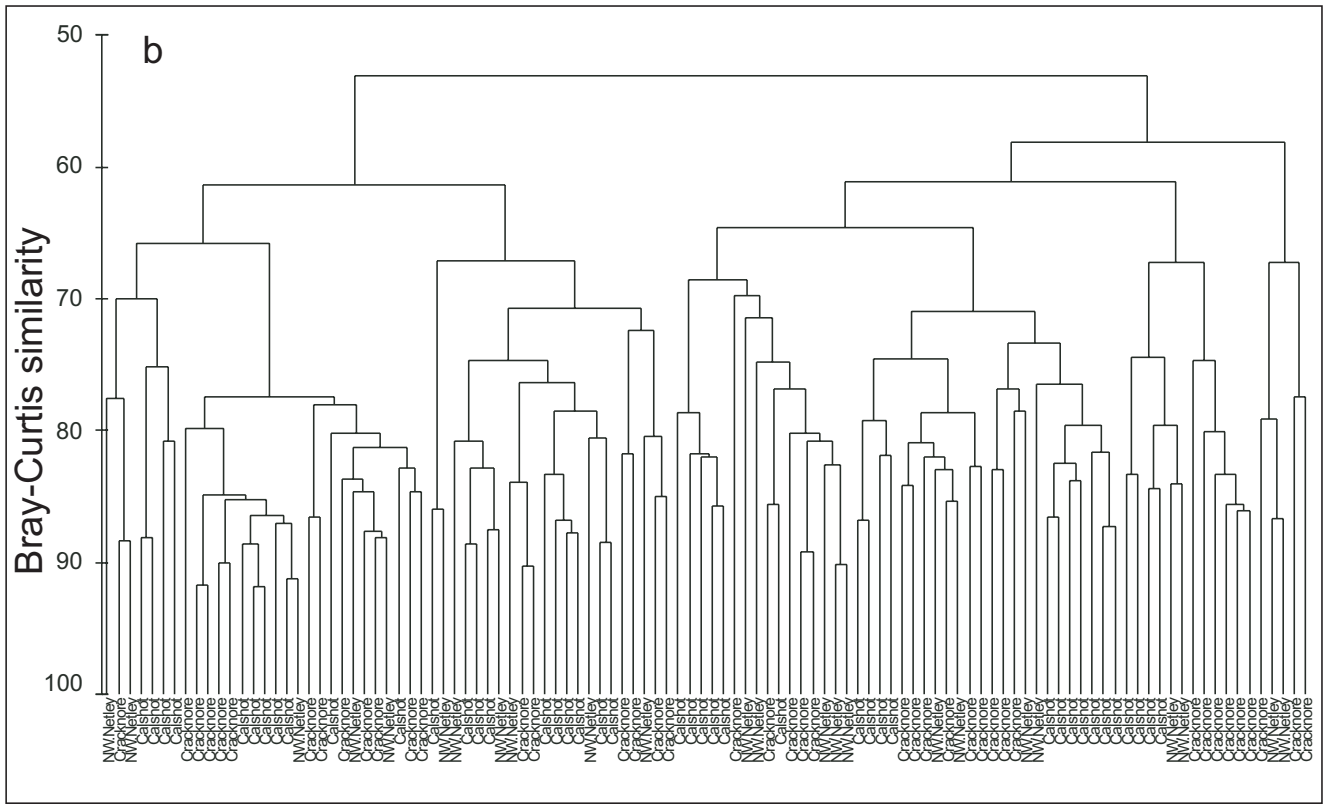
Appendix IX b. Dendrogram of the spring-summer samples, using group-average clustering from Bray-Curtis similarities on square root transformed abundance data of all mero – tycoplanktonic species/groups collected at the three sites during 2001/02. With (a) seasons and (b) stations





Appendix IX c. Dendrogram of the 108 samples, using group-average clustering from Bray-Curtis similarities on square root transformed abundance data of all species/groups found in the mesozooplankton of Southampton water at the three sites during 2001/02. With (a) seasons and (b) stations





Appendix X a. Mean weight values (µg) of naupliar stages II to VI + cypris of *Elminius modestus* and *Semibalanus balanoides* from the literature, together with the values of the present investigation. Also shown is the % of Ash and Carbon (C) considered for each stage, as well as the averaged value of one of the body measurements (M) of each larval stage used in the biomass analysis (i.e. for naupliar stages II – VI the value shown is the average carapace width (µm), while for cyprids the value shown is the averaged length (µm)

Elminius modestus

Stage	**M** ± SD (n)	**Average Weight (µg)** **DW** ± SD(n)	**AFDW** ± SD (n)	**%Ash** ±SD	****%C** ± SD	**References**
I	----	----	----	----	----	----
II	----	0.3 ****	----	----	----	(Bhatnager & Crisp, 1965)*
	----	0.40 ± 0.01 (80)	----	----	43.31 ± 0.33	(Harms, 1987)*
	----	2.4 ± 0.5 (6)	----	----	----	(Geary, 1991)
	156 ± 8.4 (10)	**0.29 ± 0.01 (4)**	**0.24 ± 0.01 (4)**	**17.03 ± 6.25**	**43.31 ± 0.33**	**Present study**
III	----	0.72 ± 0.03 (40)	----	----	44.17 ± 5.24	(Harms, 1987)*
	----	3.9 ± 0.2 (5)	----	----	----	(Geary, 1991)
	180 ± 0.0 (10)	**0.49 ± 0.05 (4)**	**0.40 ± 0.04 (4)**	**17.88 ± 4.00**	**44.17 ± 5.24**	**Present study**
IV	----	1.24 ± 0.21 (48)	----	----	40.40 ± 3.42	(Harms, 1987)*
	----	7.3 ± 0.9 (5)	----	----	----	(Geary, 1991)
	216 ± 8.4 (10)	**0.77 ± 0.70 (4)**	**0.65 ± 0.06 (4)**	**15.25 ± 6.82**	**40.40 ± 3.42**	**Present study**
V	----	2.47 ± 0.15 (62)	----	----	39.37 ± 2.22	(Harms, 1987)*
	----	10.4 ± 2.4 (5)	----	----	----	(Geary, 1991)
	262 ± 6.3 (10)	**1.20 ± 0.09 (4)**	**1.03 ± 0.08 (4)**	**13.61 ± 6.41**	**39.37 ± 2.22**	**Present study**
VI	----	4.62± 0.50(109)	----	----	44.69 ± 5.53	(Harms, 1987)*
	----	13.7± 2.4 (6)	----	----	----	(Geary, 1991)
	314 ± 9.8 (7)	**2.23 ± 0.05 (4)**	**1.90 ± 0.04 (4)**	**14.57 ± 7.74**	**44.69 ± 5.53**	**Present study**
Cypris	----	4.92 ± 0.78 (70)	----	----	51.94 ± 4.54	(Harms, 1987)*
	----	15.8 ± 0.9 (3)	----	----	----	(Geary, 1991)
	530 ± 10.9 (6)	**3.34 ± 0.04 (2)**	**3.30 ± 0.05 (2)**	**1.06 ± 0.74**	**51.94 ± 4.54**	**Present study**
	666 ± 25.0 (10)	**7.46 ± 0.21 (2)**	**7.10 ± 0.20 (2)**	**0.05 ± 2.11**	**51.94 ± 4.54**	**Present study**

Semibalanus balanoides

Stage	**M** ± SD (n)	**Average Weight (µg)** **DW** ± SD(n)	**AFDW** ± SD (n)	**%Ash** ±SD	****%C** ± SD	**References**
I	----	0.63 ***	----	----	----	(Lucas, 1979)*
	----	1.02 ± 0.04 (4)	0.90 (4)	11.3	----	(Achituv *et al.,* 1980)*
II	----	0.78 ± 0.04 (3)	0.51 (3)	35.2	----	(Achituv *et al.,* 1980)*
	196 ± 8.4 (10)	**0.69 ± 0.02 (3)**	**0.56 ± 0.02 (3)**	**18.23 ± 2.29**	**43.31 ± 0.33**	**Present study**
III	**230 ± 16.7 (6)**	**1.11 ± 0.06 (2)**	**0.86 ± 0.05 (2)**	**22.37 ± 4.13**	**44.17 ± 5.24**	**Present study**
IV	----	7.45 ± 3.32 ***	----	----	----	(Lucas, 1979)*
	313 ± 10.4 (8)	**2.47 ± 0.15 (2)**	**2.01 ± 0.12 (2)**	**18.97 ± 1.02**	**40.40 ± 3.42**	**Present study**
V	**398 ± 35.8 (10)**	**5.56 ± 0.51 (4)**	**4.49 ± 0.42 (4)**	**19.22 ± 5.42**	**39.37 ± 2.22**	**Present study**
VI	**505 ± 38.2 (8)**	**10.41 ± 0.23 (4)**	**8.51 ± 0.18 (4)**	**18.31 ± 2.39**	**44.69 ± 5.53**	**Present study**
Cypris	----	37.70 ± 2.85 (3)	33.03 ± 2.50 (3)	12.4	----	(Holland & Walker, 1975)*
	----	32.60±0.85 ***	----	----	----	(Lucas, 1979)*
	----	32.15 ± 0.35 (2)	30.15 ± 0.35 (2)	6.21 ± 1.69	----	(Lucas *et al.,* 1979)*
	797 ± 29.2 (7)	**9.79 ± 0.37 (4)**	**9.21 ± 0.35 (4)**	**5.93 ± 2.47**	**51.94 ± 4.54**	**Present study**
	930 ± 49.2 (10)	**23.19 (1)**	**21.80 (1)**	**6.01**	**51.94 ± 4.54**	**Present study**

Where: DW = Dry Weight; AFDW = Ash Free Dry Weight; C = carbon; SD = ±1 Standard Deviation; n = number of organisms measured/ or replicates; ---- = not available (the nº of larvae utilized for each weight replica in this work can be seen on Table 20 – Chapter 4).
* Values obtained after averaging the averages for different temperatures/experiments.
** %C values used were obtained from Harms (1987)
**** n were not given
***** values obtained from Harms (1987)
**** values cited in Harms (1987)

Appendix X b. Mean weight values (μg) of the naupliar stages II to VI + cypris of *Balanus eburneus* available from the literature.

Balanus eburneus						
	Average Weight (μg)					
Stage	**M** ± SD (n)	**DW** (n)	**AFDW** ± SD (n)	**%Ash** ±SD	**%C** ± SD	**References**
I	----	0.27 (25)	----	----	----	(Jorgensen & Vernberg, 1982)
II	----	----	----	----	----	
III	----	----	----	----	----	
IV	----	0.68 (19)	----	----	----	(Jorgensen & Vernberg, 1982)
V	----	----	----	----	----	
VI	----	1.50 (9)	----	----	----	(Jorgensen & Vernberg, 1982)
Cypris	----	2.28 (16)	----	----	----	(Jorgensen & Vernberg, 1982)

Where: DW = Dry Weight; AFDW = Ash Free Dry Weight; C = carbon; SD = ±1 Standard Deviation; n = number of organisms measured/ or replicates; ---- = not available .

Appendix XI a – Total length, carapace length and width of the naupliar stages I to VI + cypris of *Elminius modestus* from the present study, with reported values from literature. (All measurements in μm)

Elminius modestus **(μm)**								
	Carapace							
Stage	Width ± SD	(n)	Length ± SD	(n)	Total Length ± SD	(n)	**Source**	**L/F**
I	125 ± 8	(25)	----		250 ± 14**	(25)	(Knight-Jones & Waugh, 1949)	L
	130	(10)	----		250	(10)	(Soares, 1958)	F
	105 ± 5**	****	----		220 ± 14**	****	(Barker, 1976)	L
	123 ± 7	**(70)**	----		**242 ± 22**	**(70)**	**Present study**	F
II	161 ± 6	(25)	----		395 ± 49**	(25)	(Knight-Jones & Waugh, 1949)	F
	140	(10)	----		370	(10)	(Soares, 1958)	F
	158 ± 3**	****	----		388 ± 9**	****	(Tighe-Ford *et al.,* 1970)	L
	155 ± 7**	****	----		370 ± 14**	****	(Barker, 1976)	L
	174 ± 3***	****	----		----		(Harms, 1986)	L
	----		----		369 ± 20	****	(Geary, 1991)	F
	157 ± 13	**(1033)**	----		**392 ± 33**	**(1033)**	**Present study**	F
III	190 ± 7	(41)	----		390 ± 57 **	(41)	(Knight-Jones & Waugh, 1949)	F
	200	(10)	----		410	(10)	(Soares, 1958)	F
	195 ± 4**	****	----		438 ± 8**	****	(Tighe-Ford *et al.,* 1970)	L
	190 ± 14**	****	----		430 ± 28**	****	(Barker, 1976)	L
	206 ± 8***	****	----		----		(Harms, 1986)	L
	----		----		414 ± 17	****	(Geary, 1991)	F
	187 ± 14	**(732)**	----		**421 ± 39**	**(732)**	**Present study**	F
IV	238 ± 8	(48)	320 ± 42**	(48)	445 ± 78**	(48)	(Knight-Jones & Waugh, 1949)	F
	220	(10)	----		410	(10)	(Soares, 1958)	F
	241 ± 6**	****	299 ± 7**	****	481 ± 8**	****	(Tighe-Ford *et al.,* 1970)	L
	230 ± 14**	****	285 ± 7**	****	----		(Barker, 1976)	L
	254 ± 12***	****	----		----		(Harms, 1986)	L
	----		314 ± 10	****	459 ± 17	****	(Geary, 1991)	F
	222 ± 18	**(538)**	**299 ± 22**	**(538)**	**451 ± 45**	**(533)**	**Present study**	F
V	292 ± 15	(48)	390 ± 71**	(48)	510 ± 85**	(48)	(Knight-Jones & Waugh, 1949)	F
	270	(10)	----		470	(10)	(Soares, 1958)	F
	304 ± 16**	****	369 ± 13**	****	558 ± 12**	****	(Tighe-Ford *et al.,* 1970)	L
	280 ± 14**	****	355 ± 21**	****	----		(Barker, 1976)	L
	312 ± 6***	****	----		----		(Harms, 1986)	L
	----		387 ± 18	****	538 ± 35	****	(Geary, 1991)	F
	271 ± 21	**(440)**	**359 ± 27**	**(441)**	**500 ± 53**	**(433)**	**Present study**	F
VI	359 ± 19	(41)	485 ± 92**	(41)	595 ± 163**	(41)	(Knight-Jones & Waugh, 1949)	F
	320	(10)	----		570	(10)	(Soares, 1958)	F
	382 ± 14**	****	382 ± 14**	****	648 ± 39**	****	(Tighe-Ford *et al.,* 1970)	L
	360 ± 14**	****	460 ± 28**	****	----		(Barker, 1976)	L
	380 ± 13***	****	----		----		(Harms, 1986)	L
	----		438 ± 21	****	579 ± 32	****	(Geary, 1991)	F
	328 ± 23	**(339)**	**436 ± 28**	**(341)**	**565 ± 54**	**(330)**	**Present study**	F
Cypris	----		----		550 ± 14**	****	(Knight-Jones & Waugh, 1949)	F
	----		----		570	(10)	(Soares, 1958)	F
	-----		----		566 ± 30	****	(Tighe-Ford *et al.,* 1970)	L
	----		----		545 ± 49**	****	(Barker, 1976)	L
	----		----		554 ± 28**	****	(Harms, 1986)	L
	----		----		536 ± 39***	****	(Geary, 1991)	F
	----		----		**553 ± 53**	**(122)**	**Present study**	F

Where: SD = ±1 Standard Deviation; n = number of organisms measured/ or replicates; ---- = Value/measure not available; L/F indicates measurements were made on laboratory cultured nauplii (L) or field plankton samples (F)
** Values obtained after averaging the range of sizes given.
*** Values obtained after averaging the averages for different temperatures/experiments.
**** n were not given

Appendix XI b – Total length, carapace length and width of the naupliar stages I to VI + cypris of *Balanus crenatus* from the present study, with reported values from literature. (All measurements in μm)

Balanus crenatus ***(μm)***									
Stage	Carapace Width ± SD	(n)	Carapace Length ± SD	(n)	Total Length ± SD	(n)	**Source**	**L/F**
I	133*	----	----		280	****	(Pyefinch, 1948; 1949)	-
	140	(10)	----		290	(10)	(Soares, 1958)	F
	142*	----	----		271*	----	(Lang, 1980)	-
	125*	----	----		250*	----	(Branscomb & Vedder, 1982)	L
	144 ± 9	**(63)**	----		**274 ± 21**	**(63)**	**Present study**	F
II	183*	----	----		440	****	(Pyefinch, 1948; 1949)	-
	180	(10)	----		440	(10)	(Soares, 1958)	F
	171*	----	----		485*	----	(Lang, 1980)	-
	150*	----	----		425*	----	(Branscomb & Vedder, 1982)	L
	----		----		440	****	(Geary, 1991)	F
	172 ± 12	**(609)**	----		**433 ± 28**	**(609)**	**Present study**	F
III	----		----		570	****	(Pyefinch, 1948; 1949)	-
	200	(10)	----		530	(10)	(Soares, 1958)	F
	214*	----	----		542*	----	(Lang, 1980)	-
	250*	----	----		625*	----	(Branscomb & Vedder, 1982)	L
	----		----		560	****	(Geary, 1991)	F
	203 ± 11	**(342)**	----		**502 ± 25**	**(339)**	**Present study**	F
IV	350*	----	480	****	730	****	(Pyefinch, 1948; 1949)	-
	270	(10)	----		600	(10)	(Soares, 1958)	F
	242*	----	428*	----	571*	----	(Lang, 1980)	-
	350*	----	550*	----	----		(Branscomb & Vedder, 1982)	L
	----		480	****	700	****	(Geary, 1991)	F
	247 ± 13	**(254)**	**404 ± 22**	**(254)**	**575 ± 28**	**(249)**	**Present study**	F
V	----		590	****	840	****	(Pyefinch, 1948; 1949)	-
	360	(10)	----		760	(10)	(Soares, 1958)	F
	342*	----	514*	----	714*	----	(Lang, 1980)	-
	375*	----	600*	----	----		(Branscomb & Vedder, 1982)	L
	----		500	****	730	****	(Geary, 1991)	F
	311 ± 19	**(199)**	**502 ± 30**	**(199)**	**679 ± 39**	**(198)**	**Present study**	F
VI	433*	----	630	****	910	****	(Pyefinch, 1948; 1949)	-
	460	(10)	----		900	(10)	(Soares, 1958)	F
	450*	----	700*	----	----		(Branscomb & Vedder, 1982)	L
	----		580	****	810	****	(Geary, 1991)	F
	397 ± 29	**(165)**	**635 ± 47**	**(165)**	**814 ± 54**	**(161)**	**Present study**	F
Cypris	----		----		711*	----	(Pyefinch, 1948)	-
	----		----		875 ± 64	(10)	(Soares, 1958)	F
	----		----		**779 ± 78**	**(74)**	**Present study**	F

Where: SD = ±1 Standard Deviation; n = number of organisms measured/ or replicates; ---- = Value/measure not available; L/F indicates the measurements were made on laboratory cultured nauplii (L) or field plankton samples (F); - = not indicated.
* Values obtained from drawings.
**** n were not given

Appendix XI c – Total length, carapace length and width of the naupliar stages I to VI + cypris of *Semibalanus balanoides*, from the present study, with reported values from literature. (All measurements in μm)

Semibalanus balanoides ***(μm)***								
Stage	Carapace Width ± SD	(n)	Carapace Length ± SD	(n)	Total Length ± SD	(n)	**Source**	**L/F**
I	220	****	----		350	****	(Bassindale, 1936)	L
	130*	----	----		340*	----	(Pyefinch, 1948)	L
	170	(10)	----		400	(10)	(Soares, 1958)	L
	189 ± 10	****	----		333 ± 15	****	(Crisp, 1962)	L
	179 ± 17	(22)	----		319 ± 28	(22)	**Present study**	F
II	220	****	----		510	****	(Bassindale, 1936)	L
	260*	----	----		540*	----	(Pyefinch, 1948)	L
	220	(10)	----		460	(10)	(Soares, 1958)	F
	227 ± 22	****	----		526 ± 50	****	(Crisp, 1962)	F
	302 ± 12	****	----		702 ± 17	****	(Crisp, 1962)	F
	257*	----	----		585*	----	(Lang, 1980)	-
	----		----		550	****	(Geary, 1991)	F
	203 ± 11	(286)			475 ± 28	(286)	**Present study**	F
III	270	****	----		620	****	(Bassindale, 1936)	L
	307*	----	----		630*	----	(Pyefinch, 1948)	L
	270	(10)	----		600	(10)	(Soares, 1958)	F
	290 ± 22	****	----		625 ± 22	****	(Crisp, 1962)	F
	355 ± 9	****	----		849 ± 60	****	(Crisp, 1962)	F
	285*	----	----		714*	----	(Lang, 1980)	-
	----		----		630	****	(Geary, 1991)	F
	238 ± 13	(157)			562 ± 30	(156)	**Present study**	F
IV	290	****	410	****	690	****	(Bassindale, 1936)	L
	384*	----	----		760*	----	(Pyefinch, 1948)	L
	380	(10)	----		750	(10)	(Soares, 1958)	F
	330 ± 30	****	453 ± 34	****	725 ± 35	****	(Crisp, 1962)	F
	483 ± 14	****	635 ± 22	****	1005 ± 58	****	(Crisp, 1962)	F
	371*	----	642*	----	885*	----	(Lang, 1980)	-
	----		460	****	650	****	(Geary, 1991)	F
	298 ± 15	(89)	446 ± 22	(89)	662 ± 38	(84)	**Present study**	F
V	420	****	530	****	810	****	(Bassindale, 1936)	L
	480*	----	----		920*	----	(Pyefinch, 1948)	L
	450	(10)	----		900	(10)	(Soares, 1958)	F
	500 ± 57	****	635 ± 41	****	944 ± 83	****	(Crisp, 1962)	F
	610 ± 19	****	780 ± 25	****	1170 ± 58	****	(Crisp, 1962)	F
	571*	----	814*	----	----		(Lang, 1980)	-
	385 ± 22	(96)	556 ± 31	(96)	795 ± 40	(79)	**Present study**	F
VI	620	****	790	****	1150	****	(Bassindale, 1936)	F
	596*	----	----		1050*	----	(Pyefinch, 1948)	L
	600	(10)	----		1110	(10)	(Soares, 1958)	F
	595 ± 27	****	786 ± 52	****	1145 ± 102	****	(Crisp, 1962)	F
	888 ± 33	****	1093 ± 25	****	1559 ± 36	****	(Crisp, 1962)	F
	----		700	****	1020	****	(Geary, 1991)	F
	503 ± 33	(78)	725 ± 51	(79)	990 ± 66	(76)	**Present study**	F
Cypris	----		----		940	****	(Bassindale, 1936)	F
	----		----		1000 ± 141**	****	(Pyefinch, 1948)	L
	----		----		945 ± 92**	(10)	(Soares, 1958)	F
	----		----		1025 ± 26	****	(Crisp, 1962)	L
	----		----		1332 ± 53	****	(Crisp, 1962)	L
	----		----		835 ± 81	(42)	**Present study**	F

Where: SD = ±1 Standard Deviation; n = number of organisms measured/ or replicates; ---- = Value/measure not available; L/F indicates the measurements were made on laboratory cultured nauplii (L) or field plankton samples (F)
* Values obtained from drawings.
** Values obtained after averaging the range of sizes given.
**** n were not given

Appendix XI d – Total length, carapace length and width of the naupliar stages I to VI + cypris of *Balanus improvisus,* from the present study, with reported values from literature. (All measurements in μm)

Balanus improvisus ***(μm)***							
Stage	Carapace Width ± SD	(n)	Carapace Length ± SD	(n)	Total Length ± SD	(n)	Source	L/F
I	130**	****	----		205 ± 7**	****	(Knight-Jones & Waugh, 1949)	F
	111 ± 8	(10)	----		195 ± 20	(10)	(Jones & Crisp, 1954)	F
	118 ± 17	(10)	----		228 ± 13	(10)	(Lee *et al.,* 1998)	L
	139 ± 22	(16)	----		285 ± 59	(16)	**Present study**	F
II	155 ± 7**	****	----		345 ± 21**	****	(Knight-Jones & Waugh, 1949)	F
	147 ± 9	(10)	----		323 ± 17	(10)	(Jones & Crisp, 1954)	F
	150	(10)	----		310	(10)	(Soares, 1958)	F
	157*	----	----		342*	----	(Lang, 1980)	-
	154 ± 19	(10)	----		302 ± 13	(10)	(Lee *et al.,* 1998)	L
	148 ± 12	(282)	----		316 ± 26	(281)	**Present study**	F
III	183 ± 7	(3)	----		367 ± 8	(3)	(Jones & Crisp, 1954)	F
	200	(10)	----		390	(10)	(Soares, 1958)	F
	171*	----	----		385*	----	(Lang, 1980)	-
	187 ± 15	(10)	----		375 ± 11	(10)	(Lee *et al.,* 1998)	L
	181 ± 12	(188)	----		356 ± 27	(187)	**Present study**	F
IV	230 ± 20	(10)	267 ± 21	(10)	402 ± 15	(10)	(Jones & Crisp, 1954)	F
	230	(10)	----		400	(10)	(Soares, 1958)	F
	242*	----	343*	----	471*	----	(Lang, 1980)	-
	270 ± 21	(10)	283 ± 16	(10)	423 ± 23	(10)	(Lee *et al.,* 1998)	L
	227 ± 20	(144)	311 ± 27	(145)	412 ± 37	(137)	**Present study**	F
V	281 ± 28	(12)	354 ± 18	(12)	496 ± 23	(12)	(Jones & Crisp, 1954)	F
	290	(10)	----		480	(10)	(Soares, 1958)	F
	314 *	----	428*	----	571*	----	(Lang, 1980)	-
	282 ± 13	(10)	342 ± 19	(10)	492 ± 19	(10)	(Lee *et al.,* 1998)	L
	289 ± 27	(77)	392 ± 33	(77)	492 ± 50	(78)	**Present study**	F
VI	370 ± 14	(8)	465 ± 16	(8)	624 ± 30	(8)	(Jones & Crisp, 1954)	F
	390	(10)	----		620	(10)	(Soares, 1958)	F
	442 *	----	585*	----	----		(Lang, 1980)	-
	337 ± 18	(10)	461 ± 13	(10)	624 ± 15	(10)	(Lee *et al.,* 1998)	L
	369 ± 27	(71)	502 ± 29	(71)	621 ± 48	(65)	**Present study**	F
Cypris	----		----		523 ± 12	(8)	(Jones & Crisp, 1954)	F
	----		----		523 ± 21	(10)	(Lee *et al.,* 1998)	L
	----		----		523 ± 20	(6)	**Present study**	F

Where: SD = ±1 Standard Deviation; n = number of organisms measured/ or replicates; ---- = Value/measure not available; L/F indicates the measurements were made on laboratory cultured nauplii (L) or field plankton samples (F)
* Values obtained from drawings.
** Values obtained after averaging the range of sizes given.
**** n were not given

Appendix XI e – Total length, carapace length and width of the naupliar stages I to VI + cypris of *Verruca stroemia,* from the present study, with the reported values from literature. (All measurements in μm)

Verruca stroemia ***(μm)***							
Stage	Carapace Width ± SD	(n)	Carapace Length ± SD	(n)	Total Length ± SD	(n)	**Source**	**L/F**
I	120	****	----		270	****	(Bassindale, 1936)	L
	117*	----	----		223*	----	(Pyefinch, 1948)	-
	140 ± 28	(2)	----		280	(2)	**Present study**	F
II	190	****	----		440	****	(Bassindale, 1936)	L
	202*	----	----		400	****	(Pyefinch, 1948)	-
	170	****	----		410	****	(Soares, 1958)	F
	180 ± 9	(170)	----		412 ± 36	(169)	**Present study**	F
III	250	****	----		500	****	(Bassindale, 1936)	L
	----		----		470	****	(Pyefinch, 1948)	-
	250	****	----		490	****	(Soares, 1958)	F
	212 ± 13	(116)	----		456 ± 34	(114)	**Present study**	F
IV	280	****	340	****	580	****	(Bassindale, 1936)	L
	----		310	****	540	****	(Pyefinch, 1948)	-
	310	****	----		560	****	(Soares, 1958)	F
	256 ± 21	(37)	297 ± 26	(37)	500 ± 37	(29)	**Present study**	F
V	300	****	370	****	630	****	(Bassindale, 1936)	L
	----		390	****	620	****	(Pyefinch, 1948)	-
	340	****	----		600	****	(Soares, 1958)	F
	311 ± 18	(15)	371 ± 27	(15)	590 ± 44	(12)	**Present study**	F
VI	370	****	420	****	690	****	(Bassindale, 1936)	L
	----		470	****	730	****	(Pyefinch, 1948)	-
	390	****	----		700	****	(Soares, 1958)	F
	353 ± 31	(3)	427 ± 23	(3)	653 ± 31	(3)	**Present study**	F
Cypris	----		----		530	****	(Bassindale, 1936)	L
	----		----		480*	----	(Pyefinch, 1948)	-
	----		----		480	(1)	**Present study**	F

Where: SD = ±1 Standard Deviation; n = number of organisms measured/ or replicates; ---- = Value/measure not available; L/F indicates the measurements were made on laboratory cultured nauplii (L) or field plankton samples (F)
* Values obtained from drawings.
**** n were not given