Epipelagic zooplankton community structure: Spatial patterns in abundance, species composition and size structure.

Cook, Kathryn B

Cook, Kathryn B (2001) *Epipelagic zooplankton community structure: Spatial patterns in abundance, species composition and size structure..* thesis, Swansea University.
http://cronfa.swan.ac.uk/Record/cronfa42911

Epipelagic Zooplankton Community Structure: spatial patterns in abundance, species composition and size structure

By

Kathryn B. Cook (M.Sc., B.Sc.)

A thesis submitted to the School of Biological Sciences
for the degree of Doctor of Philosophy at the
University of Wales, Swansea,
August 2001.

DECLARATION

This work has not previously been accepted in substance for any degree and is not concurrently submitted in candidature for any degree.

Signed.. .... (candidate)

Date........2/11/01...................................

STATEMENT 1

This thesis is the result of my own investigations, except where otherwise stated. A bibliography is appended.

Signed.. .... (candidate)

Date........2/11/01...................................

STATEMENT 2

I hereby give consent for my thesis, if accepted, to be available for photocopying and for inter-library loan, and for the title and summary to be made available to outside organisations.

Signed.. .... (candidate)

Date........2/11/01...................................

CONTENTS

ACKNOWLEDGEMENTS

Thanks must first go to NERC for funding this research, and Graeme Hays for supervising the project.

I am most grateful for the opportunities to join the U-Tow trial cruises in the North Sea and Irish Sea, the BASIC cruise in the Baltic Sea, and the SEAMAR cruise in the North East Atlantic. For those, thanks to Tony Walne, Mark Rawlinson, Dave Mills, Ivan Heaney, Karl Embleton, John Gallon, Lucas Stal, Karl von Bröckel and Steve Coombs.

I am indebted to Keith Naylor and all 'volunteers' for all their hard work on the RV 'Nicola', and the crews of the RRS 'Cirolana', RV 'Lough Foyle', RV 'Valdivia' and RRS 'Challenger' for all their invaluable help. Thanks also have to go to Andrea Evans and Alun Jones for support during the Baltic Sea cruise; Colin Barrett (for technical support), Joh Sidey, Nick Halliday, Dave Conway and everyone else who made the North Atlantic cruise such an enjoyable experience.

I also have to thank all the people in Swansea who kept me going: John, Andy, Corinne, Hazel, Nick, Bob and so many others. The most thanks have to go to all my family. My apologies to anyone I have forgotten.

ABSTRACT

The U-Tow, a new instrument designed to sample zooplankton over large distances, was used to study factors affecting zooplankton community structure over large spatial scales. Zooplankton were collected from Swansea Bay, the North Sea, Irish Sea, and NE Atlantic.

The performance of the U-Tow was compared to that of the traditional WP2 net. The U-Tow significantly underestimated species abundance, but gave a good representation of species composition and size structure. It is recommended that the U-Tow be used as a tool to identify areas of change in plankton communities.

Size-fractionated biomass and abundance, as a measure of zooplankton size structure, were investigated using field collected data, theoretical models, and published data. The results show that the two methods often lead to different conclusions, and that size-fractionated abundance is generally more sensitive.

Cladoceran and copepod biomass were positively correlated with salinity in the Baltic, and there were changes in species composition with the salinity gradient. There were no changes in zooplankton size or diversity. NE Atlantic zooplankton were distinguished into communities from the Porcupine Bank, deep water, Celtic Shelf, Bay of Biscay and English Channel. *Oithona* spp. and *Para/Pseudocalanus* spp. were the dominant taxa. The relative biomass of *Calanus* was small but became more important over the continental shelf. Irish Sea zooplankton were distinguished into communities from the Welsh coast, central mixed region, summer stratified region, and Irish coast. A month later, the patterns were similar although Welsh coast zooplankton were not separate from central mixed region zooplankton.

All zooplankton samples were investigated to identify any evidence of 'top-down' control on zooplankton size structure. There were significant decreases in zooplankton size with an increase in a number of fish predation indices. The amount of variation in zooplankton size explained was relatively small indicating that other factors are involved, although there was no relationship with temperature.

SUMMARY

This thesis takes the form of seven discrete chapters that are written in the style of manuscripts, and so appear as independent units. It is hoped that individual chapters will form the basis of manuscripts that will be published. The result of this style is that there is, inevitably, some repetition of literature and methodology between chapters.

One of the fundamental aims of biological oceanography is to assess the abundance, species composition and size distribution of mesozooplankton (Greene *et al.*, 1998a; Mitson *et al.*, 1996; UNESCO, 1968). Traditionally, mesozooplankton have been sampled with simple ring nets that sample over very restricted spatial scales. This limits our ability to understand broad spatial patterns in the zooplankton community. Consequently, there is an urgent need for techniques that allow mesozooplankton to be sampled over extended spatial scales (10s or even 100s km) (Marine Zooplankton Colloquium, 1989).

To date the only system capable of such sampling is the Continuous Plankton Recorder (CPR), which is unable to sample physical parameters and is confined to sampling at one depth (Hays *et al.*, 1998). Due to these limitations in the performance of the CPR, a new vehicle, the U-Tow, has been designed in recent years (Hays *et al.*, 1998). The original version of the U-Tow was designed and built by Valeport Limited (Dartmouth, Devon) in collaboration with the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) in 1994. It is fitted with a Plankton Sampling Mechanism (PSM) which is based on the mechanisms used in the CPR and Longhurst Hardy Plankton Recorder (LHPR) (Hays *et al.*, 1998), and a Conductivity Temperature Depth sensor

(CTD). It can also be configured to carry additional sensors, and fitted with a servo control module, to actively control depth, so that an undulating depth profile can be achieved. This design has since been modified by W.S. Ocean Systems Limited (Alton, Hants.) to have improved undulating capabilities and an increased potential payload (Mills *et al.*, 1998).

The aim of this thesis is to investigate some of the factors affecting zooplankton community structure over large spatial scales using the U-Tow. Sampling took place over a range of marine systems and, therefore, individual chapters are concerned with factors within these systems. Chapter 1 is a literature review of the types of factors that can affect zooplankton abundance, species composition on horizontal and vertical scales, and body size within species and of the community as a whole.

The performance of any new piece of equipment must be investigated before use so that results can be reliably compared with other studies, and so that temporal and spatial variation in the plankton can be distinguished from variation in sampler performances (Aron *et al.*, 1965). Therefore, chapter 2 is a comparison between the sampling performance of the U-Tow and the traditionally used WP2 net. The results show that the U-Tow significantly underestimates species abundance, but gives a very good representation of species composition and community size structure. It is, therefore, recommended that the U-Tow, in its current configuration, be used as a tool to identify areas of change in plankton communities.

One of the fundamental aims of this thesis was to incorporate a chapter investigating evidence of 'top-down' control on zooplankton community size structure. Therefore, it was important to investigate whether the method chosen to represent the size structure would affect the conclusions reached. Chapter 3 compares the use of size-fractionated biomass and abundance using field collected data, theoretical models of different sampling scenarios, and published data. The results of this study show that the two methods often lead to different conclusions and that, in general, the use of size-fractionated abundance will yield a more sensitive and less variable measure.

Much of the sampling for this thesis comes from U-Tow trial cruises in the North Sea and Irish Sea, and local sampling in Swansea Bay. However, opportunities also arose to join the BASIC cruise in the Baltic Sea and the SEAMAR cruise in the North East Atlantic and Bay of Biscay. The Baltic Sea presented the ideal situation for studying the effects of a known salinity gradient on the zooplankton, and chapter 4 deals with this subject. Previous studies have noted changes in mesozooplankton biomass associated with salinity (Flinkman *et al.*, 1998; Viitasalo *et al.*, 1995a), a decrease in the biomass ratio of copepods to cladocerans with salinity (Vuorinen *et al.*, 1998), and changes in species composition associated with changes in salinity (Laprise and Dodson, 1994; Lopes, 1994; Soetaert and Van Rijswijk, 1993). The only changes in zooplankton size seen in this study seem to be associated with DVM behaviour of the animals, and not the salinity gradient in the Baltic Sea. Total cladoceran and copepod biomass were positively correlated with salinity in the range sampled. By combining this result with previous studies in a lower salinity range (Viitasalo *et al.*, 1995a), it appears that salinity and zooplankton biomass are not related in a simple monotonic manner. The decrease in biomass ratio of copepods to cladocerans with salinity was found in samples with salinity less than 7.06‰ due to the decrease in neritic copepod taxa. There were no changes in diversity associated with salinity, however significant changes in the patterns of species composition were found.

Chapter 5 deals with the spatial patterns and importance of different copepod taxa in the North East Atlantic. *Calanus spp.* are often cited as being the most abundant, and therefore most important, copepod in the North Sea and North Atlantic (Fiksen and Carlotti, 1998; Gislason and Assthorsson, 1995; Hansen *et al.*, 2000; Irigoien *et al.*, 1998; Meise and O'Reilly, 1996; Morales *et al.*, 1993; Parsons and Lalli, 1988; Planque and Batten, 2000; Planque and Fromentin, 1996; Steele, 1974; Tande, 1982; Tande and Miller, 2000; Williams, 1985). However, in this study the relative biomass of *Calanus* was small overall but became more important over the continental shelf, especially at the edge of the shelf. The most important taxa, both by number and by biomass, were generally *Oithona* spp. and *Para/Pseudocalanus* spp. Zooplankton communities were distinguished into those from the Porcupine Bank, NE Atlantic deep water, Celtic Shelf, Bay of Biscay and English Channel.

Chapter 6 looks at spatial patterns in Irish Sea zooplankton in relation to a tidal mixing front that forms seasonally (Allen *et al.*, 1998; Gowen *et al.*, 1997; Hill *et al.*, 1997; Horsburgh *et al.*, 2000). In June, zooplankton communities were distinguished into those from the Welsh coast, the central mixed region, the summer stratified region, and the Irish Sea coast. In July, the patterns were similar although the groups tended to stretch further east, and the Welsh coast zooplankton were not separate from those in the central mixed region. No obvious size differences associated with the community changes were found.

The final chapter incorporates the data from all areas to investigate evidence of 'top-down' control on zooplankton community size over much wider scales. In 1965, Brooks and Dodson (1965) put forward the size-efficiency hypothesis, from work in freshwater systems, which deals with the effects of size-selective predation. However, there has been relatively little work done in marine systems. This study found significant decreases in zooplankton size as the relative density of planktivorous fish biomass increased. The amount of variation in zooplankton size explained was relatively small indicating that other factors are involved. It is likely that, in such large and complex ecosystems as these, environmental factors play a large role although no significant relationship between zooplankton size and temperature was found.

CHAPTER 1

Zooplankton Community Structure: spatial patterns in abundance, species composition and size structure

Introduction

The marine zooplankton are one of the most diverse assemblages of animals known to man. Although the holoplankton only constitutes about 1% of all marine animal species, it is estimated that about 80% of all marine invertebrates have planktonic larval stages (Hällfors *et al.*, 1981; Wyatt, 1976). In addition, most marine invertebrates depend on zooplankton as a source of food at some stage. Therefore, zooplankton play a vital role in marine ecosystems (Savidge and Williams, 2001) and changes in the zooplankton biomass and community structure can have widespread effects on the marine ecosystem (Conversi and Hameed, 1998; Skjoldal *et al.*, 2000).

One of the most vital roles played by zooplankton in the functioning of marine ecosystems is the link they form in pelagic food webs, between producers and secondary consumers (Gislason and Assthorsson, 1995; Kane, 1993; Steele, 1974; Williams and Conway, 1984). The zooplankton, therefore, determine the amount of primary production that is converted to a form accessible to top predators (Ikeda, 1985; Lenz, 2000; Ojaveer *et al.*, 1998). This in turn can have major implications in determining the strength and distribution of fish stocks (Cushing, 1975; Rothschild, 1998). The amount of zooplankton available as food to fish larvae, especially in the first few weeks of their life, is believed to determine survival of larvae and hence the strength of the fish year class. Zooplankton are also important in regenerating nutrients through excretion (Ikeda, 1985; Zhang *et al.*, 1995), and therefore contribute towards determining the rate of production by autotrophic and heterotrophic plankton (Banse, 1995), and in the transportation of nutrients from the surface to the deeper layers of the sea through Diel

Vertical Migration (DVM) (Al-Mutairi and Landry, 2001; Dam *et al.*, 1993; Hays *et al.*, 1997a; Hernández-León *et al.*, 2001; Madin *et al.*, 2001; Morales *et al.*, 1993; Steinberg *et al.*, 2001; Zhang and Dam, 1997).

Copepod assemblages are generally the most abundant component of mesozooplankton (Morales *et al.*, 1993) and, therefore, dominate the biomass of pelagic grazers having important impacts on the phytoplankton (Morales *et al.*, 1993; Tiselius, 1988). In fact, several studies have shown that, at certain times of the year, the grazing impact of the copepod community can match or exceed daily primary production (Hansen *et al.*, 2000; Weeks *et al.*, 1993).

The size structure of zooplankton communities is also an important parameter since physiological rates of individual organisms are consistently related to body size (Blackburn *et al.*, 1993; Cyr and Pace, 1993; Dickie *et al.*, 1987) and it has been shown that, across a wide variety of ecological communities, values for rates of production, respiration, excretion and specific production show constant patterns of change with individual body mass (Cyr and Pace, 1992; Cyr and Pace, 1993; Dickie *et al.*, 1987; Reid *et al.*, 2000; Rodhouse *et al.*, 1994). Therefore, organisms of different sizes will play different roles in biogeochemical cycling and trophic interactions. For example, small zooplankters graze more per unit biomass than larger organisms (Dam *et al.*, 1993; Peters and Downing, 1984). Furthermore, the magnitude of nutrient regeneration and transport will be related to the size structure, taxonomic composition and metabolic rates of the zooplankton community (Le Borgne and Rodier, 1997; Pace, 1984). This suggests that ecological rates should also be related to the size structure of organisms in communities. Indeed, it has recently become common for ecosystem ecologists, especially in aquatic systems, to determine energy flow within communities from the broad size distributions of organisms, often with no reference to taxonomy or trophic level (Ahrens and Peters, 1991; Alvarez-Cobelas and Rojo, 2000; Boudreau and Dickie, 1992; Cyr and Pace, 1993; Cyr and Peters, 1996; Dickie *et al.*, 1987; Echevarría *et al.*, 1990; Gin *et al.*, 1999; Heath, 1995; Kerr, 1974; Kobayashi *et al.*, 1998; Pace, 1984; Platt and Denman, 1977; Platt and Denman, 1978; Rodhouse *et al.*, 1994; Rodriguez *et al.*, 1990; Rodriguez and Mullin, 1986; Rolff, 2000; Sheldon *et al.*, 1977; Sprules *et al.*, 1991; Sprules and Goyke, 1994; Sprules and Munawar, 1986; Sprules and Stockwell, 1995; Thiebaux, 1993; Tittel *et al.*, 1998; Witek and Krajewska-Soltys, 1989; Zhou and Huntley, 1997).

To be able to interpret changes in the zooplankton community and understand oceanic fluxes, it is essential to understand the mechanisms affecting these changes and to determine the type of control exerted over different temporal and spatial scales (Dufour and Torréton, 1996). Major factors driving variation in the zooplankton community will be changes in the physical environment, such as temperature and salinity (Hernroth, 1981), and oceanographic processes that influence phytoplankton production by controlling light and nutrients (Richardson and Pedersen, 1998). The relative importance of abiotic and biotic factors in regulating the zooplankton communities has been widely debated (Carpenter *et al.*, 1987; McQueen *et al.*, 1986). 'Bottom-up' models suggest that nutrient availability determines the biomass and productivity of an ecosystem, whereas 'top-down' or 'cascading trophic interaction' models emphasise the effect of predators on lower trophic levels (Carpenter *et al.*, 1987; Currie *et al.*, 1999). It is likely that, in nature, both 'bottom-up' and 'top-down' controls will operate in varying magnitudes in different temporal and spatial scales (McQueen *et al.*, 1986; Reid *et al.*, 2000).

Zooplankton abundance

One of the most obvious factors affecting the abundance of individual species seen when sampling zooplankton is the seasonal cycle of the species. Most herbivorous zooplankters have highly pronounced seasonal cycles of high and low abundance, which are closely related to the seasonal cycle of phytoplankton (Durbin *et al.*, 1995; Fransz *et al.*, 1991; Gowen *et al.*, 1998a; Irigoien, 1999; Lignell *et al.*, 1993; Madin *et al.*, 2001; Planque and Fromentin, 1996; Rodríguez *et al.*, 2000; Steinberg *et al.*, 2001; Villate, 1991) and water temperature (Durbin *et al.*, 2000; Lopes, 1994), but can differ even in closely related species. For example, in the North East Atlantic *Calanus finmarchicus* shows a single peak in abundance from April to June and plateaus until September, whereas *Calanus helgolandicus* has a peak from May to June and a second, larger, peak from September to October (Planque and Fromentin, 1996).

The classic seasonal cycle for phytoplankton in temperate seas involves a major bloom in spring and a lesser bloom in autumn (Le Fèvre, 1986). As the amount of light penetrating the water column decreases with depth, there is a critical depth at which photosynthesis can no longer exceed respiration and, therefore, phytoplankton growth can not take place. In winter, there is low light, resulting in a shallow critical depth, and high wind turbulence, which results in a deep mixed layer. During this period, there is little production so standing stocks are low and nutrient levels are high. With spring conditions, the light levels increase, which increases the critical depth, and wind mixing decreases, which stabilises the water column. At this time, the phytoplankton bloom is triggered, and lasts as long as the nutrients are not exhausted or grazing pressure is not too high. The autumn bloom is usually caused by the decrease in grazing pressure, due to increased predation on the herbivorous zooplankton, and an increase in vertical mixing, which introduces new sources of nutrients. In general, the zooplankton blooms follow phytoplankton blooms with a time lag, but the timing can vary spatially (Gaudy and Champalbert, 1998; Gislason and Assthorsson, 1995; Meise and O'Reilly, 1996; Planque and Batten, 2000; Planque *et al.*, 1997). For example, Meise and O'Reilly (1996) found that the magnitude and timing of the *Calanus finmarchicus* seasonal cycle varied within subareas of the Gulf of Maine-Georges Bank region.

The seasonal cycle is particularly noticeable in meroplanktonic species which are absent from the zooplankton during much of the year, but can appear in extremely high levels of abundance during the reproductive season of the adult animals. This reproductive season is often timed to coincide with phytoplankton blooms to facilitate higher recruitment (Hällfors *et al.*, 1981; Heath, 1995), termed the 'match/mismatch' hypothesis (Cushing, 1995a).

The second factor affecting the abundance of zooplankton species is the availability of food, and therefore productivity of the surrounding environment (Currie *et al.*, 1999; Hansson *et al.*, 1990; Schneider *et al.*, 1994; Vanni, 1987). For example, comparative studies have noted that primary productivity is three times higher in the Gulf of Aden than the Red Sea, and the difference in zooplankton biomass is of the same magnitude (Schneider *et al.*, 1994). In high food environments, the zooplankton species have increased growth and reproductive rates, thereby increasing the abundance relative to less productive areas (Currie *et al.*, 1999; Kiørboe *et al.*, 1985; Koski, 1999; Vanni, 1987). For example, Beckmann *et al.* (1987) found higher phytoplankton biomass, and an associated higher zooplankton biomass, in a cyclonic cold-core eddy compared to surrounding water in the eastern North Atlantic.

Although seasonal cycles and food availability obviously affect zooplankton abundance, the underlying causes of these effects are changes in water properties, such as nutrients, turbidity, temperature and salinity. For example, the different seasonal cycles noted previously for *Calanus finmarchicus* and *C. helgolandicus* are attributed to their different temperature tolerances. *C. finmarchicus* prefers colder water and, therefore, has its major peak in spring when phytoplankton abundance is high but temperatures low. However, *C. helgolandicus* has its major peak during the autumn phytoplankton peak when temperatures are higher (Planque and Fromentin, 1996). Similarly, Halsband and Hirche (2001) concluded that copepod egg production was controlled by temperature, by its effect on body size, in the North Sea.

Within an area, changes in the water chemistry can cause large changes in productivity and therefore zooplankton abundance (Gowen *et al.*, 1995; Le Borgne and Rodier, 1997; Scrope-Howe and Jones, 1985). Roman *et al.* (1995) noted a drop in sea surface temperature, an increase in phytoplankton, and a lagged five-fold increase in zooplankton biomass associated with the passage of a tropical instability wave through their study area at the equator. Frontal systems, where different bodies of water meet, can cause an area with sharp horizontal gradients in water properties (e.g. temperature, salinity and turbidity). These areas often support enhanced production, and therefore high phytoplankton and zooplankton stocks (Clark *et al.*, 2001a; Coyle *et al.*, 1998; Fernández *et al.*, 1993; Fransz and Gonzalez, 1997; Gaudy and Champalbert, 1998; Hays *et al.*, 2001; Le Fèvre, 1986; Marañón and Fernández, 1995; Munk, 1997; Pakhomov *et* *al.*, 2000; Scrope-Howe and Jones, 1985). For example, Pakhomov *et al.* (2000), in a study of the Southern Ocean, found highest zooplankton densities at the Antarctic Polar Front and the Subtropical Convergence.

Areas of upwelling, where nutrient rich deep waters are drawn to the surface, are also associated with high levels of phytoplankton and zooplankton abundance (Botas *et al.*, 1990; Dessier and Donguy, 1985; Paffenhöfer, 1980; Smith *et al.*, 1998; van Couwelaar, 1997; Verheye and Richardson, 1998). Paffenhöfer (1980) describes the intrusion of deep nutrient rich water into Onslow Bay, causing increased phytoplankton growth and zooplankton biomass.

In coastal areas, there is often freshwater influence from rivers and run-off from the land. This can cause a decrease in salinity (Fransz *et al.*, 1991), but also an increase in nutrient input (Allen, 1997; Lenhart *et al.*, 1997; Pätsch and Radach, 1997; Schulz *et al.*, 1991; Skogen and Moll, 2000; Smith Jr. and Demaster, 1996), and these areas can support high levels of zooplankton abundance (Dickey-Collas *et al.*, 1996a; Gaudy and Champalbert, 1998; Gislason and Assthorsson, 1995; Huntley *et al.*, 1995; Roman *et al.*, 2000; Stelfox *et al.*, 1999). However, areas affected directly by river plumes can also have high turbidity, which can decrease phytoplankton growth by decreasing light penetration into the water column (Smith Jr. and Demaster, 1996; Soetaert and Van Rijswijk, 1993; Van den Berg *et al.*, 1996). Smith Jr. and Demaster (1996), whilst investigating the Amazon River plume, found maximum chlorophyll concentrations in the transition zone between turbid, high nutrient riverine waters and clear, low nutrient saline water. They concluded that the waters influenced by the Amazon plume were light limited inshore and nutrient limited offshore. de Lafontaine (1994) found that biomass patterns were not related to water mass characteristics and freshwater runoff in the southern Gulf of St. Lawrence, but noted that there may have been changes in species composition. This was confirmed by Laprise and Dodson (1994), who found that zooplankton population centers were situated in the most abiotically stable regions.

The hydrodynamics of an area also play a role in determining local zooplankton abundance, e.g. eddies can retain animals in an area (Beckmann *et al.*, 1987; Hill *et al.*, 1997; Huntley *et al.*, 1995; Mutlu, 2001; Pinca and Dallot, 1995). Pinca and Dallot (1995) found increased abundance of certain species in an anticyclonic eddy in the Ligurian sea, whilst Hill *et al.* (1997) describe the retention of *Nephrops norvegicus* larvae by a cyclonic gyre in the Irish Sea. Similarly, White *et al.* (1998) noted a dense dome of cold and comparatively nutrient rich water over the Porcupine Bank during spring and summer.

Recent studies have begun to correlate plankton and oceanographical variability with indices of climate variability (Aebischer *et al.*, 1990; Beaugrand *et al.*, 2000; Conversi and Hameed, 1998; Frid and Huliselan, 1996; Fromentin and Planque, 1996; George and Harris, 1985; Hänninen *et al.*, 2000; Planque and Taylor, 1998; Reid *et al.*, 2001; Stephens *et al.*, 1998; Viitasalo *et al.*, 1995a; Villate *et al.*, 1997; White *et al.*, 1995). Planque and Taylor (1998) show a strong correlation of variation in plankton abundance in the North Atlantic with the position of the north wall of the Gulf Stream and the North Atlantic Oscillation (NAO). The changes in climate can produce changes in temperature, stratification levels, timing and intensity of spring phytoplankton blooms and the amount of advection into the North Sea. Stephens *et al.* (1998) found that more than half the variance of *Calanus finmarchicus* abundance in the North Sea was accounted for by the winter inflow of Atlantic water, which in turn was related to the strength of the NAO. Similarly, climatic factors affect zooplankton biomass in the Baltic Sea through effects on hydrographic variables, such as river discharge (therefore salinity) and dominating wind directions (therefore temperature) (Viitasalo *et al.*, 1995a). However, Beaugrand *et al.* (2000) found no such relationships for the Bay of Biscay, and concluded that the relationship between climate and plankton is difficult to generalise.

So far, all the factors considered are 'bottom-up' controls of zooplankton abundance. However, there has been recent debate as to the relative contributions of 'bottom-up' and 'top-down' controls. Indeed, it has been shown that predation can have marked effects on zooplankton abundance (Arrhenius and Hansson, 1993; Båmstedt, 1998; Båmstedt *et al.*, 1994; Durbin *et al.*, 2000; Hansson *et al.*, 1990; Hutchings *et al.*, 1995; Jeppesen *et al.*, 2000; Johansson and O'Gorman, 1991; Lazzaro *et al.*, 1992; Möllmann *et al.*, 2000; Nicholas and Frid, 1999; Ojaveer *et al.*, 1998; Reid *et al.*, 2000; Rudstam *et al.*, 1992; Scheffer *et al.*, 2000; Schneider and Behrends, 1998; Spencer *et al.*, 1999; Vanni *et al.*, 1990; Verheye and Richardson, 1998; Villate, 1991; Wahlström and Westman, 1999; Williams and Collins, 1985). A model developed by Scheffer *et al.* (2000), for freshwater systems, predicts that predator-prey oscillations will cause switches between overexploitation and underexploitation of zooplankton at a critical fish density. They conclude that in nature, as the zooplankton become food limited, fish predation will become a more important control on abundance. Vanni (1987) found that abundance of zooplankton was more affected by food availability than fish predation during field experiments in lakes. However, McQueen *et al.* (1986) hypothesise that:

1. The maximum possible biomass at each trophic level is determined by 'bottom-up' controls.
2. 'Bottom-up' control is strongest at the base of the food web, and weakens with each step up, making the effects less predictable.
3. 'Top-down' control is strongest at the top of the food web, and weakens with each step down.
4. Variability in 'bottom-up' effects can usually be explained by 'top-down' effects.
5. The interplay between 'top-down' and 'bottom-up' effects depends on nutrient status; i.e. in low nutrient conditions, there will be little buffering of 'top-down' effects and vice versa.

It can be seen that a wide range of interrelated factors can affect zooplankton abundance. The response of a community will generally depend, not only on the direct effect of the variable, but the growth rate of the species and the effects on the interactions between species (Ives *et al.*, 1999). The result of all these variables is to give zooplankton a very patchy distribution, on large scales as well as small scales (Currie *et al.*, 1998; Greene *et al.*, 1998b; Kidwai and Amjad, 2000; Piontkovski and Williams, 1995; Stockwell and Sprules, 1995).

Horizontal distribution of zooplankton species

As well as high variability in zooplankton abundance, there are also spatial changes in the species composition of the zooplankton communities (Beaugrand *et al.*, 2000; Duró and

Saiz, 2000; Gislason and Assthorsson, 1995; Krause *et al.*, 1995; López-Salgado and Suárez-Morales, 1998; M'harzi *et al.*, 1998; Sutton *et al.*, 2001; Viitasalo, 1992; Williams *et al.*, 1993). Much of this is due to changes in the body of water being sampled. The influx of different water bodies into a sample area can bring in different species assemblages (Ashjian *et al.*, 1998; Fransz *et al.*, 1991; Krause *et al.*, 1995; Magnesen, 1989a; Villate *et al.*, 1997), and this has resulted in attempts to quantify the influx of North Atlantic water into the North Sea using the abundance of certain indicator species (Corten, 1999; Fransz *et al.*, 1991). Frontal systems also often separate distinct zooplankton assemblages (Burkart *et al.*, 1995; Clark *et al.*, 2001a; Gowen *et al.*, 1998b; Lindley and Williams, 1994; Nielsen and Munk, 1998; Pakhomov *et al.*, 2000). Pakhomov *et al.* (2000) found that the Subantarctic Front in the Southern Ocean separated Antarctic assemblages from subantarctic/subtropical assemblages.

Within a body of water, there can be marked gradients in factors such as salinity and temperature. For example, the Baltic Sea has a gradient of increasing salinity from north to south caused by increased freshwater run-off in the north, and the influx of North Sea water in the south (Flinkman *et al.*, 1992; Segerstråle, 1969; Viitasalo, 1992; Vuorinen *et al.*, 1998). Differences in water properties can lead to different species having competitive advantages (e.g. due to different salinity and temperature tolerances) and, therefore, a different species composition being present (Collins and Williams, 1981; Flinkman *et al.*, 1992; Lopes, 1994; Möllmann *et al.*, 2000; Siokou-Frangou, 1998; Souissi *et al.*, 2000; Viitasalo *et al.*, 1990; Vuorinen *et al.*, 1998; Williams, 1984). Laboratory experiments have shown that animals outside their preferred salinity range have increased respiration rates due to the need for extra energy to osmoregulate (Gaudy *et al.*, 2000). In the Baltic Sea, associated with a decrease in salinity, Viitasalo *et al.* (1990) noted an increase in limnetic and decrease in neritic species, Vuorinen *et al.* (1998) found a decrease in the proportion of copepod biomass, and Flinkman *et al.* (1992) saw a decrease in diversity.

Estuaries also have distinct salinity gradients, which result in distinct zooplankton assemblages (Collins and Williams, 1981; Laprise and Dodson, 1994; Lopes, 1994; Soetaert and Van Rijswijk, 1993; Williams, 1984). Collins and Williams (1981) classified four distinct zooplankton assemblages along the salinity gradient from the Severn Estuary to the Celtic Sea, which related to true estuarine, estuarine and marine, euryhaline, and stenohaline species. Williams (1984) also found that, during summer when freshwater run-off decreased, the higher salinity water, with its associated zooplankton assemblages, penetrated further up the estuary.

Differences in water properties can lead to different species of food being abundant (Botas *et al.*, 1990; Gowen *et al.*, 1998b; Van den Berg *et al.*, 1996) and again the zooplankton species best adapted to feeding on, or avoiding, the particular food type will have a competitive advantage (Engström *et al.*, 2000). For example, Hansson *et al.* (1990) found no change in total abundance of copepods with a change in feeding conditions, but did notice a shift in species dominance. Engström *et al.* (2000) found that copepods able to select against toxic cyanobacteria had an advantage. However, some copepods are non-selective grazers (Turner and Tester, 1989). Surprisingly, Soetaert and Rijswijk (1993) found that the chlorophyll content of water in the Westerschelde estuary was unimportant in explaining zooplankton community structure.

Climatic variables can affect the horizontal distribution of species and species composition as well as abundance (Dippner *et al.*, 2000; Frid and Huliselan, 1996; Fromentin and Planque, 1996; Reid *et al.*, 2001; Southward *et al.*, 1995; Villate *et al.*, 1997). For example, Fromentin and Planque (1996) found that, through its affect on sea surface temperature, the North Atlantic Oscillation can affect the biogeographical boundaries of *Calanus finmarchicus* and *C. helogolandicus*. In addition, Villate *et al.* (1997) found that climatic and oceanographic changes in the Bay of Biscay had increased the abundance of *Temora stylifera*.

Once again, 'top-down' control can play a part in structuring species composition of zooplankton communities. In many areas, the principal predators of zooplankton are fish, either adult planktivorous fish or the larvae and juveniles of other species. Fish are generally selective feeders, and much work has shown that certain species of zooplankton are preferred (Brooks, 1968; Gotceitas and Brown, 1993; Hamrin, 1983; Hansson *et al.*, 1990; Mehner and Heerkloss, 1994; Munk, 1997; Rudstam *et al.*, 1992; Shaheen *et al.*, 2001). There are a number of studies that have noted a shift in zooplankton species composition with an increase in zooplanktivory (Bøhn and Amundsen, 1998; Brooks, 1968; Jeppesen *et al.*, 2000; Rudstam *et al.*, 1992).

Invertebrate predation can also play a role (Kehayias *et al.*, 1996; Omori *et al.*, 1995; Schneider and Behrends, 1998; Spencer *et al.*, 1999; Sullivan and Meise, 1996; Viherluoto and Viitasalo, 2001; Wahlström and Westman, 1999). Viitasalo and Rautio (1998) conducted feeding experiments with the mysid *Praunus flexuosus* and found that they could capture cladocerans by creating a suspension feeding current, whereas copepods had to be attacked individually due to their escape responses. Consequently, the mysids fed intensively on cladocerans whenever possible. In a further study, Viherluoto *et al.* (2000) concluded that the mysids *Mysis mixta* and *M. relicta* have to reach a minimum size of 8mm before they were able to capture copepods.

Vertical distribution of zooplankton species

Zooplankton have a very variable vertical distribution in the water column, due mainly to Diel Vertical Migration (DVM) behaviour (Al-Mutairi and Landry, 2001; Bradford-Grieve *et al.*, 1998; Dam *et al.*, 1993; Falkenhaug *et al.*, 1997; Fiksen and Carlotti, 1998; Hays, 1996; Hays *et al.*, 1996; Hays *et al.*, 1997b; Hernández-León *et al.*, 2001; Madhupratap *et al.*, 2001; Madin *et al.*, 2001; Magnesen, 1989a; Morales *et al.*, 1993; Zhang and Dam, 1997). Normal DVM is the tendency for zooplankton to migrate to depth around dawn, remain there during the day, and then come towards the surface at dusk for the duration of the night to feed (Hays *et al.*, 1997b). The magnitude of DVM can range from a few meters to several hundreds of meters, with the larger species generally undertaking the larger migrations.

The predator-evasion hypothesis suggests that the migrations, to light limited depths during the day, decrease the risk from visual predators that rely on light to perceive their prey (Zaret and Suffern, 1976). It has been shown that night feeding reduces predation risk as fish feed on copepods with full guts at significantly higher rates than those without (Tsuda *et al.*, 1998). However, not all species, or individuals of a species, migrate (Checkley *et al.*, 1992; Falkenhaug *et al.*, 1997; Madhupratap *et al.*, 2001), and it has been noted that different stages of a species migrate to different degrees (Besiktepe and Unsal, 2000; Durbin *et al.*, 1995; Falkenhaug *et al.*, 1997; Fiksen and Carlotti, 1998; Irigoien, 1999; Pedersen *et al.*, 1995; Williams and Conway, 1980). The predator-evasion argument has been supported by evidence that mainly the larger, more visible, and less mobile species migrate (Al-Mutairi and Landry, 2001; Dam *et al.*, 1993; Hays, 1996; Hays *et al.*, 1997b; Madin *et al.*, 2001; Magnesen, 1989a; Morales *et al.*, 1993). De Robertis *et al.* (2000) have also shown that smaller species migrate to the surface earlier, and migrate from the surface later, than larger species. This is attributed to the level of light at which visual predation becomes less of a risk. In addition, it has been noted that *Chiridius armatus* ceases DVM in periods of midnight sun, staying at depth, and winter darkness (Falkenhaug *et al.*, 1997). It has also been suggested that long-term changes in visual predator abundance can cause long-term changes in the DVM behaviour of zooplankton (Hays *et al.*, 1996).

It is possible that whether an animal migrates or not is a trade-off between body condition and the risk of predation (Andersen *et al.*, 1997; Fiksen and Carlotti, 1998; Zaret and Suffern, 1976) since DVM is often reduced during the winter (Hays *et al.*, 1996). In other words, if an animal is starving it is more likely to remain at the surface during the day, despite the increased the risk of predation, because it is more in need of food. However, Durbin *et al.* (1995) concluded that DVM patterns showed no simple relationship with food availability, and suggested that predation played a more important role.

Other factors that affect the vertical distribution of animals are seasonal features, such as stratification boundaries (e.g. thermoclines and haloclines), which can produce seasonal patterns in the vertical distribution of species (Magnesen, 1989b). Although many species migrate through these (van Couwelaar, 1997), certain species or stages of species, have been shown to remain below (e.g. *Calanus finmarchicus* in the Celtic Sea; Williams (1985), above (e.g. *Calanus helgolandicus* in the Celtic Sea; Williams (1985); juvenile *Sagitta setosa* in the Black Sea; Besiktepe and Unsal (2000), or associated with the thermocline (Plounevez and Champalbert, 2000). These patterns can change in different areas; Fransz *et al.* (1998) noted that adjacent subregions of the North Sea could differ widely in the vertical distribution of *Calanus finmarchicus* biomass. These differences may be determined by the gradient in the relevant water property over the boundary layer in question, i.e. in certain cases it may range beyond the tolerances of the animal (Besiktepe and Unsal, 2000; Luo *et al.*, 2000; Madhupratap *et al.*, 2001; Scrope-Howe and Jones, 1986; Smith *et al.*, 1998; Wishner *et al.*, 1998). For example, in the Arabian Sea, Smith *et al.* (1998) found virtually no DVM at a station with strong, persistent subsurface suboxic conditions. Gaudy *et al.* (2000) have shown that metabolic rate is increased in levels of salinity outside the tolerance range of an animal, therefore the animal needs more food and competes less well with animals within their salinity tolerance range.

An associated factor affecting the vertical distribution of zooplankton is the seasonal cycle and vertical distribution of the phytoplankton. Falkenhaug *et al.* (1997) noted that the vertical distribution of *Calanus finmarchicus* was dominated by seasonal migration, being found in surface waters during phytoplankton blooms and staying at depth in the autumn and winter. Similarly in the Barents Sea, *Metridia longa* only occupies surface waters between April and May (Pedersen *et al.*, 1995). There is often a seasonal vertical maximum in phytoplankton, the position of which can be determined by the position of a stratification boundary (Ahel *et al.*, 1996; Botas *et al.*, 1990; Harris, 1988; Laborde *et al.*, 1999; Nielsen *et al.*, 1993; Richardson and Pedersen, 1998; Smith Jr. and Demaster, 1996; Steinberg *et al.*, 2001). Turbidity of the water will also play a role in determining the level of the phytoplankton maxima, as turbidity determines the depth to which sunlight can penetrate (Allen, 1997). It has been noted that certain species associate around the phytoplankton maxima (Harris, 1988; Scrope-Howe and Jones, 1986).

It has also been shown that different stages of a species may prefer different depths (Irigoien, 1999), and that this can change with season. For example, *Calanus pacificus* in the Santa Barbara Basin, have been shown to form deep water aggregations as diapausing fifth copepodites in autumn (Osgood, 1997; Osgood and Checkley, 1997). Richter (1995) has also shown that, in the Greenland Sea Gyre, omnivorous and carnivorous species showed no seasonal depth migrations, but showed vertical partitioning between the species. However, the herbivorous species showed pronounced seasonal vertical migration between the surface in the summer and great depths during the winter when surface chlorophyll levels were low. Falkenhaug *et al.* (1997) conclude that seasonal variations in vertical behaviour are related to food and light conditions, whereas inter- and intraspecific differences may be due to life history, diet and susceptibility to predation.

Zooplankton size

There are three main factors affecting the size of zooplankton, and there are many debates over the relative importance of each. It is important to note that some of these factors affect the size of individuals within a species, and some affect whether large or small-bodied species are found in an area. The first factor is the temperature of the surrounding water. There has been much work concerning the effect of temperature on physiological rates, generation time, and body size of individuals within a species (Escribano and Hidalgo, 2000; Gillooly, 2000; Huntley and Lopez, 1992; Ikeda, 1985; Klein Breteler *et al.*, 1995; Viitasalo *et al.*, 1995b). In short, a rise in temperature increases growth rate, which in turn shortens generation time and therefore decreases body size (Gillooly, 2000). Huntley and Lopez (1992) found that temperature alone explained more than 90% of the variance in marine copepod growth rate, and predicted a trend of decreasing size with increasing environmental temperature. They conclude that the influence of temperature on growth rates may override that of food availability in nature. Similarly, Dickey-Collas *et al.* (1996b) have shown that, as water temperature increases, the mature size of *Sagitta elegans* decreases in the Irish Sea. However, this does not mean that all species found in warmer waters will be smaller than all species found in colder waters.

The second factor is predation, especially by fish. As noted earlier, fish are highly selective feeders preying preferentially on certain species. They are also highly size-selective predators, generally feeding preferentially on larger animals (Akopian *et al.*, 1999; Bøhn and Amundsen, 1998; Brooks, 1968; Flinkman *et al.*, 1998; Flinkman *et al.*, 1992; Gardner, 1981; Gotceitas and Brown, 1993; Hamrin, 1983; Munk, 1997; O'Brien and Kettle, 1979; Plounevez and Champalbert, 2000; Shaheen *et al.*, 2001; Wahlström *et al.*, 2000; Wahlström and Westman, 1999). In addition, all components of planktivory, such as gape-limitation, encounter rate, prey avoidance capacity, capture success and handling time, are size dependent. Predation can affect both the size of animals within a species (because the larger individuals are taken), and the size of the dominant species present (through increased mortality of the larger species).

In 1965, Brooks and Dodson (1965), from work in freshwater systems, put forward the size-efficiency hypothesis:

1. Planktonic herbivores all compete for fine particulate matter.
2. Larger zooplankters are more efficient at grazing and can utilise larger particles.
3. When planktivory is low, the small planktonic herbivores will be eliminated by large forms.
4. When planktivory is high, the size-dependent predation will eliminate the larger forms allowing the small herbivores to become dominant.
5. When planktivory is intermediate, predation will keep the larger forms to sufficiently low numbers so that the smaller competitors are not eliminated.

Since this work, there has been much corroborating evidence from further freshwater studies, and the formulation of the trophic cascade hypothesis (Almond *et al.*, 1996; Bøhn and Amundsen, 1998; Brooks, 1968; Carpenter *et al.*, 1987; Dahl-Hansen, 1995; Devries and Stein, 1992; He *et al.*, 1994; Hurlbert and Mulla, 1981; Jeppesen *et al.*, 2000; Lazzaro, 1987; Lazzaro *et al.*, 1992; Persson *et al.*, 1992; Rudstam *et al.*, 1993; Vanni, 1986; Vanni and Findlay, 1990; Vanni and Layne, 1997; Vanni *et al.*, 1997; Wootton and Power, 1993; Zaret and Suffern, 1976). It has also been noted, in freshwater systems, that the presence of fish and fish kairomones, alters life-history traits so that reproduction is increased and mature body size is decreased (Lampert, 1993; Rose *et al.*, 2001; Vanni, 1987).

There has been relatively little work done in marine systems, although Verheye and Richardson (1998) did note an increase in the proportion of <0.9mm zooplankton coupled with an increase in anchovy abundance. Similarly, Villate (1991) noted that variations in zooplankton size spectra were synchronised with the annual development of the main predators. Koslow (1983) put forward a simulation model to examine if predation can regulate the size structure of marine zooplankton communities, which resulted in the general agreement that a large increase or decrease in planktivorous fish led to the dominance of small or large zooplankton. However, his model failed to explain the 1965-70 decline seen in zooplankton communities of the North Atlantic and herring and mackerel stock of the North Sea. Similarly, Rudstam *et al.* (1994) failed to find any correlation between clupeid and zooplankton biomass in the Baltic Sea.

Invertebrate predation also tends to be size-selective, although falls more heavily on the smaller animals (Almond *et al.*, 1996; O'Brien, 2001; O'Brien and Kettle, 1979; Wahlström and Westman, 1999). Suchman and Sullivan (2000) found that, although scyphomedusae selected larger animals, the avoidance behaviour of adult copepods diminished the risk associated with larger size. However, it is generally believed that invertebrate predation is less intensive, and therefore less important in affecting zooplankton size, than fish predation (Vanni, 1987). There are some instances described in the literature where invertebrate predation could be important (Arnott and Vanni, 1993; Manca and Ruggiu, 1998; O'Brien, 2001; Pearre Jr., 1980; Wahlström and Westman, 1999). For example, O'Brien (2001) showed that the introduction of the predatory copepod *Heterocope septentrionalis*, to a previously predator free pond, could eliminate or reduce small and medium sized zooplankton. Similarly, Wahlström and Westman (1999) concluded that predation by invertebrate planktivores results in a zooplankton community consisting of larger individuals. Duró and Saiz (2000) found that the impact of chaetognath predation on copepod standing stock in the Mediterranean appeared to be extremely low, but became more relevant once prey size and species specificity was taken into account.

Associated with size-selective predation, the depth of water can also affect the size structure of zooplankton communities. In deeper water, there is more refuge from visual predators available to the zooplankton and larger forms tend to dominate. Similarly, in shallow waters such as coastal regions, this refuge is decreased and so smaller animals dominate. However, these small animals, with high egg production rates, may also have a competitive advantage by being able to take advantage of variable food regimes (Tiselius, 1988). In addition, Lougheed and Chow-Fraser (1998) noted that high turbidity, which is often associated with coastal sites, selected against large filter feeders and allowed smaller zooplankton to dominate.

A third factor that can also be important in structuring the size of zooplankton communities is the amount of phytoplankton available as food (Gallienne *et al.*, 2001; Viitasalo *et al.*, 1995b; Wagner *et al.*, 1998), which can again act on both the species and community level. Wagner *et al.* (1998) found that food limited copepods were smaller than those reared in excess food conditions. However, on the community scale, Piontkovski *et al.* (1995) noted that, in areas of maximum primary productivity in the

Indian Ocean, the smallest zooplankton dominated. Koslow (1983) put forward the hypothesis that zooplankton are food-limited rather than predator limited, and Gallienne *et al.* (2001) found changes in the zooplankton size structure associated with regions of high surface chlorophyll concentration. However, Huntley and Lopez (1992) suggest that, on the small scales appropriate to individual copepods, food may be reliably available and that predation mortality may eradicate the effect of food limitation on growth rates.

The type of phytoplankton available as food will also be important. Obviously, certain phytoplankton species are 'better' sources of food than others, i.e. are have higher per capita productivity (Norberg, 2000). In areas dominated by these food species, the zooplankton will be able to grow more efficiently and therefore larger, and produce larger eggs. In laboratory experiments it has been shown that copepod growth rates can depend on food supply (Steele and Henderson, 1995). Stelfox *et al.* (1999) noted that a shift in size structure, from large to small zooplankton, occurred in response to a shift from large to small phytoplankton cells. Rodríguez *et al.* (2001) found that mesoscale vertical motion, which is found in eddies and frontal systems, increases the relative proportion of large phytoplankton. This implies that hydrographic features could also exert control on zooplankton size structure.

Warren *et al.* (1986) found surface water temperature and fish abundance were both inversely correlated to adult copepod weight, and that standing stocks of important phytoplankton groups were positively correlated with copepod weight. Similarly, Steele and Frost (1977) concluded that predation is at least as important in determining herbivore size structure as physical or nutrient parameters, and that no single factor was predominant. Viitasalo *et al.* (1995b) found that the relative importance of temperature and food availability on zooplankton size varied according to species, developmental stage and study area. It would appear, not surprisingly, that there is not one factor affecting zooplankton size, but a number of interrelated variables that play a role. Reid *et al.* (2000), in a review of 'top-down' control in marine systems, concluded that as ecosystem complexity increases, environmental factors become more important and 'top-down' factors less easy to distinguish.

CHAPTER 2

Comparison of the epipelagic zooplankton samples from a U-Tow and the traditional WP2 net

Cook, K.B. and Hays, G.C. (2001). Comparison of the epipelagic zooplankton samples from a U-Tow and the traditional WP2 net. *Journal of Plankton Research* 23: 953-962.

Abstract

The performance of a new mesozooplankton sampler, the U-Tow, was compared to that of the traditional WP2 net. The U-Tow significantly underestimated species abundance, but gave a very good representation of species composition and community size structure. WP2 net samples could be used to calibrate the U-Tow allowing absolute abundance to be determined. It is recommended that the U-Tow, in its current configuration, be used in conjunction with WP2 net samples to give measures of abundance, or as a tool to identify areas of change in plankton communities.

Introduction

The assessment of the abundance, species composition and size distribution of mesozooplankton is a fundamental goal of biological oceanography (Greene *et al.*, 1998a; Mitson *et al.*, 1996; UNESCO, 1968). Traditionally, however, mesozooplankton have been sampled with simple ring nets which sample over very restricted spatial scales, with individual deployments being made over a few 10s of metres. The resulting lack of spatial detail in mesozooplankton surveys limits our ability to understand, for example, the trophic interactions and biogeochemical impact of mesozooplankton, their life-history strategies, and the impact of physical and biological processes on secondary production (Benfield *et al.*, 1998; Greenstreet *et al.*, 1997; Liao *et al.*, 1999; Piontkovski *et al.*, 1995; Stockwell and Sprules, 1995; Zhang *et al.*, 2000). Consequently, there is an urgent need for techniques that allow mesozooplankton to be sampled over extended spatial scales (10s or even 100s km) (Marine Zooplankton Colloquium, 1989). To this end acoustic and optical techniques have been extensively explored in recent years, although both techniques have limited ability to resolve species composition and may also suffer from the presence of too many, or non-living, particles in the water (Benfield *et al.*, 1998; Brierley *et al.*, 1998a; Brierley *et al.*, 1998b; Liao *et al.*, 1999; Mitson *et al.*, 1996; Osgood, 1997; Stanton *et al.*, 1996; Zhang, *et al.*, 2000). Systems that actually collect zooplankton samples at high speed and over extended transects would, therefore, be most valuable.

To date the only system capable of such sampling is the Continuous Plankton Recorder (CPR). This instrument has been routinely, and consistently, surveying the

North Sea and North Atlantic plankton since 1948 (Oceanographic Laboratory Edinburgh, 1973; Warner and Hays, 1994). The main reason that the CPR is not used more widely is its inability to sample physical parameters and confinement to sampling at one depth (Hays *et al.*, 1998). Due to these limitations in the performance of the CPR, a new vehicle, the U-Tow, has been designed in recent years for sampling of mesozooplankton and physical parameters at high speeds (maximum tested speed of 22 $km.h^{-1}$) and over extended spatial scales (Hays *et al.*, 1998).

The original version of the U-Tow was designed and built by Valeport Limited (Dartmouth, Devon) in collaboration with the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) in 1994. It is fitted with a Plankton Sampling Mechanism (PSM, Valeport Model 140) (Figure 2.1), which is based on the mechanisms used in the CPR and Longhurst Hardy Plankton Recorder (LHPR) (Hays *et al.*, 1998), and a Conductivity Temperature Depth sensor (CTD). It can also be configured to carry additional sensors, and fitted with a servo control module, to actively control depth, so that an undulating depth profile can be achieved. This design has since been modified by W.S. Ocean Systems Limited (Alton, Hants.) to have improved undulating capabilities and an increased potential payload (Mills *et al.*, 1998). However, both models use the same PSM (Figure 2.1). Water enters the PSM via an aperture at the front of the U-Tow, and passes through a filtering mesh supported by a series of fine stainless steel rods. At pre-determined intervals, the filtering mesh and a covering mesh advance on to a take-up spool, situated in a storage chamber that contains a formaldehyde reservoir, giving a series of discrete samples. The U-Tow has a comparatively small inlet aperture (18mm

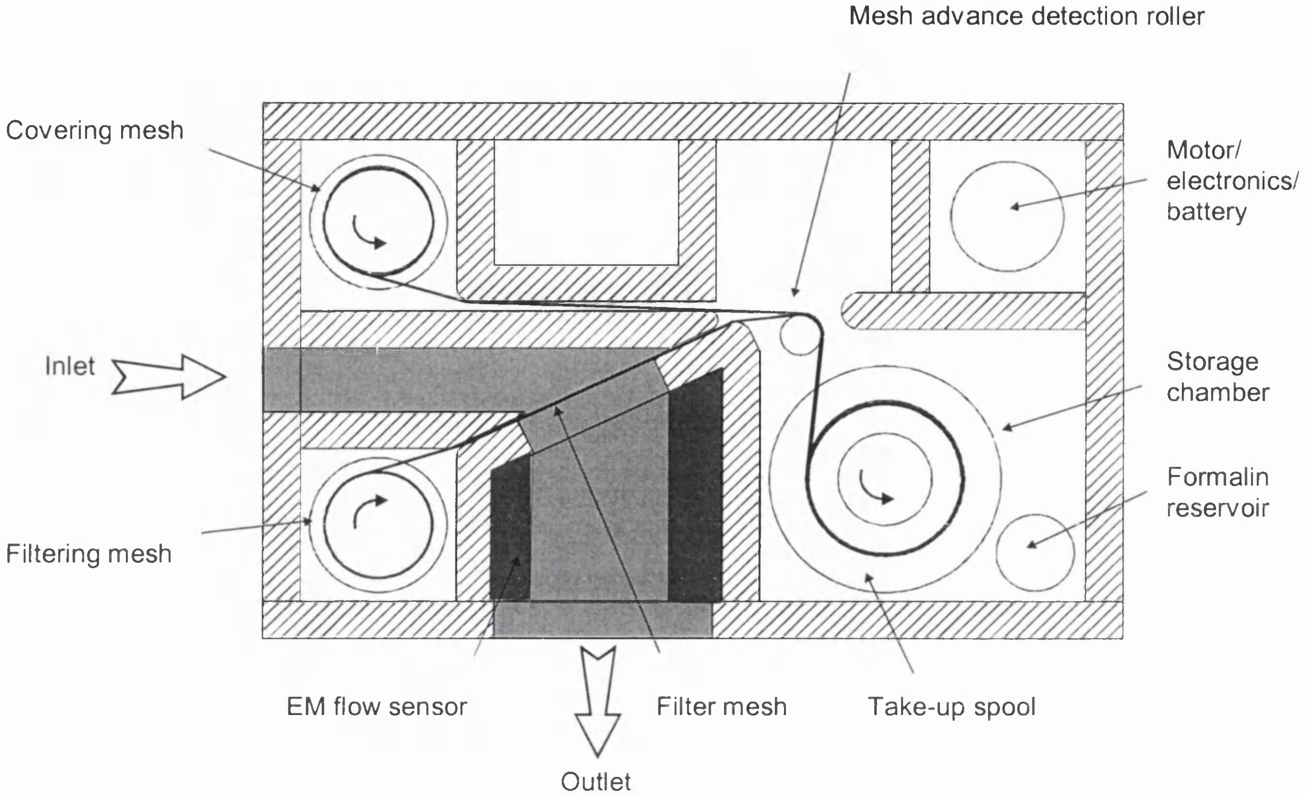

Fig. 2.1 A schematic illustration of the Plankton Sampling Mechanism (PSM). Hatched shading represents the PVC used in the basic construction. When submerged, all the chambers in the PSM become flooded and then the only flow through the unit is along the water tunnel (grey shading). Holes in the formalin reservoir allow formalin to gradually seep out into the storage chamber so that the sample is preserved. The EM flow sensor (black shading) measures the flow rate.

diameter) which prevents problems with clogging of the mesh when too large a volume of water is filtered.

Ideally, the performance of any new piece of equipment should be investigated before use so that results can be reliably compared with other studies, and so that temporal and spatial variation in the plankton can be distinguished from variation in sampler performances (Aron *et al.*, 1965). Gear inter-comparisons, although not "exciting" science, are a vital component of sampling. For example, Hernroth (1987) found that the sampling and filtration efficiency of the Nansen net was 50-70% compared to the WP2 net under ideal conditions and 25-30% during periods of high particle abundance or long hauls; while DeVries and Stein (1991) discovered a discrepancy in densities of the rotifer *Diaphanosoma* found by a tube sampler, a vertical tow net and the Schindler-Patalas trap, although they performed equally for most species, emphasising the need for a taxon specific approach when evaluating samplers. More recently, whilst calibrating an optical plankton counter (OPC), Sprules *et al.* (1998) found it to be accurate up to concentrations of 100 organisms.liter^{-1}. Above this concentration, there was an increasing level of coincident counts, where multiple animals are counted as one, resulting in underestimation of zooplankton abundance and inaccurate size distributions. Similarly, Zhang *et al.* (2000) suggests that the OPC is able to produce reasonable estimates of zooplankton abundance in waters with less than 100 particles of detritus liter^{-1} but only after correcting for the influence of background detritus. The most extensive gear inter-comparisons have concentrated on acoustic techniques. For example, Greene *et al.* (1998a) used a Dual-Beam Acoustics Deployed on a Multiple Opening/Closing Net and Environmental Sensing System (D-BAD MOCNESS) to collect acoustic data and net samples simultaneously. The results from the two samplers were consistent, except for samples with high quantities of siphonophores where predicted backscattering coefficients exceeded observed backscattering coefficients.

The most widely used mesozooplankton sampler is the simple ring net, or WP2 net (UNESCO, 1968), which has been shown to be suitable for quantitative sampling (Hernroth, 1987). The WP2 net is generally used to give an integrated sample of mesozooplankton from either a vertical or a horizontal haul at slow speeds, usually not more than 3.7 $km.h^{-1}$, and therefore samples over a relatively small distance (metres). The aim of this study is to compare the performance of the U-Tow with that of the traditional WP2 net. Estimates of abundance, species composition, and community size structure are evaluated from samples collected in Swansea Bay, the North Sea and the Irish Sea.

Methods

Three different U-Tow systems were used in this study. A fixed depth Valeport Ltd. U-Tow (Hays *et al.*, 1998) was deployed in Swansea Bay (December 1997, April, May, September and November 1998), an undulating Valeport Ltd. U-Tow (Hays *et al.*, 1998) was deployed in the North Sea (February 1998), and an undulating W.S. Ocean Systems Ltd. U-Tow (Mills *et al.*, 1998) was deployed in the Irish Sea (June and July 1998). This gave a total of 28 deployments over about 1668km. Tow speeds ranged between 13 and 18.5$km.h^{-1}$. All U-Tows were fitted with the same Plankton Sampling Mechanism (PSM) and 200 μm filtering mesh. The only difference in the three systems with respect to sampling zooplankton was the electromagnetic flowmeter fitted to the PSM used in the Valeport systems (Valeport Model 802) (Hays *et al.*, 1998). The W.S. Ocean Systems Ltd. model did not have a flowmeter fitted to the PSM. In these cases, the volume of water filtered per sample was calculated using the distance towed multiplied by the area of the inlet aperture. Although this method has been shown not to be ideal due to clogging (Hays, 1994; Hays *et al.*, 1998), the short duration of each sample (average 20min) means that this was not a significant problem. In addition, the average efficiency of the U-Tow was calculated from the North Sea tows, which were of a comparable speed, and was not significantly different from 100%.

Deployments in Swansea Bay involved towing the fixed depth U-Tow, at a depth of 9m and speed of 13.9km.h^{-1}, round a triangular course, with each leg approximately 4.5km, for approximately 3 hours. The PSM was set to a sample interval of 15 minutes. 5-minute WP2 net tows at 9m, made possible by using a real time depth sensor, were taken at each corner of the triangular course. Deployments in the North Sea and Irish Sea involved towing the undulating U-Tow along a straight-line course, with a vertical WP2 net haul taken at the beginning and end of each tow. As the purpose of these cruises was to test the capabilities of the U-Tow, the length of tow and depth range varied between tows. Tow duration ranged between 1.5 hours and 16 hours (average 4.5 hours) and depth ranged between 5m and 40m. The PSM was set at sample intervals between 15 and 30 minutes (average 22.5 minutes). For each tow, vertical net hauls were taken from the maximum depth of the undulation profile to the surface. In all cases, a 56cm diameter WP2 net fitted with a General Oceanics flowmeter and Aladin Pro dive computer, for an accurate reading of depth, was deployed. After each deployment samples were immediately washed off the mesh and preserved in 4% borax buffered seawater formaldehyde.

Animals from both sets of samples were identified as far as possible, to at least genus for copepods and at least order for other animals, using a binocular microscope. Where possible the whole sample was analysed but in some cases, where total zooplankton abundance was very high, a sub-sample was analysed. Where possible, at least a hundred animals of a size that is caught 95% quantitatively by a 200μm mesh, calculated using mesh selection curves calculated by Nichols and Thompson (1991) were counted from each sample. Measurements of length and width were also made of at least 100 animals, or all the animals present if there were less than 100, from each sample using a calibrated eyepiece graticule. Animal lengths were sorted into length groups of 50μm intervals between 100μm and 1000μm, and 1000μm intervals between 1000μm and 10000μm.

In the analysis to compare the two gear types, only the U-Tow samples at either end of the tow, and therefore directly comparable to the net samples, were used. However, samples left on the filtering section of the PSM during retrieval of the U-Tow were discarded. This was due to the possibility of plankton being washed off by turbulent water from the ships wash, and as water is drained out of the PSM. Bray-Curtis similarity coefficients between individual sample measures of species abundance (numbers.m^{-3}), species composition (proportion contributed by each species to total abundance), and length frequency distributions were calculated using the CLUSTER routine from Plymouth Routines In Multivariate Ecological Research, (PRIMER) (Carr, 1997; Clarke and Warwick, 1994). These were mapped as non-metric multi-dimensional scaling (MDS) plots. Analyses of similarities (ANOSIMs) were performed to test for differences between all WP2 net samples and all U-Tow samples with respect to species abundance, species composition, and length frequency distribution. These multivariate techniques were used as they compare samples on the extent to which particular species are found at similar levels of abundance (Clarke and Warwick, 1994). This was shown to be important by DeVries and Stein (1991).

To further examine the proportion of animals retained by the PSM in the laboratory, a known number of adult *Calanus* (a large copepod) and *Sagitta* (a large chaetognath), that are quantitatively retained by a 200μm mesh, were pumped through the PSM at flow rates comparable to those on operational tows (average 1958 $l.h^{-1}$). The number of animals retained on the mesh and the number of animals found floating in the tank having passed through the PSM were counted.

Results

Absolute abundance

51 WP2 net samples and 66 U-Tow samples were analysed. In total, about 25000 animals were identified and about 13000 measured. In almost all cases, the average total zooplankton abundance estimated using U-Tow samples was markedly lower than that estimated using WP2 net samples (Figure 2.2a). This observation was confirmed by a

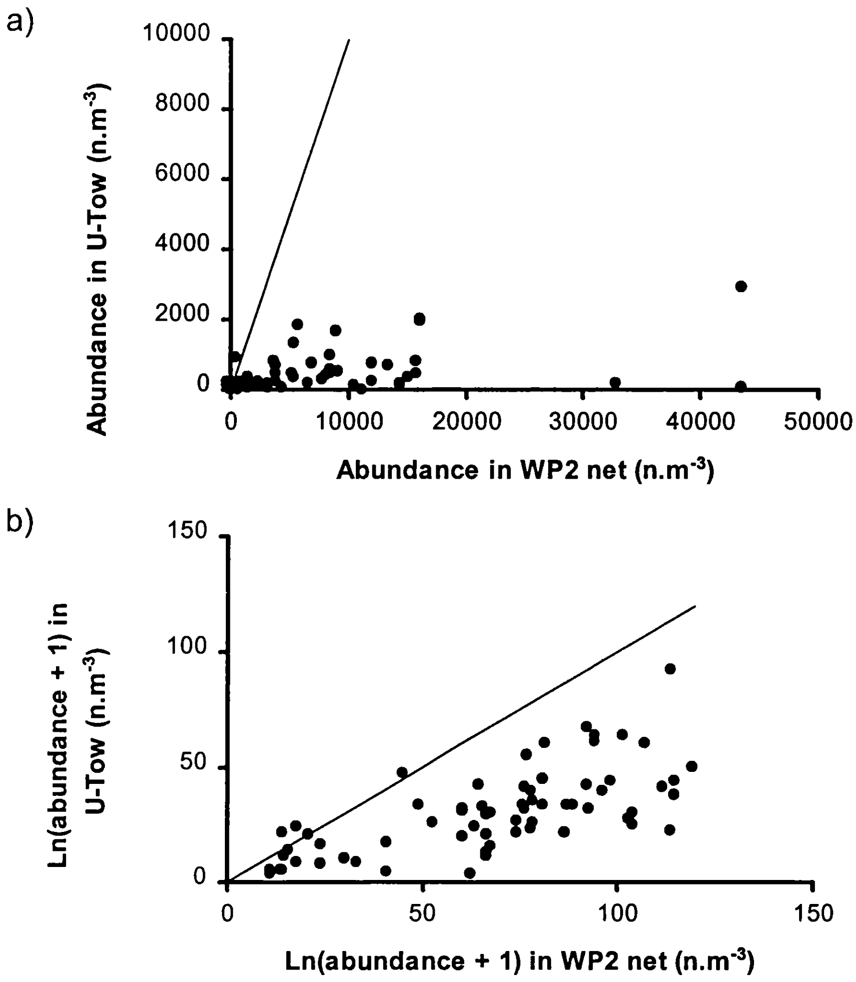

Fig 2.2 Comparison between levels of abundance (a) and natural log transformed abundance (b) from samples taken with the U-Tow and WP2 net. Solid line represents the line of equivalence.

one-way ANOSIM analysis which showed that sample similarities between species abundance measures from the U-Tow and WP2 net groups were significantly different to sample similarities within groups (Global $R = 0.219$, $p = 0.027$). To test whether this difference was due to skewing by unusually high measures of abundance in some samples, the analysis was repeated with a ln(abundance + 1) transformation. The abundance estimated from U-Tow samples were still lower than that estimated from WP2 samples (Figure 2.2b). An ANOSIM showed this difference to be significant (Global $R=0.203$, $p<0.001$).

The average abundance from U-Tow samples, expressed as a percentage of abundance from WP2 net samples, of all taxa was 24.41% ($n = 66$, $SD = 44.02$), although this was very variable even within tows (Figure 2.3) and a paired t-test showed the values from the beginning and end of a tow to be significantly different ($t_{28} = 2.3$, $p < 0.05$). To test whether WP2 net measures of abundance could be used to calibrate the U-Tow measures of abundance, correlation analysis was performed between the average abundance from U-Tow samples, expressed as a percentage of abundance from WP2 net samples, at the beginning and end of tows where the values were less than 100%, and would therefore need calibrating. A significant positive correlation was found at the 1% level ($F_{1,27} = 57.13$, $r^2 = 0.68$, $p < 0.001$) (Figure 2.4) showing that a reasonable measure of abundance could be estimated using the WP2 net samples to calibrate abundance measures. From Figure 2.4 it appears that the average abundance from U-Tow samples, expressed as a percentage of abundance from WP2 net samples, decreases from the beginning to the end of the tow. However, regression analysis showed no significant

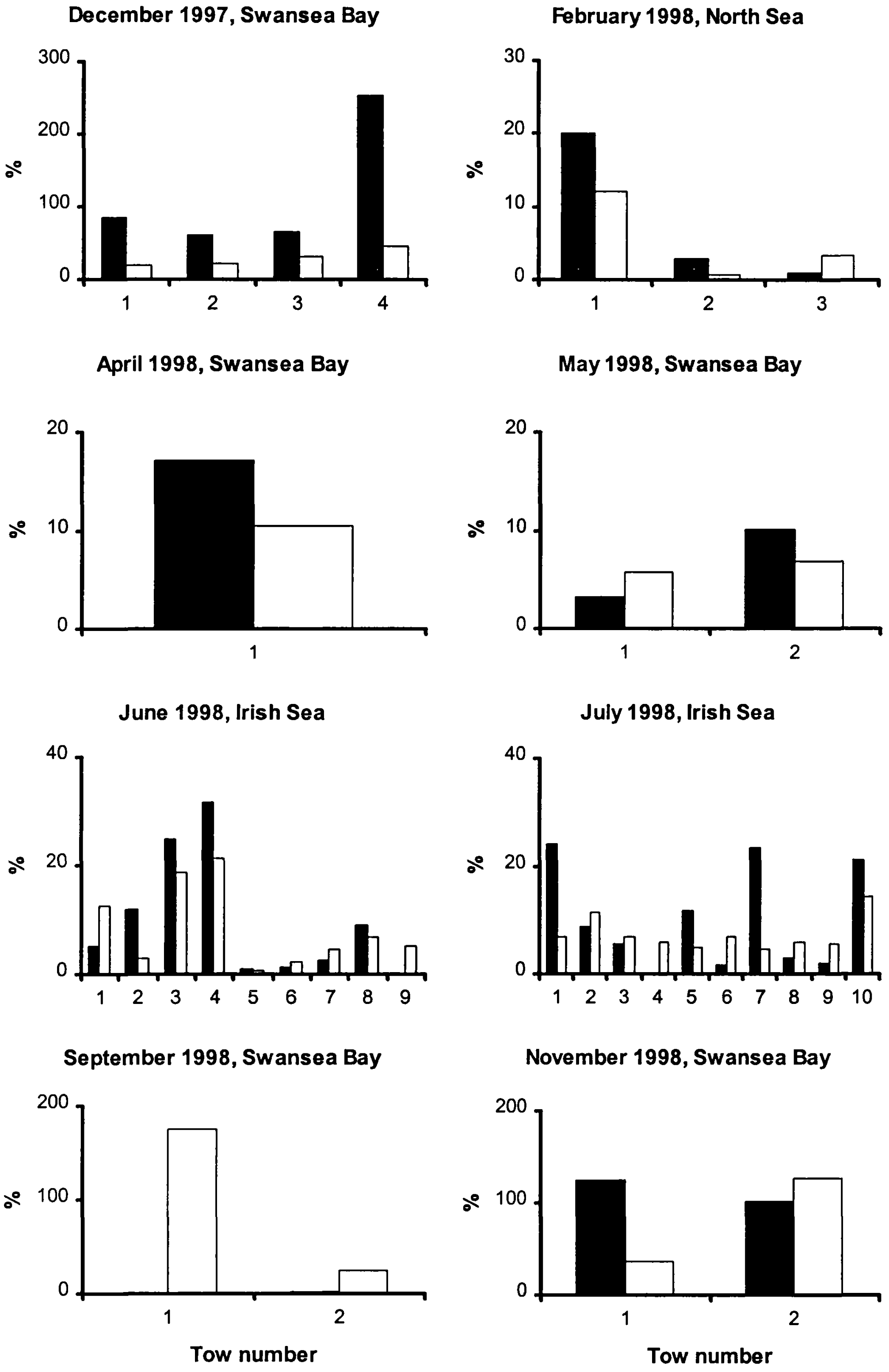

Fig. 2.3 Ratios of U-Tow abundance : WP2 net abundance, expressed as a percentage, for the beginning (filled) and end (open) of each tow. Note different scales on y-axes.

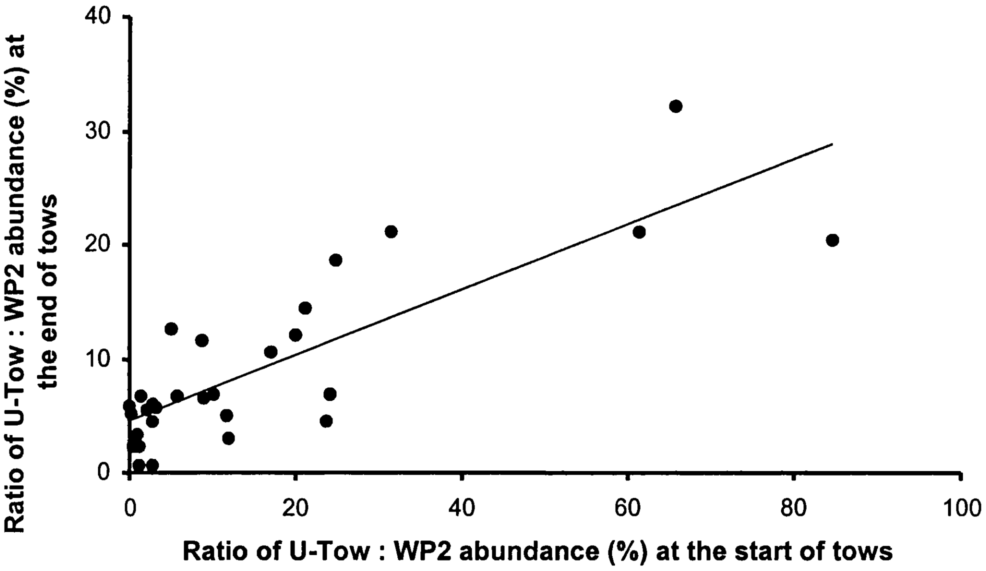

Fig. 2.4 Comparison between average abundance from U-Tow samples, expressed as a percentage of abundance from WP2 net samples, at the beginning and end of tows, showing the line of best fit.

relationship between the change in performance during the tow and the length of tow ($F_{1,27} = 2.61$, $r^2 = 0.09$, $p > 0.05$). Figure 2.5 shows the result of assuming a linear relationship between the average abundance from U-Tow samples, expressed as a percentage of abundance from WP2 net samples, at the beginning and end of the June tows in the Irish Sea and, using this relationship, calibrating the intermediate U-Tow samples.

The laboratory trials showed that on average 27.45% (n = 3, SD = 6.74) *Calanus* and 37.83% (n = 3, SD = 4.36) *Sagitta* were retained on the mesh. Overall an average of 29.04% (n = 3, SD = 5.86) of all the animals were retained on the mesh inside the PSM.

Species composition and size structure

When species composition was considered (i.e. for each sample, individual species abundances were expressed as a percentage of the total zooplankton abundance) the samples from the U-Tow and the WP2 net gave very similar values (Figure 2.6a) and an MDS plot showed no obvious separation of similarity coefficients (Figure 2.6b). A one-way ANOSIM analysis (Global R = -0.000, p = 0.451) showed that, on average, similarities between groups and within groups are the same.

Similarly, when comparing the size structure (i.e. proportion contributed by each length interval, as described in the methods, to the total number of animals measured) from samples taken by the U-Tow and WP2 net, the average length frequency distributions were comparable (Figure 2.7a) and an MDS plot showed no separation of sample similarity coefficients (Figure 2.7b). This was confirmed by a one-way ANOSIM

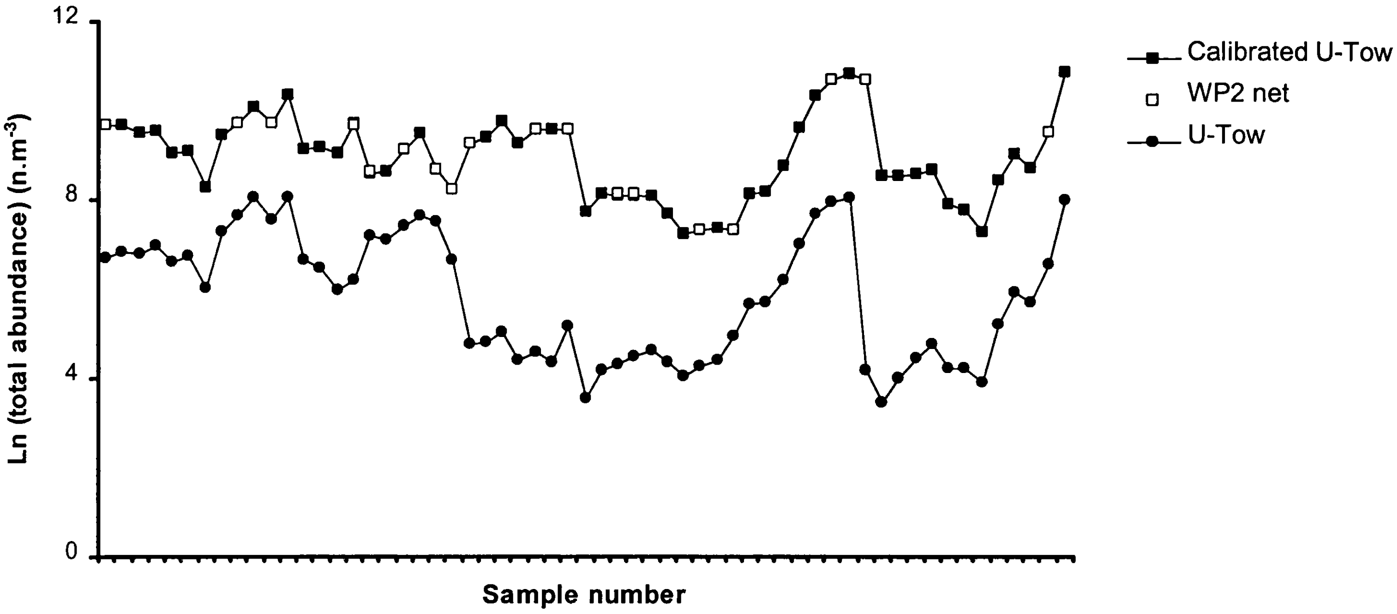

Fig. 2.5 Absolute abundance measured in U-Tow samples and WP2 net samples during June tows in the Irish Sea, and calibrated abundance from the U-Tow samples using the WP2 net samples.

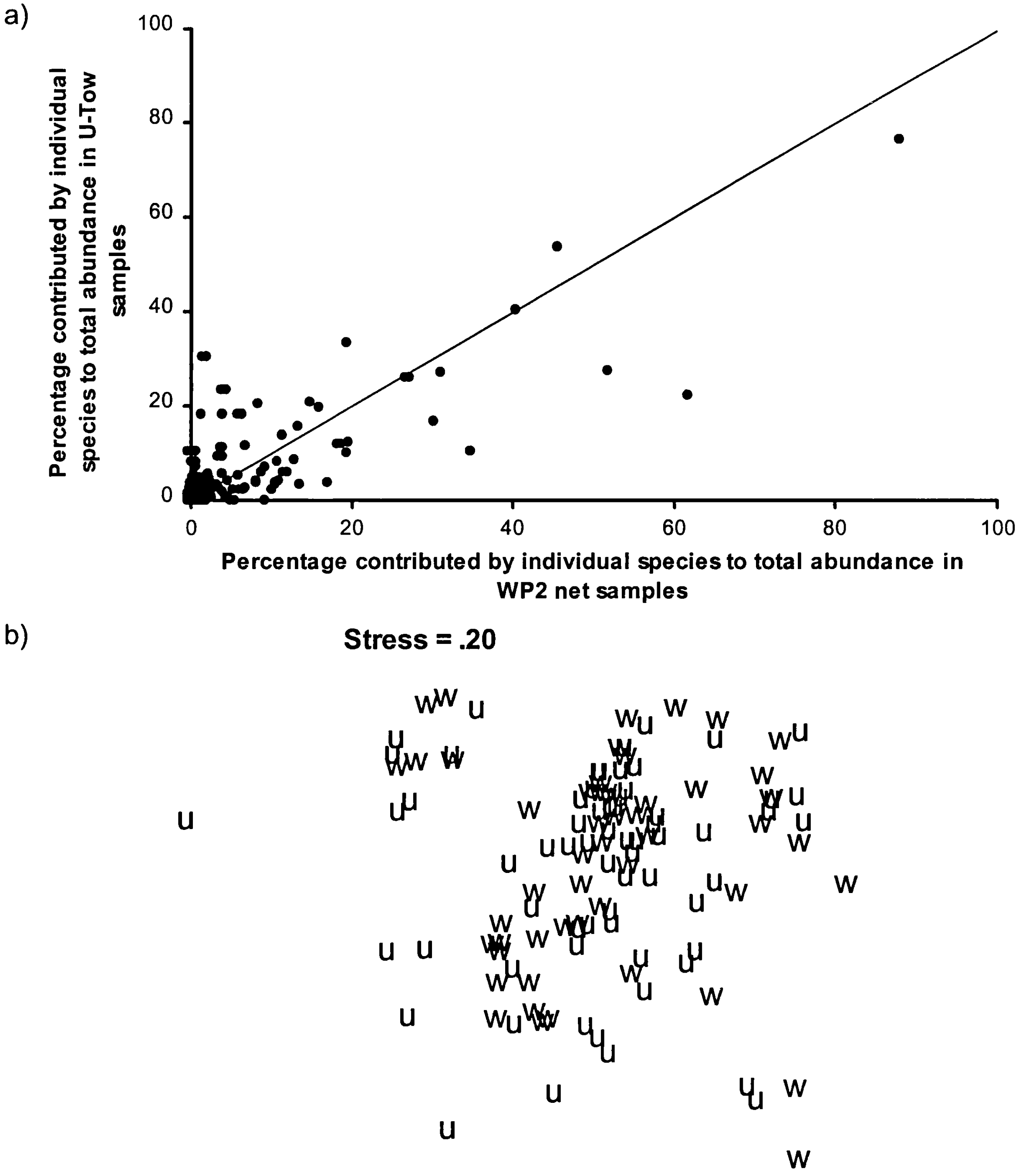

Fig. 2.6 Comparison between percentages contributed by individual species to total abundance from samples taken with the U-Tow (U) and WP2 net (W). (a) shows a scatter plot with line of equivalence. (b) shows a non-metric MDS plot of all samples based on the rank order of sample similarities.

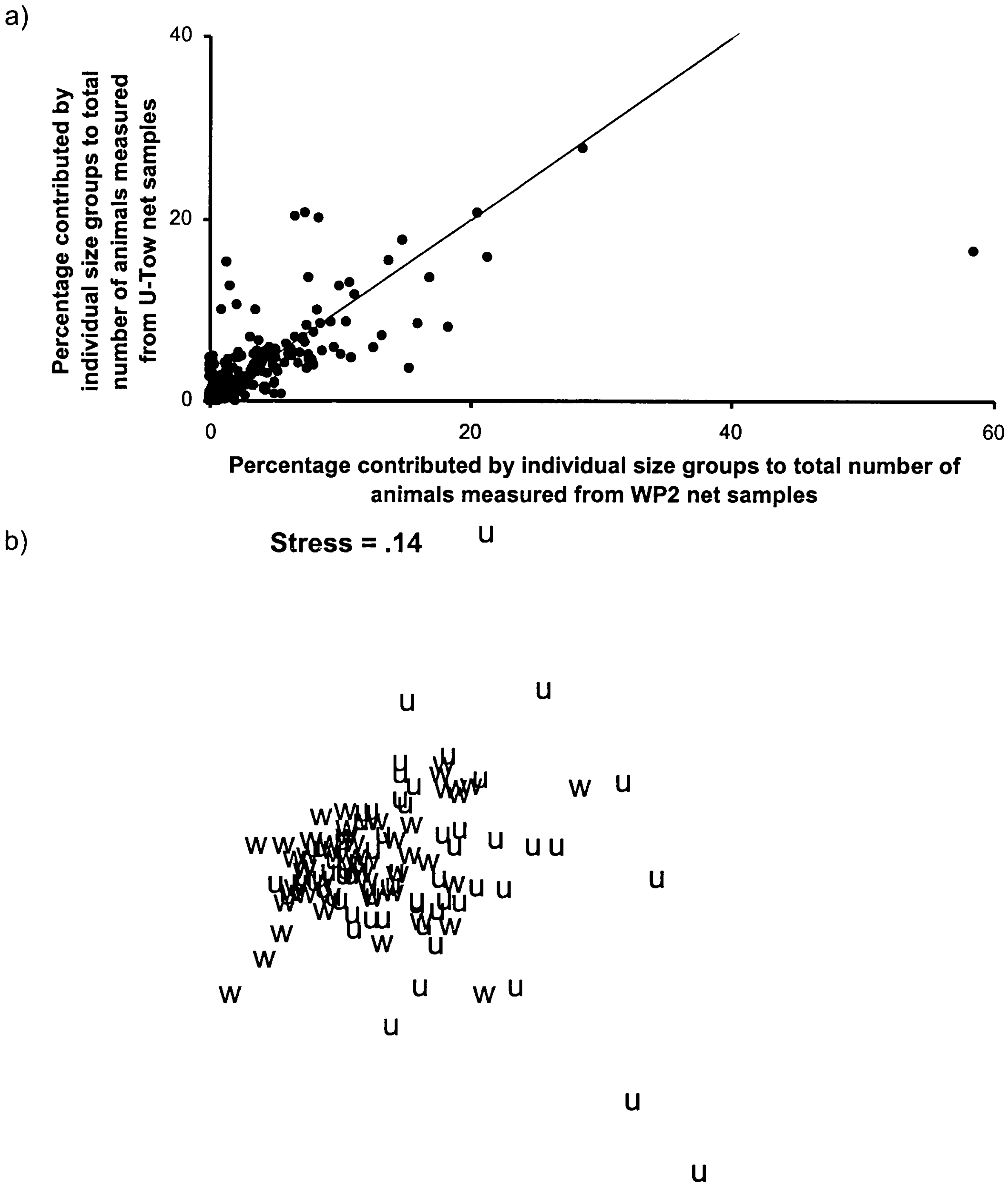

Fig. 2.7 Comparison between percentages contributed by individual size groups (see methods) to total number of animals measured from samples taken with the U-Tow (U) and WP2 net (W). (a) shows a scatter plot with line of equivalence. (b) shows a non-metric MDS plot of all samples based on the rank order of sample similarities.

analysis with p-value of 0.39 (Global R = 0.002).

Discussion

Data from any sampler may, broadly speaking, be internally consistent (e.g. the CPR) but combining or comparing data from other samplers is not possible unless the performance of that sampler has been thoroughly investigated. However, all too frequently, this important component of sampling is ignored and rigorous intercomparisons are hard to find in the literature.

One of the most common parameters investigated in zooplankton studies is the abundance of different species (numbers.m^{-3}). In this investigation it is obvious that the U-Tow seriously underestimates levels of abundance (Figure 2.2a) even after a ln(abundance + 1) transformation to reduce the effect of any skewing by unusually high measures of abundance (Figure 2.2b). There are several potential reasons that could lead to differing estimates of absolute abundance. The first consideration is the patchiness of plankton. The long tows of the U-Tow mean that patches of plankton will be integrated to give an estimate of average abundance. On the other hand, when sampling with the net, the samples may come entirely from a very dense or a very sparse patch of plankton. If this were the case, one would expect occasions where the U-Tow greatly overestimated abundance compared to the WP2 net but overall levels of abundance in the two nets would be the same. However, this was not the case since the U-Tow is always underestimating abundance (Figure 2.2).

Further variation could be introduced by the extrusion of smaller plankton through the mesh and avoidance of the sampler by the larger and more mobile animals. It is generally expected that extrusion will be higher in high-speed samplers due to the higher water pressures pushing animals through the mesh. In contrast, avoidance will be lower in high-speed samplers due to the animal's speed not being sufficient to escape. However, small inlet apertures are also associated with increased avoidance as the distance that has to be crossed to escape the sampler is so much smaller (Clutter and Anraku, 1968). In this case, extrusion and avoidance cannot explain the discrepancy between the U-Tow and WP2 nets. Firstly, there is no difference in percentage species composition relative to total abundance (Figures 2.5a and b), whereas you would expect to find less of the smaller species in the U-Tow compared to the WP2 net due to increased extrusion, and also less of the larger species in the net suffering most from avoidance. Secondly, and most obviously, there is no difference in the size structure of the samples (Figures 2.6a and b). Thus, despite the much increased speed and reduced inlet aperture, there appears to be no increase in extrusion or avoidance in the U-Tow relative to the WP2 net.

An additional consideration for deriving absolute abundance is the filtration efficiency of the samplers, which decreases as the mesh clogs, and the measurement of the flow rates. Filtration efficiency is defined as the percentage of the water presented to a sampler that is filtered (UNESCO, 1968). A drop in efficiency causes a larger acceleration front that is more easily detected by animals. Consequently, this could cause an increase in avoidance. If flow is underestimated, the volume of water filtered will be underestimated and, therefore, the measure of abundance will be overestimated. It is possible that, due to the lack of flowmeter on the PSM, the volumes of water filtered in samples from the Irish Sea tows were overestimated resulting in an underestimation of abundance. However, a one-way ANOVA, performed on the average ratios of U-Tow abundance to WP2 net abundance, showed no significant differences between tows from Swansea Bay, the North Sea or the Irish Sea ($F = 1.575$, $p > 0.05$), i.e. our assumption of flow rates through the PSM when no flowmeter was fitted are probably valid.

Pumping experiments in the laboratory resulted in an average 29.04% of animals being retained on the PSM mesh, the rest being found in the outlet water or in other parts of the PSM. The animals were not extruded through the mesh since they were much wider than the mesh size (Nichols and Thompson, 1991), implying that they travelled through the PSM without being retained on the plankton mesh. This would explain why, although there are large discrepancies in abundance estimates, species composition and size structure does not differ between the two samplers. Variations in the tautness of the mesh, which could differ with each tow and between PSMs, could also allow different numbers of animals to pass under the mesh. This could explain the variation in the levels of discrepancy between the WP2 net and the U-Tow. In a recent comparison between CPR data and that derived from WP2 nets, it has been shown that levels of abundance were much lower in the CPR (Clark *et al.*, 2001b). It therefore seems to be a general feature that high speed samplers may underestimate zooplankton abundance. It is widely known that for many samplers performance may vary from deployment to deployment due to changes in conditions, e.g. particle abundance in the Nansen net (Hernroth, 1987) and the OPC (Sprules *et al.*, 1998). It is also possible that some of the variation is caused by differences in the performance of the WP2 net, although this has been shown to be relatively stable (UNESCO, 1968).

Evidence suggests that if the average abundance from U-Tow samples, expressed as a percentage of abundance from WP2 net samples, is low at the beginning of a tow it will also be low at the end of a tow, and vice versa. Therefore, it is probably justifiable to assume a linear relationship of sampling performance within a tow.

The main conclusion from this study is that the U-Tow cannot be the only sampler used for investigations that require accurate measures of abundance or, therefore, biomass. It is necessary to take samples with another sampler, such as the WP2 net, at the beginning and end of a tow to calibrate the results from the U-Tow. However, it would be perfectly acceptable to use the U-Tow in studies based on the species composition and size structure of plankton communities. The U-Tow would be an ideal tool to use between sampling stations to identify where changes in plankton communities occur.

Conclusions

- The average total zooplankton abundance estimated using U-Tow samples was always markedly lower than that using WP2 net samples, and was very variable within and between tows.
- Laboratory trials showed that on average 29% of animals (too large to be extruded through the mesh) pumped through the PSM were retained. This implies that water is passing through the PSM without passing through the mesh.

- Samples from the U-Tow and WP2 net gave significantly similar measures of species composition and size structure.
- The U-Tow cannot be used for studies that require accurate measures of abundance unless additional samples are taken with another sampler, such as the WP2 net, to calibrate the U-Tow results.
- The U-Tow would be an ideal tool to use between sampling stations to identify where changes in plankton communities occur.

CHAPTER 3

Biomass versus abundance for investigating mesozooplankton community size structure

Abstract

The use of size-fractionated measures of biomass and abundance, as a measure of zooplankton community size structure, was investigated to make conclusions on the most useful method. This was done using field collected data, theoretical models of different sampling scenarios, and published data. The results of this study show that the two methods often lead to different conclusions and that, in general, the use of size-fractionated abundance will yield a more sensitive and less variable measure.

Introduction

Zooplankton play an essential role in the functioning of marine ecosystems as they form a link in pelagic food webs between producers and secondary consumers. The amount of zooplankton available as food to fish larvae, especially in the first few weeks of their life, is believed to determine survival of larvae and hence the strength of the fish year class. This has major implications in fisheries biology (Cushing, 1975). Zooplankton are also important in regenerating nutrients, and transporting nutrients from the surface to the deeper layers of the sea through Diurnal Vertical Migration (DVM) (Hays *et al.*, 1997a; Zhang and Dam, 1997).

The assessment of the abundance, species composition and size distribution of mesozooplankton is a fundamental goal of biological oceanography (Greene *et al.*, 1998a; Mitson *et al.*, 1996; UNESCO, 1968). The size structure of zooplankton communities is an important parameter since organisms of different sizes play different roles in biogeochemical cycling and trophic interactions. For example, small zooplankters graze more per unit biomass than larger organisms (Peters and Downing, 1984). Furthermore, the magnitude of nutrient regeneration and transport will be related to the size structure, taxonomic composition and metabolic rates of the zooplankton community (Le Borgne and Rodier, 1997). The trophic cascade hypothesis (Pace *et al.*, 1999; Vanni and Findlay, 1990) describes how phytoplankton and nutrients at the base of the food web, and hence primary production, can be governed by predatory effects on the size and composition of zooplankton. Similarly, factors affecting predator-prey relationships, such as encounter rate, prey avoidance ability and handling time, are also strongly influenced by size

(Gardner, 1981; Wahlström *et al.*, 2000). Many models describing the structure and function of pelagic communities are based on allometric relationships between body size and biological processes (e.g. food intake, growth and metabolism) (Kerr, 1974; Platt and Denman, 1977; Platt and Denman, 1978; Sheldon *et al.*, 1977) and the distribution of sizes within animal groups in the community (Dickie *et al.*, 1987).

Given the importance of the zooplankton community, it is essential that the size structure can be measured accurately so that the influence of environmental, biological and anthropogenic variables can be identified. Generally, for simplicity, zooplankton community ecologists have focused on measuring the abundance or biomass of animals falling within size classes to describe patterns of community structure, production and nutrient recycling (Dam *et al.*, 1993; Morales *et al.*, 1991; Morales *et al.*, 1993; Roman *et al.*, 2000; Roman *et al.*, 1995). The measurement of both the abundance and biomass of zooplankton populations have inherent problems associated with the spatial and temporal variability of the zooplankton, especially in the larger size-fractions where animals are rarer (Echevarría *et al.*, 1990). In addition, biomass measurements can be greatly skewed by the occurrence of a single large animal, or detritus, making patterns difficult to distinguish (Rojo and Rodriguez, 1994).

The aim of this study is to investigate the use of size-fractionated measures of biomass and abundance, and make conclusions on the most accurate method for determining zooplankton community size structure. This has been done using field collected data, theoretical models of different sampling scenarios, and published data.

Methods

Field sampling

Sampling took place in Swansea Bay (December 1997, April, May, September and November 1998), the North Sea (February 1998), and the Irish Sea (June and July 1998). Five-minute WP2 net tows at 9m, made possible by using a real time depth sensor, were taken in Swansea Bay. Vertical WP2 net hauls, to a depth of between 10m and 50m depending on the water depth, were taken in the North Sea and Irish Sea. In all cases, a 56cm diameter WP2 net fitted with 200μm mesh, a General Oceanics flowmeter and Aladin Pro dive computer, for an accurate reading of depth, was deployed.

After each deployment, samples were immediately split into two. Half was preserved in 4% borax buffered seawater formaldehyde for subsequent sizing. Length and width of at least a hundred animals of a size that is caught 95% quantitatively by a 200μm mesh, using mesh selection curves calculated by Nichols and Thompson (1991) were measured using a calibrated eyepiece graticule. Animal widths were sorted into groups corresponding to 200-500μm, 500-1000μm and 1000-2000μm.

The other half of the sample immediately underwent size-fractionation and dry weight analysis. The zooplankton were wet-sieved through 200μm, 500μm, 1000μm and 2000μm meshes. These size-fractions were then filtered onto 47mm ashless filters, washed with distilled water to remove salt, placed in a drying oven at 50°C for 48 hours and weighed.

Models of different sampling scenarios

The initial model was based on a virtual population of 1000000 animals, with 900000 animals in the 200-500μm size-fraction, 90000 in the 500-1000μm fraction and 10000 in the 1000-2000μm fraction. The coefficient of variation (i.e. CV = (SD / mean) × 100, where CV is coefficient of variation and SD is standard deviation) associated with sampling the populations in each size-fraction were calculated from samples taken in Swansea Bay, where ten samples were taken at the same position on three different occasions. The respective coefficients of variation for the 200-500μm, 500-1000μm and 1000-2000μm size-fractions were 5%, 15% and 30%. The same samples were also used to determine that the variation in abundance was normally distributed using a Kolmogorov-Smirnov test for goodness of fit ($D = 0.14$, $df = 10$, $p = 0.200$).

The first step was to investigate whether the proportion of the population sampled made any difference to the results obtained, so models were run for sampling 100%, 75%, 50%, 25%, 10%, 5%, 1%, 0.1% and 0.01% of the population. In each case, the mean number of animals expected in each size-fraction was calculated (e.g. when sampling 75% of the population, the mean number of animals caught in the 200-500μm fraction would be: $(75 \times 900000) / 100 = 675000$). The expected standard deviation of animals caught in the 200-500μm fraction was then calculated using this expected mean and the coefficient of variation calculated previously. Sampling was simulated by generating a random number from a normal distribution with the expected mean and standard deviation calculated. Each random number represents the abundance of animals in that size fraction of a simulated sample. This process was repeated 10000 times, for each size fraction, to represent 10000 simulated samples for each size fraction. Biomass was calculated by multiplying the abundance by an average biomass measure for each size-fraction. This was obtained from the average length of animals in each size-fraction using the length-weight regression for total copepods from Uye (1982). The average length or average biomass was calculated for each 'sample' using the formulae:

Average length: $W = \sum_{S=1}^{S=i} ((M_L + M_U) / 2) \times P_S$

$$L = W \times 3$$

Average biomass: $B = \sum_{S=1}^{S=i} b \times P_S$

where W is the average width of animals in the sample, S is the size fraction, M_L is the lower mesh size for the size fraction, M_U is the upper mesh size for the size fraction, P_S is the proportion of total animals or total biomass in that size fraction, L is the average length of animals in the sample, B is the average biomass of animals in the sample, and b is the average biomass of animals in the appropriate size fraction. W was then converted to an average length by assuming a typical width:length ratio for mesozooplankton of 1:3 (Herman *et al.*, 1992). This process is shown schematically in Figure 3.1.

The next step was to simulate sampling populations with different size structure. As the coefficients of variation were calculated from samples where about 100 animals were measured, it was decided to use simulated samples of the same size. To this end, the same random number generation process was repeated with the population size structures shown in Table 3.1. The average lengths from a sample were then tested against all other samples using an independent samples t-test to find populations that significantly differ, and the same was done for the biomass samples to see if differences occurred between the same populations.

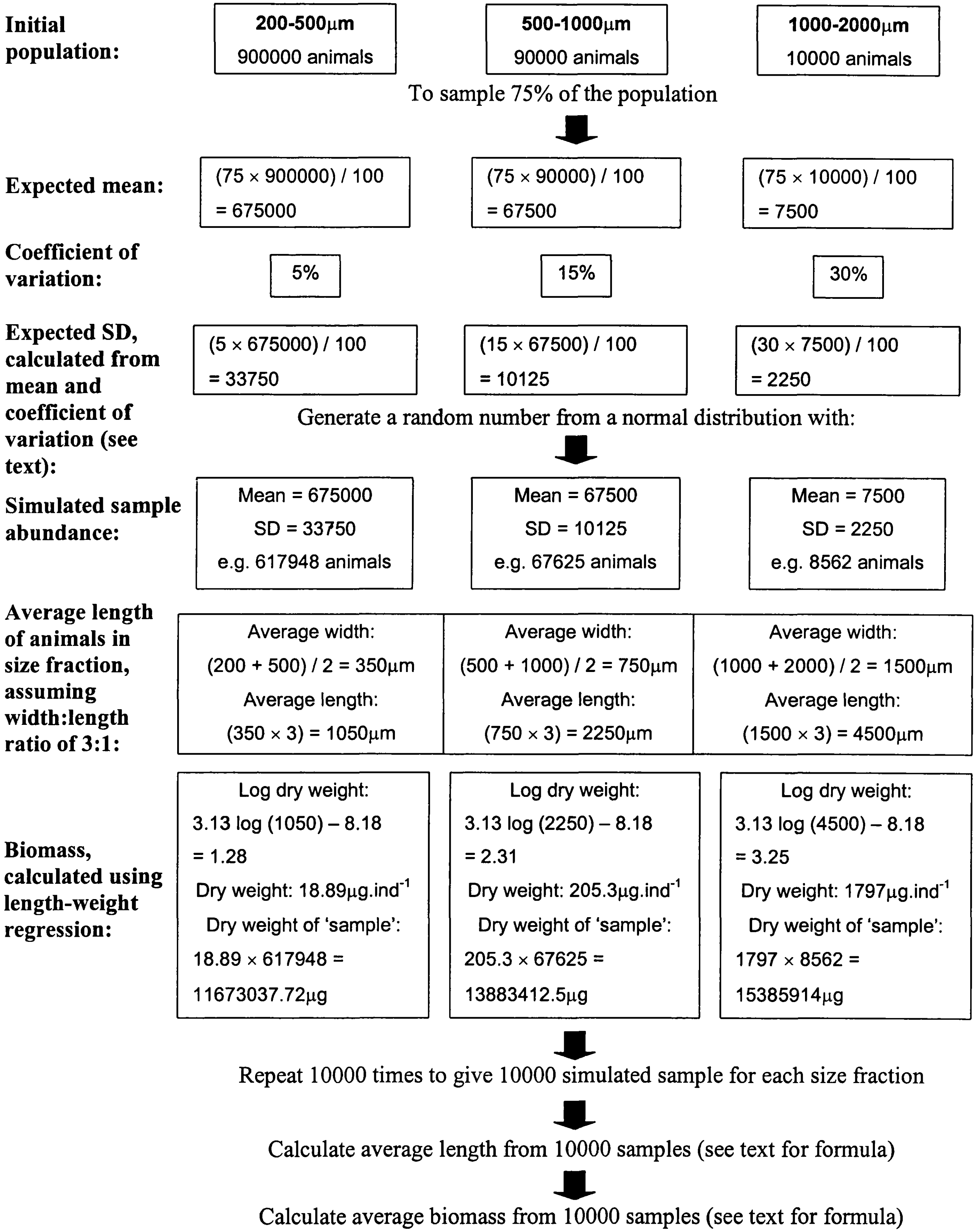

Fig. 3.1 Schematic illustration of simulated sample generation (SD = standard deviation)

200-500μm	**500-1000μm**	**1000-2000μm**
90	10	0
90	9	1
90	0	10
80	10	10
70	20	10
70	10	20
60	20	20
50	30	20
50	25	25
50	20	30
34	33	33
30	40	30
30	30	40
25	50	25
25	25	50
20	40	40
10	50	40
10	40	50
0	90	10
0	50	50
0	10	90

Table 3.1 Average population size structures used to generate random samples for models.

Published data

Three studies were used for this part of the investigation. Brooks and Dodson (1965) were the first study to formulate the Size Efficiency Hypothesis, which describes the size selective effects of fish predation and competition, from an investigation into the numbers of animals falling into different length classes. Dam *et al.* (1993) investigated the trophic role of mesozooplankton using size-fractionated dry weight measurements in the North Atlantic, and Nielsen and Munk (1998) measured zooplankton biomass ($mgCm^{-2}$) at the Fisher Banks in the North Sea.

Data from Brooks and Dodson (1965) were taken from their Figure 4, and converted to dry weight using the total copepod length-weight regression from Uye (1982). Data from Dam *et al.* (1993) were taken from their Figure 1, and converted to abundance by dividing by an average carbon value calculated using the Uye (1982) equation and the Wiebe (1988) relationship between dry weight and carbon. Data from Nielsen and Munk (1998) were taken from their Table 1, and converted to abundance in the same way.

Results

In the literature there are a number of studies where the average body size of a sample is characterised by sieving the sample through a series of meshes, and then calculating the slope of a line fitted through the cumulative biomass in each size fraction against the $\log_{10}$ of the mesh size (Magnesen, 1989b; Seda and Dostalkova, 1996). However, a quick comparison of this method and using the average length in a sample revealed that the latter method represented the actual size structure better (Figure 3.2). For example, the slope index indicates that animals are larger in a sample where all animals fall into the 500-1000μm fraction than a sample where all animals fall into the 1000-2000μm fraction. In addition, average length is an easier index to visualise, and therefore understand what is happening.

Field sampling

Figure 3.3 shows the average length (μm) and the average biomass (μg dry weight) of animals in samples from Swansea Bay, the North sea and the Irish Sea at different times of the year. In general, the patterns of change in average length or biomass are similar. However, there are exceptions such as the December sample from Swansea Bay, which has one of the smallest average lengths of animals, but the highest average biomass. Also, the February North Sea sample has a smaller average length of animals than the June Irish Sea sample, but a higher average biomass value. A one-way ANOVA finds a significant difference in the three sample areas with respect to average animal length ($F_{2,64} = 9.6$, $p < 0.001$) but not with respect to biomass ($F_{2,64} = 0.05$, $p = 0.952$).

Models of different sampling scenarios

There were no significant differences in the estimates of average length ($F_{8,89991} = 1.1$, $p = 0.335$) or average biomass ($F_{8,89991} = 0.7$, $p = 0.649$) obtained when sampling different proportions of the zooplankton 'population'. When the population size structures were

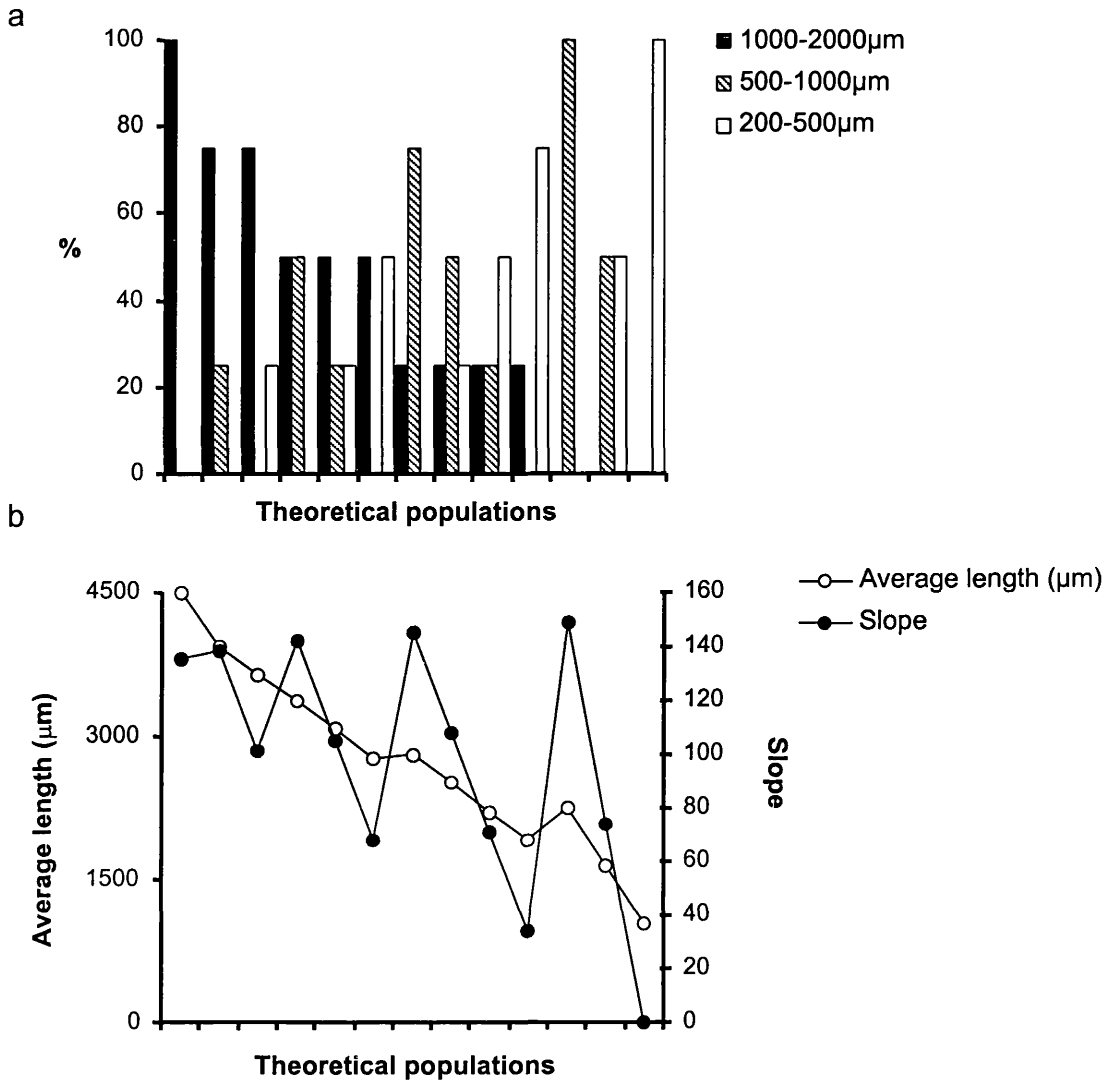

Fig. 3.2 Theoretical zooplankton community size structure represented as percentage of animals in 200-500μm, 500-1000μm and 1000-2000μm size fractions (a), and the average length (μm) and slope (see text) calculated from these size structures.

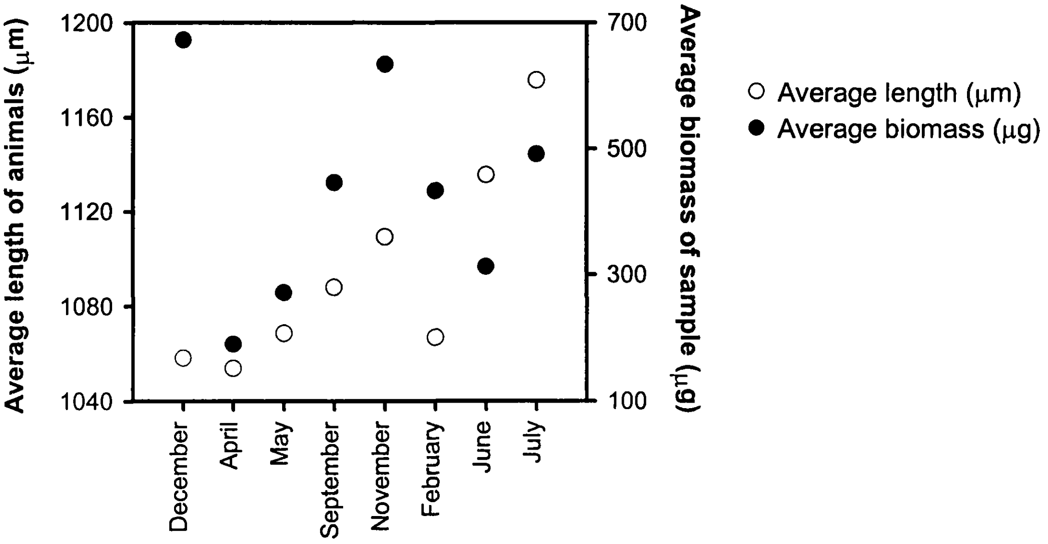

Fig 3.3 The average length (µm) and biomass (µg) of animals in samples from Swansea Bay (December, April, May, September, November), the North sea (February) and the Irish Sea (June, July).

altered and tested against each other, most samples were significantly different from each other using an independent samples t-test. However, there were a few exceptions (Table 3.2). Overall, when using the average length significant differences were found between 92 out of 94 populations, whilst when using the average biomass significant differences were found between 77 out of 94 populations.

Published data

Brooks and Dodson (1965) investigated the length of zooplankton in Crystal Lake before and after the introduction of the planktivorous fish *Alosa aestivalis*. They found that the modal length decreased from 0.8mm to 0.3mm in the presence of the fish. Figure 3.4a shows the results from their study using the numbers of animals in length classes, whereas figure 3.4b shows the results after they have been converted to dry weight in the same length classes. Although the conclusions made from both sets of data would be the same, it is much more clearly seen when using the numbers of animals in the length classes.

Dam *et al.* (1993) measured biomass ($mgCm^{-3}$) in 0.2-0.5mm, 0.5-1.0mm and 1.0-2.0mm size-fractions for day and night zooplankton samples. Figure 3.5 shows the increase seen in both average biomass and average animal length at night compared to during the day. An independent samples t-test found this difference to be significant when considering average biomass ($t_9 = -3.2$, $p < 0.05$) but not when considering average length ($t_9 = -1.0$, $p = 0.36$).

Nielsen and Munk (1998) investigated zooplankton biomass across the front off the Jutlandic coast in the size classes 460-560μm, 560-700μm, 700-880μm, 880-1120μm a)

	34,33,33
30,40,30	0.307
25,50,25	0.254

b)

	80,10,10	60,20,20	50,30,20	50,25,25	50,20,30	34,33,33	30,30,40	20,40,40	10,50,40
90,0,10	0.062	0.532	0.247	0.418					
80,10,10			0.452						
70,10,20					0.701				
60,20,20			0.063	0.847					
20,40,40						0.856			
30,30,40						0.063			
10,50,40						0.465		0.586	
10,40,50							0.377		0.189
0,50,50						0.560	0.202	0.446	

Table 3.2 P-values of non-significant independent sample t-tests between average lengths (a) and average biomass (b) from samples with population size structure represented as percentage of animals in 200-500μm, 500-1000μm and 1000-2000μm fractions

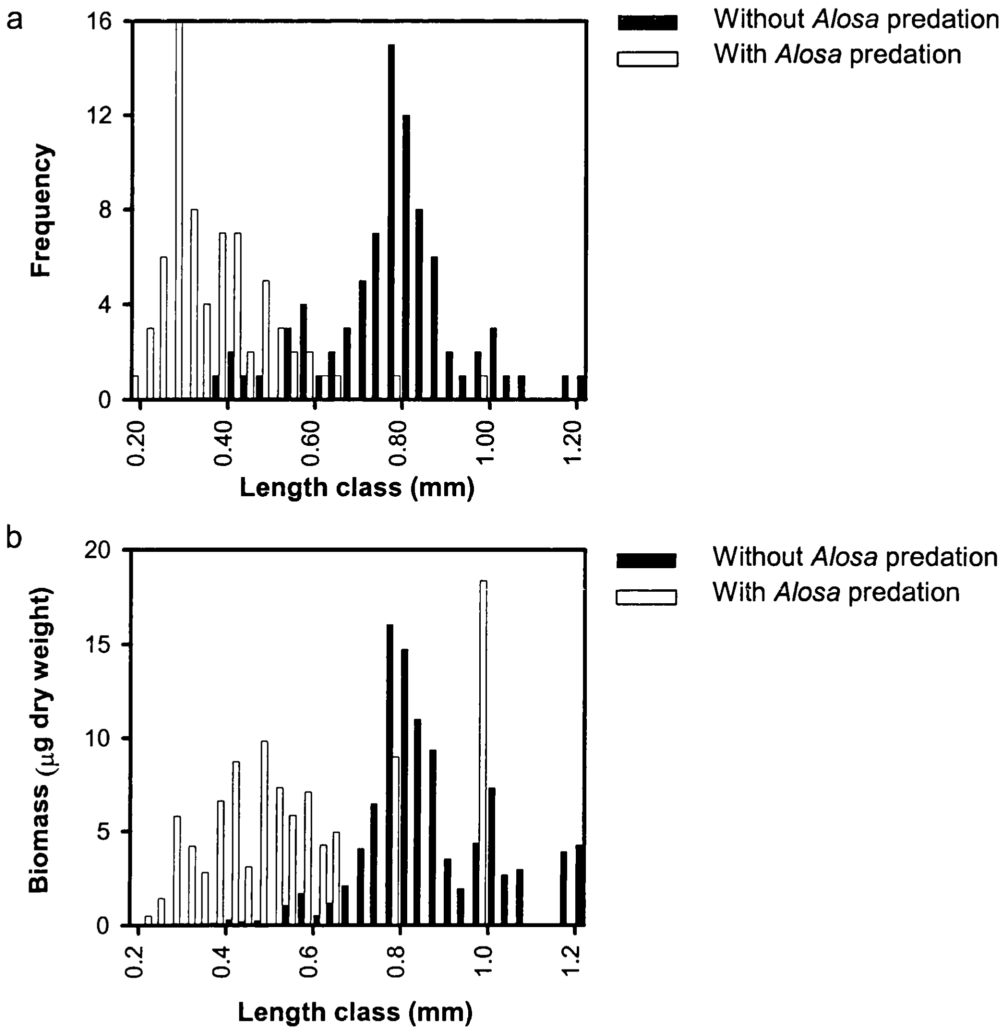

Fig 3.4 Zooplankton numbers (a) and biomass (b) distributions among length classes from lakes with and without *Alosa* predation. Data taken from Brooks and Dodson (1965).

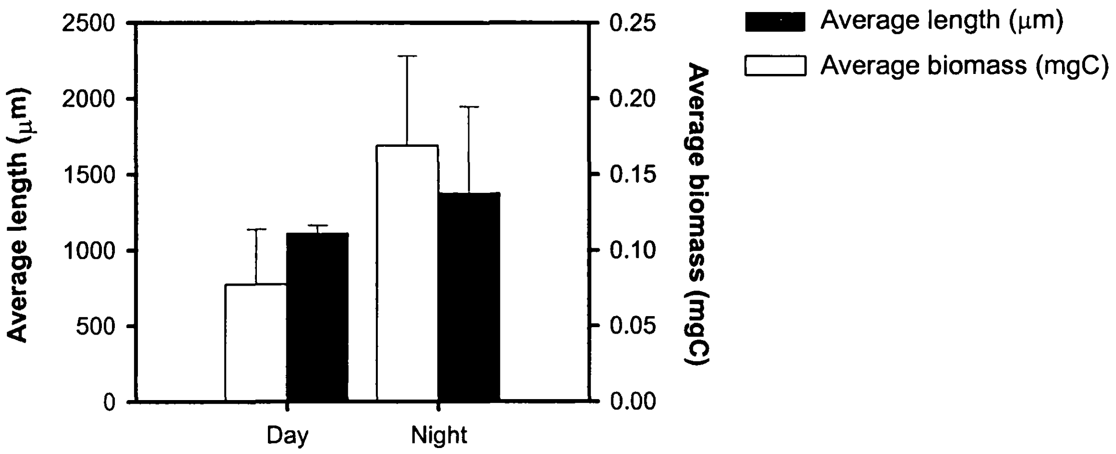

Fig 3.5 The average length (μm) and biomass (mgC) of animals in samples taken at night and during the day in the North Atlantic. Data taken from Dam *et al.* (1993).

and >1120μm. The open ended nature of the last size class means that it is impossible to calculate an average length of animal expected, and therefore this data was ignored. Figure 3.6 shows the increase seen in both average biomass and average animal length in coastal water compared to frontal water. An independent samples t-test found this difference to be significant when considering average length ($t_3 = -4.3$, $p < 0.05$) but not when considering average biomass ($t_3 = -2.7$, $p = 0.08$). When comparing the North Sea data from Nielsen and Munk (1998) with the North Atlantic data from Dam *et al.* (1993), there is another discrepancy in the conclusions made when using biomass or length. An independent samples t-test found the sampling areas significantly different when considering average length ($t_{14} = -4.3$, $p < 0.001$) but not when considering average biomass ($t_{14} = 1.0$, $p = 0.32$).

Discussion

Several studies have found zooplankton biomass to be an inadequate descriptor of changes in phytoplankton (Elser *et al.*, 1987) and phosphorous-chlorophyll *a* relationships (Pace, 1984), these factors being better related to the taxonomic composition of zooplankton. Others have found that different elements of a community relate to either total biomass or size structure of zooplankton. For example, Currie (1999) found that zooplankton size structure, rather than biomass, was related to the trophic status of the water and piscivore presence; but that algal biomass was related to zooplankton biomass and not size structure. Similarly, Cyr (1992) found zooplankton grazing rates to be related to biomass but not size structure, although taxonomic

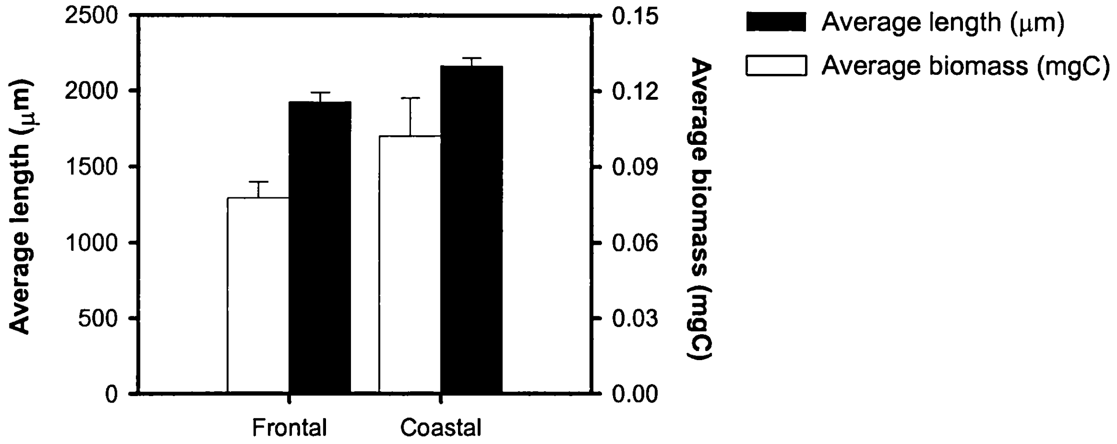

Fig 3.6 The average length (μm) and biomass (mgC) of animals in samples from frontal and coastal water in the North Sea. Data taken from Nielsen and Munk (1998).

composition was also a significant factor in explaining grazing rates. Therefore, the method of defining zooplankton size structure is obviously important.

The results from each aspect of this study demonstrate the variability in results obtained from using average zooplankton length or biomass. The method of getting biomass data used in this field study means there will be problems associated with detrital contamination. This could explain the high average biomass values found in samples from Swansea Bay and the North Sea with small average length values. Both these sampling dates occurred in periods of rough weather, which can increase problems with detritus and suspended sediments. However, the models of different sampling scenarios is free of such problems, and yet still shows average length to be, on the whole, a more sensitive measure of zooplankton size than biomass. The very large number of replicate 'samples' used in the model decreases problems with zooplankton spatial variability that would be found in real sampling. Obviously, it would be impossible to take 10000 replicate samples in a real situation and, for this reason, the models used may have been over sensitive. However, the nature of biomass measurements mean that the value is heavily influenced by the large size-fraction which, due to the lower numbers involved, is the most variable size-fraction (Echevarría *et al.*, 1990; Rojo and Rodriguez, 1994). On the other hand, values of average length, calculated using the abundance in each size-fraction, is heavily influenced by the small, least variable, size-fraction. This is probably the reason for the significant day/night differences in average biomass, but not average length, found in the data from Dam *et al.* (1993). At night larger animals come to the surface but the proportion of large to small animals is still very low, and does not result in a significant increase in average length. However, because a small increase in the length of an animal can lead to a proportionately much larger increase in biomass, a small increase in the numbers of large animals will heavily influence the average biomass leading to the significant difference seen in these results. In the results from Nielsen and Munk (1998), and when comparing their North Sea data to the North Atlantic data from Dam *et al.* (1993), the difference in biomass results are probably masked to some degree by biomass variability and hence is not significant.

Despite these minor problems, it is obvious from this study that it is essential to choose the method of describing size structure very carefully. Clearly, the choice you make depends on the aim of the study. There are two main types of study that look at the size structure of communities: those looking to understand community production dynamics and yield (Boudreau and Dickie, 1989; Boudreau and Dickie, 1992; Carpenter *et al.*, 1987; Dickie *et al.*, 1987; Ikeda, 1985), and those looking to understand factors that affect individual body sizes and patterns of community organisation (Bogdan and Gilbert, 1984; Brooks and Dodson, 1965; Munk, 1997; Omori, 1997; Suchman and Sullivan, 1998; Twombly and Tisch, 2000; Warren *et al.*, 1986). Studies looking at community production dynamics will obviously need to measure biomass as the processes involved, such as metabolism and respiration, are a function of body weight (Dickie *et al.*, 1987; Platt and Denman, 1977). However, the results of this study show that, when trying to understand factors affecting size structure, the use of size-fractionated abundance will yield a more sensitive and less variable measure.

Conclusions

- A quick comparison of the slope index method (Seda and Dostalkova, 1996) and average length of animals in a sample as a measure of zooplankton size found the latter to be more accurate.

- From field sampling the use of average length or average biomass, to describe zooplankton size, yielded similar results except for one occasion where increased detritus and suspended sediment probably produced inaccurate biomass results.
- From models of different sampling scenarios, where population size structures were altered and tested against each other, the use of average length as the measure of size structure found significant differences between a greater number of populations than the use of average biomass.
- From published data it is concluded that biomass measurements are heavily influenced by the number of animals in the large size fraction which tends to be more variable due to the lower numbers involved. As such, differences in size structure are often masked whereas when comparing average length measurements (which are influenced by the small, least variable, size fraction) differences in size structure are seen more clearly.
- It is essential to choose the method of describing size structure very carefully to reflect the aims of the individual study.

CHAPTER 4

Mesozooplankton community structure along a salinity gradient in the Baltic Sea

Abstract

The Baltic Sea has a known salinity gradient from more saline water in the south to less saline water in the north. The aim of this study was to test the hypotheses that there are changes in mesozooplankton biomass associated with salinity, the biomass ratio of copepods to cladocerans decreases with salinity, and there are patterns in species composition associated with changes in salinity. The only changes in zooplankton size seen in this study seem to be associated with DVM behaviour of the animals, and not the salinity gradient in the Baltic Sea. However, cladoceran and copepod biomass was positively correlated with salinity. The decrease in biomass ratio of copepods to cladocerans with salinity was only found in samples with salinity less than 7.06‰. There were no changes in diversity associated with salinity. However, there were significant changes in the patterns of species abundance with the salinity gradient.

Introduction

Zooplankton play a vital role in the pelagic food web by determining the amount of primary production that is converted to a form accessible to top predators (Lenz, 2000; Ojaveer *et al.*, 1998) and hence have major implications in determining strength and distribution of fish stocks (Cushing, 1975). As most marine species have planktonic life stages, or depend on zooplankton as a source of food at some stage, changes in the zooplankton biomass and community structure can have widespread effects on the whole marine ecosystem (Conversi and Hameed, 1998; Skjoldal *et al.*, 2000). Major factors driving variation in the zooplankton community will be changes in the physical environment. For example, temperature and salinity tolerances can determine the horizontal and vertical distributions of zooplankters (Hernroth, 1981).

There have been many observations concerning the effects of salinity on zooplankton communities, although formulation of these observations into generally applicable hypotheses is scarce. With a decrease in salinity, Viitasalo *et al.* (1995a) found an increase in total biomass and that of cladocerans and many dominant species, whilst Vuorinen *et al.* (1998) detected a decrease in the ratio of copepods to cladocerans. Flinkman *et al.* (1998) stated that numbers of animals of larger biomass (greater than 20μg wet weight) also decreased with salinity, although there was no decreasing trend in total mesozooplankton biomass. Similarly, Soetaert and Van Rijswijk (1993), Laprise and Dodson (1994), and Lopes (1994) all found that a salinity gradient explained most variation in zooplankton species composition, and Flinkman *et al.* (1992) discovered a decrease in the diversity of planktonic species along a gradient from high to low salinity. Vuorinen and Ranta (1987) studied long-term variations in zooplankton in the Northern

Baltic Sea and concluded that, although most mesozooplankton taxa responded either positively or negatively to salinity change, the changes were not distinguishable from random fluctuations. Viitasalo *et al.* (1990) stated that salinity was the most influential factor for crustacean zooplankton living mostly below the thermocline, whilst temperature and nutrients were more important for those living above it. However, there have also been studies that have found no relation between salinity and zooplankton species abundance (Pedersen *et al.*, 1995) or biomass (de Lafontaine, 1994).

The Baltic Sea is an ideal environment to examine the interaction between salinity and zooplankton community structure since there is a gradient in salinity from 1-4‰ in the north to 7-8‰ in the south (Rudstam *et al.*, 1994), and salinity is the most important environmental factor affecting zooplankton in the Baltic (Viitasalo *et al.*, 1990). The Baltic Sea is one of the largest bodies of brackish water in the world, virtually an enclosed sea, with only a narrow connection, the Öresund, to the North Sea. Sporadic saline water pulses enter via this channel forming layers of more saline deep waters. There is also considerable run-off from the surrounding land masses which generates a brackish surface layer (Ehlin, 1981; Kullenberg, 1981). These saline pulses and run-off are, in turn, controlled by climatic factors such as the North Atlantic Oscillation index and westerly winds (Hänninen *et al.*, 2000).

The aim of this study was to collect zooplankton in a consistent manner throughout the Baltic in order to test the following hypotheses: initially, that there are changes in mesozooplankton biomass associated with salinity (Flinkman *et al.*, 1998; Viitasalo *et al.*, 1995a); secondly, that the biomass ratio of copepods to cladocerans decreases with salinity (Vuorinen *et al.*, 1998); and finally, that there are patterns in species composition associated with changes in salinity (Laprise and Dodson, 1994; Lopes, 1994; Soetaert and Van Rijswijk, 1993).

Methods

Zooplankton samples were collected at a depth of 18m with a U-Tow, a towed body designed to sample continuously over extended spatial scales (Hays *et al.*, 1998) and so overcome effects of zooplankton patchiness. The U-Tow was fitted with a Plankton Sampling Mechanism (PSM), containing 200μm mesh, an electromagnetic flowmeter, and a CTD. Sampling took place between 12 and 19 June 1999. Sunrise and sunset were defined as the time when the elevation of the sun was 0°, and was determined using almanacs (TELONICS Real-Time Satellite Display).

After each deployment, samples were immediately washed off the mesh and preserved in a 4% borax buffered seawater formaldehyde solution. Alternate samples were wet sieved into the size fractions 200-500μm, 500-1000μm, and 1000-2000μm. Using a binocular microscope, the animals in each size fraction were identified, to at least genus for copepods and at least order for other animals, and counted to give measures of abundance for the species present and the size structure of the zooplankton community. The average size of animals in a sample was calculated using the formula:

$$W = \sum_{S=1}^{S=i} ((M_L + M_U) / 2) \times P_S$$

where W is the average width of animals in the sample, S is the size fraction, M_L is the lower mesh size for the size fraction, M_U is the upper mesh size for the size fraction, and P_S is the proportion of animals in that size fraction. W was then converted to an average length by assuming a typical width:length ratio for mesozooplankton of 1:3 (Herman *et al.*, 1992). Biomass was calculated using wet weight values ($\mu g.ind^{-1}$) from Flinkman *et al.* (1998).

Bray-Curtis similarity coefficients between individual sample measures of species composition (proportion contributed by each species to total abundance) were calculated using the CLUSTER routine from Plymouth Routines In Multivariate Ecological Research (PRIMER) (Carr, 1997; Clarke and Warwick, 1994). These were mapped as non-metric multi-dimensional scaling (MDS) plots.

Results

There were four individual tows covering a total distance of 665 km (Figure 4.1). Twenty samples were collected, each constituting approximately 18.5 km of sampling. There was a strong relationship between latitude and mean salinity per sample ($F_{1,18} = 85.2$, $r^2 = 0.83$, $p < 0.001$), confirming the salinity gradient from south to north (Figure 4.2). There were also weaker trends with latitude and temperature ($F_{1,18} = 6.4$, $r^2 = 0.26$, $p < 0.05$), and temperature and salinity ($F_{1,18} = 7.4$, $r^2 = 0.29$, $p < 0.05$) (Figure 4.2).

Acartia spp. (mostly *Acartia bifilosa*) were the most abundant constituting 43% of all identified zooplankton. *Evadne* spp., *Temora* spp., and *Pseudocalanus* spp. made up a further 15%. The remainder consisted of, in descending order, *Centropages* spp., bivalve larvae, *Podon* spp., copepod nauplii, *Eurytemora affinis*, *Bosmina* spp., larvaceans (mainly *Fritillaria* spp.), mysids, fish eggs, and *Sagitta* spp. The average length of mesozooplankton from all samples

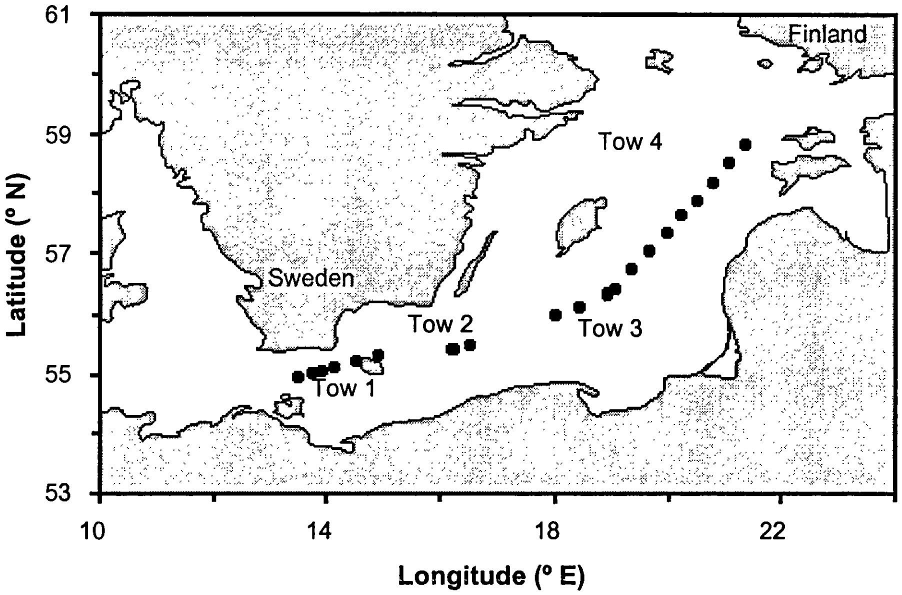

Fig 4.1 Spatial distribution of mesozooplankton samples between Kiel and Helsinki. Filled circles represent the midpoint of each sample.

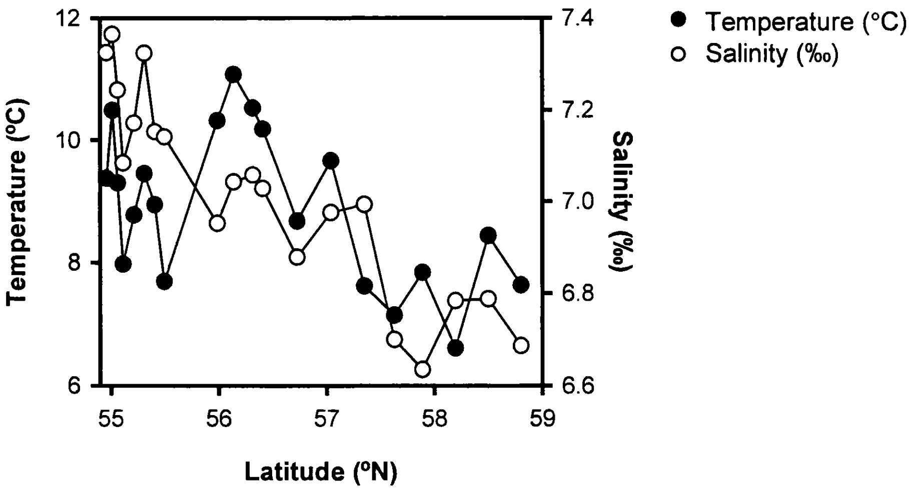

Fig 4.2 Patterns of salinity (‰) and temperature (°C) with latitude from all tows.

was 1.11mm, with the ratio of mean abundance of animals in the size ranges 200-500μm, 500-1000μm, and 1000-2000μm being 1:0.06:0.0002.

There was no significant relationship between salinity and the average length of animals in a sample ($F_{1,18} = 2.0$, $r^2 = 0.10$, $p = 0.173$). The average length of animals from samples taken in daylight hours (mean = 1.10 mm, n = 10, SD = 0.01) was slightly lower than the average length of animals from samples taken during the night (mean = 1.13 mm, n = 10, SD = 0.05), but this was not significant (t-test: $t_{10} = 1.9$, $p = 0.082$).

Log-transformed total copepod biomass ($F_{1,18} = 8.5$, $r^2 = 0.32$, $p < 0.01$) and total cladoceran biomass ($F_{1,18} = 7.0$, $r^2 = 0.28$, $p < 0.05$) were both positively correlated with salinity (Figure 4.3a). There was no relationship between the biomass ratio of copepods to cladocerans and salinity ($F_{1,18} = 0.0$, $r^2 = 0.00$, $p = 0.923$). However, the average biomass ratio of copepods to cladocerans in samples taken during the night (mean = 1.19, n = 10, SD = 0.12) was significantly higher than in samples taken in daylight hours (mean = 1.10, n = 10, SD = 0.06) (t-test: $t_{14} = 2.2$, $p < 0.05$). This was due to the fact that the average log-transformed biomass of copepods in samples taken during the night (mean = 9.62 μg, n = 10, SD = 0.51) was significantly higher than in samples taken in daylight hours (mean = 8.78 μg, n = 10, SD = 0.80) (t-test: $t_{18} = 2.8$, $p < 0.05$), but no such pattern was found for the log-transformed biomass of cladocerans (t-test: $t_{18} = 0.4$, $p = 0.664$). To remove possible effects of Diel Vertical Migration (DVM) behaviour by copepods, the biomass ratio of copepods to cladocerans for day and night samples were standardised separately, by reducing values to zero mean and unit variance, and reanalysed. However, the relationship between ratio of copepods to cladocerans and salinity was still not significant ($F_{1,18} = 0.5$, $r^2 = 0.03$, $p = 0.504$).

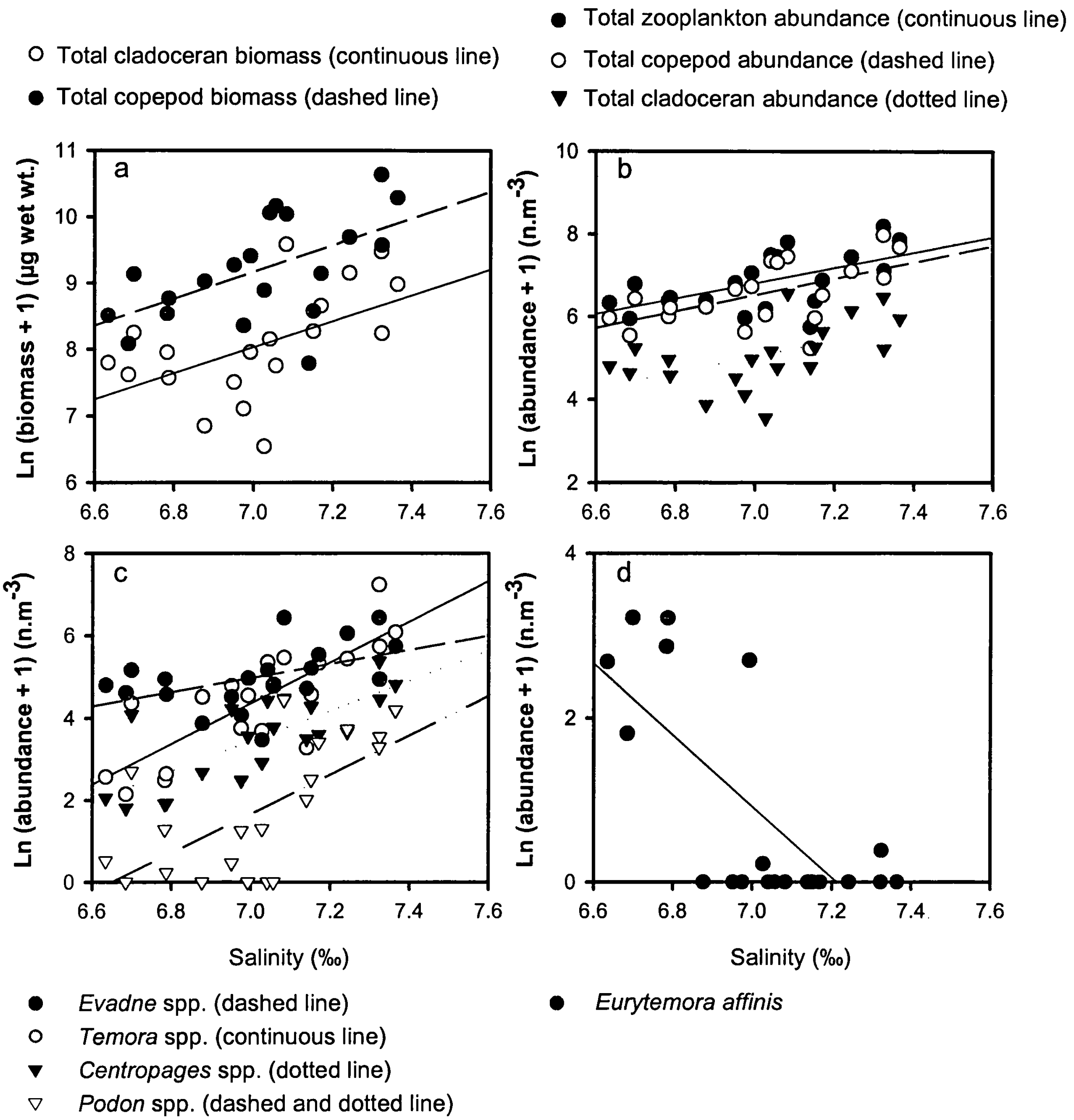

Fig 4.3 Patterns in log-transformed biomass (a) and abundance (b, c, d) change with salinity.

Significant patterns in log-transformed abundance and salinity were found. Total zooplankton, total copepods, total cladocerans (Figure 4.3b), *Evadne*, *Temora*, *Centropages*, and *Podon* (Figure 4.3c) were positively correlated with salinity; whilst *Eurytemora affinis* (Figure 4.3d) was negatively correlated with salinity (also see Table 4.1). There was no significant relationship between salinity and the log-transformed abundance of *Acartia*, *Pseudocalanus*, polychaete larvae, *Sagitta*, *Bosmina*, *Fritillaria*, mysids, and bivalve larvae (Table 4.1).

There were no significant changes with salinity in measures of diversity such as total number of species ($F_{1,18} = 0.0$, $r^2 = 0.00$, $p = 0.941$), richness ($F_{1,18} = 2.2$, $r^2 = 0.11$, $p = 0.151$), the Shannon index ($F_{1,18} = 0.6$, $r^2 = 0.03$, $p = 0.440$), or evenness ($F_{1,18} = 0.6$, $r^2 = 0.03$, $p = 0.455$). When the Bray-Curtis similarity coefficients between all samples were plotted as a non-metric multi-dimensional scaling (MDS) plot, the samples divided into three distinct groups which can be related to the salinity gradient (Figure 4.4a). The average salinity of the groups was 7.23‰ (n = 8, SD = 0.10) for group A, 6.99‰ (n = 6, SD = 0.07) for group B and 6.76‰ (n = 6, SD = 0.13) for group C. These were confirmed as significantly different by a one-way ANOVA ($F_{2,17} = 35.1$, $p < 0.001$). Figure 4.4b shows where, along the transect, the groups occurred and Figure 4.5 shows the species composition of these three groups.

Those taxa which showed significance between group differences in log-transformed abundance, from a one-way ANOVA, were *Centropages* ($F_{2,17} = 7.5$, $p < 0.005$), *Temora* ($F_{2,17} = 8.9$, $p < 0.005$), *Eurytemora* ($F_{2,17} = 41.4$, $p < 0.001$), *Evadne* ($F_{2,17} = 10.2$, $p < 0.001$), *Podon* ($F_{2,17} = 25.6$, $p < 0.001$), and bivalve larvae ($F_{2,17} = 7.1$, $p < 0.01$). *Centropages* and *Temora* showed a gradual decrease along the groups from A to C, while *Acartia* were dominant in all three groups but showed a decrease in group B that was coupled with an increase in

SPECIES	**df**	**F**	**r^2**	**SIGNIFICANCE**
Centropages spp.	19	23.5	0.57	0.001
Temora spp.	19	33.6	0.65	0.001
Acartia spp.	19	4.1	0.18	NS
Pseudocalanus spp.	19	1.3	0.07	NS
Eurytemora affinis	19	9.2	0.34	0.01
Polychaete larvae	19	0.6	0.03	NS
Sagitta spp.	19	2.2	0.11	NS
Evadne spp.	19	5.5	0.23	0.05
Podon spp.	19	13.5	0.43	0.005
Bosmina spp.	19	4.0	0.18	NS
Fritillaria	19	4.3	0.19	NS
Mysids	19	0.0	0.00	NS
Bivalve larvae	19	3.6	0.17	NS
Total zooplankton	19	9.2	0.34	0.01
Total cladocerans	19	6.8	0.28	0.05
Total copepods	19	8.8	0.33	0.01

Table 4.1 Results from regressions of log-transformed abundance ($n.m^{-3}$) against salinity (‰).

NS = not significant.

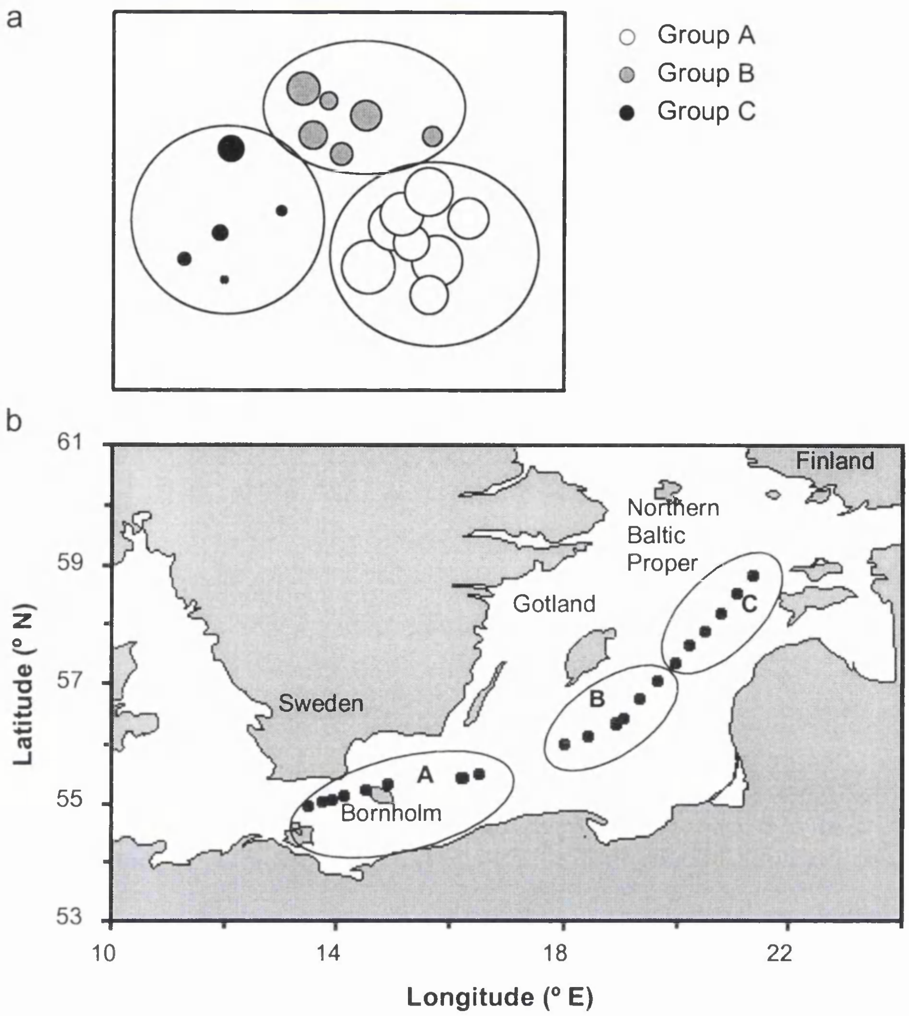

Fig 4.4 a) Two-dimensional MDS bubble plot of Bray-Curtis similarity coefficients, based on proportion contributed by each species to total abundance, between all samples. The size of the bubble represents the salinity of the water. b) Spatial distribution of samples comprising groups A, B and C.

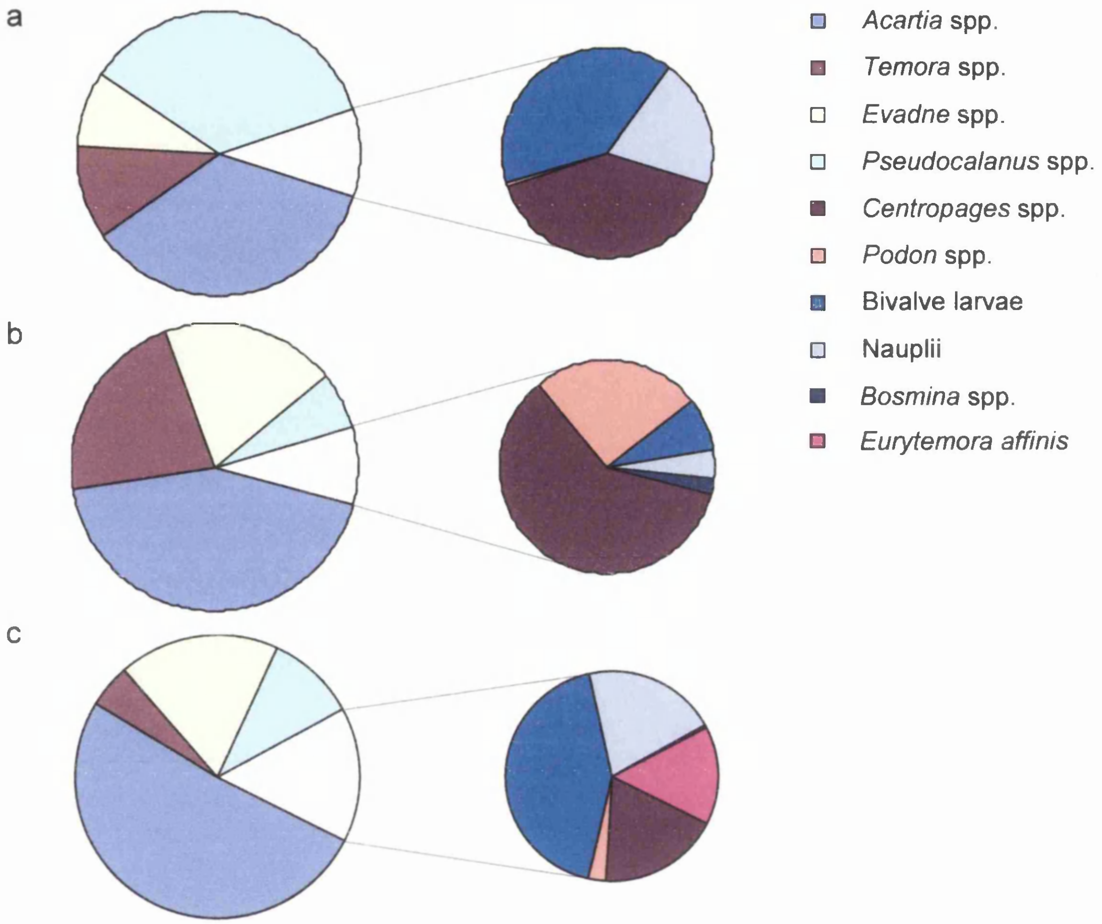

Fig. 4.5 Log-transformed species abundance of a) group A, b) group B, and c) group C. The smaller pie charts represent the composition of the less abundant species making up the white segments.

Pseudocalanus. *Eurytemora affinis* was only present in group C. *Evadne* was present in similar proportions in groups A and C but reduced in group B, whereas *Podon* was present in group A but virtually absent in groups B and C. Bivalve larvae and nauplii were both present at a similar abundance in groups B and C, but at a reduced level in group A.

Discussion

There has been a substantial amount of work on the zooplankton in the Baltic Sea (Dippner *et al.*, 2000; Flinkman *et al.*, 1998; Flinkman *et al.*, 1992; Möllmann *et al.*, 2000; Ojaveer *et al.*, 1998; Viitasalo, 1992; Viitasalo *et al.*, 1990; Viitasalo *et al.*, 1995a; Vuorinen *et al.*, 1998; Vuorinen and Ranta, 1987), but these studies concentrated on temporal changes, or relied on net samples from fixed stations. Sampling at fixed stations can produce biased results due to the patchiness of zooplankton (Viitasalo *et al.*, 1995a). This study is the first to employ a continuous, large scale, sampler that overcomes this problem, and can identify where, in the horizontal range, changes occur in the zooplankton community.

The broad composition of the zooplankton found in this study compares well to that found in earlier studies (Dippner *et al.*, 2000; Flinkman *et al.*, 1992; Hernroth, 1981; Ojaveer *et al.*, 1998; Rudstam *et al.*, 1994; Viitasalo, 1992; Viitasalo *et al.*, 1990; Vuorinen *et al.*, 1998; Vuorinen and Ranta, 1987). However, Möllmann *et al.* (2000) found *Pseudocalanus* spp. to be the most abundant copepod. It has previously been noted that *Pseudocalanus*, especially adults, are more abundant below 100m in the deeper basins of the Baltic (Möllmann *et al.*, 2000;

Ojaveer *et al.*, 1998). This means that, with the sampling depth of 18m in this study, many *Pseudocalanus* will have been missed.

The ratio of animals in the size ranges 200-500µm, 500-1000µm, and 1000-2000µm (1:0.06:0.0002) indicates that the plankton found in the Baltic Sea is dominated by smaller planktonic species in comparison to other oceans, such as the Pacific where at times the biomass in the > 1000µm size fraction can be dominant (White *et al.*, 1995), and the Arabian Sea where most of the biomass occurs in the large size fraction (Wishner *et al.*, 1998). The lack of large organisms in the Baltic is probably due to the low salinity, but may also indicate high predation pressure from planktivorous fish, which are known to selectively feed on larger animals (Flinkman *et al.*, 1998; Flinkman *et al.*, 1992). This high predation pressure is derived from the high level of planktivorous fish present (Rudstam *et al.*, 1994) and the relatively shallow water (Segerstråle, 1969) which reduces the refuge available to zooplankters through DVM.

It is thought that zooplankton may undergo DVM to reduce the risk of predation from visual planktivores (Zaret and Suffern, 1976). Large amplitude migrators (i.e. species moving hundreds of meters) are generally large (> 2mm) or heavily pigmented, making them very visible (Hays, 1996; Hays *et al.*, 1994). The zooplankton sampled in this study were comparatively small, however DVM in smaller taxa has been documented (Harris, 1988). Although there were no changes in the average length of zooplankton associated with time of day, there was a difference in average day and night copepod biomass which suggests that DVM of copepods may take place.

Contrasting patterns of biomass change with salinity have been reported with, for example, Viitasalo *et al.* (1995a) showing that seasonally adjusted biomass of total mesozooplankton biomass and cladoceran biomass were negatively correlated with salinity, while Flinkman *et al.* (1998) and this study show that total cladoceran and total copepod biomass were positively correlated to salinity. These differences may reflect differences in the levels of salinity in which sampling took place. The study by Viitasalo *et al.* (1995a) took place further north than the present study, off the coast of Finland, where the salinity range was lower (5.8 – 6.6‰) and limnetic species are more prevalent (Viitasalo, 1992; Viitasalo *et al.*, 1990; Vuorinen and Ranta, 1987) creating different spatial patterns. This suggests that salinity does not influence zooplankton biomass in a simple monotonic manner, with limnetic species decreasing, and eventually disappearing, before salinity increases up to 6.6‰, and neritic species appearing, and increasing, as salinity increases further.

Vuorinen *et al.* (1998) found a decrease in the ratio of copepod to cladoceran biomass with salinity. These results confirm and extend his conclusion. The study by Vuorinen *et al.* (1998) was conducted in the salinity range 5.8 – 6.8‰. Samples from this study that had a salinity below 7.06‰ did show a significant decrease in the ratio of copepod to cladoceran biomass with salinity ($F_{1,11} = 13.2$, $r^2 = 0.57$, $p < 0.005$). This was caused by the decrease, with salinity, in the biomass of neritic copepod taxa such as *Temora* ($F_{1,11} = 7.3$, $r^2 = 0.42$, $p < 0.05$) and *Pseudocalanus* ($F_{1,11} = 7.2$, $r^2 = 0.42$, $p < 0.05$). However, above 7.06‰ there is no obvious decrease in the abundance of these taxa with salinity ($F_{1,7} = 2.9$, $r^2 = 0.32$, $p = 0.141$ and $F_{1,7} = 2.9$, $r^2 = 0.33$, $p = 0.138$). It has previously been shown that, in low salinity, marine copepods have increased respiration rates due to the need for extra energy to osmoregulate (Gaudy *et al.*, 2000). Consequently, as salinity declines, it becomes more difficult for the neritic species to compete efficiently.

While strong relationships between salinity and abundance were not found for some taxa (e.g. polychaete larvae, *Sagitta*, *Fritillaria*, *Bosmina*, and mysids) this may simply be due to the low observed numbers in samples reflecting that sampling took place too early in the year to observe high abundance for these taxa. However, for taxa routinely caught in high numbers, the patterns of abundance with salinity were generally consistent with those reported previously (Flinkman *et al.*, 1998; Viitasalo *et al.*, 1990; Viitasalo *et al.*, 1995a; Vuorinen *et al.*, 1998) and can be related to the salinity tolerances of the individual taxa. Care must be taken when interpreting the correlation between salinity and *Eurytemora* spp. due to the high number of zero values in the southern part of the transect. However, this area has salinity higher than that preferred by *Eurytemora* (Viitasalo, 1992). Salinity alone could not explain the patterns in *Pseudocalanus* suggesting that, for this taxa, other factors may play a role. Again, this may be an artifact due to the under-sampling of *Pseudocalanus* caused by deeper distributions. *Acartia bifilosa* is known to be a brackish water species and abundant throughout the Baltic Sea (Ojaveer *et al.*, 1998; Viitasalo, 1992). There is some evidence that they may have a competitive advantage over some other copepods by avoiding feeding on toxic cyanobacteria that occur widely in the Baltic Sea (Engström *et al.*, 2000). Further evidence suggests that other species of copepods, such as *Eurytemora*, that carry egg sacs, and larger *Temora* and *Centropages*, are more heavily preyed on (Flinkman *et al.*, 1992). These facts may explain the dominance of *Acartia* in the Baltic, but also may reflect differing seasonal cycles of the species.

Given the observed changes in the abundance of individual taxa with salinity, it is not surprising that groups of taxa, related to the salinity gradient, were identified by cluster analysis (Figure 4.4a). Most of the differences in species composition in the groups (Figure 4.5) can be explained by changes in abundance with salinity described earlier, with neritic taxa more abundant in higher salinity (group A) and brackish water taxa more abundant in lower salinity (group C). *Evadne* showed a definite minimum in the middle of the transect (group B) rather than a monotonic change with salinity. As well as significant salinity differences between the three groups, there were also significant temperature differences ($F_{2,17} = 15.2$, $p < 0.001$). As group B has the highest temperature, this may explain the decrease in *Evadne*. Although *Evadne* is not significantly negatively correlated with temperature alone ($F_{1,18} = 0.5$, $r^2 = 0.00$, $p = 0.818$), a stepwise multiple regression ($F_s = 0.1$) enters salinity and temperature into the equation and explains more of the variation than salinity alone ($F_{2,17} = 5.0$, $r^2 = 0.37$, $p < 0.05$).

Species diversity was shown to be unrelated to salinity, which is probably because, although some species decreased in numbers with salinity, none disappeared completely; and as one species declined another species increased. This result may also reflect the very low diversity found in the Baltic (Hernroth, 1981) which reduces the possible amount of variability in diversity.

Conclusions

- There was a strong salinity gradient decreasing from north to south in the Baltic Sea.
- Animals were generally small (average length was 1.11mm) and there was no relationship between length of animals and salinity or time of day, although increased copepod biomass at night indicates that DVM may take place.
- Total zooplankton and total copepod biomass were negatively correlated with salinity. By combining this result with previous studies in a lower salinity range (Viitasalo *et al.*, 1995a), it appears that salinity and zooplankton biomass are not related in a simple monotonic manner.

- A decrease in biomass ratio of copepods to cladocerans with salinity was found in samples with salinity less than 7.06‰ due to the decrease in neritic copepod taxa.
- Total zooplankton, total copepods, total cladocerans, *Evadne*, *Temora*, *Centropages*, and *Podon* were positively correlated with salinity; whilst *Eurytemora affinis* was negatively correlated with salinity. These can be related to the salinity tolerances of the individual taxa. However, salinity alone could not explain the patterns in *Pseudocalanus* suggesting that other factors play a role.
- Groups of taxa, related to the salinity gradient, were identified by cluster analysis. They correspond to samples from the Bornholm, Gotland and Northern Baltic proper areas of the Baltic Sea.
- Species diversity was unrelated to salinity, probably due to the very low diversity found which reduces the possible amount of variability in diversity.

CHAPTER 5

Spatial patterns and the importance of different copepod taxa in North East Atlantic epipelagic mesozooplankton

Abstract

Epipelagic mesozooplankton were collected from the NE Atlantic, Celtic Sea and Bay of Biscay, using the U-Tow (a continuous plankton sampler). Zooplankton communities could be distinguished into those from the Porcupine Bank, NE Atlantic deep water, Celtic Shelf, Bay of Biscay and English Channel. The most important taxa, both by number and by biomass, were generally *Oithona* spp. and *Para/Pseudocalanus* spp. Overall, the relative biomass of *Calanus* was small but became more important over the continental shelf, especially at the edge of the shelf.

Introduction

Zooplankton play a fundamental role in the functioning of pelagic food webs as they form a link in between producers and secondary consumers (Gislason and Assthorsson, 1995; Kane, 1993; Steele, 1974; Williams and Conway, 1984), and can be important in determining the rate of production by autotrophic and heterotrophic plankton through nutrient regeneration (Banse, 1995). It is also considered that epipelagic plankton can provide a useful monitor of climate change (Villate *et al.*, 1997).

Copepod assemblages are generally the most abundant component of mesozooplankton (Morales *et al.*, 1993) and, therefore, dominate the biomass of pelagic grazers having important impacts on the phytoplankton (Morales *et al.*, 1993; Tiselius, 1988). In fact, several studies have shown that, at certain times of the year, the grazing impact of the copepod community can match or exceed daily primary production (Hansen *et al.*, 2000; Weeks *et al.*, 1993). A large amount of marine plankton research has concentrated on the larger copepod taxa such as *Calanus*, *Metridia* and *Pleuromamma* species, for example, describing horizontal distribution and seasonal cycle (Durbin *et al.*, 2000; Gaard, 2000; Planque and Batten, 2000; Planque and Fromentin, 1996; Planque *et al.*, 1997), vertical distribution (Williams, 1985; Williams and Conway, 1980; Williams and Conway, 1984), grazing impact (Hansen *et al.*, 2000), optimal life history (Fiksen and Carlotti, 1998), and population structure (Irigoien *et al.*, 1998; Meise and O'Reilly, 1996; Tande, 1982). *Calanus spp.* are often cited as being the most abundant, and therefore most important, copepod in the North Sea and North Atlantic (Fiksen and Carlotti, 1998; Gislason and Assthorsson, 1995; Hansen *et al.*, 2000; Irigoien *et al.*, 1998; Meise and O'Reilly, 1996; Morales *et al.*, 1993; Parsons and Lalli, 1988; Planque and Batten, 2000;

Planque and Fromentin, 1996; Steele, 1974; Tande, 1982; Tande and Miller, 2000; Williams, 1985) and have been assigned roles in structuring the North Atlantic pelagic community (Fiksen and Carlotti, 1998), and controlling the growth rate of commercially important fish stocks such as herring (Steele and Frost, 1977), cod, haddock (Irigoien *et al.*, 1998), sprat, pilchard and mackerel in the North Atlantic and Celtic Sea (Williams and Conway, 1984). However, recent evidence has suggested that smaller copepods are generally dominant not only in numbers, but also sometimes in biomass and grazing pressure (Dam *et al.*, 1993; Fernández *et al.*, 1993; Gallienne *et al.*, 2001; Lochte *et al.*, 1993; Morales *et al.*, 1991; Morales *et al.*, 1993; Valdés and Moral, 1998). The aim of this study was to quantify the importance of different copepod taxa, in terms of numbers and biomass, in the epipelagic zooplankton community of the North East Atlantic.

Methods

Zooplankton samples were collected at a depth of 10m with a U-Tow, a towed body designed to sample over extended spatial scales (Hays *et al.*, 1998) and so overcome effects of zooplankton patchiness. The U-Tow was fitted with a Plankton Sampling Mechanism (PSM), containing 200μm mesh, an electromagnetic flowmeter, and a CTD. Sampling took place between 29 June and 25 July 1999. Sunrise and sunset were defined as the time when the elevation of the sun was 0°, and was determined using almanacs (TELONICS Real-Time Satellite Display).

After each deployment, samples were immediately washed off the mesh and preserved in a 4% borax buffered seawater formaldehyde solution. Alternate samples were wet sieved into the size fractions 200-500µm, 500-1000µm, and 1000-2000µm. Using a binocular microscope, the animals in each size fraction were identified, to at least genus for copepods and at least order for other animals, and counted to give measures of abundance for the species present and the size structure of the zooplankton community. The average size of animals in a sample was calculated using the formula:

$$W = \sum_{S=1}^{S=j}((M_L + M_U) / 2) \times P_S$$

where W is the average width of animals in the sample, S is the size fraction, M_L is the lower mesh size for the size fraction, M_U is the upper mesh size for the size fraction, and P_S is the proportion of animals in that size fraction. W was then converted to an average length by assuming a typical width:length ratio for mesozooplankton of 1:3 (Herman *et al.*, 1992). Biomass was calculated by taking widths from Hays (1996) and Sars (1903), converting to lengths, and then to dry weight using length-weight regressions for total copepods from Uye (1982) and multiplying by the animals abundance corrected for mesh selectivity (Nichols and Thompson, 1991).

Bray-Curtis similarity coefficients between individual sample measures of species composition (proportion contributed by each species to total abundance) were calculated using the CLUSTER routine from Plymouth Routines In Multivariate Ecological Research (PRIMER) (Carr, 1997; Clarke and Warwick, 1994). These were mapped as non-metric multi-dimensional scaling (MDS) plots.

Results

There were fifty individual tows covering a total of 2902 km from the North Atlantic, Celtic Sea and Bay of Biscay (Figure 5.1). 109 samples were analysed, each constituting approximately 18.5 km of sampling. Figure 5.2 shows the percentage of all samples in which different species were ranked among the top three most numerically abundant species. By far the most abundant copepod overall was *Oithona* spp., which was ranked in the top three most abundant species in 83% of all samples. *Para/Pseudocalanus* spp. (composed of *Paracalanus*, *Pseudocalanus*, *Ctenocalanus*, and *Clausocalanus*), *Acartia* spp. and larvaceans were also abundant overall, ranking in the top three most abundant species in 66%, 38% and 33% of all samples respectively. *Calanus* spp. only ranked in the three most abundant species in less than 1% of all samples.

There were no distinct spatial patterns in the average size of the zooplankton, although the plankton on the continental shelf tended to be larger than that off the shelf (one-way ANOVA: $F_{1,83} = 11.2$, $p < 0.001$). There were also day and night differences in size, with the average length of animals 6% (one-way ANOVA: $F_{1,40} = 0.9$, $p = 0.351$) and 8% larger at night (one-way ANOVA: $F_{1,41} = 6.3$, $p < 0.05$) on and off the shelf respectively, although the pattern was only significant for off shelf samples.

When the Bray-Curtis similarity coefficients between all samples were plotted as a cluster diagram, at the 50% similarity level the samples divided into three groups. This does not mean that the samples within the groups are completely different to those in other groups. 0% similarity means samples are completely dissimilar in terms of species composition and abundance, and 100% similarity means the samples are identical. Therefore, division at the 50%

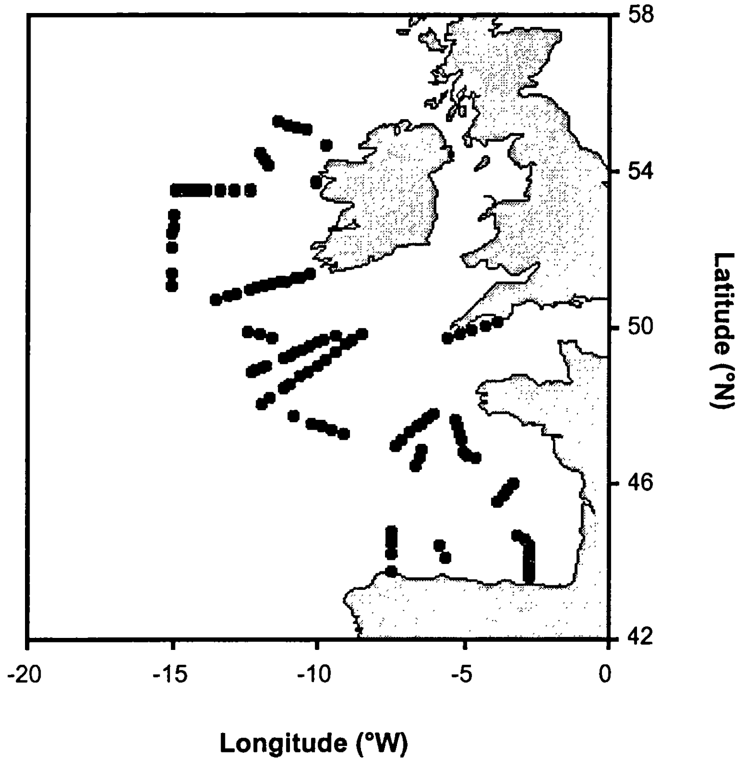

Fig 5.1 Spatial distribution of mesozooplankton samples. Filled circles represent the midpoint of each sample.

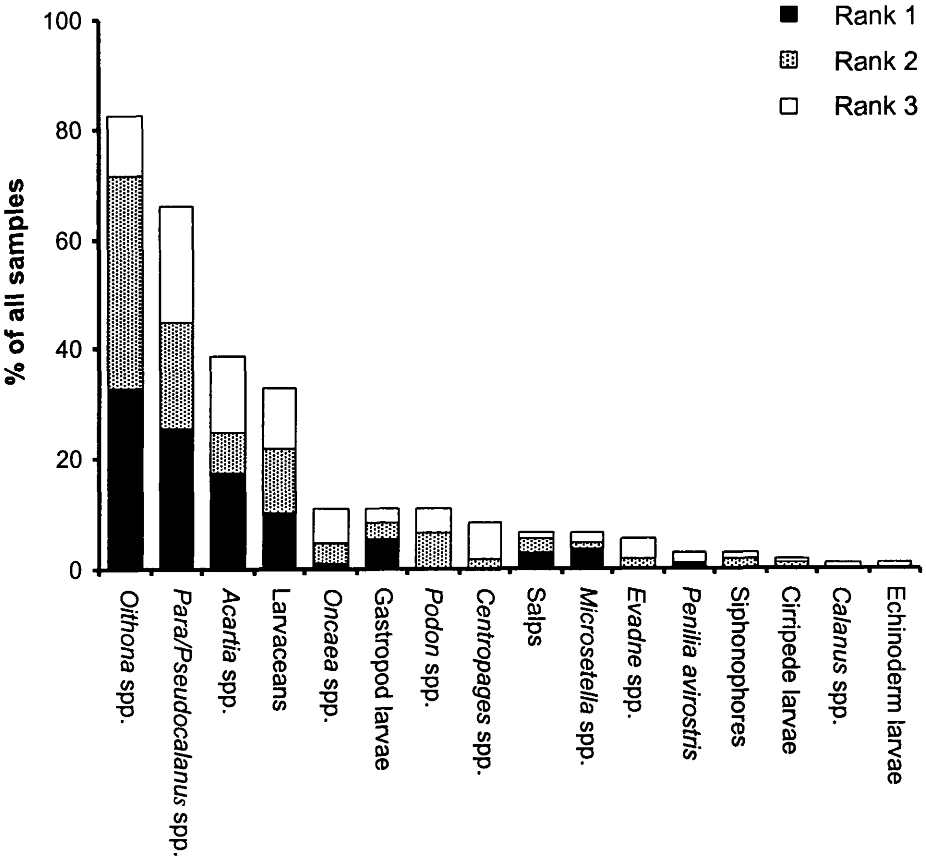

Fig 5.2 Percentage of all samples in which different species were ranked among the top three most abundant species.

similarity level means that the samples within one group show more than 50% similarity to each other and less than 50% similarity to the samples in the other groups. The three groups correspond to deep water and the Bay of Biscay, the Celtic Shelf and west/northwest of Ireland, except for one sample at the north west tip of France which stood by itself. However, at the 54% similarity level the samples divided into seven distinct groups (Figure 5.3). Figure 5.4 shows the broad species composition (species contributing greater than 10% of the total abundance) of these groups. Group 1 occurs over the Porcupine Bank and is characterised by a large proportion of the copepod *Acartia* spp. Within group 1, at the 55% similarity level, the samples divide into those on the bank and those crossing the edge of the bank. Although both sub-groups are dominated by *Acartia* spp., the second most dominant group in samples over the edge is cladocerans whereas it is *Oithona* spp. in samples on the Bank. Group 2 occurs off the continental shelf in the North Atlantic and is dominated by the cyclopoid copepod *Oithona* spp., but also contains a relatively large amount of *Acartia* spp. and the copepods *Para/Pseudocalanus* spp. Group 3 occurs on the Celtic shelf to the southwest of Ireland and is also dominated by *Oithona* spp., but contains similar amounts of gastropod larvae, larvaceans and salps. Group 4 occurs in the Celtic Sea and English Channel and is dominated by larvaceans. Group 5 consists of a single sample that is heavily dominated by larvaceans. However, this sample occurs within the range covered by group 4 and is only distinguished because of the lack of other species. Group 6 occurs in the Bay of Biscay and is dominated by *Para/Pseudocalanus* but also contains a large proportion of *Oithona* spp. Within group 6, at the 60% similarity level, the samples divide into three groups corresponding to samples on the north of the Armorican shelf on the west coast of France, those on the south of the Armorican shelf,

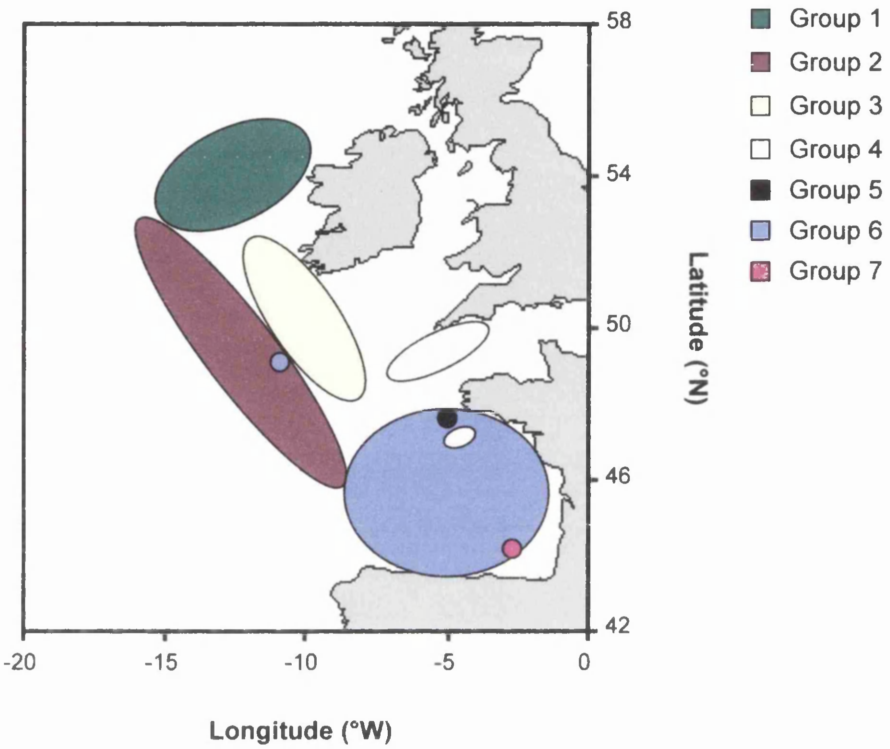

Fig 5.3 Spatial distribution of samples comprising groups determined by cluster analysis.

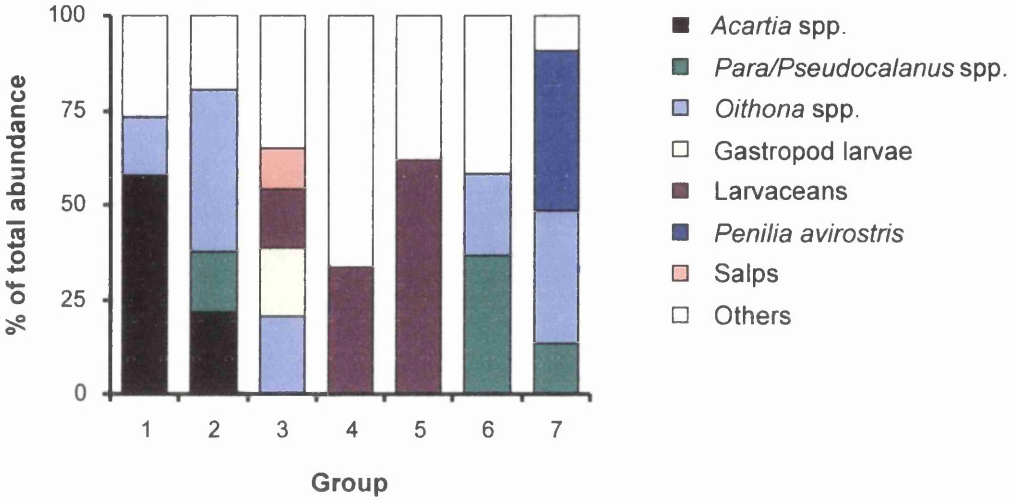

Fig 5.4 Broad species composition (species contributing greater than 10% of the total abundance) of groups determined by cluster analysis.

and all other samples taken from the Bay of Biscay. Group 7 consists of two samples in the southeast corner of the Bay of Biscay and, although otherwise similar to group 6, is dominated by the cladoceran *Penilia avirostris*. Out of the 56 species found, a one-way ANOVA showed significant between group differences in the abundance of 30 species (Table 5.1). Of the non-significant species, 23 out of 26 never contributed more than 1% of the total abundance in any sample. Table 5.2 shows the average salinity and temperature of the groups of samples.

Copepods contributed between 10 and virtually 100% of the total numbers of zooplankters sampled overall, but most frequently contributed between 90 and 100% (Figure 5.5a). *Calanus* spp. contributed between 0 and 30% of the total copepod numbers overall, but most frequently between 0 and 10% (Figure 5.5b), and between 0 and 88% of the total copepod biomass overall, but most frequently contributed between 0 and 10% (Figure 5.5c). All cases where *Calanus* contributed more than 10% of the copepod biomass occurred on the continental shelf, and all cases where *Calanus* contributed more than 70% occurred on the edge of the continental shelf. Figure 5.6 shows the percentage of all samples that species were ranked among the top three contributors to total copepod biomass. Again the most dominant copepod is *Oithona* spp., ranking in the top three in 88% of all samples, followed by *Para/Pseudocalanus* spp., ranking in the top three in 71% of all samples, but *Calanus* spp. rank as the third most dominant copepod, ranking in the top three in 38% of all samples and ranking first in 17% of all samples. Of the samples that *Calanus* ranked in the top three, 30 were daytime samples and 11 were nighttime samples.

Significant between group differences		**Non-significant between group differences**	
Species	**p-value**	**Species**	**p-value**
Acartia spp.	0.000	*Calanus tenuicornis*	0.761
Calanus spp.	0.000	*Candacia armata*	0.142
Calocalanus spp.	0.012	*Eucalanus* spp.	0.695
Centropages spp.	0.000	*Euchaeta* spp.	0.916
Para/Pseudocalanus spp.	0.000	*Heterorhabdus* spp.	0.906
Mecynocera clausii	0.026	*Ischnocalanus* spp.	0.873
Oithona spp.	0.000	*Isias clavipes*	0.906
Coryceaus spp.	0.000	*Metridia* spp.	0.346
Euterpina spp.	0.000	*Nannocalanus minor*	0.906
Microsetella spp.	0.050	*Parapontella* spp.	0.588
Oncaea spp.	0.000	*Pleuromamma* spp.	0.744
copepod nauplii	0.001	*Rhincalanus* spp.	0.612
Evadne spp.	0.000	*Scolecithricella* spp.	0.977
Podon spp.	0.000	*Temora longicornis*	0.227
Penilia avirostris	0.000	*Temora stylifera*	0.872
euphausiids	0.000	*Undeuchaeta* spp.	0.906
hyperiid amphipods	0.003	*Clytemnestra* spp.	0.790
Clione spp.	0.023	Harpacticoids	0.906
larvaceans	0.000	gammarid amphipods	0.858
Sagitta spp.	0.008	mysids	0.896
salps	0.000	ostracods	0.896
siphonophores	0.000	pteropods	0.381
barnacle larvae	0.008	anchovy eggs	0.413
bivalve larvae	0.000	hydromedusae	0.402
bryozoan larvae	0.006	phoronid larvae	0.906
decapod larvae	0.000		
echinoderm larvae	0.000		
fish larvae	0.012		
gastropod larvae	0.000		
polychaete larvae	0.000		

Table 5.1 Results from one-way ANOVA on species abundance (n.m^{-3}) in groups identified by cluster analysis.

	Average salinity (‰)	**Average temperature (°C)**
Group 1	36.22	13.81
Group 2	36.49	15.50
Group 3	36.32	15.99
Group 4	36.01	16.16
Group 5	35.89	15.07
Group 6	35.86	17.57
Group 7	35.00	20.05

Table 5.2 Average salinity (‰) and temperature (°C) of the groups identified by cluster analysis.

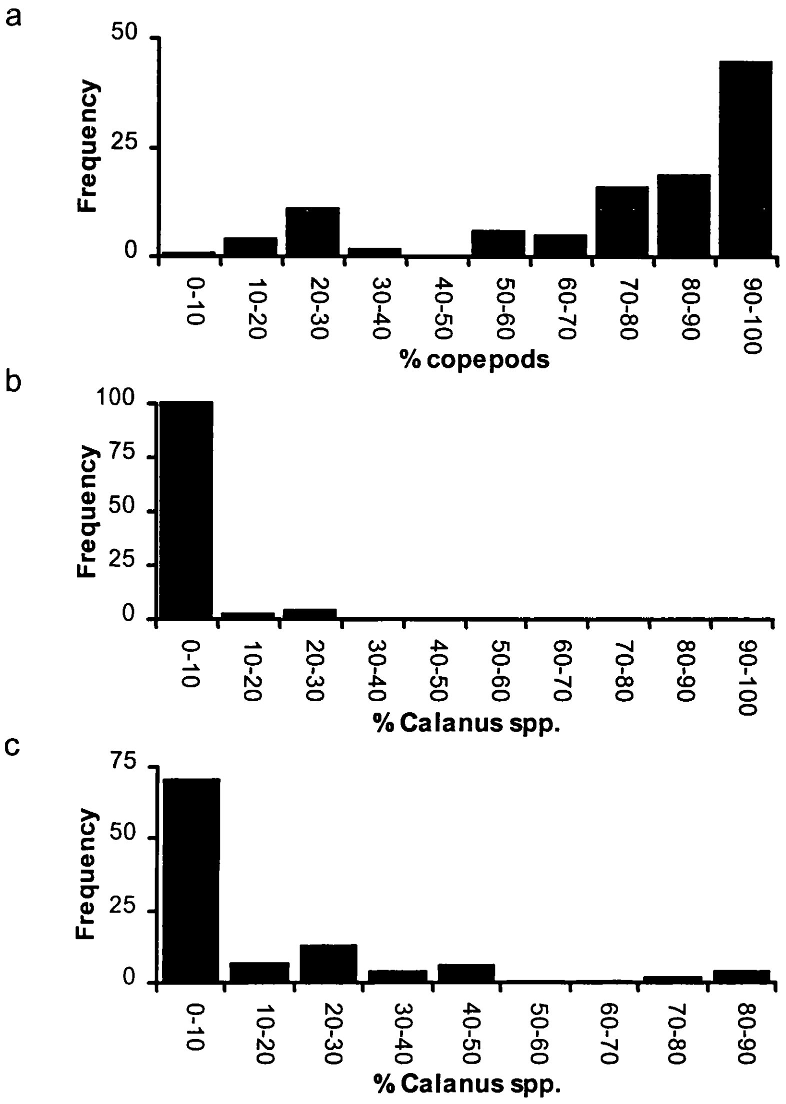

Fig. 5.5 a) Percent contributed by copepods to total zooplankton abundance. b) Percent contributed by *Calanus* spp. to total copepod abundance. c) Percent contributed by *Calanus* spp. to total copepod biomass.

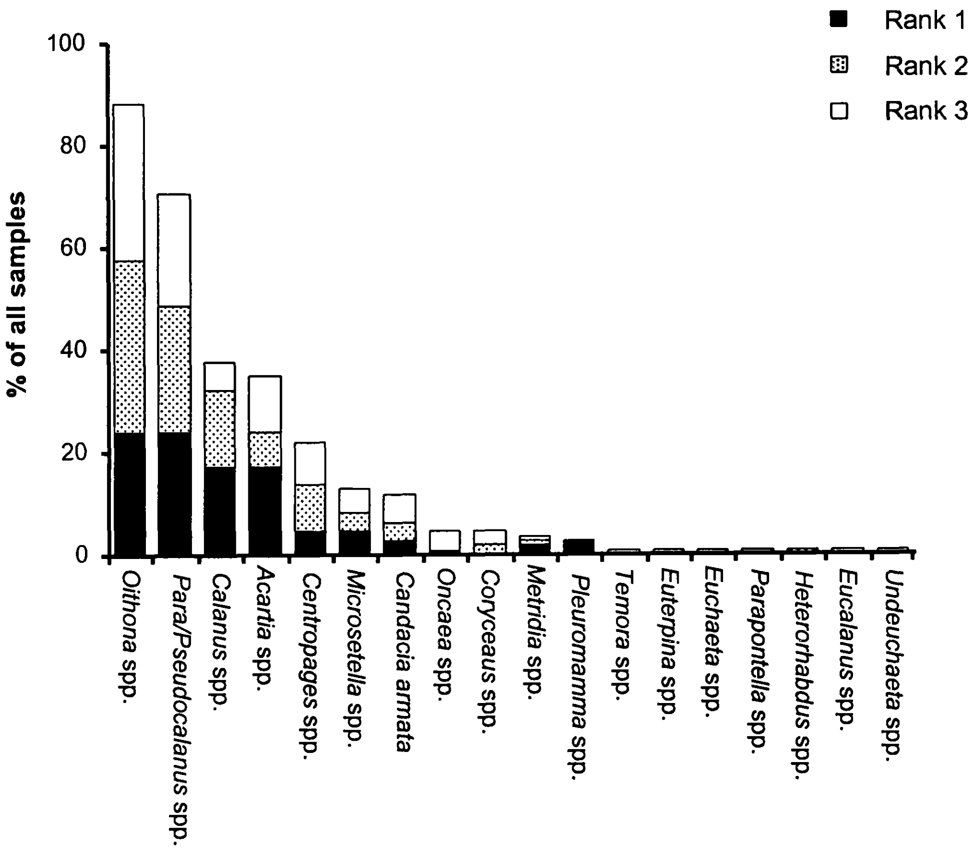

Fig. 5.6 Percentage of all samples in which different species were ranked among the top three contributors to total copepod biomass.

Discussion

It is widely recognised that zooplankton biomass provides an important index for estimating the secondary production in marine ecosystems (Kane, 1993), so the study of large-scale spatial patterns in planktonic communities is central to a wider understanding of the dynamics of marine environments (Beaugrand *et al.*, 2000; Morales *et al.*, 1991).

The zooplankton of the North East Atlantic has been fairly intensively studied, although much of the work concentrates on the mid-oceanic plankton due to programs such as the Biogeochemical Ocean Flux Study (BOFS), Joint Global Oceanic Flux Study (JGOFS) and Plankton Reactivity in the Marine Environment (PRIME) (Clark *et al.*, 2001a; Dam *et al.*, 1993; Hays *et al.*, 2001; Irigoien *et al.*, 2000; Koppelmann and Weikert, 1999; Lochte *et al.*, 1993; Morales *et al.*, 1991; Morales *et al.*, 1993; Weeks *et al.*, 1993). The Continuous Plankton Recorder (CPR) survey has been routinely sampling North Atlantic zooplankton since the end of the 1950s resulting in a number of studies concerned with spatial and temporal patterns (Beaugrand *et al.*, 2000; Colebrook, 1979; Colebrook, 1984; Fromentin and Planque, 1996; Hays, 1996; Hays *et al.*, 1996; Hays *et al.*, 1997b; Planque and Batten, 2000; Planque and Fromentin, 1996; Planque *et al.*, 1997). However, the Bay of Biscay is not completely covered by the CPR survey, with the innermost area and the continental shelf being missed (Villate *et al.*, 1997). There has been a certain amount of work describing Bay of Biscay zooplankton (Fernández *et al.*, 1993; Valdés and Moral, 1998; Villate, 1991; Villate *et al.*, 1997), but none using large-scale continuous samplers.

The general species composition and species distributions found in this study compare well with those described previously for these areas (Beaugrand *et al.*, 2000; Fernández *et al.*, 1993; Oceanographic Laboratory Edinburgh, 1973; Valdés and Moral, 1998; Villate, 1991). High abundance of *Oithona* spp. has previously been noted by several studies (Gallienne *et al.*, 2001; Harris *et al.*, 1997; Morales *et al.*, 1991; Morales *et al.*, 1993; Nielsen and Sabatini, 1996; Valdés and Moral, 1998; Weeks *et al.*, 1993) and confirmed by this study, even though *Oithona* is not sampled quantitatively by the 200 μm mesh used in this study. According to the mesh selectivity equation from Nichols and Thompson (1991), a 200 μm mesh will only catch 96% of an animal the width of an adult *Oithona* implying that these animals are the most dominant and ubiquitous zooplankters in this study area.

Finding larger zooplankton on the continental shelf, compared with off the shelf, is a surprising find. It is generally accepted that zooplankton will be larger in deeper water due to an increased refuge from planktivorous predators during the day (Hays, 1996). It may be the case that, in the deeper water off the continental shelf, the larger animals never migrate fully to the surface, hence being missed by the U-Tow, which samples at a depth of 10m. Parsons and Lalli (1988) noted that of the larger copepods in the North Atlantic (*Calanus finmarchicus*, *Metridia lucens*, *Euchaeta novergica*, and *Pleuromamma robusta*) found in the top 500m of water, *Calanus* has a shallower distribution than the rest, and therefore has a greater relative contribution to the surface 150m. However, Falkenhaug *et al.* (1997) found that, *Calanus finmarchicus* and Metridia spp. stages CI-III were often found in the top 25m but the maxima for older stages was generally below 25m.

White *et al.* (1998) described a dense dome of cold and relatively less-saline water with higher nutrient values and reduced shelf-ocean exchange over the Porcupine Bank that persisted from at least May to July. This may explain the separation of group 1 samples from the rest of the North Atlantic samples, either through the retention of plankton over the Bank, or the higher available nutrients. In this study, group 1 has a lower average temperature and salinity than the surrounding samples (groups 2 and 3) implying that this cold dome was present. The difference between the group 1 sub-groups is probably caused by enhanced vertical mixing or upwelling at the shelf edge providing additional nutrient input to the surface waters in this area, allowing the cladocerans *Podon* spp. and *Evadne* spp. to increase in numbers. These frontal regions between coastal and oceanic waters are known to contain sharp gradients in nutrients (White *et al.*, 1998). Group 6 relates to Bay of Biscay water which is known to be different from the North Atlantic water (Villate *et al.*, 1997). Group 6 further divides into samples relating to deep water, and north and south Armorican shelf. This splitting of the Armorican shelf samples is probably due to temperature differences as the southern groups has an average temperature of 19.1°C compared to 16.5°C for the northern groups. The southern samples also have a slightly lower salinity, 35.2‰ compared to 36.0‰. Group 7 is also distinguishable from the rest of the Bay of Biscay due to the high dominance of *Penilia avirostris* which may be related to the very high average temperature (20.1°C) and low average salinity (35‰) at these sampling points. *Penilia avirostris* is known to be a tropical coastal thermophilic species (Siokou-Frangou, 1998) that can be found in large numbers in polluted bays and estuaries in temperate waters, and feeds exclusively on small particles (Paffenhöfer, 1986). Villate *et al.* (1997) describes how the inner Bay of Biscay is heavily influenced by river run-off from the Loire and Garone rivers which may explain both the high temperature and low salinity in group 7 and the southern Armorican shelf, and the high numbers of *Penilia avirostris* in this area.

Beaugrand *et al.* (2000), found that the SW Channel, the Ushant front, the Celtic Sea and the Bay of Biscay had separable zooplankton assemblages based on PCA analysis, which is mainly confirmed by this study, although no difference was found between the Ushant front and the Celtic Sea. Beaugrand *et al.* (2000) found the Bay of Biscay and Celtic Sea to be dominated by *Clausocalanus* and *Oithona*, and the west Channel dominated by *Acartia* spp., *Calanus helgolandicus* and *Para/Pseudocalanus*. This agrees with the present findings for the Bay of Biscay, but the Celtic Sea samples, although dominated by *Oithona*, did not contain much *Para/Pseudocalanus* (which includes *Clausocalanus*). However, Beaugrand *et al.* (2000) also found that the Celtic Sea had stronger year to year fluctuations than the Bay of Biscay. In addition, this study found the West Channel to be heavily dominated by larvaceans rather than the copepods described by Beaugrand *et al.* (2000). However, Beaugrand *et al.* (2000) was using CPR data that incorporated samples from all seasons over a number of years whereas this study is limited to samples taken in July of one year.

The dominance of copepods in the zooplankton agrees well with previous studies (Hansen *et al.*, 2000; Morales *et al.*, 1993; Tiselius, 1988). However, the unimportance of *Calanus* spp. seen in this study goes against many previously published data (Fiksen and Carlotti, 1998; Gislason and Assthorsson, 1995; Hansen *et al.*, 2000; Irigoien *et al.*, 1998; Meise and O'Reilly, 1996; Morales *et al.*, 1993; Parsons and Lalli, 1988; Planque and Fromentin, 1996; Steele, 1974; Tande, 1982; Williams, 1985). Although sometimes noted that *Calanus* is not dominant in numbers it is generally reported that, due to its large size, *Calanus* is dominant in terms of biomass (Meise and O'Reilly, 1996). This was only the case in 17% of all samples taken and only in on shelf waters. This may be due to the older *Calanus* stages not migrating up as far as the surface 10m in the deeper water off the continental shelf. Koppelmann and Weikert (1999) found that, during the day in oceanic waters, the maximum numbers of *Metridia* were found below 750m and Morales *et al.* (1993), working in the same area found adult *Pleuromamma* and *Metridia* below 400m. However, Irigoien (1999) found that most of the

Calanus finmarchicus population remained in the upper 50m at the oceanic station India in the North Atlantic (59°N, 19°W). Similarly, Durbin *et al.* (1995) found almost all *Calanus finmarchicus* were found in the top 20m during the night in the southern Gulf of Maine. In any case, when referring to the North East Atlantic epipelagic plankton, it is clear that *Calanus* is certainly not always an abundant group and, as such, estimates of grazing or secondary production based on *Calanus* will be underestimates. However, Planque and Batten (2000) states that 1997 had the lowest recorded biomass of *Calanus* in the North Atlantic and this, if the trend has continued, may explain the low numbers found in this study. In addition, the relative importance of *Calanus* will be larger in different geographical areas, such as the western North Atlantic, the northern North Sea, and the Norwegian Sea (Planque and Batten, 2000; Planque *et al.*, 1997). In these areas, *Oithona* will be less important. Indeed, Sherman *et al.* (1998), in a biodiversity study of the Northeast Shelf ecosystem, makes no mention of *Oithona*. Similarly, Nielsen and Sabatini (1996) noted that in the northern North Sea, where *Calanus* is dominant, the contribution of *Oithona* biomass to total copepod biomass decreased from 50-70% to 10-20%.

Conclusions

- There were no spatial patterns in zooplankton size, although significant day/night differences were found in samples taken in the deeper water off the continental shelf.
- Using cluster analysis, samples were divided into groups corresponding to the Porcupine Bank (divided into sub-groups on the bank and crossing the edge of the bank), North Atlantic deep water, the Celtic shelf, the English Channel, the Bay of Biscay (divided into

sub-groups on the north Armorican shelf, south Armorican shelf and other Bay of Biscay samples) and the south-east corner of the Bay of Biscay which was heavily dominated by *Penilia avirostris*.

- *Oithona* was the most abundant copepod overall ranking in the top three most abundant species in 83% of all samples, and the top three contributors to total biomass in 88% of all samples. *Calanus*, which is often cited as the most important copepod in the North Atlantic, only ranked in the top three most abundant species in less than 1% of all samples, and the top three contributors to total biomass in 38% of all samples.
- *Calanus* was most important in samples taken from the edge of the continental shelf.

CHAPTER 6

Spatial patterns in Irish Sea epipelagic mesozooplankton in relation to a tidal mixing front

Abstract

Epipelagic mesozooplankton were collected from Liverpool Bay to Dundalk Bay in the Irish Sea, a transect which passes through the Liverpool Bay salinity front and the western Irish Sea front, using the U-Tow (a continuous plankton sampler), in June and July 1998. In June, zooplankton communities could be distinguished into those from the Welsh coast, the central mixed region, the summer stratified region, and the Irish Sea coast. In July, the patterns were similar although the groups tended to stretch further east, and the Welsh coast zooplankton were not separated from that in the central mixed region. There were no obvious size differences associated with the community changes.

Introduction

Zooplankton play many fundamental roles in the functioning of pelagic food webs: they are the primary grazers of phytoplankton (Steele, 1974), have a role in nutrient regeneration and transport (Al-Mutairi and Landry, 2001; Dam *et al.*, 1993; Hays *et al.*, 1997a; Ikeda, 1985; Zhang *et al.*, 1995), provide food for secondary consumers (Ikeda, 1985; Lenz, 2000; Ojaveer *et al.*, 1998) and, through this last role, can determine fishery strength (Cushing, 1975; Rothschild, 1998). It is, therefore, important to understand the trophic interactions, biogeochemical impact, life-history strategies of mesozooplankton, and the impact of physical and biological processes on them (Dufour and Torréton, 1996).

Major factors driving variation in the zooplankton community will be changes in the physical environment and oceanographic processes that influence phytoplankton production by controlling light and nutrients (Gowen *et al.*, 1995; Le Borgne and Rodier, 1997; Richardson and Pedersen, 1998; Scrope-Howe and Jones, 1985; Smith Jr. and Demaster, 1996). For example, vertical and horizontal water stratification causes sharp changes in water chemistry (Hill *et al.*, 1997; Smith *et al.*, 1998; White *et al.*, 1998), water mixing allows even distribution of nutrients (Le Fèvre, 1986) but can also result in greater turbidity reducing light penetration (Allen, 1997; Coombs *et al.*, 1994; Van den Berg *et al.*, 1996), and upwelling results in a large input of new nutrients (Paffenhöfer, 1980). In addition, regions where different water masses, such as mixed and stratified waters, come into contact create a new set of conditions that can result in biomass accumulation associated with the fronts (Pakhomov *et al.*, 2000; Richardson and Pedersen, 1998).

The Irish Sea is semi-enclosed, connected to the North Atlantic via relatively narrow channels to the north and south, with relatively long hydrodynamic residence times (Allen *et al.*, 1998; Young *et al.*, 2000). In the western Irish Sea there is a deep basin (60-120m) but the rest is relatively shallow (less than 50m) (Coombs *et al.*, 1994; Dickey-Collas *et al.*, 1996a). In spring the deeper region south west of the Isle of Man becomes thermally stratified (known as the summer stratified region), due to the relatively weak tidal mixing, forming the western Irish Sea front at the boundary between mixed and stratified regions (Burkart *et al.*, 1995; Dickey-Collas *et al.*, 1996a; Dickey-Collas *et al.*, 1996b; Gowen *et al.*, 1997; Gowen *et al.*, 1995). Within the stratified region there is a near-surface cyclonic gyre, which develops over a cushion of cold water, and may retain zooplankton in the stratified region (Allen *et al.*, 1998; Gowen *et al.*, 1997; Hill *et al.*, 1997; Horsburgh *et al.*, 2000). There is also a Liverpool Bay salinity front separating the Welsh coastal waters from offshore waters (Burkart *et al.*, 1995).

There have been a number of studies investigating physical and biological properties of the Summer Stratified Region (SSR) in the Irish Sea; for example, the spatial distribution of zooplankton (Scrope-Howe and Jones, 1985), copepod and barnacle nauplii (Burkart *et al.*, 1995), *Calanus* spp. (Gowen *et al.*, 1997), fish larvae and 0-group fish (Dickey-Collas *et al.*, 1996a). Peaks in zooplankton abundance (Scrope-Howe and Jones, 1985; Scrope-Howe and Jones, 1986) and suspended particulates (Coombs *et al.*, 1994) have been found above the thermocline in stratified regions, although the stratified region also has a lower suspended detrital content than the mixed region. In terms of environments for phytoplankton growth, the Irish Sea has been divided into north and south coastal regions, the SSR, and north and south mixed regions (Gowen *et al.*, 1995). However, there have been no studies concerning changes in the size structure of zooplankton communities across the fronts. The purpose of this study is to investigate changes in zooplankton community and size structure in the Irish Sea with respect to the western Irish Sea coastal front.

Methods

Zooplankton samples were collected between 5 and 50m with an undulating U-Tow, a towed body designed to sample over extended spatial scales (Hays *et al.*, 1998; Mills *et al.*, 1998) and so overcome effects of zooplankton patchiness. The U-Tow was fitted with a Plankton Sampling Mechanism (PSM) containing 200μm mesh, and a CTD. There was no flowmeter fitted to the PSM, so the volume of water filtered per sample was calculated using the distance towed multiplied by the area of the inlet aperture. Although this method has been shown not to be ideal due to clogging (Hays, 1994; Hays *et al.*, 1998), the short duration of each sample (average 20mins) means that this was not a significant problem. The average efficiency of the U-Tow was calculated from previous tows in the North Sea, which were of a comparable speed, and was not significantly different from 100% (Cook and Hays, 2001). In addition, vertical WP2 net hauls, fitted with a General Oceanics flowmeter and Aladin Pro dive computer (for an accurate reading of depth), were taken from the maximum depth of the undulation profile to the surface, at the beginning and end of each tow. Sampling took place 15 to 18 June and 27 to 30 July 1998 and, to ensure sampling occurred across the western Irish Sea front, the U-Tow was deployed on a transect from Liverpool Bay to Dundalk Bay on both occasions.

After each deployment, samples were immediately washed off the mesh and preserved in a 4% borax buffered seawater formaldehyde solution. Animals from both sets of samples were identified as far as possible, to at least genus for copepods and at least order for other animals, using a binocular microscope. Where possible the whole sample was analysed but in some cases, where total zooplankton abundance was very high, a sub-sample was analysed. Where possible, at least a hundred animals of a size that is caught 95% quantitatively by a 200μm mesh, calculated using mesh selection curves calculated by (Nichols and Thompson, 1991) were counted from each sample. Measurements of length were also made of at least 100 animals, where possible, from each sample using a calibrated eyepiece graticule and an average length calculated for each sample.

Bray-Curtis similarity coefficients between individual sample measures of species composition (proportion contributed by each species to total abundance) and length frequency distributions were calculated using the CLUSTER routine from Plymouth Routines In Multivariate Ecological Research (PRIMER) (Carr, 1997; Clarke and Warwick, 1994). These were mapped as non-metric multi-dimensional scaling (MDS) plots.

Results

There were eight individual tows covering a total of 337 km (Figure 6.1). 35 U-Tow samples, each constituting approximately 5.6 km of sampling, and 10 WP2 net samples were analysed.

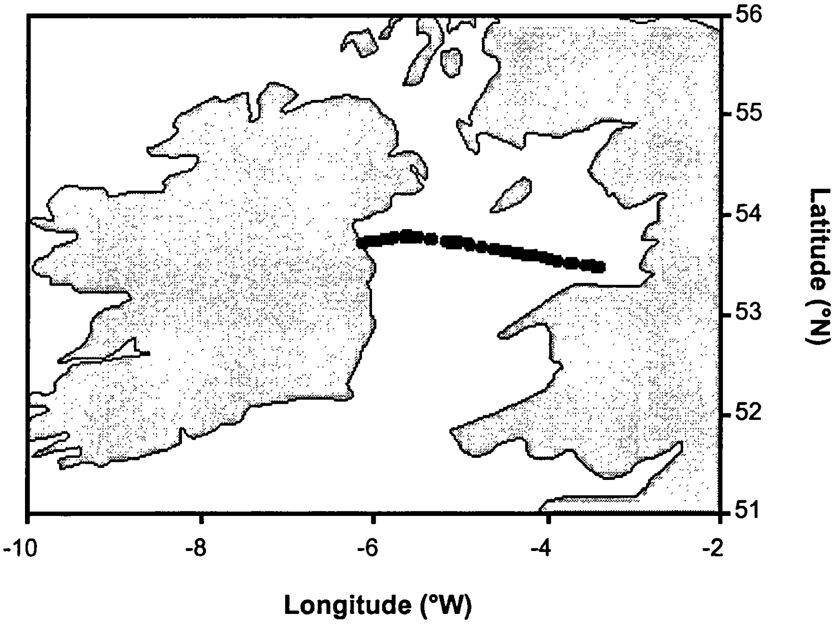

Fig 6.1 Spatial distribution of mesozooplankton samples. Filled circles represent the midpoint of each sample.

Liverpool Bay to Dundalk Bay transect, June 1998.

When the Bray-Curtis similarity coefficients between species composition of all samples were plotted as a non-metric multi-dimensional scaling (MDS) plot, the samples divided into five groups (Figure 6.2a) at the 50% similarity level. Group 1 consists of a single sample very close to the Irish coast, that was very dissimilar to the other samples, and group 2 consists of the rest of the Irish coast samples. Group 3 consists of samples to the south west of the Isle of Man, which is where the SSR occurs. Group 4 consists of samples south of the Isle of Man and group 5 consists of samples from Liverpool Bay.

Figure 6.2b shows the broad species composition of these five groups. *Acartia* spp. is the most widespread species, being found in high numbers in all groups. *Temora* spp. is also found in high numbers in all groups bar group 2. Groups 1 and 2 stand out due to the dominance of echinoderm larvae, and group 1 also contains a number of Cyphonautes larvae that only contribute a very small proportion in all other groups. Group 3 has the largest proportion of *Acartia* spp., and contains *Oithona* spp. and larvaceans that occur in negligible amounts in the other groups. In fact, larvaceans did not occur at all in groups 1 and 2. *Para/Pseudocalanus* spp. only occur in significant amounts in groups 3, 4 and 5, and *Centropages* spp. only occur in large amounts in groups 4 and 5. Polychaete larvae, cirripede larvae and bivalve larvae only occur in relatively large numbers in group 4. Group 5 contains a number of echinoderm larvae, but the most distinguishing feature of group 5 is the large number of the cladocerans *Evadne* spp. and *Podon* spp. that are not seen in the other groups. *Calanus* spp., although only present in very low numbers, had its peak in group 3.

A one-way ANOVA showed significant between group differences for *Acartia* spp. ($F_{4,29} = 18.1, p < 0.001$), *Calanus* spp. ($F_{4,29} = 6.3, p < 0.001$), *Centropages* spp. ($F_{4,29} = 14.0, p <$

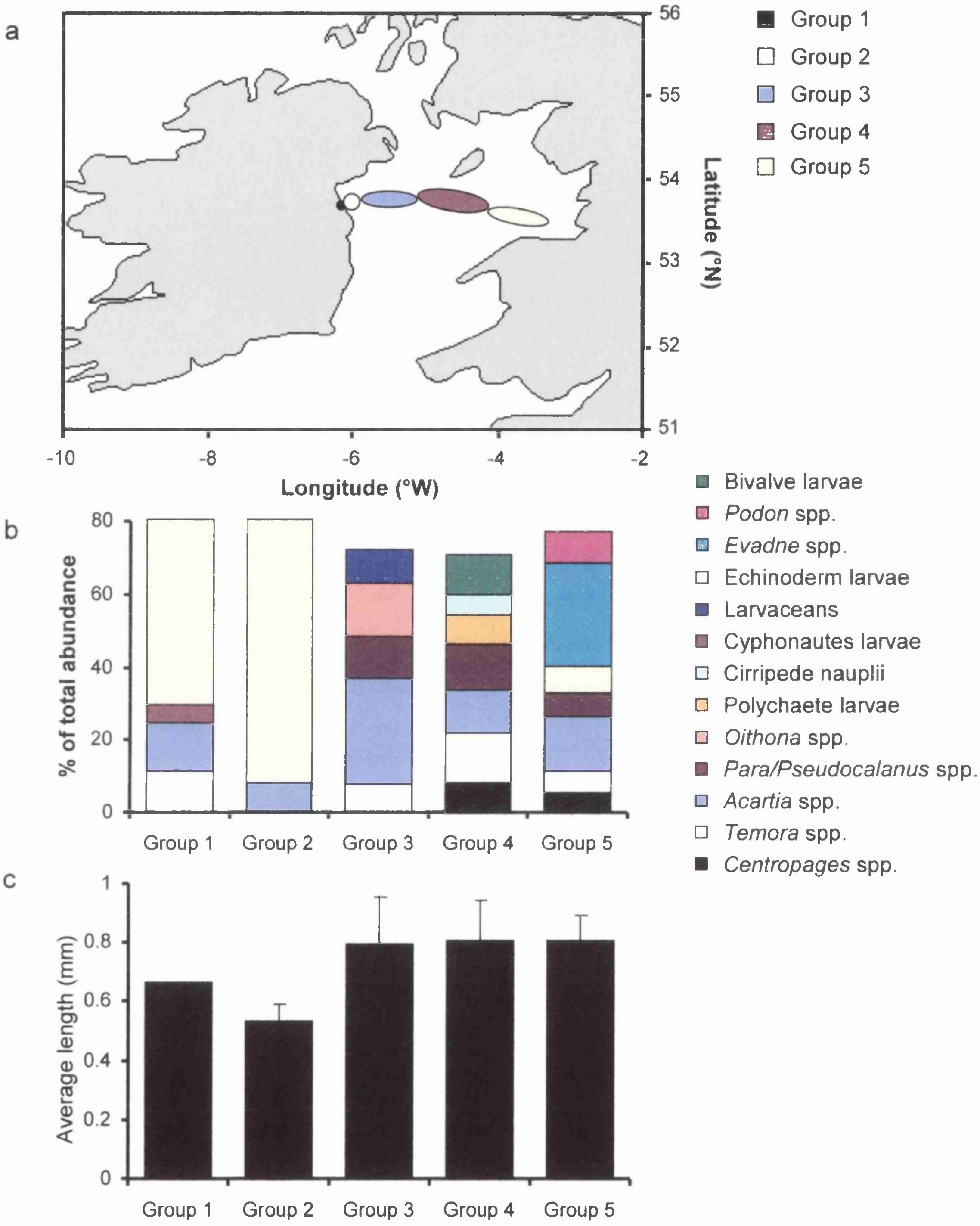

Fig 6.2. a) Spatial distribution of June 1998 groups determined by cluster analysis. b) Broad species composition of groups determined by cluster analysis. c) Average length (mm) of zooplankton in June 1998 groups determined by cluster analysis.

0.001), *Oithona* spp. ($F_{4,29} = 15.2$, $p < 0.001$), *Para/Pseudocalanus* spp. ($F_{4,29} = 3.6$, $p < 0.05$), *Temora* spp. ($F_{4,29} = 10.9$, $p < 0.001$), *Evadne* spp. ($F_{4,29} = 17.3$, $p < 0.001$), *Podon* spp. ($F_{4,29} = 3.0$, $p < 0.05$), bivalve larvae ($F_{4,29} = 14.8$, $p < 0.001$), cirripede nauplii ($F_{4,29} = 9.3$, $p < 0.001$), cyphonautes larvae ($F_{4,29} = 5.3$, $p < 0.001$), echinoderm larvae ($F_{4,29} = 204.4$, $p < 0.001$), and polychaete larvae ($F_{4,29} = 4.9$, $p < 0.001$). However, larvaceans did not show significant differences between the groups ($F_{4,29} = 2.2$, $p = 0.10$). Figure 6.2c shows the average length of zooplankton in the five groups. There were significant between group differences in average length of zooplankton ($F_{4,29} = 3.2$, $p < 0.05$). However, Figure 6.2c shows that groups 3, 4 and 5 have a similar average zooplankton length, with groups 1 and 2 having significantly smaller zooplankton.

As group 1 consists of only one WP2 net sample, there is no water data available. Table 6.1 shows the average values of salinity and temperature in the other groups. There were significant between group differences in salinity ($F_{3,24} = 10.9$, $p < 0.001$), and temperature ($F_{3,24} = 10.2$, $p < 0.001$). Salinity is about 35‰ in groups 3 and 4, but lower at the coastal sites. Temperature is about 12°C in groups 3 and 4, but about 13°C in the coastal sites.

Liverpool Bay to Dundalk Bay transect, July 1998.

When the Bray-Curtis similarity coefficients between species composition of all samples were plotted as a non-metric multi-dimensional scaling (MDS) plot, the samples divided into four groups (Figure 6.3a) at the 55% similarity level with very similar spatial distribution to those found in June. Group 1 again consists of a single sample very close to the Irish coast, which was very dissimilar to the other samples. Group 2 consists of Irish coastal samples but extends much further away from the coast than in June. Group 3 consists of samples to the

	Group 2	**Group 3**	**Group 4**	**Group 5**
Salinity (‰)	34.73	35.02	35.02	33.87
Temperature (˚C)	12.57	11.94	12.00	13.02

Table 6.1 Average salinity (‰) and temperature (°C) of June 1998 samples comprising groups determined by cluster analysis.

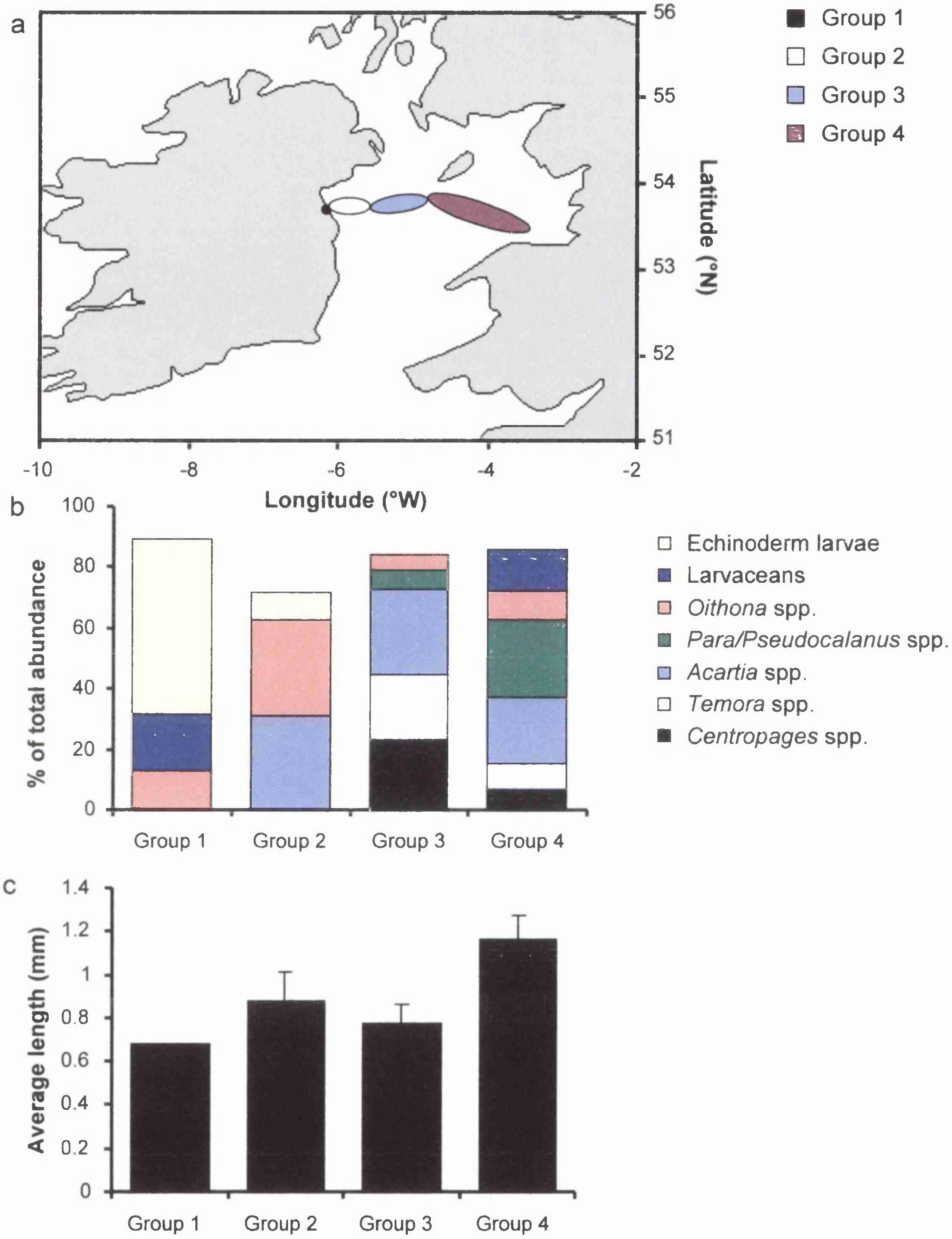

Fig 6.3 a) Spatial distribution of July 1998 groups determined by cluster analysis. b) Broad species composition of groups determined by cluster analysis. c) Average length (mm) of zooplankton in July 1998 samples comprising groups determined by cluster analysis.

south west of the Isle of Man and again extends further east than on the June transect. Group 4 extends from south of the Isle of Man to the Welsh coast.

Figure 6.3b shows the broad species composition of these four groups. In this transect *Oithona* spp. is the most widespread species, occurring in relatively high numbers in all groups. *Acartia* spp. is present in significant amounts in all groups except group 1, the single sample Irish coast group. *Temora* spp. and *Centropages* spp. are found in high numbers in groups 3 and 4, but not in the Irish coast groups (groups 1 and 2). Groups 1 and 2 again stand out due to the dominance of echinoderm larvae. Larvaceans only contribute a significant proportion of the zooplankton in groups 1 and 4. *Para/Pseudocalanus* spp. only occur in significant amounts in groups 3, and 4. *Calanus* spp. was again only present in very low numbers, but had peaks in groups 2 and 4. *Podon* spp. is present in very low numbers in all groups, but *Evadne* spp. is only present in groups 2 and 4, although again in very low numbers. Bivalve larvae, cyphonautes larvae and polychaete larvae no longer show the peaks in abundance found in June and are found in low numbers in all groups. The peak in cirripede larvae is also no longer seen, but the low numbers present are restricted to groups 3 and 4.

A one-way ANOVA showed significant between group differences for *Acartia* spp. ($F_{3,21} = 3.8$, $p < 0.05$), *Centropages* spp. ($F_{3,21} = 15.3$, $p < 0.001$), *Oithona* spp. ($F_{3,21} = 13.5$, $p < 0.001$), *Para/Pseudocalanus* spp. ($F_{3,21} = 23.1$, $p < 0.001$), *Temora* spp. ($F_{3,21} = 27.6$, $p < 0.001$), larvaceans ($F_{3,21} = 10.5$, $p < 0.001$) and echinoderm larvae ($F_{3,21} = 21.4$, $p < 0.001$). Figure 6.3c shows the average length of zooplankton in the four groups. The largest zooplankton was found in group 4, and was relatively much larger than the rest of the zooplankton in the survey (1.16mm compared to about 0.7mm). Group 2 had the second largest zooplankton community, followed by group 3, with the smallest zooplankton in group1. There were significant between group differences in average length of zooplankton ($F_{3,19} = 9.2$, $p < 0.001$).

As in June, group 1 consists of only one WP2 net sample and there is no water data available. Table 6.2 shows the average values of salinity and temperature in the other groups. There were significant between group differences in temperature ($F_{2,10} = 4.5$, $p < 0.05$). Salinity decreases from west to east, whereas temperature increases in the same direction.

Discussion

It is well known that, within areas, different water properties can lead to spatial patterns in plankton species composition and biomass, nutrients, and therefore primary and secondary production. Since zooplankton play an essential role in the pelagic ecosystem, it is vital to understand the factors that contribute to these spatial patterns.

The plankton of the Irish Sea has been fairly intensively studied, although much of the work has concentrated on phytoplankton (Gowen and Bloomfield, 1996; Gowen *et al.*, 1995), nutrients (Allen *et al.*, 1998), fish larvae (Dickey-Collas *et al.*, 1996a), and *Nephrops* larvae (Hill *et al.*, 1997; Horsburgh *et al.*, 2000), or zooplankton as an indication of fish food (Burkart *et al.*, 1995; Coombs *et al.*, 1994; Thompson and Harrop, 1991). There has been a number of studies on the spatial patterns of zooplankton species composition and behaviour in relation to the seasonal fronts found in the Irish Sea (Dickey-Collas *et al.*, 1996b; Gowen *et al.*, 1998a; Gowen *et al.*, 1998b; Scrope-Howe and Jones, 1985; Scrope-Howe and Jones, 1986). However, apart from naupliar size distributions (Burkart *et al.*, 1995) and general suspended particulate

	Group 2	**Group 3**	**Group 4**
Salinity (‰)	34.85	34.76	34.04
Temperature (°C)	13.65	14.33	15.05

Table 6.2 Average salinity (‰) and temperature (°C) of July 1998 samples comprising groups determined by cluster analysis.

size distributions (Coombs *et al.*, 1994), changes in size distribution associated with frontal systems in the Irish Sea have not been investigated.

The general species composition found in this study compare well with those described previously for the Irish Sea (Gowen *et al.*, 1997; Gowen *et al.*, 1998a; Scrope-Howe and Jones, 1985). The groups distinguished by the MDS plot in June also correspond well to areas previously described in the Irish Sea. Groups 1 and 2 fall in the mixed Irish coast region inside the 50m contour line. Group 3 falls in the summer stratified region demarcated by the western Irish Sea front. Group 4 falls in the mixed central channel and group 5 falls in the Welsh coastal waters separated from the mixed channel by the Liverpool Bay salinity front (Burkart *et al.*, 1995; Coombs *et al.*, 1994; Dickey-Collas *et al.*, 1996a; Dickey-Collas *et al.*, 1996b; Gowen and Bloomfield, 1996; Gowen *et al.*, 1997; Gowen *et al.*, 1998a; Gowen *et al.*, 1995; Scrope-Howe and Jones, 1985; Scrope-Howe and Jones, 1986). In July, there are similar groups, but they seem less well defined. Groups 1 and 2 still fall in Irish coastal waters, but are not confined within the 50m contour. Group 3 still corresponds to the summer stratified region, but this seems to extend further east than in June. Group 4 is again in the mixed central channel, but in this transect the Welsh coastal samples are not separated from these samples. It is known that stormy weather can act to break down stratification (Scrope-Howe and Jones, 1985), and the July cruise did suffer from some bad conditions. This may explain why the two coastal frontal zones are not as distinct as in June. However, the cyclonic gyre that is associated with the SSR may help to retain the zooplankton community in the area in spite of bad weather. It has also been noted that the zooplankton in these areas is highly temporally variable (Gowen *et al.*, 1997; Scrope-Howe and Jones, 1985). As the zooplankton maximum generally occurs in April to June (Scrope-Howe and Jones, 1985) you would expect relatively higher proportions of certain species in June compared to July, which may magnify differences between the areas when comparing species composition by proportion rather than absolute abundance. This would also explain the lack of meroplanktonic forms, except echinoderm larvae, in July compared the high numbers seen in June. This very high proportion of meroplankton, especially cirripede larvae, is the most likely cause of the significantly smaller zooplankton in the Irish coastal sites in June and July.

During the June transect the Welsh and Irish coastal sites both had lower salinity and higher temperature compared to the other sites. This is easily explained by freshwater input from rivers and a more shallow depth allowing the water to be heated quicker (White *et al.*, 1988). However, there is no obvious difference in the mixed and stratified oceanic regions. This may be due to the sampling range of the U-Tow deployments. The summer thermocline in the stratified region has been found at depths around 20m (Burkart *et al.*, 1995; Coombs *et al.*, 1994; Scrope-Howe and Jones, 1986). However, due to the nature of the research cruises (to test the undulation capabilities of the new U-Tow), sampling took place down to 50m where possible. This means that sampling also took place below the thermocline and, therefore, the average temperature will have been lowered by measurements taken in the colder deep waters. In July the temperature decreased and salinity increased from east to west, which has previously been found by Burkart *et al.* (1995).

The formation of stratification allows different nutrient and phytoplankton regimes to develop compared to mixed waters, for example, Coombs *et al.* (1994) found the stratified region to have larger phytoplankton species, less detritus and therefore a more direct and efficient food web compared to mixed waters which contained smaller copepods and bacterial cycling. This would explain the different zooplankton communities found in the different areas.

It is not at all surprising that the coastal, and therefore shallow, sites are different due to increased meroplanktonic species as you would expect to find more of these larval stages in close proximity to the spawning adults. Gowen *et al.* (1997) found a greater abundance of *Calanus* spp. in stratified waters in May/June and Burkart *et al.* (1995), found *Calanus* nauplii only in stratified water in May. In this study, the June transect agrees with their findings as *Calanus* had its peak in the SSR. However, in July *Calanus* was found in greater abundance in the Irish coastal group and the central mixed group. Scrope-Howe and Jones (1985) found cladocerans to be confined to the stratified region in April and May. In the present study cladocerans were confined to the Welsh coast in June, whereas in July, *Podon* spp. were found throughout and *Evadne* spp were only found in the Irish coastal site and the central mixed region. Gowen *et al.* (1998a) describe *Pseudocalanus* spp. as being abundant throughout the Irish Sea, with *Temora* spp. mainly restricted to coastal waters, and *Acartia* spp. and *Oithona* spp. mainly in offshore waters. In this study *Para/Pseudocalanus* spp. are widespread in June, although absent from the Irish coastal sites, but in July are only present in significant amounts in the central mixed and Welsh coastal regions. *Temora* spp. are also widespread in June, and concentrated in the central mixed and welsh coastal sites in July, and not restricted to coastal sites as described by Gowen *et al.* (1998a). Similarly, *Acartia* spp. is widespread in both surveys, and *Oithona* spp., although only found in the SSR in June, are widespread in July.

These results seem to indicate that, although the zooplankton communities can be separated according to areas of different water characteristics, these communities are highly variable from month to month and even year to year. In addition, there was no obvious size changes associated with the different areas, apart from the significantly smaller zooplankton at the Irish coastal sites caused by the large number of cirripede nauplii. In July, the Welsh coastal zooplankton appears to be significantly larger than the rest of the zooplankton in both surveys. However, this may be an artifact caused by Diel Vertical Migration (DVM) behaviour as a number of these samples were taken on the only tow deployed overnight.

Conclusions

- In June 1998, samples were divided into groups, using cluster analysis, corresponding to the Irish coast, the SSR, the mixed Irish Sea, and Liverpool Bay. The only difference in size were the significantly smaller zooplankton found at the Irish coast due to the dominance of echinoderm larve.
- In July 1998, samples were divided into groups from the Irish coast, the SSR and all other samples from the mixed region to the Welsh coast. All groups extended further east than in June. The mixed region/Welsh coast group had significantly larger zooplankton.
- The species composition of the groups also changed between the two sampling dates, although the Irish coastal sites were consistently dominated by meroplanktonic species.
- These results indicate that stratification can separate water into areas of different production regimes giving rise to different zooplankton communities. However, these communities are highly variable in terms of species composition.

CHAPTER 7

Mesozooplankton community size structure: evidence of 'top-down' control

Abstract

Epipelagic mesozooplankton were collected from Swansea Bay, the North Sea, the Irish Sea, the Baltic Sea, the North Atlantic and the Bay of Biscay with the aim of looking at the size structure of zooplankton communities over large spatial scales to determine if any evidence of 'top-down' control could be identified. There were significant decreases in zooplankton size as recruitment and numbers of planktivorous fish increased. However, the amount of variation in zooplankton size explained by these variables was relatively small indicating that there are other factors involved. It is likely that, in such large and complex ecosystems as these, environmental factors play a large role although there was no significant relationship between zooplankton size and temperature.

Introduction

One of the fundamental aims of ecology is to measure the production and energy flux of a community (Boudreau and Dickie, 1989; Boudreau and Dickie, 1992; Cyr and Peters, 1996; Platt and Denman, 1977; Platt and Denman, 1978; Sheldon *et al.*, 1977; Sprules and Goyke, 1994; Sprules and Munawar, 1986; Sprules and Stockwell, 1995). Physiological rates of individual organisms are consistently related to body size (Blackburn *et al.*, 1993; Cyr and Pace, 1993; Dickie *et al.*, 1987) and it has been shown that, across a wide variety of ecological communities, values for rates of production, respiration, excretion and specific production show constant patterns of change with individual body mass (Cyr and Pace, 1992; Cyr and Pace, 1993; Reid *et al.*, 2000; Rodhouse *et al.*, 1994). This suggests that ecological rates should also be related to the size structure of organisms in communities. Indeed, it has recently become common for ecosystem ecologists, especially in aquatic systems, to determine energy flow within communities from the broad size distributions of organisms, usually with no reference to taxonomy or trophic level (Cyr and Pace, 1993; Dickie *et al.*, 1987; Rodhouse *et al.*, 1994). However, to be able to interpret changes in the size distribution of animals in an ecosystem, it is essential to understand the mechanisms relating the size structure and the underlying ecological dynamics (Rudjakov *et al.*, 1995; Thiebaux, 1993) and to determine the type of control exerted over different temporal and spatial scales (Dufour and Torréton, 1996).

The relative importance of abiotic and biotic factors in regulating the size structure of communities has been widely debated (Carpenter *et al.*, 1987; McQueen *et al.*, 1986). 'Bottom-up' models suggest that nutrient availability determines the biomass and productivity of an ecosystem, whereas ‘top-down’ or ‘cascading trophic interaction’ models emphasise the effect of predators on lower trophic levels (Carpenter *et al.*, 1987; Currie *et al.*, 1999).

Epipelagic zooplankton are considered to be active agents of organic matter transfer from primary producers to large carnivores, and of nutrient regeneration through excretion (Ikeda, 1985; Lenz, 2000; Ojaveer *et al.*, 1998; Zhang *et al.*, 1995), and therefore determining the type of control exerted on planktonic populations is essential in order to understand oceanic fluxes (Dufour and Torréton, 1996). Predation appears to be one of the most obvious controls on zooplankton size structure, as most planktivores swallow their prey whole and it has been shown that most planktivorous fish selectively prey on larger zooplankton (Flinkman *et al.*, 1992; Gardner, 1981; Gotceitas and Brown, 1993; Hamrin, 1983; Munk, 1997; Plounevez and Champalbert, 2000; Shaheen *et al.*, 2001; Wahlström *et al.*, 2000; Wahlström and Westman, 1999). In addition, all components of planktivory, such as encounter rate, prey avoidance capacity, capture success and handling time, are size dependent.

In 1965, Brooks and Dodson (1965) put forward the size-efficiency hypothesis, which states that:

1. Planktonic herbivores all compete for fine particulate matter.
2. Larger zooplankters are more efficient grazers and can utilise larger particles.
3. When planktivory is low, the small planktonic herbivores will be eliminated by large forms.
4. When planktivory is high, the size-dependent predation will eliminate the larger forms allowing the small herbivores to become dominant.
5. When planktivory is intermediate, predation will keep the larger forms to sufficiently low numbers so that the smaller competitors are not eliminated.

Since this work, there has been much corroborating evidence from further freshwater studies (Almond *et al.*, 1996; Bøhn and Amundsen, 1998; Brooks, 1968; Dahl-Hansen, 1995; Devries and Stein, 1992; He *et al.*, 1994; Hurlbert and Mulla, 1981; Lazzaro *et al.*, 1992; Rudstam *et al.*, 1993; Vanni, 1986; Vanni, 1987). It is likely that, in nature, both 'bottom-up' and 'top-down' controls will operate in varying magnitudes in different temporal and spatial scales (McQueen *et al.*, 1986; Reid *et al.*, 2000). However, there has been relatively little work done in marine systems with most studies concentrating on species or total biomass changes (Cushing, 1995b; Flinkman *et al.*, 1998; Reid *et al.*, 2000; Rudstam *et al.*, 1994; Verheye and Richardson, 1998) although Verheye and Richardson (1998) did note an increase in the proportion of <0.9mm zooplankton coupled with an increase in anchovy abundance. Koslow (1983) put forward a simulation model to examine if predation can regulate the size structure of marine zooplankton communities which resulted in the general agreement that a large increase or decrease in planktivorous fish led to the dominance of small or large zooplankton. However, his model failed to explain the 1965-70 decline seen in zooplankton communities of the North Atlantic and herring and mackerel stock of the North Sea. Reid *et al.* (2000), in a review of 'top-down' control in marine systems, concluded that as ecosystem complexity increases, environmental factors become more important and 'top-down' factors less easy to distinguish.

The aim of this study is to look at the size structure of epipelagic mesozooplankton communities over large spatial scales and from a number of ocean systems, and determine if any evidence of 'top-down' control can be identified.

Methods

Zooplankton samples were collected from Swansea Bay, the North Sea, the Irish Sea, the Baltic Sea, the Bay of Biscay and the North Atlantic using a U-Tow, a high speed towed body designed to sample over extended spatial scales (Hays *et al.*, 1998; Mills *et al.*, 1998) and so overcome effects of zooplankton patchiness. In addition, WP2 net samples were taken at the beginning and end of all deployments except those in the Bay of Biscay and North Atlantic.

Three different U-Tow systems were used in this study. A fixed depth Valeport Ltd. U-Tow (Hays *et al.*, 1998) was deployed in Swansea Bay (December 1997, April, May, September and November 1998), the Baltic Sea (June 1999), and the Bay of Biscay and North Atlantic (July 1999). An undulating Valeport Ltd. U-Tow (Hays *et al.*, 1998) was deployed in the North Sea (February 1998), and an undulating W.S. Ocean Systems Ltd. U-Tow (Mills *et al.*, 1998) was deployed in the Irish Sea (June and July 1998). Tow speeds ranged between 13 and 18.5km.h^{-1}. All U-Tows were fitted with the same Plankton Sampling Mechanism (PSM) and 200 μm filtering mesh and CTD. The only difference in the three systems with respect to sampling zooplankton was the electromagnetic flowmeter fitted to the PSM used in the Valeport systems (Valeport Model 802) (Hays *et al.*, 1998). The W.S. Ocean Systems Ltd. model did not have a flowmeter fitted to the PSM. In these cases, the volume of water filtered per sample was calculated using the distance towed multiplied by the area of the inlet aperture. Although this method has been shown not to be ideal due to clogging (Hays, 1994; Hays *et al.*, 1998), the short duration of each sample (average 20mins) means that this was not a significant problem. In addition, the average efficiency of the U-Tow was calculated from the North Sea tows, which were of a comparable speed, and was not significantly different from 100% (Cook and Hays, 2001).

Deployments in Swansea Bay involved towing the fixed depth U-Tow, at a depth of 9m, round a triangular course, with each leg approximately 4.5km, for approximately 3 hours. The PSM was set to a sample interval of 15 minutes. 5-minute WP2 net tows at 9m, made possible by using a real time depth sensor, were taken at each corner of the triangular course. Deployments in the North Sea and Irish Sea involved towing the undulating U-Tow along a straight-line course, with a vertical WP2 net haul taken at the beginning and end of each tow. As the purpose of these cruises was to test the capabilities of the U-Tow, the length of tow and depth range varied between tows. Tow duration ranged between 1.5 hours and 16 hours and depth ranged between 5m and 40m. The PSM was set at sample intervals between 15 and 30 minutes. For each tow, vertical net hauls were taken from the maximum depth of the undulation profile to the surface. Deployments in the Baltic Sea involved towing the fixed depth U-Tow on a straight-line course, at a depth of 18m and sample interval of between 40 and 55 minutes, with vertical WP2 net hauls to 20m taken at the beginning and end of each tow. In all cases, a 56cm diameter WP2 net fitted with a General Oceanics flowmeter and Aladin Pro dive computer, for an accurate reading of depth, was deployed. Deployments in the Bay of Biscay and North Atlantic involved towing the fixed depth U-Tow on a straight-line course at a depth of 10m and sample interval of between 40 and 60 minutes. After each deployment samples were immediately washed off the mesh and preserved in 4% borax buffered seawater formaldehyde. In all cases samples left on the filtering section of the PSM during retrieval of the U-Tow were discarded. This was due to the possibility of plankton being washed off by turbulent water from the ships wash, and as water is drained out of the PSM.

For samples from Swansea Bay, the North Sea and the Irish Sea, measurements of length and width were made of at least 100 animals, or all the animals present if there were less than 100, from each sample using a calibrated eyepiece graticule. Animal widths were sorted into groups relating to animals that would be caught quantitatively by meshes in the size ranges 200-500µm, 500-1000µm, and 1000-2000µm. For samples from the Baltic Sea, the Bay of Biscay and the North Atlantic, samples were wet sieved into the size fractions 200-500µm, 500-1000µm, and 1000-2000µm. Using a binocular microscope, the animals in each size fraction were counted to give measures of the size structure of the zooplankton community.

Due to the variability in sample interval and tow speed for U-Tow samples, and the inclusion of WP2 net samples, the proportion of animals in each size fraction, rather than absolute numbers, was used in the data analysis. The average size of animals in a sample was calculated using the formula:

$$W = \sum_{S=1}^{S=i} ((M_L + M_U) / 2) \times P_S$$

where W is the average width of animals in the sample, S is the size fraction, M_L is the lower mesh size for the size fraction, M_U is the upper mesh size for the size fraction, and P_S is the proportion of animals in that size fraction. W was then converted to an average length by assuming a typical width:length ratio for mesozooplankton of 1:3 (Herman *et al.*, 1992). It is well known that, in any community, small organisms are generally more abundant than large organisms, often by orders of magnitude (Cyr and Pace, 1993; Zhou and Huntley, 1997). Therefore, to compare the size structure of the zooplankton in this study, the proportion of animals in the 500-2000µm size range was used as an indication of the size of the community.

Fisheries data were taken from ICES stock assessment reports, which are based on Virtual Population Analysis (VPA) and comprised total biomass, spawning stock biomass, recruitment and estimated total stock number for a number of individual species (Table 7.1) for 1998. The figures were divided by the relative areas of each ICES division involved to get fish density values for each division. Zooplankton size data were also divided into groups corresponding to the ICES divisions. Figure 7.1 shows the ICES divisions used.

Results

There were 82 individual tows covering a total of 5235 km (Figure 7.2). 288 U-Tow samples and 109 WP2 net samples were analysed. The average ratio of small (200-500μm) to large (500-2000μm) animals was 1:0.2 in the North Atlantic (average length of 1.32mm), 1:0.1 in the Bay of Biscay (average length of 1.22mm), 1:0.08 in the Irish Sea (average length of 1.17mm), 1:0.04 in the North Sea (average length of 1.10mm), 1:0.03 in the Baltic Sea (average length of 1.09mm) and 1:0.01 in Swansea Bay (average length of 1.07mm). Figure 7.3 shows the average proportion of large zooplankton in the different oceanic systems. A one-way ANOVA found significant between group differences in the proportion of large zooplankton in the different oceanic systems ($F_{5,391} = 369.0$, $p < 0.001$) and a Dunnett's T3 post-hoc test (Sokal and Rohlf, 1981) found significant differences between all pairs of means except Swansea Bay and the Baltic Sea, the North Sea and the Baltic Sea, and the Irish Sea and the Bay of Biscay.

There was a significant linear relationship between latitude and temperature ($F_{1,248} = 518.6$, $r^2 = 0.68$, $p < 0.001$) (Figure 7.4a) and a weak relationship between temperature and the proportion of large animals in a sample ($F_{1,248} = 22.0$, $r^2 = 0.08$, $p < 0.001$) (Figure 7.4b),

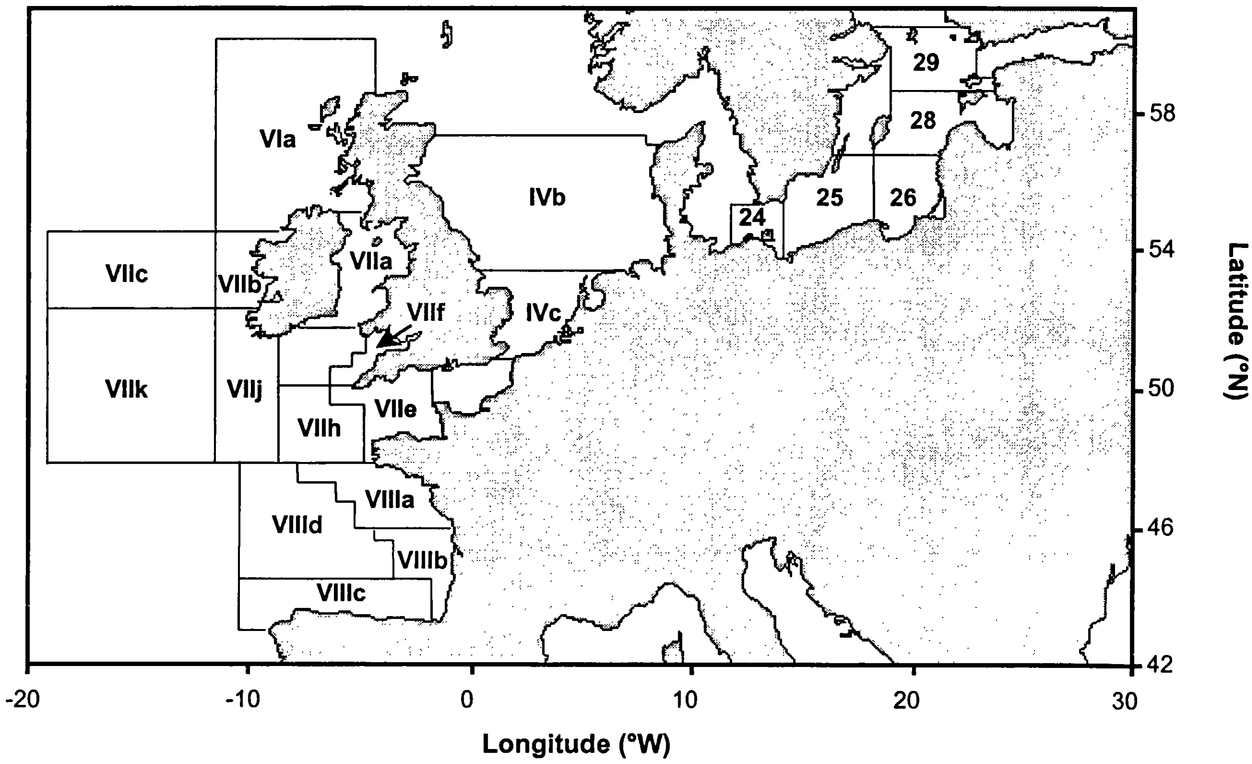

Fig 7.1 Approximate positions of ICES divisions sampled.

Species	**ICES divisions**
Anchovy (*Engraulis encrasicolus*)	Sub-area VIII
Anglerfish (*Lophius piscatorius, Lophius budegassa*)	Divisions VIIb-k, VIIIa,b
Blue whiting (*Micromesistius poutassou*	Sub-areas I-IX, XII, XIV
Cod (*Gadus morhua*)	Sub-divisions 25-32 Sub-area IV, divisions VIId, IIIa Division VIa Division VIIa Divisions VIIe-k
Haddock (*Melanogrammus aeglefinus*)	Sub-area IV, division IIIa Division VIa Division VIIa
Herring (*Clupea harengus*)	Sub-divisions 25-29,32 Sub-area IV, divisions VIId, IIIa Division VIa Divisions VIa (south), VIIb, c Division VIa (north) Division VIIa Divisions VIIf, g, j
Hake (*Merluccius merluccius*)	Divisions IIIa, VIIIa, b, Sub-areas IV, VI, VII Divisions VIIIc, IXa
Horse mackerel (*Trachurus trachurus*)	Divisions IIa, IVa, Vb, VIa, VIIa-c, e-k, VIIIa, b, d, e Divisions IIIa (east), IVb, c, VIId Divisions VIIIc, IXa
Mackerel (*Scomber scombrus*)	Sub-areas IV, VI, VII, VIII, divisions IIa, IIIa, Vb, IXa
Megrim (*Lepidorhombus whiffiagonis Lepidorhombus boscii*)	Sub-area VII, divisions VIIIa, b, d, e Divisions VIIIc, IXa
Norway pout (*Trisopterus esmarkii*)	Sub-area IV, division IIIa
Plaice (*Pleuronectes platessa*)	Sub-area IV Division VIIa Division VIIe Divisions VII f, g
Saithe (*Pollachius virens*)	Sub-area IV, VI, division IIIa
Sandeel (*Ammodytes spp.*)	Sub-area IV
Sardine (*Sardina pilchardus*)	Divisions VIIIc, IXa
Sole (*Solea solea*)	Sub-area IV Division VIIa Division VIIe Divisions VIIf, g Divisions VIIIa, b
Sprat (*Sprattus sprattus*)	Sub-divisions 22-32 Sub-area IV Divisions VIId, e
Whiting (*Merlangus merlangus*)	Sub-area IV, division VIId Division VIa Division VIIa Divisions VIIe-k

Table 7.1 Species and ICES divisions for which fisheries data were compiled.

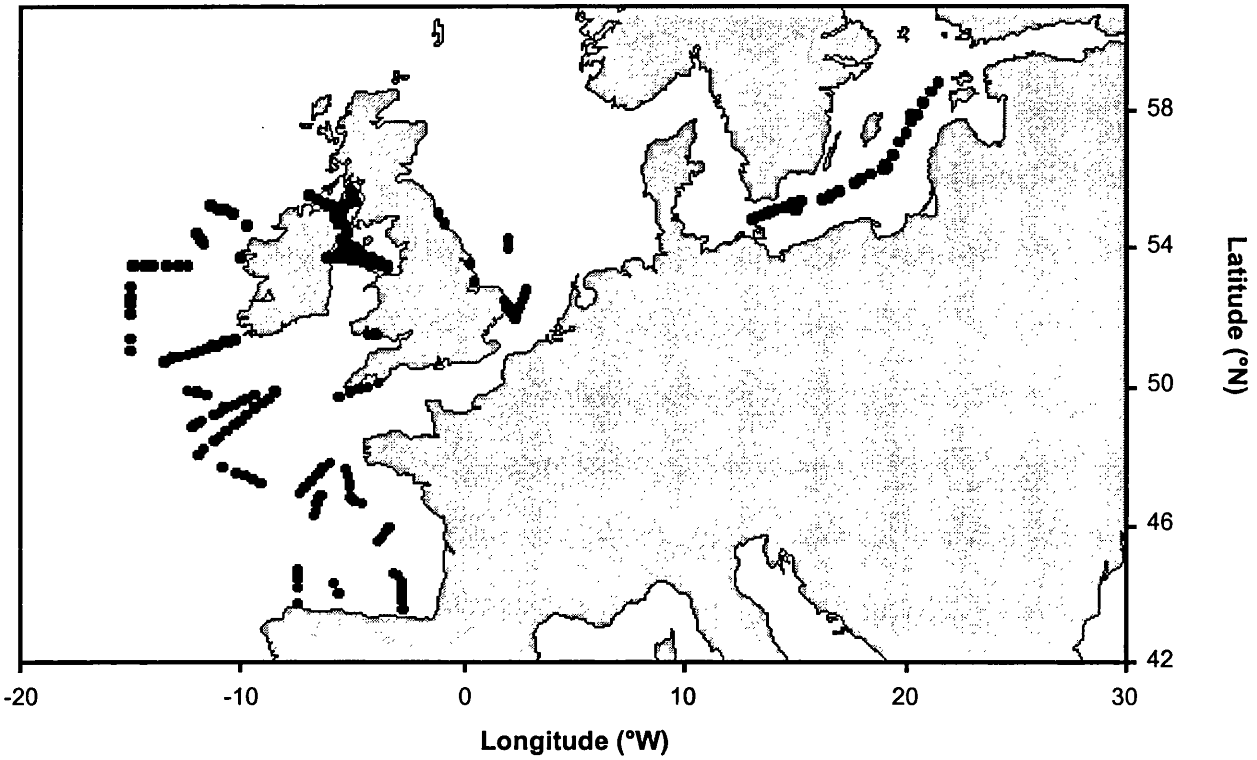

Fig 7.2 Spatial distribution of mesozooplankton samples. Filled circles represent the midpoint of each sample.

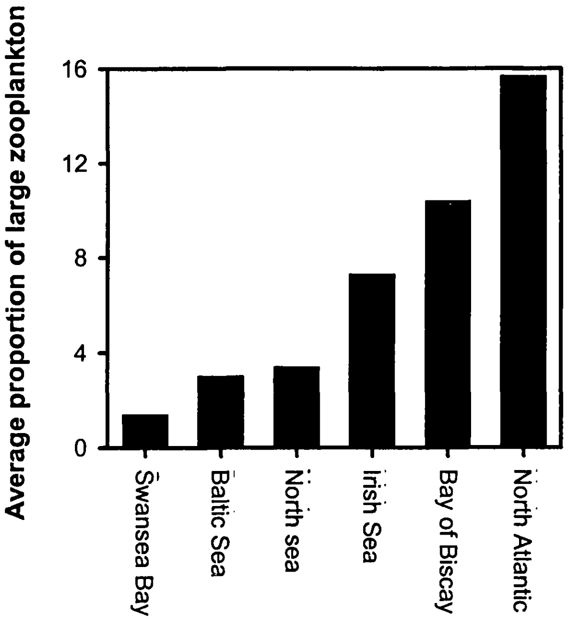

Fig 7.3 Average proportion of large zooplankton in the different oceanic systems

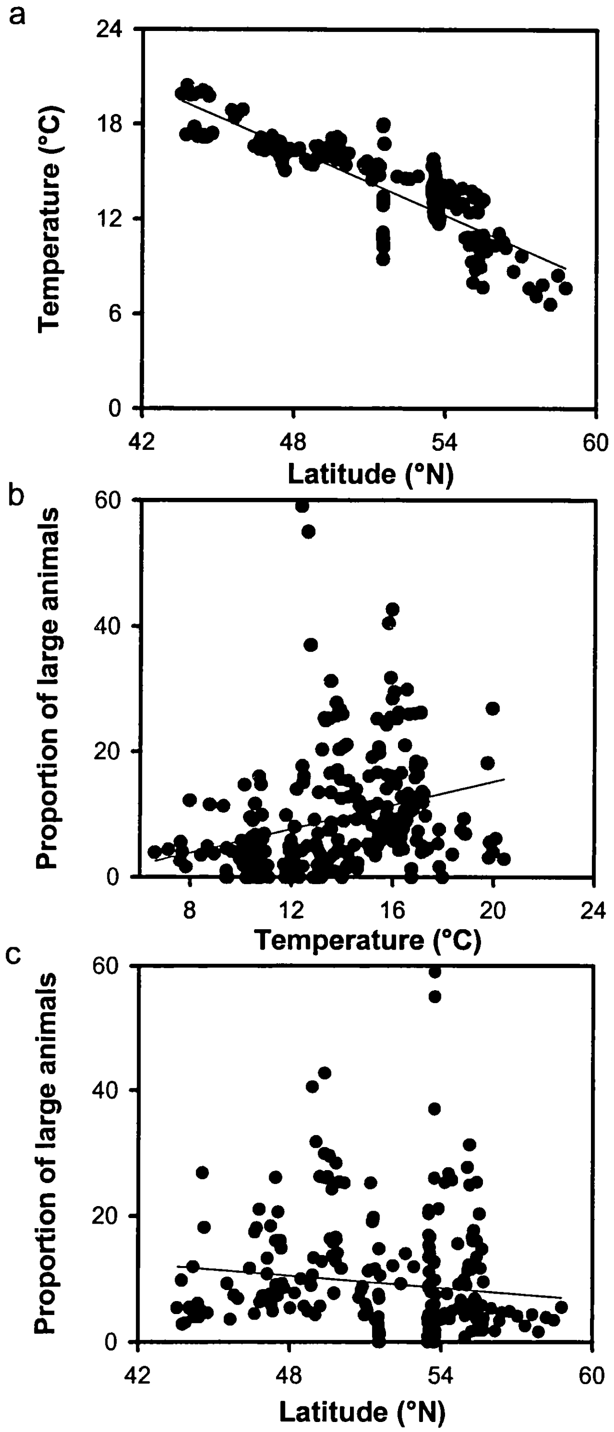

Fig 7.4 Relationships between: a) temperature (°C) and latitude (°N). b) proportion of large animals in a sample and temperature (°C). c) proportion of large animals in a sample and latitude (°N).

however the relationship between latitude and proportion of large animals in a sample was not significant ($F_{1,248} = 3.4$, $r^2 = 0.01$, $p = 0.068$) (Figure 7.4c).

There were significant negative relationships between the average proportion of large zooplankton in an ICES division and ln(relative density of total fish biomass) ($F_{1,18} = 18.8$, $r^2 = 0.51$, $p < 0.001$), ln(relative density of total planktivorous fish biomass ($F_{1,18} = 20.0$, $r^2 = 0.53$, $p < 0.001$), ln(relative density of total fish spawning stock biomass) ($F_{1,18} = 12.7$, $r^2 = 0.41$, $p < 0.05$), ln(relative density of total fish recruitment) ($F_{1,18} = 14.1$, $r^2 = 0.44$, $p < 0.005$), ln(relative density of total fish numbers) ($F_{1,18} = 8.0$, $r^2 = 0.31$, $p < 0.05$), and ln(relative density of total planktivorous fish numbers) ($F_{1,18} = 7.0$, $r^2 = 0.28$, $p < 0.05$) (Figure 7.5). There was also a significant positive relationship between the average proportion of large zooplankton in an ICES division and the average water depth ($F_{1,18} = 10.1$, $r^2 = 0.36$, $p < 0.01$). However, a step-wise multiple regression with all the variables found the best descriptor of average proportion of large zooplankton to be ln(relative density of total planktivorous fish biomass) on its own. It would be impossible to test for evidence of 'top-down' control on zooplankton community size structure if fish predation increased with temperature, as they would both produce the same results (Figure 7.6a). However, in this study the general trend was for the indices of fish predation to decrease with temperature (Figure 7.6b).

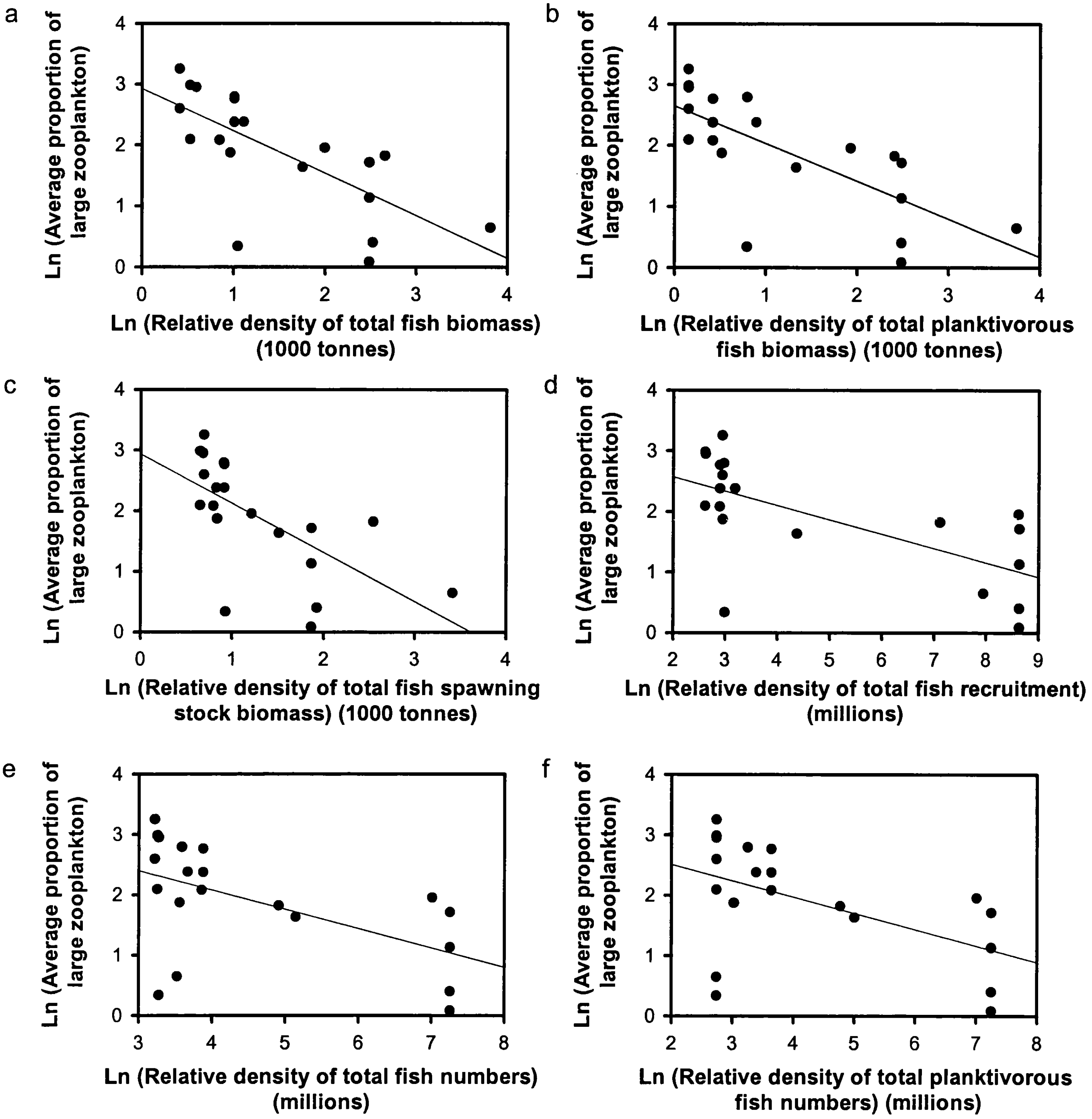

Fig 7.5 Relationships between natural log transformed average proportion of large zooplankton and relative densities of: a) total fish biomass (1000 tonnes), b) total planktivorous fish biomass, c) total fish spawning stock biomass (1000 tonnes), d) fish recruitment (millions), e) total fish numbers (millions), and f) total planktivorous fish numbers (millions).

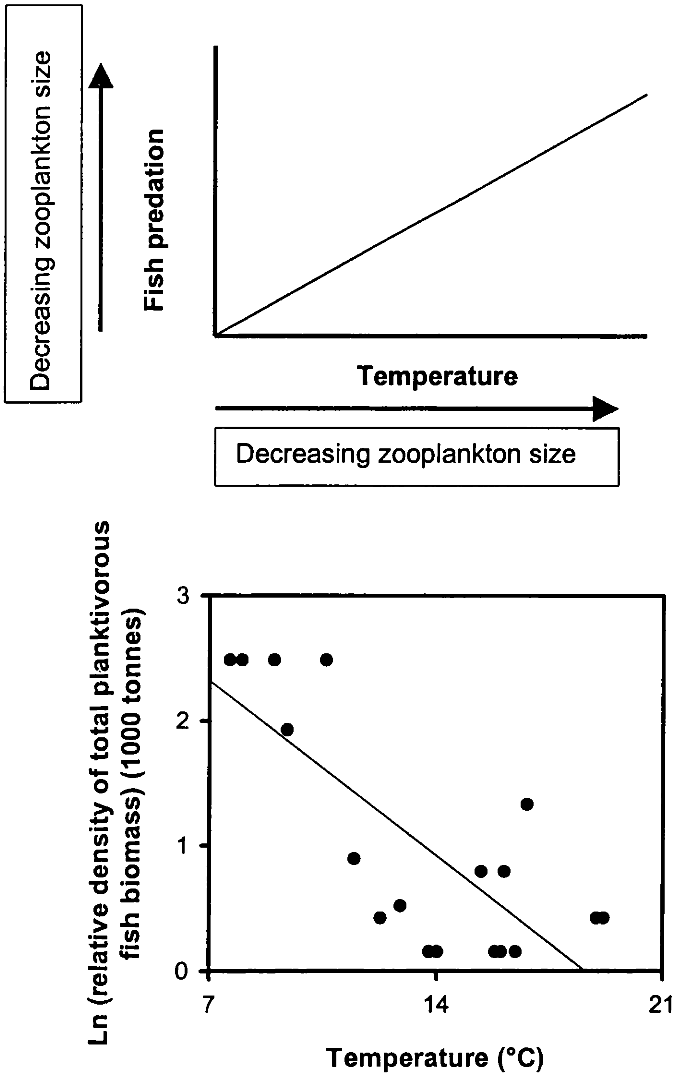

Fig 7.6 a) Schematic representing the hypothesised patterns of change in zooplankton size with temperature and fish predation, indicating that increasing temperature and increasing fish predation would produce the same effect on zooplankton size. b) Trend in ln (relative density of total planktivorous fish biomass) with temperature.

Discussion

In freshwater systems it is widely accepted that predation from planktivorous fish can structure the size distribution in zooplankton communities (Almond *et al.*, 1996; Brooks, 1968; Devries and Stein, 1992; Lazzaro *et al.*, 1992). However, in marine systems there has been relatively little work concerning this relationship, and the evidence is much less convincing (Cushing, 1995b; Flinkman *et al.*, 1998; Koslow, 1983; Reid *et al.*, 2000; Verheye and Richardson, 1998). One of the reasons for this is the large scale of the oceans compared to average freshwater systems. Plankton tend to have a very patchy spatial distribution (Currie *et al.*, 1998; Folt and Burns, ; Greene *et al.*, 1998b; Piontkovski and Williams, 1995; Stockwell and Sprules, 1995) so you need to have a very spatially intensive sampling program to accurately estimate the abundance. Most plankton sampling is done using net hauls, which sample a few tens or hundreds of meters. It is relatively easy to extensively sample an average lake using this method. However, when trying to describe the plankton in large oceanic regions this would be impossible due to time and money constraints. Large-scale samplers, such as the U-Tow and Continuous Plankton Recorder (CPR) make such intensive sampling easier, cheaper, and overcome the effects of plankton patchiness to give measures of average abundance or size structure over larger areas. Reid *et al.* (2000) studied the effects of different fish species on zooplankton species in the North Sea using CPR data and concludes that at times ‘top-down’ control may be an important factor in the North Sea ecosystem, but no large-scale studies of the effects on zooplankton size structure have been attempted.

There are also hypotheses on the effect of temperature on the size of individuals within a species of zooplankton (Gillooly, 2000; Huntley and Lopez, 1992; Ikeda, 1985; Klein Breteler *et al.*, 1995), and it is generally accepted that as environmental temperature decreases the size of zooplankton increases, forming a latitudinal pattern of decreasing zooplankton size as you approach the equator. From this hypothesis you would predict that, in this study, the largest zooplankton would be found in the Baltic Sea and the smallest zooplankton in the Bay of Biscay. However, the Baltic had one of the smallest zooplankton communities and the Bay of Biscay one of the largest. Although there was a significant trend in decreasing temperature with latitude there was no relationship between latitude and zooplankton size. Indeed, the relationship seen between temperature and zooplankton size, although very weak, showed an increase in the proportion of large animals in a sample as temperature increased. This implies that there are other additional factors controlling the size of zooplankton.

Significant relationships between zooplankton size and fish variables were found, with the most variation in zooplankton size being accounted for by the relative density of total planktivorous fish biomass. It is surprising that the number of planktivorous fish did not have more of an effect. However, this could be a reflection that fish biomass is a better index of fish predation than fish numbers, as the amount of plankton eaten by a fish will depend on its size.

In all cases where there was a significant relationship between fish and zooplankton size, the amount of variation explained was relatively low (between 28 and 53%). However, the plankton from Swansea Bay (ICES division VIIf) seems to be unusual as it is much smaller than you would expect from the levels of fish predation indices. When these data are removed from the regression, the variation in proportion of large zooplankton explained by the relative density of planktivorous fish biomass rises to 67% ($F_{1,18} = 33.8$, $p < 0.001$). There are a number of factors that could account for this. Firstly, sampling in ICES division VIIf only took place in Swansea Bay, and therefore the fish data, which covers the whole area, may not actually reflect levels in Swansea Bay. Secondly, Swansea Bay is a very shallow coastal site with strong tidal conditions and a relatively low salinity, which implies that turbidity may be higher than other sites due to disturbance and coastal run-off. Lougheed and Chow-Fraser (1998) noted that high turbidity, which is often associated with coastal sites, selected against large filter feeders and allowed smaller zooplankton to dominate.

There are also a number of other factors that could account for the low amount of variation in zooplankton size explained by fish predation indices. Firstly, as the larger zooplankton are much scarcer than the small zooplankton, sometimes they are missed when sampling. Secondly, the ICES stock assessment reports only deal with fish for which there is a fishery. There could be a large number of other fish species present in these areas for which there is no data available. In addition, the ICES data are constructed from virtual population analysis, which is based on stock assessment cruises and catch data, but may not reflect the natural population accurately. Thirdly, many young fish tend to cluster in certain hydrographic features, such as gyres (Dickey-Collas *et al.*, 1997; Dickey-Collas *et al.*, 1996a), and so the predation on zooplankton may be more concentrated in certain areas. However, the sampling for this study was very spatially intensive.

There are other factors which could also be affecting zooplankton size. For example, the amount of invertebrate predation (which tends to fall more heavily on smaller animals (Almond *et al.*, 1996; O'Brien, 2001; O'Brien and Kettle, 1979; Wahlström and Westman, 1999), 'bottom-up' control through the availability of food and nutrients for phytoplankton, and environmental factors such as temperature and salinity (that could affect both the zooplankton directly and other members of the food web such as phytoplankton and fish). As the sample area in this study was so large, it is likely that all of these factors may also vary considerably. A further factor could be the amount of refuge from fish available to zooplankton. It is hypothesised that Diel Vertical Migration (DVM), or the tendency for zooplankton to stay at depth during the day and return to the surface to feed at night, is a behaviour designed to minimise the risk of predation from visual feeders such as planktivorous fish (Zaret and Suffern, 1976). It follows from this that you would expect to find smaller zooplankton in shallow water as this refuge from predation is unavailable. From this hypothesis you would predict that the largest zooplankton would be found in the North Atlantic and the smallest zooplankton would be found in Swansea Bay, and this is what is seen in the present study, and was further confirmed by the positive relationship between zooplankton size and water depth in ICES divisions.

So, to conclude, some evidence of 'top-down' control by fish on the size structure of epipelagic mesozooplankton communities was identified. However, the amount of variation in zooplankton size explained by these variables was relatively small indicating that there are other factors, such as water depth, involved. It is likely that, in such large and complex ecosystems as these, environmental factors play a large role (Reid *et al.*, 2000).

Conclusions

- From the hypothesis of decreasing zooplankton size with increasing temperature, you would predict that there would be larger zooplankton in the Baltic Sea compared to the Bay of Biscay, but in this study the opposite was found. A relationship was found, although very weak, of increasing size with increasing temperature. This implies that other factors are controlling zooplankton size over large spatial scales.
- Using ICES fisheries data, it was found that the relative density of planktivorous fish biomass explained the most variation in zooplankton size, indicating that there is top-down control of zooplankton size.
- There was a much better relationship with the biomass of fish than the numbers of fish indicating that biomass is a better index of fish predation, probably because the amount of plankton eaten by a fish will depend on its size.
- Plankton from Swansea Bay was much smaller than you would predict from the levels of fish predation indices. This may be due to the strong tidal conditions and very shallow water found in the bay leading to high turbidity which can select against larger filter feeders.

REFERENCES

Aebischer, N.J., Coulson, J.C. and Colebrook, J.M. (1990) Parallel long-term trends across four marine trophic levels and weather. *Nature* 347:753-755.

Ahel, M., Barlow, R.G. and Mantoura, R.F.C. (1996) Effect of salinity gradients on the distribution of phytoplankton pigments in a stratified estuary. *Mar. Ecol. Prog. Ser.* 143:289-295.

Ahrens, M.A. and Peters, R.H. (1991) Patterns and limitations in limnoplankton size spectra. *Can. J. Fish. Aquat. Sci.* 48:1967-1978.

Akopian, M., Garnier, J. and Pourriot, R. (1999) A large reservoir as a source of zooplankton for the river: structure of the populations and influence of fish predation. *J. Plankton Res.* 21:285-297.

Allen, J.I. (1997) A modelling study of ecosystem dynamics and nutrient cycling in the Humber plume, UK. *J. Sea Res.* 38:333-359.

Allen, J.R., Slinn, D.J., Shammon, T.M., Hartnoll, R.G. and Hawkins, S.J. (1998) Evidence for eutrophication of the Irish Sea over four decades. *Limnol. Oceanogr.* 43:1970-1974.

Almond, M.J.R., Bentzen, E. and Taylor, W.D. (1996) Size structure and species composition of plankton communities in deep Ontario lakes with and without *Mysis relicta* and planktivorous fish. *Can. J. Fish. Aquat. Sci.* 53:315-325.

Al-Mutairi, H. and Landry, M.R. (2001) Active export of carbon and nitrogen at Station ALOHA by diel migrant zooplankton. *Deep-Sea Res. II* 48:2083-2103.

Alvarez-Cobelas, M. and Rojo, C. (2000) Ecological goal functions and plankton communities in lakes. *J. Plankton Res.* 22:729-748.

Andersen, V., Sardou, J. and Gasser, B. (1997) Macroplankton and micronekton in the northeast tropical Atlantic: abundance, community composition and vertical distribution in relation to different trophic environments. *Deep-Sea Res. I* 44:193-222.

Arnott, S.E. and Vanni, M.J. (1993) Zooplankton assemblages in fishless bog lakes: influence of biotic and abiotic factors. *Ecology* 74:2361-2380.

Aron, W., Ahlstrom, E.H., Bary, B.M., Bé, A.W.H. and Clarke, W.D. (1965) Towing characteristics of plankton sampling gear. *Limnol. Oceanogr.* 10:333-340.

Arrhenius, F. and Hansson, S. (1993) Food consumption of larval, young and adult herring and sprat in the Baltic Sea. *Mar. Ecol. Prog. Ser.* 96:125-137.

Ashjian, C.J., Smith, S.L., Flagg, C.N. and Wilson, C. (1998) Patterns and occurrence of diel vertical migration of zooplankton biomass in the Mid-Atlantic Bight described by an acoustic Doppler current profiler. *Cont. Shelf. Res.* 18:831-858.

Båmstedt, U. (1998) Trophodynamics of *Pleurobrachia pileus* (Ctenophora, Cydippida) and ctenophore summer occurrence off the Norwegian north-west coast. *Sarsia* 83:169-181.

Båmstedt, U., Martinussen, M.B. and Matsakis, S. (1994) Trophodynamics of the two scyphozoan jellyfishes, *Aurelia aurita* and *Cyanea capillata*, in western Norway. *ICES J. Mar. Sci.* 51:369-382.

Banse, K. (1995) Zooplankton: pivotal role in the control of ocean production. *ICES J. Mar. Sci.* 52:265-277.

Beaugrand, G., Ibanez, F. and Reid, P.C. (2000) Spatial, seasonal and long-term fluctuations of plankton in relation to hydroclimatic features in the English Channel, Celtic Sea and Bay of Biscay. *Mar. Ecol. Prog. Ser.* 200:93-102.

Beckmann, W., Auras, A. and Hemleben, C. (1987) Cyclonic cold-core eddy in the eastern North Atlantic. III. Zooplankton. *Mar. Ecol. Prog. Ser.* 39:165-173.

Benfield, M.C., Wiebe, P.H., Stanton, T.K., Davis, C.S., Gallager, S.M. and Greene, C.H. (1998) Estimating the spatial distribution of zooplankton biomass by combining Video Plankton Recorder and single-frequency acoustic data. *Deep-Sea Res. II* 45:1175-1199.

Besiktepe, S. and Unsal, M. (2000) Population structure, vertical distribution and diel migration of *Sagitta setosa* (Chaetognatha) in the south-western part of the Black sea. *J. Plankton Res.* 22:669-683.

Blackburn, T.M., Brown, V.K., Doube, B.M., Greenwood, J.D., Lawton, J.H. and Stork, N.E. (1993) The relationship between abundance and body size in natural animal assemblages. *J. Anim. Ecol.* 62:519-528.

Bogdan, K.G. and Gilbert, J.J. (1984) Body size and food size in freshwater zooplankton. *Proc. Natl. Acad. Sci. USA* 81:6427-6431.

Bøhn, T. and Amundsen, P. (1998) Effects of invading vendace (*Coregonus albula* L.) on species composition and body size in two zooplankton communities of the Pasvik River System, northern Norway. *J. Plankton Res.* 20:243-256.

Botas, J.A., Fernandez, E., Bode, A. and Anadon, R. (1990) A persistent upwelling off the central Cantabrian Coast (Bay of Biscay). *Est. Coast. Shelf Sci.* 30:185-199.

Boudreau, P.R. and Dickie, L.M. (1989) Biological model of fisheries production based on physiological and ecological scalings of body size. *Can. J. Fish. Aquat. Sci.* 46:614-623.

Boudreau, P.R. and Dickie, L.M. (1992) Biomass spectra of aquatic ecosystems in relation to fisheries yield. *Can. J. Fish. Aquat. Sci.* 49:1528-1538.

Bradford-Grieve, J., Murdoch, R., James, M., Oliver, M. and McLeod, J. (1998) Mesozooplankton biomass, composition, and potential grazing pressure on phytoplankton during austral winter and spring 1993 in the Subtropical Convergence region near New Zealand. *Deep-Sea Res. I* 45:1709-1737.

Brierley, A.S., Brandon, M.A. and Watkins, J.L. (1998a) An assessment of the utility of an acoustic Doppler current profiler for biomass estimation. *Deep-Sea Res. I* 45:1555-1573.

Brierley, A.S., Ward, P., Watkins, J.L. and Goss, C. (1998b) Acoustic discrimination of Southern Ocean zooplankton. *Deep-Sea Res. II* 45:1155-1173.

Brooks, J.L. (1968) The effects of prey size selection by lake planktivores. *Syst. Zool.* 17:272-291.

Brooks, J.L. and Dodson, S.I. (1965) Predation, body size, and composition of plankton. *Science* 150:28-35.

Burkart, C.A., Kleppel, G.S., Brander, K., Holliday, D.V. and Pieper, R.E. (1995) Copepod and barnacle nauplius distributions in the Irish Sea: relation to springtime hydrographic variability. *J. Plankton Res.* 17:1177-1188.

Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., Cochran, P.A., Elser, J.J., Elser, M.M., Lodge, D.M., Kretchmer, D. and He, X. (1987) Regulation of lake primary productivity by food web structure. *Ecology* 68:1863-1876.

Carr, M.R. (1997) *PRIMER user manual. Plymouth Routines In Multivariate Ecological Research.* Plymouth: Plymouth Marine Laboratory.

Checkley, D.M.J., Dagg, M.J. and Uye, S. (1992) Feeding, excretion and egg production by individuals and populations of the marine, planktonic copepods, *Acartia* spp. and *Centropages furcatus*. *J. Plankton Res.* 14:71-96.

Clark, D.R., Aazem, K.V. and Hays, G.C. (2001a) Zooplankton abundance and community structure over a 4000 km transect in the north-east Atlantic. *J. Plankton Res.* 23:365-372.

Clark, R.A., Frid, C.L.J. and Batten, S. (2001b) A critical comparison of two long-term zooplankton time series from the central-west North Sea. *J. Plankton Res.* 23:27-39.

Clarke, M.R. and Warwick, R.M. (1994) *Change in marine communities. An approach to statistical analysis and interpretation.* Bournemouth: Natural Environment Research Council.

Clutter, R.I. and Anraku, M. (1968) Avoidance of samplers. In: *Zooplankton sampling.* Tranter, D. J. (ed.) Paris: UNESCO, pp. 57-76.

Colebrook, J.M. (1979) Continuous plankton records: seasonal cycles of phytoplankton and copepods in the North Atlantic Ocean and the North Sea. *Mar. Biol.* 51:23-32.

Colebrook, J.M. (1984) Continuous plankton records: relationships between species of phytoplankton and zooplankton in the seasonal cycle. *Mar. Biol.* 83:313-323.

Collins, N.R. and Williams, R. (1981) Zooplankton of the Bristol channel and Severn estuary. The distribution of four copepods in relation to salinity. *Mar. Biol.* 64:273-283.

Conversi, A. and Hameed, S. (1998) Common signals between physical and atmospheric variables and zooplankton biomass in the Subarctic Pacific. *ICES J. Mar. Sci.* 55:739-747.

Cook, K.B. and Hays, G.C. (2001) Comparison of the epi-pelagic zooplankton samples from a U-Tow and the traditional WP2 net. *J. Plankton Res.* 23: 953-962.

Coombs, S.H., Robins, D.B., Conway, D.V.P., Halliday, N.C. and Pomroy, A.J. (1994) Suspended particulates in the Irish Sea and feeding conditions for fish larvae. *Mar. Biol.* 118:7-15.

Corten, A. (1999) Evidence from plankton for multi-annual variations of Atlantic inflow in the northwestern North Sea. *J. Sea Res.* 42:191-205.

Coyle, K.O., Weingartner, T.J. and Hunt, G.L.J. (1998) Distribution of acoustically determined biomass and major zooplankton taxa in the upper mixed layer relative to water masses in the western Aleutian Islands. *Mar. Ecol. Prog. Ser.* 165:95-108.

Currie, D.J., Dilworth-Christie, P. and Chapleau, F. (1999) Assessing the strength of top-down influences on plankton abundance in unmanipulated lakes. *Can. J. Fish. Aquat. Sci.* 56:427-436.

Currie, W.J.S., Claereboudt, M.R. and Roff, J.C. (1998) Gaps and patches in the ocean: a one-dimensional analysis of planktonic distributions. *Mar. Ecol. Prog. Ser.* 171:15-21.

Cushing, D. (1995a) *Population production and regulation in the sea.* Cambridge: Cambridge University Press, pp. 354.

Cushing, D.H. (1975) *Marine ecology and fisheries.* Cambridge: Cambridge University Press, pp. 278.

Cushing, D.H. (1995b) The long-term relationship between zooplankton and fish. *ICES J. Mar. Sci.* 52:611-626.

Cyr, H. and Pace, M.L. (1992) Grazing by zooplankton and its relationship to community structure. *Can. J. Fish. Aquat. Sci.* 49:1455-1465.

Cyr, H. and Pace, M.L. (1993) Allometric theory: extrapolations from individuals to communities. *Ecology* 74:1234-1245.

Cyr, H. and Peters, R.H. (1996) Biomass-size spectra and the prediction of fish biomass in lakes. *Can. J. Fish. Aquat. Sci.* 53:994-1006.

Dahl-Hansen, G.A.P. (1995) Long-term changes in crustacean zooplankton- the effects of a mass removal of Arctic charr, *Salvelinus alpinus* (L), from an oligotrophic lake. *J. Plankton Res.* 17:1819-1833.

Dam, H.G., Miller, C.A. and Jonasdottir, S.H. (1993) The trophic role of mesozooplankton at 47°N, 20°W during the North Atlantic Bloom Experiment. *Deep-Sea Res. II* 40:197-212.

de Lafontaine, Y. (1994) Zooplankton biomass in the southern Gulf of St. Lawrence: spatial patterns and the influence of freshwater runoff. *Can. J. Fish. Aquat. Sci.* 51:617-635.

De Robertis, A., Jaffe, J.S. and Ohman, M.D. (2000) Size-dependent visual predation risk and the timing of vertical migration in zooplankton. *Limnol. Oceanogr.* 45:1838-1844.

Dessier, A. and Donguy, J.R. (1985) Planktonic copepods and environmental properties of the eastern equatorial Pacific: seasonal and spatial variations. *Deep-Sea Res.* 32:1117-1133.

DeVries, D.R. and Stein, R.A. (1991) A comparison of three zooplankton samplers- a taxon specific assessment. *J. Plankton Res.* 13:53-59.

Devries, D.R. and Stein, R.A. (1992) Complex interactions between fish and zooplankton: Quantifying the role of an open water planktivore. *Can. J. Fish. Aquat. Sci.* 49:1216-1227.

Dickey-Collas, M., Brown, J., Fernand, L., Hill, A.E., Horsburgh, K.J. and Garvine, R.W. (1997) Does the western Irish Sea gyre influence the distribution of pelagic juvenile fish? *J. Fish. Biol.* 51:206-229.

Dickey-Collas, M., Gowen, R.J. and Fox, C.J. (1996a) Distribution of larval and juvenile fish in the western Irish Sea: relationship to phytoplankton, zooplankton biomass and recurrent physical features. *Mar. Freshwater Res.* 47:169-181.

Dickey-Collas, M., Stewart, B.M. and Gowen, R.J. (1996b) The role of thermal stratification on the population dynamics of *Sagitta elegans* Verrill in the western Irish Sea. *J. Plankton Res.* 18:1659-1674.

Dickie, L.M., Kerr, S.R. and Boudreau, P.R. (1987) Size-dependent processes underlying regularities in ecosystem structure. *Ecol. Mon.* 57:233-250.

Dippner, J.W., Kornilovs, G. and Sidrevics, L. (2000) Long-term variability of mesozooplankton in the Central Baltic Sea. *J. Mar. Sys.* 25:23-31.

Dufour, P.H. and Torréton, J.-P. (1996) Bottom-up and top-down control of bacterioplankton from eutrophic to oligotrophic sites in the tropical northeastern Atlantic Ocean. *Deep-Sea Res. I* 43:1305-1320.

Durbin, E.G., Garrahan, P.R. and Casas, M.C. (2000) Abundance and distribution of *Calanus finmarchicus* on the Georges Bank during 1995 and 1996. *ICES J. Mar. Sci.* 57:1664-1685.

Durbin, E.G., Gilman, S.L., Campbell, R.G. and Durbin, A.G. (1995) Abundance, biomass, vertical migration and estimated development rate of the copepod *Calanus finmarchicus* in the southern Gulf of Maine during late spring. *Cont. Shelf. Res.* 15:571-591.

Duró, A. and Saiz, E. (2000) Distribution and trophic ecology of chaetognaths in the western Mediterranean in relation to an inshore-offshore gradient. *J. Plankton Res.* 22:339-361.

Echevarría, F., Carrillo, P., Jimenez, F., Sanchez-Castillo, P., Cruz-Pizarro, L. and Rodriguez, J. (1990) The size-abundance distribution and taxonomic composition of plankton in an oligotrophic, high mountain lake (La Caldera, Sierra Nevada, Spain). *J. Plankton Res.* 12:415-422.

Ehlin, U. (1981) Hydrology of the Baltic Sea. In: *The Baltic Sea.* Voipio, A. (ed.) Amsterdam: Elsevier Science Publishers, pp. 123-134.

Elser, J.J., Goff, N.C., MacKay, N.A., St. Amand, A.L., Elser, M.M. and Carpenter, S.R. (1987) Species-specific algal responses to zooplankton: experimental and field observations in three nutrient-limited lakes. *J. Plankton Res.* 9:699-717.

Engström, J., Koski, M., Viitasalo, M., Reinikainen, M., Repka, S. and Sivonen, K. (2000) Feeding interactions of the copepods *Eurytemora affinis* and *Acartia bifilosa* with the cyanobacterium *Nodularia* sp. *J. Plankton Res.* 22:1403-1409.

Escribano, R. and Hidalgo, P. (2000) Influence of *El Niño* and *La Niña* on the population dynamics of *Calanus chilensis* in the Humboldt Current ecosystem of northern Chile. *ICES J. Mar. Sci.* 57:1867-1874.

Falkenhaug, T., Tande, K.S. and Semenova, T. (1997) Diel, seasonal and ontogenetic variations in the vertical distributions of four marine copepods. *Mar. Ecol. Prog. Ser.* 149:105-119.

Fernández, E., Cabal, J., Acuña, J.L., Bode, A., Botas, A. and García-Soto, C. (1993) Plankton distribution across a slope current-induced front in the southern Bay of Biscay. *J. Plankton Res.* 15:619-641.

Fiksen, Ø. and Carlotti, F. (1998) A model of optimal life history and diel vertical migration in *Calanus finmarchicus*. *Sarsia* 83:129-147.

Flinkman, J., Aro, E., Vuorinen, I. and Viitasalo, M. (1998) Changes in northern Baltic zooplankton and herring nutrition from 1980s to 1990s: top-down and bottom-up processes at work. *Mar. Ecol. Prog. Ser.* 165:127-136.

Flinkman, J., Vuorinen, I. and Aro, E. (1992) Planktivorous Baltic herring (*Clupea harengus*) prey selectively on reproducing copepods and cladocerans. *Can. J. Fish. Aquat. Sci.* 49:73-77.

Folt, C.L. and Burns, C.W. Biological drivers of zooplankton patchiness. .

Fransz, H.G., Colebrook, J.M., Gamble, J.C. and Krause, M. (1991) The zooplankton of the North Sea. *Neth. J. Sea Res.* 28:1-52.

Fransz, H.G. and Gonzalez, S.R. (1997) Latitudinal metazoan plankton zones in the Antarctic Circumpolar Current along 6°W during austral spring 1992. *Deep-Sea Res. II* 44:395-414.

Fransz, H.G., Gonzalez, S.R. and Steeneken, S.F. (1998) Metazoan plankton and the structure of the plankton community in the stratified North Sea. *Mar. Ecol. Prog. Ser.* 175:191-200.

Frid, C.L.J. and Huliselan, N.V. (1996) Far-field control of long-term changes in Northumberland (NW North Sea) coastal zooplankton. *ICES J. Mar. Sci.* 53:972-977.

Fromentin, J. and Planque, B. (1996) *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. *Mar. Ecol. Prog. Ser.* 134:111-118.

Gaard, E. (2000) Seasonal abundance and development of *Calanus finmarchicus* in relation to phytoplankton and hydrography on the Faroe Shelf. *ICES J. Mar. Sci.* 57:1605-1611.

Gallienne, C.P., Robins, D.B. and Woodd-Walker, R.S. (2001) Abundance, distribution and size structure of zooplankton along a 20° west meridional transect of the northeast Atlantic Ocean in July. *Deep-Sea Res. II* 48:925-949.

Gardner, M.B. (1981) Mechanisms of size selectivity by planktivorous fish: A test of hypothesis. *Ecology* 62:571-578.

Gaudy, R., Cervetto, G. and Pagano, M. (2000) Comparison of the metabolism of *Acartia clausi* and *A. tonsa*: influence of temperature and salinity. *J. Exp. Mar. Biol. Ecol.* 247:51-65.

Gaudy, R. and Champalbert, G. (1998) Space and time variations in zooplankton distribution south of Marseilles. *Ocean. Acta* 21:793-802.

George, D.G. and Harris, G.P. (1985) The effect of climate on long-term changes in the crustacean zooplankton biomass of Lake Windermere, UK. *Nature* 318:536-539.

Gillooly, J.F. (2000) Effect of body size and temperature on generation time in zooplankton. *J. Plankton Res.* 22:241-251.

Gin, K.Y.H., Chisholm, S.W. and Olson, R.J. (1999) Seasonal and depth variation in microbial size spectra at the Bermuda Atlantic time series station. *Deep-Sea Res. I* 46:1221-1245.

Gislason, A. and Assthorsson, O.S. (1995) Seasonal cycle of zooplankton southwest of Iceland. *J. Plankton Res.* 17:1959-1976.

Gotceitas, V. and Brown, J.A. (1993) Risk of predation to fish larvae in the presence of alternative prey: effects of prey size and number. *Mar. Ecol. Prog. Ser.* 98:215-222.

Gowen, R.J. and Bloomfield, S.P. (1996) Chlorophyll standing crop and phytoplankton production in the western Irish Sea during 1992 and 1993. *J. Plankton Res.* 18:1735-1751.

Gowen, R.J., Dickey-Collas, M. and McCullough, G. (1997) The occurrence of *Calanus finmarchicus* (Gunnerus) and *Calanus helgolandicus* (Claus) in the western Irish Sea. *J. Plankton Res.* 19:1175-1182.

Gowen, R.J., McCullough, G., Dickey-Collas, M. and Kleppel, G.S. (1998a) Copepod abundance in the western Irish Sea: relationship to physical regime, phytoplankton production and standing stock. *J. Plankton Res.* 20:315-330.

Gowen, R.J., Raine, R., Dickey-Collas, M. and White, M. (1998b) Plankton distributions in relation to physical oceanographic features on the southern Malin Shelf, August 1996. *ICES J. Mar. Sci.* 55:1095-1111.

Gowen, R.J., Stewart, B.M., Mills, D.K. and Elliott, P. (1995) Regional differences in stratification and its effect on phytoplankton production and biomass in the northwestern Irish Sea. *J. Plankton Res.* 17:753-769.

Greene, C.H., Wiebe, P.H., Pelkie, C., Benfield, M.C. and Popp, J.M. (1998b) Three-dimensional acoustic visualisation of zooplankton patchiness. *Deep-Sea Res. II* 45:1201-1217.

Greene, C.H., Wiebe, P.H., Pershing, A.J., Gal, G., Popp, J.M., Copley, N.J., Austin, T.C., Bradley, A.M., Goldsborough, R.G., Dawson, J., Hendershott, R. and Kaartvedt, S. (1998a) Assessing the distribution and abundance of zooplankton: a comparison of acoustic and net-sampling methods with D-BAD MOCNESS. *Deep-Sea Res. II* 45:1219-1237.

Greenstreet, S.P.R., Bryant, A.D., Broekhuizen, N., Hall, S.J. and Heath, M.R. (1997) Seasonal variation in the consumption of food by fish in the North Sea and implications for food web dynamics. *ICES J. Mar. Sci.* 54:243-266.

Hällfors, G., Niemi, Å., Ackefors, H., Lassig, J. and Leppäkoski, E. (1981) Biological oceanography. In: *The Baltic Sea.* Voipio, A. (ed.) Amsterdam: Elsevier Science Publishers, pp. 219-274.

Halsband, C. and Hirche, H.J. (2001) Reproductive cycles of dominant calanoid copepods in the North Sea. *Mar. Ecol. Prog. Ser.* 209:219-229.

Hamrin, S.F. (1983) The food preference of vendace (*Coregonus albula*) in south Swedish forest lakes including the predation effect on zooplankton populations. *Hydrobiologia* 101:121-128.

Hänninen, J., Vuorinen, I. and Hjelt, P. (2000) Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. *Limnol. Oceanogr.* 45:703-710.

Hansen, B.W., Hygum, B.H., Brozek, M., Jensen, F. and Rey, C. (2000) Food web interactions in a *Calanus finmarchicus* dominated pelagic ecosystem- a mesocosm study. *J. Plankton Res.* 22:569-588.

Hansson, S., Larsson, U. and Johansson, S. (1990) Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. *J. Plankton Res.* 12:1099-1116.

Harris, R.P. (1988) Interactions between diel vertical migratory behaviour of marine zooplankton and the subsurface chlorophyll maximun. *Bull. Mar. Sci.* 43:663-674.

Harris, R.P., Boyd, P., Harbour, D.S., Head, R.N., Pingree, R.D. and Pomroy, A.J. (1997) Physical, chemical and biological features of a cyclonic eddy in the region of 61°10'N 19°50'W in the North Atlantic. *Deep-Sea Res. I* 44:1818-1839.

Hays, G.C. (1994) Mesh selection and filtration efficiency of the Continuous Plankton Recorder. *J. Plankton Res.* 16:403-412.

Hays, G.C. (1996) Large-scale patterns of diel vertical migration in the North Atlantic. *Deep-Sea Res. I* 43:1601-1615.

Hays, G.C., Clark, D.R., Walne, A.W. and Warner, A.J. (2001) Large-scale patterns of zooplankton abundance in the NE Atlantic in June and July 1996. *Deep-Sea Res. II* 48:951-961.

Hays, G.C., Harris, R.P. and Head, R.N. (1997a) The vertical nitrogen flux caused by zooplankton diel vertical migration. *Mar. Ecol. Prog. Ser.* 160:57-62.

Hays, G.C., Proctor, C.A., John, A.W.G. and Warner, A.J. (1994) Interspecific differences in the diel vertical migration of marine copepods: the implication of size, colour and morphology. *Limnol. Oceanogr.* 39:1621-1629.

Hays, G.C., Walne, A.W. and Quartley, C.P. (1998) The U-Tow: a system for sampling mesozooplankton over extended spatial scales. *J. Plankton Res.* 20:135-144.

Hays, G.C., Warner, A.J. and Lefevre, D. (1996) Long-term changes in the diel vertical migration behaviour of zooplankton. *Mar. Ecol. Prog. Ser.* 141:149-159.

Hays, G.C., Warner, A.J. and Tranter, P. (1997b) Why do the two most abundant copepods in the North Atlantic differ so markedly in their diel vertical migration behaviour? *J. Sea Res.* 38:85-92.

He, X., Scheurell, M.D., Soranno, P.A. and Wright, R.A. (1994) Recurrent response patterns of a zooplankton community to whole-lake fish manipulation. *Fresh. Biol.* 32:61-72.

Heath, M.R. (1995) Size spectrum dynamics and the planktonic ecosystem of Loch Linnhe. *ICES J. Mar. Sci.* 52:627-642.

Herman, A.W., Sameoto, D.D., Shunnian, C., Mitchell, M.R., Petrie, B. and Cochrane, N. (1992) Design and calibration of a new optical plankton counter capable of sizing small zooplankton. *Deep-Sea Res.* 39:395-415.

Hernández-León, S., Gómez, M., Pagazaurtundua, M., Portillo-Hahnefeld, A., Montero, I. and Almeida, C. (2001) Vertical distribution of zooplankton in Canary Island waters: implications for export flux. *Deep-Sea Res. I* 48:1071-1092.

Hernroth, L. (1981) Zooplankton in the Baltic Sea. *Mar. Poll. Bull.* 12:206-209.

Hernroth, L. (1987) Sampling and filtration efficiency of two commonly used plankton nets. A comparative study of the Nansen net and the Unesco WP 2 net. *J. Plankton Res.* 9:719-728.

Hill, A.E., Brown, J. and Fernand, L. (1997) The summer gyre in the western Irish Sea: shelf sea paradigms and management implications. *Est. Coast. Shelf Sci.* 44:83-95.

Horsburgh, K.J., Hill, A.E., Brown, J., Fernand, L., Garvine, R.W. and Angelico, M.M.P. (2000) Seasonal evolution of the cold pool gyre in the western Irish Sea. *Prog. Oceanogr.* 46:1-58.

Huntley, M.E. and Lopez, M.D.G. (1992) Temperature-dependent production of marine copepods: a global synthesis. *Am. Nat.* 140:201-242.

Huntley, M.E., Zhou, M. and Nordhausen, W. (1995) Mesoscale distribution of zooplankton in the California Current in late spring, observed by Optical Plankton Counter. *J. Mar. Res.* 53:647-674.

Hurlbert, S.H. and Mulla, M.S. (1981) Impacts of mosquitofish (*Gambusia affinis*) predation on plankton communities. *Hydrobiologia* 83:125-151.

Hutchings, L., Verheye, H.M., Mitchell-Innes, B.A., Peterson, W.T., Huggett, J.A. and Painting, S.J. (1995) Copepod production in the southern Benguela system. *ICES J. Mar. Sci.* 52:439-455.

Ikeda, T. (1985) Metabolic rates of epipelagic marine zooplankton as a function of body mass and temperature. *Mar. Biol.* 85:1-11.

Irigoien, X. (1999) Vertical distribution and population structure of *Calanus finmarchicus* at station India (59°N, 19°W) during the passage of the great salinity anomaly, 1971-1975. *Deep-Sea Res. I* 47:1-26.

Irigoien, X., Harris, R.P., Head, R.N., Lindley, J.A. and Harbour, D. (2000) Physiology and population structure of *Calanus finmarchicus* (Copepoda: Calanoida) during a Lagrangian tracer release experiment in the North Atlantic. *J. Plankton Res.* 22:205-221.

Irigoien, X., Head, R., Klenke, U., Meyer-Harms, B., Harbour, D., Niehoff, B., Hirche, H.-J. and Harris, R. (1998) A high frequency time series at weathership M, Norwegian Sea, during the 1997 spring bloom: feeding of adult female *Calanus finmarchicus*. *Mar. Ecol. Prog. Ser.* 172:127-137.

Ives, A.R., Carpenter, S.R. and Dennis, B. (1999) Community interaction webs and zooplankton responses to planktivory manipulations. *Ecology* 80:1405-1421.

Jeppesen, E., Lauridsen, T.L., Mitchell, S.F., Christoffersen, K. and Burns, C.W. (2000) Trophic structure in the pelagial of 25 shallow New Zealand lakes: changes along nutrient and fish gradients. *J. Plankton Res.* 22:951-968.

Johansson, O.E. and O'Gorman, R. (1991) Roles of predation, food and temperature in structuring the epilimnetic zooplankton populations in Lake Ontario, 1981-1986. *Trans. Am. Fish. Soc.* 120:193-208.

Kane, J. (1993) Variability of zooplankton biomass and dominant species abundance on Georges Bank, 1977-1986. *Fish. Bull.* 91:464-474.

Kehayias, G., Lykakis, J. and Fragopoulu, N. (1996) The diets of the chaetognaths *Sagitta enflata*, *S. serratodentata atlantica* and *S. bipunctata* at different seasons in Eastern Mediterranean coastal waters. *ICES J. Mar. Sci.* 53:837-846.

Kerr, S.R. (1974) Theory of size distribution in ecological communities. *J. Fish. Res. Bd. Can.* 31:1859-1862.

Kidwai, S. and Amjad, S. (2000) Zooplankton: pre-southwest and northeast monsoons of 1993 to 1994, from the North Arabian Sea. *Mar. Biol.* 136:561-571.

Kiørboe, T., Møhlenberg, F. and Hamburger, K. (1985) Bioenergetics of the planktonic copepod *Acartia tonsa*: relation between feeding, egg production and respiration, and composition of specific dynamic action. *Mar. Ecol. Prog. Ser.* 26:85-97.

Klein Breteler, W.C.M., Gonzalez, S.R. and Schogt, N. (1995) Development of *Pseudocalanus elongatus* (Copepoda, Calanoida) cultured at different temperature and food conditions. *Mar. Ecol. Prog. Ser.* 119:99-110.

Kobayashi, T., Shiel, R.J. and Gibbs, P. (1998) Size structure of river zooplankton: seasonal variation, overall pattern and functional aspect. *Mar. Freshwater Res.* 49:547-552.

Koppelmann, R. and Weikert, H. (1999) Temporal changes of deep-sea mesozooplankton abundance in the temperate NE Atlantic and estimates of carbon budget. *Mar. Ecol. Prog. Ser.* 179:27-40.

Koski, M. (1999) Carbon:nitrogen ratios of Baltic Sea copepods- indication of mineral limitation? *J. Plankton Res.* 21:1565-1573.

Koslow, J.A. (1983) Zooplankton community structure in the North Sea and Northeast Atlantic: Development and test of a biological model. *Can. J. Fish. Aquat. Sci.* 40:1912-1924.

Krause, M., Dippner, J.W. and Beil, J. (1995) A review of hydrographic controls on the distribution of zooplankton biomass and species in the North Sea with particular reference to a survey conducted in January-March 1987. *Prog. Oceanogr.* 35:81-152.

Kullenberg, G. (1981) Physical Oceanography. In: *The Baltic Sea.* Voipio, A. (ed.) Amsterdam: Elsevier Science Publishers, pp. 135-181.

Laborde, P., Urrutia, J. and Valencia, V. (1999) Seasonal variability of primary production in the Cap-Ferret Canyon area (Bay of Biscay) during the ECOFER cruises. *Deep-Sea Res. II* 46:2057-2079.

Lampert, W. (1993) Phenotypic plasticity of the size at first reproduction in *Daphnia*: the importance of maternal size. *Ecology* 74:1455-1466.

Laprise, R. and Dodson, J.J. (1994) Environmental variability as a factor controlling spatial patterns in distribution and species diversity of zooplankton in the St. Lawrence estuary. *Mar. Ecol. Prog. Ser.* 107:67-81.

Lazzaro, X. (1987) A review of planktivorous fishes: their evolution, feeding behaviours, selectivities, and impacts. *Hydrobiologia* 146:97-167.

Lazzaro, X., Drenner, R.W., Stein, R.A. and Smith, J.D. (1992) Planktivores and plankton dynamics: Effects of fish biomass and planktivore type. *Can. J. Fish. Aquat. Sci.* 49:1466-1473.

Le Borgne, R. and Rodier, M. (1997) Net zooplankton and the biological pump: a comparison between the oligotrophic and mesotrophic equatorial Pacific. *Deep-Sea Res. II* 44:2003-2023.

Le Fèvre, J. (1986) Aspects of the biology of frontal systems. *Adv. Mar. Biol.* 23:163-299.

Lenhart, H., Radach, G. and Ruardij, P. (1997) The effects of river input on the ecosystem dynamics in the continental coastal zone of the North Sea using ERSEM. *J. Sea Res.* 38:249-274.

Lenz, J. (2000) Introduction. In: *ICES Zooplankton methodology manual.* Harris, R. P., Wiebe, P. H., Lenz, J., Skjoldal, H. R. and Huntley, M. (ed.) London: Academic Press, pp. 1-32.

Liao, C.H., Lee, K.T., Lee, M.A. and Lu, H.J. (1999) Biomass distribution and zooplankton composition of the sound-scattering layer in the waters of southern East China Sea. *ICES J. Mar. Sci.* 56:766-778.

Lignell, R., Heiskanen, A.-S., Kuosa, H., Gundersen, K., Kuupo-Leinikki, P., Pajuniemi, R. and Uitto, A. (1993) Fate of a phytoplankton spring bloom: sedimentation and carbon flow in the planktonic food web in the northern Baltic. *Mar. Ecol. Prog. Ser.* 94:239-252.

Lindley, J.A. and Williams, R. (1994) Relating plankton assemblages to environmental variables using instruments towed by ships-of-opportunity. *Mar. Ecol. Prog. Ser.* 107:245-262.

Lochte, K., Ducklow, H.W., Fasham, M.J.R. and Stienen, C. (1993) Plankton succession and carbon cycling at 47°N 20°W during the JGOFS North Atlantic Bloom experiment. *Deep-Sea Res. II* 40:91-114.

Lopes, R.M. (1994) Zooplankton distribution in the Guaraú river estuary (south-eastern Brazil). *Est. Coast. Shelf Sci.* 39:287-302.

López-Salgado, I. and Suárez-Morales, E. (1998) Copepod assemblages in surface waters of the western Gulf of Mexico. *Crustaceana* 71:312-330.

Lougheed, V.L. and Chow-Fraser, P. (1998) Factors that regulate the zooplankton community structure of a turbid, hypereutrophic Great Lakes wetland. *Can. J. Fish. Aquat. Sci.* 55:150-161.

Luo, J., Ortner, P.B., Forcucci, D. and Cummings, S.R. (2000) Diel vertical migration of zooplankton and mesopelagic fish in the Arabian Sea. *Deep-Sea Res. II* 47:1451-1473.

Madhupratap, M., Gopalakrishnan, T.C., Haridas, P. and Nair, K.K.C. (2001) Mesozooplankton biomass, composition and distribution in the Arabian Sea during the fall intermonsoon: implications of oxygen gradients. *Deep-Sea Res. II* 48:1345-1368.

Madin, L.P., Horgan, E.F. and Steinberg, D.K. (2001) Zooplankton at the Bermuda Atlantic Time-series Study (BATS) station: diel, seasonal and interannual variation in biomass, 1994-1998. *Deep-Sea Res. II* 48:2063-2082.

Magnesen, T. (1989a) Vertical distribution of size-fractions in the zooplankton community in Lindåspollene, western Norway. 2. Diel variations. *Sarsia* 74:69-77.

Magnesen, T. (1989b) Vertical distributon of size-fractions in the zooplankton community in Lindåspollene, western Norway. 1. Seasonal variations. *Sarsia* 74:59-68.

Manca, M. and Ruggiu, D. (1998) Consequences of pelagic food-web changes during a long-term lake oligotrophication process. *Limnol. Oceanogr.* 43:1368-1373.

Marine Zooplankton Colloquium (1989) Future marine zooplankton research- a perspective. *Mar. Ecol. Prog. Ser.* 55:197-206.

Marañón, E. and Fernández, E. (1995) Changes in phytoplankton ecophysiology across a coastal upwelling front. *J. Plankton Res.* 17:1999-2008.

McQueen, D.J., Post, J.R. and Mills, E.L. (1986) Trophic relationships in freshwater pelagic ecosystems. *Can. J. Fish. Aquat. Sci.* 43:1571-1581.

Mehner, T. and Heerkloss, R. (1994) Direct estimation of food consumption of juvenile fish in a shallow inlet of the southern Baltic. *Int. Rev. ges. Hydrobiol.* 79:295-304.

Meise, C.J. and O'Reilly, J.E. (1996) Spatial and seasonal patterns in abundance and age-composition of *Calanus finmarchicus* in the Gulf of Maine and on Georges Bank: 1977-1987. *Deep-Sea Res. II* 43:1473-1501.

M'harzi, A., Tackx, M., Daro, M.H., Kesaulia, I., Caturao, R. and Podoor, N. (1998) Winter distribution of phytoplankton and zooplankton around some sandbanks of the Belgian coastal zone. *J. Plankton Res.* 20:2031-2052.

Mills, D.K., Walne, A., Reid, P.C. and Heaney, S.I. (1998) Updating the Continuous Plankton Recorder: an improved tool for integrated plankton monitoring. *ICES J. Mar. Sci.* 55:814-817.

Mitson, R.B., Simard, Y. and Goss, C. (1996) Use of a two-frequency algorithm to determine size and abundance of plankton in three widely spaced locations. *ICES J. Mar. Sci.* 53:209-215.

Möllmann, C., Kornilovs, G. and Sidrevics, L. (2000) Long-term dynamics of main mesozooplankton species in the central Baltic Sea. *J. Plankton Res.* 22:2015-2038.

Morales, C.E., Bedo, A., Harris, R.P. and Tranter, P.R.G. (1991) Grazing of copepod assemblages in the north-east Atlantic: the importance of the small size fraction. *J. Plankton Res.* 13:455-472.

Morales, C.E., Harris, R.P., Head, R.N. and Tranter, P.R.G. (1993) Copepod grazing in the oceanic northeast Atlantic during a 6 week drifting station: the contribution of size classes and vertical migrants. *J. Plankton Res.* 15:185-211.

Munk, P. (1997) Prey size spectra and prey availability of larval and small juvenile cod. *J. Fish. Biol.* 51:340-351.

Mutlu, E. (2001) Distribution and abundance of moon jellyfish (*Aurelia aurita*) and its zooplankton food in the Black Sea. *Mar. Biol.* 138:329-339.

Nicholas, K.R. and Frid, C.L.J. (1999) Occurrence of hydromedusae in the plankton off Northumberland (western central North Sea) and the role of planktonic predators. *J. Mar. Biol. Ass. U.K.* 79:979-992.

Nichols, J.H. and Thompson, A.B. (1991) Mesh selection of copepodite and nauplius stages of four calanoid copepod species. *J. Plankton Res.* 13:661-671.

Nielsen, T.G., Løkkegaard, B., Richardson, K., Pedersen, F.B. and Hansen, L. (1993) Structure of plankton communities in the Dogger Bank area (North Sea) during a stratified situation. *Mar. Ecol. Prog. Ser.* 95:115-131.

Nielsen, T.G. and Munk, P. (1998) Zooplankton diversity and the predatory impact by larval and small juvenile fish at the Fisher Banks in the North Sea. *J. Plankton Res.* 20:2313-2332.

Nielsen, T.G. and Sabatini, M. (1996) Role of cyclopoid copepods *Oithona* spp. in North Sea plankton communities. *Mar. Ecol. Prog. Ser.* 139:79-93.

Norberg, J. (2000) Resource-niche complementarity and autotrophic compensation determines ecosystem-level responses to increased cladoceran species richness. *Oecologia* 122:264-272.

O'Brien, W.J. (2001) Long-term impact of an invertebrate predator, *Heterocope septentrionalis*, on an arctic pond zooplankton community. *Fresh. Biol.* 46:39-45.

O'Brien, W.J. and Kettle, D. (1979) Helmets and invisible armor: structures reducing predation from tactile and visual planktivores. *Ecology* 60:287-294.

Oceanographic Laboratory Edinburgh (1973) Continuous Plankton Records: a plankton atlas of the North Atlantic and North Sea. *Bull. Mar. Ecol.* 7:1-174.

Ojaveer, E., Lumberg, A. and Ojaveer, H. (1998) Highlights of zooplankton dynamics in Estonian waters (Baltic Sea). *ICES J. Mar. Sci.* 55:748-755.

Omori, K. (1997) Mature size determination in copepods. The adaptive significance of mature size in copepods: output or efficiency selection. *Ecol. Model.* 99:203-215.

Omori, M., Ishii, H. and Fujinaga, A. (1995) Life history strategy of *Aurelia aurita* (Cnidaria, Scyphomedusae) and its impact on the zooplankton community of Tokyo Bay. *ICES J. Mar. Sci.* 52:597-603.

Osgood, K.E. (1997) Observations of a deep aggregation of *Calanus pacificus* in the Santa Barbara Basin. *Limnol. Oceanogr.* 42:997-1001.

Osgood, K.E. and Checkley, D.M.J. (1997) Seasonal variations in a deep aggregation of *Calanus pacificus* in the Santa Barbara Basin. *Mar. Ecol. Prog. Ser.* 148:59-69.

Pace, M.L. (1984) Zooplankton community structure, but not biomass, influences the phosphorous-chloropyll *a* relationship. *Can. J. Fish. Aquat. Sci.* 41:1089-1096.

Pace, M.L., Cole, J.J., Carpenter, S.R. and Kitchell, J.F. (1999) Trophic cascades revealed in diverse ecosystems. *TREE* 14:483-488.

Paffenhöfer, G.A. (1980) Zooplankton distribution as related to summer hydrographic conditions in Onslow Bay, North Carolina. *Bull. Mar. Sci.* 30:819-832.

Paffenhöfer, G.A. (1986) Feeding, growth and food conversion of the marine cladoceran *Penilia avirostris*. *J. Plankton Res.* 8:741-754.

Pakhomov, E.A., Perissinotto, R., McQuaid, C.D. and Froneman, P.W. (2000) Zooplankton structure and grazing in the Atlantic sector of the Southern Ocean in late austral summer 1993. Part 1. Ecological zonation. *Deep-Sea Res. I* 47:1663-1686.

Parsons, T.R. and Lalli, C.M. (1988) Comparative oceanic ecology of the plankton communities of the subarctic Atlantic and Pacific Oceans. *Oceanogr. Mar. Biol. Ann. Rev.* 26:317-359.

Pätsch, J. and Radach, G. (1997) Long-term simulation of the eutrophication of the North Sea: temporal development of nutrients, chlorophyll and primary production in comparison to observations. *J. Sea Res.* 38:275-310.

Pearre Jr., S. (1980) Feeding by Chaetognatha: the relation of prey size to predator size in several species. *Mar. Ecol. Prog. Ser.* 3:125-134.

Pedersen, G., Tande, K.S. and Nilssen, E.M. (1995) Temporal and regional variation in the copepod community in the central Barents Sea during spring and early summer 1988 and 1989. *J. Plankton Res.* 17:263-282.

Persson, L., Diehl, S., Johansson, L., Andersson, G. and Hamrin, S.F. (1992) Trophic interactions in temperate lake ecosystems: a test of food chain theory. *Am. Nat.* 140:59-84.

Peters, R.H. and Downing, J.A. (1984) Empirical analysis of zooplankton filtering and feeding rates. *Limnol. Oceanogr.* 29:763-784.

Pinca, S. and Dallot, S. (1995) Meso- and macrozooplankton composition patterns related to hydrodynamic structures in the Ligurian Sea (Trophos-2 experiment, April-June 1986). *Mar. Ecol. Prog. Ser.* 126:49-65.

Piontkovski, S.A. and Williams, R. (1995) Multiscale variability of tropical ocean zooplankton biomass. *ICES J. Mar. Sci.* 52:643-656.

Piontkovski, S.A., Williams, R. and Melnik, T.A. (1995) Spatial heterogeneity, biomass and size structure of plankton of the Indian Ocean: some general trends. *Mar. Ecol. Prog. Ser.* 117:219-227.

Planque, B. and Batten, S.D. (2000) *Calanus finmarchicus* in the North Atlantic: the year of *Calanus* in the context of interdecadal change. *ICES J. Mar. Sci.* 57:1528-1535.

Planque, B. and Fromentin, J. (1996) *Calanus* and environment in the eastern North Atlantic. I. Spatial and temporal patterns of *C. finmarchicus* and *C. helgolandicus*. *Mar. Ecol. Prog. Ser.* 134:101-109.

Planque, B., Hays, G.C., Ibanez, F. and Gamble, J.C. (1997) Large scale variations in the seasonal abundance of *Calanus finmarchicus*. *Deep-Sea Res. I* 44:315-326.

Planque, B. and Taylor, A.H. (1998) Long-term changes in zooplankton and the climate of the North Atlantic. *ICES J. Mar. Sci.* 55:644-654.

Platt, T. and Denman, K. (1977) Organisation in the pelagic ecosystem. *Helgo. wiss Meeres.* 30:575-581.

Platt, T. and Denman, K. (1978) The structure of pelagic marine ecosystems. *Rapp. P.-v. Reun. Cons. int. Explor. Mer.* 173:60-65.

Plounevez, S. and Champalbert, G. (2000) Diet, feeding behaviour and trophic activity of the anchovy (*Engraulis encrasicolus* L.) in the Gulf of Lions (Mediterranean Sea). *Ocean. Acta* 23:175-192.

Reid, P.C., Battle, E.J.V., Batten, S.D. and Brander, K.M. (2000) Impacts of fisheries on plankton community structure. *ICES J. Mar. Sci.* 57:495-502.

Reid, P.C., Borges, M.F. and Svendsen, E. (2001) A regime shift in the North Sea circa 1988 linked to changes in the North Sea horse mackerel fishery. *Fish. Res.* 50:163-171.

Richardson, K. and Pedersen, F.B. (1998) Estimation of new production in the North Sea: consequences for temporal and spatial variability of phytoplankton. *ICES J. Mar. Sci.* 55:574-580.

Richter, C. (1995) Seasonal changes in the vertical distribution of mesozooplankton in the Greenland Sea Gyre (75°N): distribution strategies of calanoid copepods. *ICES J. Mar. Sci.* 52:533-539.

Rodhouse, P.G., Piatkowski, U., Murphy, E.J., White, M.G. and Bone, D.G. (1994) Utility and limits of biomass spectra: the nekton community sampled with the RMT 25 in the Scotia Sea during austral summer. *Mar. Ecol. Prog. Ser.* 112:29-39.

Rodríguez, F., Fernández, E., Head, R.N., Harbour, D.S., Bratbak, G., Heldal, M. and Harris, R.P. (2000) Temporal variability of viruses, bacteria, phytoplankton and zooplankton in the western English Channel off Plymouth. *J. Mar. Biol. Ass. U.K.* 80:575-586.

Rodriguez, J., Echevarría, F. and Jiménez-Gómez, F. (1990) Physiological and ecological scalings of body size in an oligotrophic, high mountain lake (La Caldera, Sierra Nevada, Spain). *J. Plankton Res.* 12:593-599.

Rodriguez, J. and Mullin, M.M. (1986) Relation between biomass and body weight of plankton in a steady state oceanic ecosystem. *Limnol. Oceanogr.* 31:361-370.

Rodríguez, J., Tintoré, J., Allen, J.T., Blanco, J.M., Gomis, D., Reul, A., Ruiz, J., Rodríguez, V., Echevarría, F. and Jiménez-Gómez, F. (2001) Mesoscale vertical motion and the size structure of phytoplankton in the ocean. *Nature* 410:360-363.

Rojo, C. and Rodriguez, J. (1994) Seasonal variability of phytoplankton size structure in a hypertrophic lake. *J. Plankton Res.* 16:317-335.

Rolff, C. (2000) Seasonal variation in δ^{13}C and δ^{15}N of size-fractionated plankton at a coastal station in the northern Baltic proper. *Mar. Ecol. Prog. Ser.* 203:47-65.

Roman, M., Smith, S., Wishner, K., Zhang, X. and Gowing, M. (2000) Mesozooplankton production and grazing in the Arabian sea. *Deep-Sea Res. II* 47:1423-1450.

Roman, M.R., Dam, H.G., Gauzens, A.L., Urban-Rich, J., Foley, D.G. and Dickey, T.D. (1995) Zooplankton variability on the equator at 140°W during the JGOFS EqPac study. *Deep-Sea Res. II* 42:673-693.

Rose, R.M., Warne, M.S.J. and Lim, R.P. (2001) Factors associated with fish modify life history traits of the cladoceran *Ceriodaphnia* cf. *dubia*. *J. Plankton Res.* 23:11-17.

Rothschild, B.J. (1998) Year class strengths of zooplankton in the North Sea and their relation to cod and herring abundance. *J. Plankton Res.* 20:1721-1741.

Rudjakov, A., Tseitlin, V.B. and Kitain, V.J. (1995) Seasonal variations of mesozooplankton biomass in the upper layer of the Bering Sea; understanding biomass oscillations in the ocean. *ICES J. Mar. Sci.* 52:747-753.

Rudstam, L.G., Aneer, G. and Hildén, M. (1994) Top-down control in the pelagic Baltic ecosystem. *Dana* 10:105-129.

Rudstam, L.G., Hansson, S., Johansson, S. and Larsson, U. (1992) Dynamics of planktivory in a coastal area of the northern Baltic Sea. *Mar. Ecol. Prog. Ser.* .

Rudstam, L.G., Lathrop, R.C. and Carpenter, S.R. (1993) The rise and fall of a dominant planktivore: direct and indirect effects on zooplankton. *Ecology* 74:303-319.

Sars, G.O. (1903) *An account of the crustacea of Norway. Vol. IV. Copepoda calanoida.* Bergen: Bergen Museum, pp. 171.

Savidge, G. and Williams, P.J.l. (2001) The PRIME 1996 cruise: an overview. *Deep-Sea Res. II* 48:687-704.

Scheffer, M., Rinaldi, S. and Kuznetsov, Y.A. (2000) Effects of fish on plankton dynamics: a theoretical analysis. *Can. J. Fish. Aquat. Sci.* 57:1208-1219.

Schneider, G. and Behrends, G. (1998) Top-down control in a neritic plankton system by *Aurelia aurita* medusae- a summary. *Ophelia* 48:71-82.

Schneider, G., Lenz, J. and Rolke, M. (1994) Zooplankton standing stock and community size structure within the epipelagic zone: a comparison between the central Red Sea and the Gulf of Aden. *Mar. Biol.* 119:191-198.

Schulz, S., Kaiser, W. and Breuel, G. (1991) Trend analysis of biological parameters in the Baltic (1976-1988). *Int. Rev. ges. Hydrobiol.* 76:351-359.

Scrope-Howe, S. and Jones, D.A. (1985) Biological studies in the vicinity of a shallow-sea tidal mixing front. V. Composition, abundance and distribution of zooplankton in the western Irish Sea, April 1980 to November 1981. *Phil. Trans. Roy. Soc. Lon. B* 310:501-519.

Scrope-Howe, S. and Jones, D.A. (1986) The vertical distribution of zooplankton in the western Irish Sea. *Est. Coast. Shelf Sci.* 22:785-802.

Seda, J. and Dostalkova, I. (1996) Live sieving of freshwater zooplankton: a technique for monitoring community size structure. *J. Plankton Res.* 18:513-520.

Segerstråle, S.G. (1969) Biological fluctuations in the Baltic Sea. *Prog. Oceanogr.* 5:169-184.

Shaheen, P.A., Stehlik, L.L., Meise, C.J., Stoner, A.W., Manderson, J.P. and Adams, D.L. (2001) Feeding behaviour of newly settled winter flounder (*Pseudopleuronectes americanus*) on calanoid copepods. *J. Exp. Mar. Biol. Ecol.* 257:37-51.

Sheldon, R.W., Sutcliffe Jr., W.H. and Paranjape, M.A. (1977) Structure of pelagic food chain and relationship between plankton and fish production. *J. Fish. Res. Bd. Can.* 34:2344-2353.

Sherman, K., Solow, A., Jossi, J. and Kane, J. (1998) Biodiversity and abundance of the zooplankton of the Northeast Shelf ecosystem. *ICES J. Mar. Sci.* 55:730-738.

Siokou-Frangou, I. (1998) Zooplankton assemblages and influence of environmental parameters on them in a Mediterranean coastal area. *J. Plankton Res.* 20:847-870.

Skjoldal, H.R., Wiebe, P.H. and Foote, K.G. (2000) Sampling and experimental design. In: *ICES Zooplankton methodology manual.* Harris, R. P., Wiebe, P. H., Lenz, J., Skjoldal, H. R. and Huntley, M. (ed.) London: Academic Press, pp. 33-53.

Skogen, M.D. and Moll, A. (2000) Interannual variability of the North Sea primary production: comparison from two model studies. *Cont. Shelf. Res.* 20:129-151.

Smith Jr., W.O. and Demaster, D.J. (1996) Phytoplankton biomass and productivity in the Amazon River plume: correlation with seasonal river discharge. *Cont. Shelf. Res.* 16:291-319.

Smith, S., Roman, M., Prusova, I., Wishner, K., Gowing, M., Codispoti, L.A., Barber, R., Marra, J. and Flagg, C. (1998) Seasonal response of zooplankton to monsoonal reversals in the Arabian Sea. *Deep-Sea Res. II* 45:2369-2403.

Soetaert, K. and Van Rijswijk, P. (1993) Spatial and temporal patterns of the zooplankton in the Westerschelde estuary. *Mar. Ecol. Prog. Ser.* 97:47-59.

Sokal, R.R. and Rohlf, F.J. (1981) *Biometry.* W.H. Freeman and Company, pp. 859.

Souissi, S., Yahia-Kéfi, O.D. and Yahia, M.N.D. (2000) Spatial characterization of nutrient dynamics in the Bay of Tunis (south-western Mediterranean) using multivariate analyses: consequences for phyto- and zooplankton distribution. *J. Plankton Res.* 22:2039-2059.

Southward, A.J., Hawkins, S.J. and Burrows, M.T. (1995) Seventy years' observations of changes in distribution and abundance of zooplankton and intertidal organisms in the western English Channel in relation to rising sea temperature. *J. Therm. Biol.* 20:127-155.

Spencer, C.N., Potter, D.S., Bukantis, R.T. and Stanford, J.A. (1999) Impact of predation by *Mysis relicta* on zooplankton in Flathead Lake, Montana, USA. *J. Plankton Res.* 21:51-64.

Sprules, W.G., Brandt, S.B., Stewart, D.J., Munawar, M., Jin, E.H. and Love, J. (1991) Biomass size spectrum of the Lake Michigan pelagic food web. *Can. J. Fish. Aquat. Sci.* 48:105-115.

Sprules, W.G. and Goyke, A.P. (1994) Size-based structure and production in the pelagia of Lakes Ontario and Michigan. *Can. J. Fish. Aquat. Sci.* 51:2603-2611.

Sprules, W.G., Jin, E.H., Herman, A.W. and Stockwell, J.D. (1998) Calibration of an optical plankton counter for use in fresh water. *Limnol. Oceanogr.* 43:726-733.

Sprules, W.G. and Munawar, M. (1986) Plankton size spectra in relation to ecosystem productivity, size, and perturbation. *Can. J. Fish. Aquat. Sci.* 43:1789-1794.

Sprules, W.G. and Stockwell, J.D. (1995) Size-based biomass and production models in the St. Lawrence Great Lakes. *ICES J. Mar. Sci.* 52:705-710.

Stanton, T.K., Chu, D. and Wiebe, P.H. (1996) Acoustic scattering characteristics of several zooplankton groups. *ICES J. Mar. Sci.* 53:289-295.

Steele, J.H. (1974) *The structure of marine ecosystems.* Cambridge, Massachusetts: Harvard University Press, pp. 128.

Steele, J.H. and Frost, B.W. (1977) The structure of plankton communities. *Roy. Soc. Lon. B* 280:43-48.

Steele, J.H. and Henderson, E.W. (1995) Predation control of plankton demography. *ICES J. Mar. Sci.* 52:565-573.

Steinberg, D.K., Carlson, C.A., Bates, N.R., Johnson, R.J., Micheals, A.F. and Knap, A.H. (2001) Overview of the US JGOFS Bermuda Atlantic Time-series Study (BATS): a decade-scale look at ocean biology and biogeochemistry. *Deep-Sea Res. II* 48:1405-1447.

Stelfox, C.E., Burkill, P.H., Edwards, E.S., Harris, R.P. and Sleigh, M.A. (1999) The structure of zooplankton communities, in the 2 to 2000 μm size range, in the Arabian Sea during and after the SW monsoon, 1994. *Deep-Sea Res. II* 46:815-842.

Stephens, J.A., Jordan, M.B., Taylor, A.H. and Proctor, R. (1998) The effects of fluctuations in North Sea flows on zooplankton abundance. *J. Plankton Res.* 20:943-956.

Stockwell, J.D. and Sprules, W.G. (1995) Spatial and temporal patterns of zooplankton biomass in Lake Eerie. *ICES J. Mar. Sci.* 52:557-564.

Suchman, C.L. and Sullivan, B.K. (1998) Vulnerability of the copepod *Acartia tonsa* to predation by the schyphomedusa *Chrysaora quinquecirrha*: effect of prey size and behaviour. *Mar. Biol.* 132:237-245.

Suchman, C.L. and Sullivan, B.K. (2000) Effect of prey size on vulnerability of copepods to predation by the scyphomedusae *Aurelia aurita* and *Cyanea* sp. *J. Plankton Res.* 22:2289-2306.

Sullivan, B.K. and Meise, C.J. (1996) Invertebrate predators of zooplankton on Georges Bank, 1977-1987. *Deep-Sea Res. II* 43:1503-1519.

Sutton, T., Hopkins, T., Remsen, A. and Burghart, S. (2001) Multisensor sampling of pelagic ecosystem variables in a coastal environment to estimate zooplankton grazing impact. *Cont. Shelf. Res.* 21:69-87.

Tande, K.S. (1982) Ecological investigations on the zooplankton community of Balsfjorden, northern Norway: generation cycles, and variations in body weight and body content of carbon and nitrogen related to overwintering and reproduction in the copepod *Calanus finmarchicus* (Gunnerus). *J. Exp. Mar. Biol. Ecol.* 62:129-142.

Tande, K.S. and Miller, C.B. (2000) Population dynamics of *Calanus* in the North Atlantic: results from the Trans-Atlantic Study of *Calanus finmarchicus*. *ICES J. Mar. Sci.* 57:1527.

Thiebaux, M.L. (1993) Structure of the body-size spectrum of the biomass in aquatic ecosystems: a consequence of allometry in predator-prey interactions. *Can. J. Fish. Aquat. Sci.* 50:1308-1317.

Thompson, A.B. and Harrop, R.T. (1991) Feeding dynamics of fish larvae on Copepoda in the western Irish Sea, with particular reference to cod *Gadus morhua*. *Mar. Ecol. Prog. Ser.* 68:213-223.

Tiselius, P. (1988) Effects of diurnal feeding rhythms, species composition and vertical migration on the grazing impact of calanoid copepods in the Skagerrak and Kattegat. *Ophelia* 28:215-230.

Tittel, J., Zippel, B. and Geller, W. (1998) Relationships between plankton community structure and plankton size distribution in lakes of northern Germany. *Limnol. Oceanogr.* 43:1119-1132.

Tsuda, A., Saito, H. and Hirose, T. (1998) Effect of gut content on the vulnerability of copepods to visual predation. *Limnol. Oceanogr.* 43:1944-1947.

Turner, J.T. and Tester, P.A. (1989) Zooplankton feeding ecology: nonselective grazing by copepods *Acartia tonsa* Dana, *Centropages velificatus* De Oliveira, and *Eucalanus pileatus* Giesbrecht in the plume of the Mississippi River. *J. Exp. Mar. Biol. Ecol.* 126:21-43.

Twombly, S. and Tisch, N. (2000) Body size regulation in copepod crustaceans. *Oecologia* 122:318-326.

UNESCO (1968) *Zooplankton sampling.* Paris: UNESCO, pp. 174.

Uye, S. (1982) Length-weight relationships of important zooplankton from the inland sea of Japan. *J. Ocean. Soc. Japan* 38:149-158.

Valdés, L. and Moral, M. (1998) Time-series analysis of copepod diversity and species richness in the southern Bay of Biscay off Santander, Spain, in relation to environmental conditions. *ICES J. Mar. Sci.* 55:783-792.

van Couwelaar, M. (1997) Zooplankton and micronekton biomass off Somalia and in the southern Red Sea during the SW monsoon of 1992 and the NE monsoon of 1993. *Deep-Sea Res. II* 44:1213-1234.

Van den Berg, A.J., Ridderinkhof, H., Riegman, R., Ruardij, P. and Lenhart, H. (1996) Influence of variability in water transport on phytoplankton biomass and composition in the southern North Sea: a modelling approach (FYFY). *Cont. Shelf. Res.* 16:907-931.

Vanni, M.J. (1986) Competition in zooplankton communities: Suppression of small species by *Daphnia pulex. Limnol. Oceanogr.* 31:1039-1056.

Vanni, M.J. (1987) Effects of food availability and fish predation on a zooplankton community. *Ecol. Mon.* 57:61-88.

Vanni, M.J. and Findlay, D.L. (1990) Trophic cascades and phytoplankton community structure. *Ecology* 71:921-937.

Vanni, M.J. and Layne, C.D. (1997) Nutrient recycling and herbivory as mechanisms in the "top-down" effect of fish on algae in lakes. *Ecology* 78:21-40.

Vanni, M.J., Layne, C.D. and Arnott, S.E. (1997) "Top-down" trophic interactions in lakes: effects of fish on nutrient dynamics. *Ecology* 78:1-20.

Vanni, M.J., Luecke, C., Kitchell, J.F., Allen, Y., Temte, J. and Magnuson, J.J. (1990) Effects on lower trophic levels of massive fish mortality. *Nature* 344:333-335.

Verheye, H.M. and Richardson, A.J. (1998) Long-term increase in crustacean zooplankton abundance in the southern Benguela upwelling region (1951-1996): bottom-up or top-down control? *ICES J. Mar. Sci.* 55:803-807.

Viherluoto, M., Kuosa, H., Flinkman, J. and Viitasalo, M. (2000) Food utilisation of pelagic mysids, *Mysis mixta* and *M. relicta*, during their growing season in the northern Baltic Sea. *Mar. Biol.* 136:553-559.

Viherluoto, M. and Viitasalo, M. (2001) Temporal variability in functional responses and prey selectivity of the pelagic mysid, *Mysis mixta*, in natural prey assemblages. *Mar. Biol.* 138:575-583.

Viitasalo, M. (1992) Mesozooplankton of the Gulf of Finland and northern Baltic proper- a review of monitoring data. *Ophelia* 35:147-168.

Viitasalo, M., Koski, M., Pellikka, K. and Johansson, S. (1995b) Seasonal and long-term variations in the body size of planktonic copepods in the northern Baltic Sea. *Mar. Biol.* 123:241-250.

Viitasalo, M. and Rautio, M. (1998) Zooplanktivory by *Praunus flexosus* (Crustacea: Mysidacea): functional responses and prey selection in relation to prey escape responses. *Mar. Ecol. Prog. Ser.* 174:77-87.

Viitasalo, M., Vuorinen, I. and Ranta, E. (1990) Changes in crustacean mesozooplankton and some environmental parameters in the archipelago sea (northern Baltic) in 1976-1984. *Ophelia* 31:207-217.

Viitasalo, M., Vuorinen, I. and Saesma, S. (1995a) Mesozooplankton dynamics in the northern Baltic Sea: implications of variations in hydrography and climate. *J. Plankton Res.* 17:1857-1878.

Villate, F. (1991) Annual cycle of zooplankton community in the Abra Harbour (Bay of Biscay): abundance, composition and size spectra. *J. Plankton Res.* 13:691-706.

Villate, F., Moral, M. and Valencia, V. (1997) Mesozooplankton community indicates climate changes in a shelf area of the inner Bay of Biscay throughout 1988 to 1990. *J. Plankton Res.* 19:1617-1636.

Vuorinen, I., Hänninen, J., Viitasalo, M., Helminen, U. and Kuosa, H. (1998) Proportion of copepod biomass declines with decreasing salinity in the Baltic Sea. *ICES J. Mar. Sci.* 55:767-774.

Vuorinen, I. and Ranta, E. (1987) Dynamics of marine meso-zooplankton at Seili, northern Baltic Sea, in 1967-1975. *Ophelia* 28:31-48.

Wagner, M., Durbin, E. and Buckley, L. (1998) RNA:DNA ratios as indicators of nutritional condition in the copepod *Calanus finmarchicus*. *Mar. Ecol. Prog. Ser.* 162:173-181.

Wahlström, E., Persson, L., Diehl, S. and Byström, P. (2000) Size-dependant foraging efficiency, cannabalism and zooplankton community structure. *Oecologia* 123:138-148.

Wahlström, E. and Westman, E. (1999) Planktivory by the predacious cladoceran *Bythotrephes longimanus*: effects on zooplankton size structure and abundance. *Can. J. Fish. Aquat. Sci.* 56:1865-1872.

Warner, A.J. and Hays, G.C. (1994) Sampling by the Continuous Plankton Recorder survey. *Prog. Oceanogr.* 34:237-256.

Warren, G.J., Evans, M.S., Jude, D.J. and Ayers, J.C. (1986) Seasonal variations in copepod size: effects of temperature, food abundance, and vertebrate predation. *J. Plankton Res.* 8:841-853.

Weeks, A., Conte, M.H., Harris, R.P., Bedo, A., Bellan, I., Burkill, P.H., Edwards, E.S., Harbour, D.S., Kennedy, H., Llewellyn, C., Mantoura, R.F.C., Morales, C.E., Pomroy, A.J. and Turley, C.M. (1993) The physical and chemical environment and changes in community structure associated with bloom evolution: the Joint Global Flux Study North Atlantic Bloom Experiment. *Deep-Sea Res. II* 40:347-368.

White, J.R., Zhang, X., Welling, L.A., Roman, M.R. and Dam, H.G. (1995) Latitudinal gradients in zooplankton biomass in the tropical Pacific at 140°W during the JGOFS EqPac study: Effects of El Niño. *Deep-Sea Res. II* 42:715-733.

White, M., Mohn, C. and Orren, M.J. (1998) Nutrient distributions across the Porcupine Bank. *ICES J. Mar. Sci.* 55:1082-1094.

White, R.G., Hill, A.E. and Jones, D.A. (1988) Distribution of *Nephrops norvegicus* (L.) larvae in the western Irish Sea: an example of advective control on recruitment. *J. Plankton Res.* 10:735-747.

Wiebe, P. (1988) Functional regression equations for zooplankton displacement volume, wet weight, dry weight, and carbon: a correction. *Fish. Bull.* 86:833-835.

Williams, R. (1984) Zooplankton of the Bristol channel and Severn estuary. *Mar. Poll. Bull.* 15:66-70.

Williams, R. (1985) Vertical distribution of *Calanus finmarchicus* and *C. helgolandicus* in relation to the development of the seasonal thermocline in the Celtic Sea. *Mar. Biol.* 86:145-149.

Williams, R. and Collins, N.R. (1985) Chaetognaths and ctenophores in the holoplankton of the Bristol Channel. *Mar. Biol.* 85:97-107.

Williams, R. and Conway, D.V.P. (1980) Vertical distributions of *Calanus finmarchicus* and *C. helgolandicus* (Crustacea: Copepoda). *Mar. Biol.* 60:57-61.

Williams, R. and Conway, D.V.P. (1984) Vertical distribution, and seasonal and diurnal migration of *Calanus helgolandicus* in the Celtic Sea. *Mar. Biol.* 79:63-73.

Williams, R., Lindley, J.A., Hunt, H.G. and Collins, N.R. (1993) Plankton community structure and geographical distribution in the North Sea. *J. Exp. Mar. Biol. Ecol.* 172:143-156.

Wishner, K.F., Gowing, M.M. and Gelfman, C. (1998) Mesozooplankton biomass in the upper 1000m in the Arabian Sea: overall seasonal and geographic patterns, and relationship to oxygen gradients. *Deep-Sea Res. II* 45:2405-2432.

Witek, Z. and Krajewska-Soltys, A. (1989) Some examples of the epipelagic plankton size structure in high latitude oceans. *J. Plankton Res.* 11:1143-1155.

Wootton, T. and Power, M.E. (1993) Productivity, consumers, and the structure of a river food chain. *Proc. Natl. Acad. Sci. USA* 90:1384-1387.

Wyatt, T. (1976) Plants and animals of the sea. In: *The ecology of the seas.* Cushing, D. H. and Walsh, J. J. (ed.) Philadelphia: Blackwell Scientific Publications, pp. 467.

Young, E.F., Aldridge, J.N. and Brown, J. (2000) Development and validation of a three-dimensional curvilinear model for the study of fluxes through the North Channel of the Irish Sea. *Cont. Shelf. Res.* 20:997-1035.

Zaret, T.M. and Suffern, J.S. (1976) Vertical migration in zooplankton as a predator avoidance mechanism. *Limnol. Oceanogr.* 21:804-813.

Zhang, X. and Dam, H.G. (1997) Downward export of carbon by diel migrant mesozooplankton in the central equatorial Pacific. *Deep-Sea Res. II* 44:2191-2202.

Zhang, X., Dam, H.G., White, J.R. and Roman, M.R. (1995) Latitudinal variations in mesozooplankton grazing and metabolism in the central tropical Pacific during the U.S. JGOFS EqPac study. *Deep-Sea Res. II* 42:695-714.

Zhang, X., Roman, M., Sanford, A., Adolf, H., Lascara, C. and Burgett, R. (2000) Can an optical plankton counter produce reasonable estimates of zooplankton abundance and biovolume in water with high detritus? *J. Plankton Res.* 22:137-150.

Zhou, M. and Huntley, M.E. (1997) Population dynamics theory of plankton based on biomass spectra. *Mar. Ecol. Prog. Ser.* 159:61-73.