PRE- AND POST-SETTLEMENT PROCESSES INFLUENCING THE DISTRIBUTION OF BARNACLES ALONG ESTUARINE GRADIENTS

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by

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To my parents and grandmothers

Rosana and Alice

And in loving memory of my grandfathers,

Antônio Gerardo Ferreira Gomes   &   Apolônio Ibiapina de Moura
1915 - 2001   1920 - 2003

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ABSTRACT

Estuaries are the interface between freshwater systems and the sea, with clearly recognizable changes in the distribution of organisms along various environmental gradients from riverine to fully marine conditions. This thesis studied ecological processes affecting the distribution of marine species along estuarine gradients using both field and laboratory experiments with barnacles as a tractable model system. *Elminius modestus* Darwin, *Semibalanus balanoides* Linneaus, *Chthamalus montagui* Southward are the most common barnacle species found in the intertidal of British estuaries. Surveys performed in the Plym and the Yealm Estuaries revealed that *E. modestus* occurred furthest up estuaries and was dominant along most of their length, with the exception of sites closest to the sea; *C. montagui* had the most restricted degree of penetration up-estuary; and *S. balanoides* occurred at low abundances, with limits of penetration located between those of *C. montagui* and *E. modestus*. Transplants of adult specimens to sites along the marine-to-freshwater gradient revealed that *E. modestus* was better adapted to environmental conditions found in inner areas of the estuaries than *C. montagui* and *S. balanoides*. Survival of the latter two species was negatively correlated with deposition of silt and decreasing salinity. Laboratory experiments showed that, in contrast to the other two species, *E. modestus* was highly tolerant to burial by silt. A comparison of observed distributions along the gradients with survivability showed that *C. montagui* was able to survive in areas where adults were absent, indicating that early life cycle stages were a potential limiting factor to the distribution of this species. Examination of patterns of cyprid settlement and recruitment to the benthic phase reinforced the suggestion that pre-settlement processes contribute to restrictions in the distribution of both *C. montagui* and *S. balanoides*. The abundance of these species, post-settlement, was also affected by physico-chemical conditions in the upper estuary. Pre-settlement processes did not limit the distribution of *E. modestus* and post-settlement processes appeared to be more important in limiting its abundance at sites closest to the sea.

CONTENTS

LIST OF FIGURES

LIST OF TABLES

ACKOWLEDGEMENTS

AUTHOR'S DECLARATION

At no time during the registration for the degree of Doctor of Philosophy has the author been registered for any other University award without prior agreement of the Graduate Committee.

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CHAPTER 1
GENERAL INTRODUCTION

Estuaries are the interface between freshwater systems and the sea with recognizable changes in the distribution of species along steep environmental gradients from riverine to fully marine conditions (McLusky, 1989; Day et al., 1989). They are sites of considerable human settlement and industrial activity and better understanding of estuarine ecology is essential for sustainable development of estuaries and the adjacent coastal zone (McLusky & Elliot, 2004).

The majority of work on the distribution of estuarine organisms has been based on the study of correlations between observed biological distributions and environmental variables. Relatively few studies have used experimental work to examine the causes of these patterns of species distribution, and even fewer have combined information from surveys, field manipulations and laboratory experiments (e. g. Khfaji & Norton, 1979; Leonard et al., 1999; Satumanatpan & Keough, 2001; Ellis et al., 2002). This thesis combined surveys, field and laboratory experiments, including transplants of individuals, to test explanatory models for patterns of distribution in estuaries in order to examine the ecological processes operating along estuarine gradients using intertidal barnacles as a tractable model system.

In the remainder of this introduction, I set the scene for the rest of the thesis by reviewing relevant literature. I firstly present the definition of an estuary that informed my work and provide a brief overview of the estuarine environment, before considering in turn: distribution patterns of marine species in estuaries; explanatory models for species diversity and distribution; and gradients influencing hard substratum species. The advantages of using barnacles as a model system are then outlined and the information on barnacle species inhabiting British estuaries reviewed. The overall rationale of the thesis and specific aims and objectives are then presented.

1

1.1. Definition and overview of estuaries

Estuaries comprise a very diverse group of systems that share the fundamental attribute of mixing between fresh water and sea water. Estuaries can vary considerably in their geomorphological, physical and biological properties. As a result, numerous definitions of estuaries have been suggested and there has been significant debate about the effectiveness of these definitions in describing such a heterogeneous group of coastal systems (For reviews see Fairbridge, 1980; Kjerfve, 1989; McLusky, 1989; Day et al., 1989; Perillo, 1995a). The most comprehensive definition, which includes most known types of estuaries and mentions their biological component, was provided by Perillo (1995): *"An estuary is a semi-enclosed coastal body of water that extends to the effective limit of tidal influence, within which sea water entering from one or more free connections with the open sea, or any other saline coastal body of water, is significantly diluted with freshwater derived from land drainage, and can sustain euryhaline biological species from either part or the whole of their life cycle"*. This definition informed the work in my thesis.

Estuaries are characterized by variability in physico-chemical and biological properties, which are mainly dictated by the patterns of water circulation (McLusky & Elliot, 2004; Dyer, 1997). Such variability occurs at a range of temporal and spatial scales. Horizontal gradients in physico-chemical properties occur from sea to freshwater and fluctuate with the tides (Dyer, 1997); interaction between freshwater and seawater flow along estuaries can generate stratification in salinity, dissolved oxygen and plankton composition (Pritchard 1955; Cameron & Pritchard, 1963; Borsuk et al., 2001). Over longer time-scales there can be seasonal variations in salinity distribution and fluctuation (Attrill & Thomas, 1996), biological occupation of habitats (Reise, 1985) and sedimentation (Dyer, 1986). Freshwater discharge and tidal fluctuation have

the most influence on water circulation, and consequently, on physico-chemical and biological variables that affect ecological processes in most estuaries. Although mudflats are predominant in most estuaries, several other intertidal and subtidal habitats can be found in estuaries, including salt marshes, mussel beds and oyster reefs, rocky shores, mangrove forests and other natural habitats along with much artificial hard substrata such as docks, jetties and wharfs, buoys and moorings.

1.2. Distribution of marine species in estuaries

Patterns of diversity, abundance and distribution of marine species along estuarine horizontal gradients have long been recognized (e.g. Remane 1934; Doty & Newhouse, 1954). Briefly, marine euryhaline species form the principal biological component of estuaries. They colonize most of the length of the estuary and decrease in numbers towards the riverine end (Remane 1934; Doty & Newhouse, 1954; Remane & Schilieper, 1971; McLusky, 1989). These patterns apply consistently to benthic invertebrate (Remane 1934; Remane & Schilieper, 1971; McLusky, 1989; Attrill, 2002) and algal (Mathieson & Penniman, 1986; Doty & Newhouse, 1954; Den Hartog, 1971; Josselyn & West, 1985; Ketchum, 1983; Mathieson et al., 1981; Wilkinson, 1980) species in estuaries. The freshwater component is less predominant and normally restricted to the upper reaches of estuaries.

Although general patterns of marine species distribution exist in estuaries, to understand and predict the responses of individual species to estuarine variables requires detailed knowledge of their behaviour, physiology and ecology. Several physico-chemical and biological factors may account for variation in community structure and the distribution of species in estuaries, including the nature of the substratum and sediment types (Boyden & Little, 1973; Warwick & Davies, 1977, Elliot

3

& Kingston, 1987; Frusher et al., 1994; Bachelet et al. 1996), salinity regime (Attrill &

Thomas, 1996); water currents (Boyden & Little, 1973; Elliot & Kingston, 1987),

bathymetry (Elliot & Kingston, 1987; Bachelet et al., 1996; Watson et al., 2005),

turbidity and suspended sediment concentrations (Boyden & Little, 1973; Ellis et al.,

2002), food and larval supply larval supply (Satumanatpan & Keough, 2001, Pineda et

al., 2002) and biological interactions (Reise, 1985; Peterson, 1979; Leonard et al.,

1999).

The relative importance of physico-chemical and biological variables in causing

distributional patterns and determining limits of penetration by marine species up

estuaries depends largely on the specific functional group and habitat to which a

particular species belongs. For example, epifaunal suspension feeders living on the

surface of soft bottom habitats are particularly influenced by high loads of suspended

silt and low hydrodynamics, which are known to affect their feeding mechanisms

(Barnes, 1989), while infaunal species are more influenced by aspects of the sediment

such as grain size and organic contents (e.g. Boyden & Little, 1973; Ellis et al., 2002).

The use of species that belong to a similar functional group and habitat facilitates the

test of ecological models that describe the mechanisms responsible for distributions of

organisms in estuaries. Therefore, the present study focuses on epibenthic species, using

intertidal rocky-shore barnacles as a tractable model for the investigation of factors

affecting the distribution of species along estuaries.

1.3. Ecological models for distribution of estuarine epibenthic invertebrates

Remane (1934), working primarily in the Baltic, proposed a model that

correlated general patterns of diversity and distribution of species in estuaries with the

horizontal salinity gradient. According to this model diversity of marine species

decreased predictably towards the upper reaches of estuaries. Further research demonstrated that, although this model was relevant for estuarine systems with stable salinity regimes, such as the Baltic (Segerstråle, 1957; Cognetti & Maltagliati, 2000), it has limitations in describing diversity patterns in many estuaries and as a quantitative descriptor of estuarine communities (Attrill, 2002). In non-tidal brackish seas, such as the Baltic, salinity clearly determines the range of distribution and colonization potential of most species, and the distribution of organisms tends to reflect their salinity tolerances (Segerstråle, 1957; Remane & Shilieper, 1971; Bonsdorff & Pearson, 1999; Cognetti & Maltagliati, 2000). However, for most estuaries, patterns of water circulation are more complex and generate fluctuations in salinity and other physico-chemical parameters which prevent organisms from occupying their potential range of distribution and obscure the correlations between these physico-chemical variables and their distributions (Carriker, 1967).

Any model intending to explain patterns of distribution and abundance of populations of marine species must take into consideration the complexity of the life cycle of the organisms, which in most cases include a larval pelagic stage before the adult benthic phase (Thorson, 1950). Therefore, the relative importance of pre- and post-settlement processes need to be contemplated. Much early work on benthic ecology focused on the role of post-settlement interactions in shaping marine assemblages (e.g. Connell, 1961a, b; 1970; Paine 1969, 1974; Dayton, 1971; Menge, 1976; Menge & Sutherland, 1976). Subsequent work has demonstrated, however, that models for community structuring based exclusively on these interactions did not fit many situations, in which limitations at the recruitment stage were of primary importance (Doherty, 1981; Hawkins & Hartnoll, 1982; Underwood & Denley, 1984; Caffey, 1985; Connell, 1985; Gaines & Roughgarden, 1985; 1987; Raimondi, 1990; Sutherland, 1990).

The importance of larval supply as opposed to post-settlement processes has been an intense area of research in marine ecology (for reviews see Underwood & Denley, 1984; Underwood and Fairweather, 1989; Raimondi, 1990; Eckman, 1996; Todd, 1998; Underwood & Keough, 2001). Work on intertidal barnacles has been particularly important in demonstrating the links between larval supply and benthic stages of populations and the importance of larval supply in setting patterns of adult distribution and abundance (Hawkins & Hartnoll, 1982; Kendall et al., 1982; Underwood & Denley, 1984; Caffey, 1985; Connell, 1985; Gaines & Roughgarden, 1985; Roughgarden & Iwasa, 1986, Raimondi, 1990; Sutherland, 1990). Syntheses of these studies have demonstrated that at high settlement densities populations are mainly regulated by post-settlement interactions (competition, predation, interactions with physical variables), while at lower levels of settlement/recruitment larval supply is more important in regulating assemblage structure (Connell, 1985; Gaines & Roughgarden, 1985, Booth & Brosnan, 1995; Menge, 2000; Underwood & Keough, 2001).

1.4. Estuarine gradients affecting the distribution of rocky-shore epibenthos

Compared to the open coast a reduction in wave action is a common feature of estuaries. Gradients in wave action also exist among areas of the open coast and a considerable amount of research has been done on the effects of this gradient and on comparisons between assemblages inhabiting sheltered and exposed shores (for a review see Raffaelli & Hawkins, 1996). The main effects of reduction in wave action on epibenthic species are linked to the consequent reductions in water circulation, which tend to cause greater deposition of sediment and turbidity of water and influence the transport and distribution of larvae and food for suspension feeders. Disturbance due to wave action is also reduced in sheltered conditions, reducing the risk of dislodgement.

Although the effects of this reduction in wave action present some similarities with sheltered locations found on open coasts (Lewis, 1964), estuarine habitats also present other gradual modifications. Other physico-chemical gradients in estuaries frequently exceed the importance of simple reduction in wave action. Two of the most obvious gradients of particular importance for epibenthic species being salinity and sedimentation.

Freshwater inflow and seawater intrusion are the main factors controlling salinity in estuaries. Consequently, at any given location in an estuary, benthic organisms are subjected to considerable salinity fluctuations with both tidal (Milne, 1938; Bassindale, 1943; Day, 1951; Sanders et al., 1965; Stickle and Denoux, 1976; Cawthorne, 1979a; Hardwick-Witman et al, 1983) and seasonal periodicity (Bassindale, 1943; Day, 1951; Sanders et al., 1965; Attrill and Thomas, 1996; Berger, 2006). Distinct salinity gradients are present in most estuaries, where the range of salinity fluctuations and the persistence of low salinity water are greater at upper estuarine regions and decrease towards the sea (Milne, 1938; Sanders et al., 1965).

Salinity fluctuations and low salinities clearly play an important role in determining the distribution of marine organisms in estuaries (Sanders et al., 1965; Carriker, 1967; Wolff, 1983; Attrill & Thomas, 1996). Despite this, salinity cannot be considered as a factor of universal importance. Tolerance to salinity of any given species, and in fact to any potentially limiting environmental factor, does not necessarily correspond to observed ranges of distribution. It can be assumed that in estuaries, salinity acts by setting broad limits to species distribution, particularly the limits of upstream penetration for marine species. However, within the potential area of occurrence of a particular species, a range of different factors will probably define the exact distribution (see McLusky, 1989; Herman et al., 1999; Little, 2000). Low salinity events and salinity fluctuations may be particularly important by interacting with other

environmental stresses. In particular, sublethal effects on organisms will affect their ability to grow, reproduce and compete by influencing their physiological condition. The importance of salinity may also increase during periods of extreme conditions in other environmental variables, such as temperature and sedimentation.

Estuaries are areas where considerable influx and accumulation of sediments can take place (Emery & Stevenson, 1957, Van Straaten & Kuenen, 1957, 1958; Postma, 1967; Meade, 1969). The dynamics of estuarine sediments includes continual processes of transport, deposition and resuspension. As a result, turbidity, sediment load and silting-up in estuaries exhibit considerable spatial and temporal variation and are typically mush greater than on open coasts (Dyer, 1997). High fluxes of suspended sediment are known to have adverse effects on epifauna and to affect their distribution in estuaries (Levinton & Bambach, 1970; Rhoads and Young, 1970; Aller and Dodge, 1974, Ellis et al., 2002). Suspension feeders under such conditions may experience clogging of the filtering apparatus (Loosanoff, 1962) and many of them display mechanisms to cope with particles entering the mantle cavity (Jorgensen, 1966, 1996). Hard substrata in estuaries are frequently covered by a layer of deposited sediment (Percival, 1929; Day, 1959) which apparently has adverse effects on epibenthic organisms (Korringa, 1951; Day and Morgans, 1956; Day, 1959; Carriker, 1961), and may cover them completely, acting as a physical barrier to feeding, settlement and reproduction (Percival, 1929; Korringa, 1951; Day, 1959; Carriker, 1961).

1.5. Barnacles as model organisms for experimental estuarine ecology

Epibenthic organisms constitute an important group in estuaries and include species that colonise the upper sediment layer of intertidal flats; reef building organisms such as oysters, mussels and some polychaetes; slow-moving species that occur in the

sediment-water interface, such as gastropods, amphipods, isopods and polychaetes; and also sessile forms associated with hard substrata, such as barnacles, hydroids and bryozoans. Hard substrata are scarce in many estuaries, but whenever present they are usually densely colonized. Barnacles are typically the dominant colonizers of hard substrata in estuaries and other coastal inlets, and occur on both natural and artificial substrata.

Barnacles used in this study belong to the order Sessilia (Lamarck, 1818) which is characterised by the presence of a hard carapace that envelops the segmented body and six pairs of thoracic cirri used for gathering food. These species are sessile, hermaphrodite and reproduce by internal cross-fertilization. The life-cycle of a barnacle comprises six naupliar planktotrophic stages and one non-feeding cypris settlement stage (Fig. 1.1).

Some key features of barnacles make them especially useful for ecological investigations, and in particular for intertidal ecology. These include the sessile nature of their benthic stage; the feasibility of collection and identification of their planktonic stages; the practicability of quantifying settlement in the field since newly settled cyprids are clearly visible, either on natural substrata or settlement panels; the fact that adult populations are conspicuous at mid-low intertidal rocky shores, and therefore, accessible during low tide. Due to this tractability, barnacles were successfully used in pioneering studies leading to modern experimental ecological approaches in intertidal ecology (e.g. Southward & Crisp, 1954; Connell, 1961a, 1961b, 1970). The importance of larval supply and recruitment to adult population regulation (e.g. Hawkins & Hartnoll, 1982; Caffey, 1985, Connell, 1985; Gaines & Roughgarden, 1985; Gaines et al., 1985; Raimondi, 1990, Sutherland, 1990; Minchinton & Scheibling, 1991; 1993; Bertness et al., 1992; Miron et al., 1995) and the roles of predation (Paine, 1974; Menge, 1976) and competition (Menge & Sutherland, 1987) in structuring communities

and determining species distribution in the intertidal, have been successfully demonstrated by using barnacles.
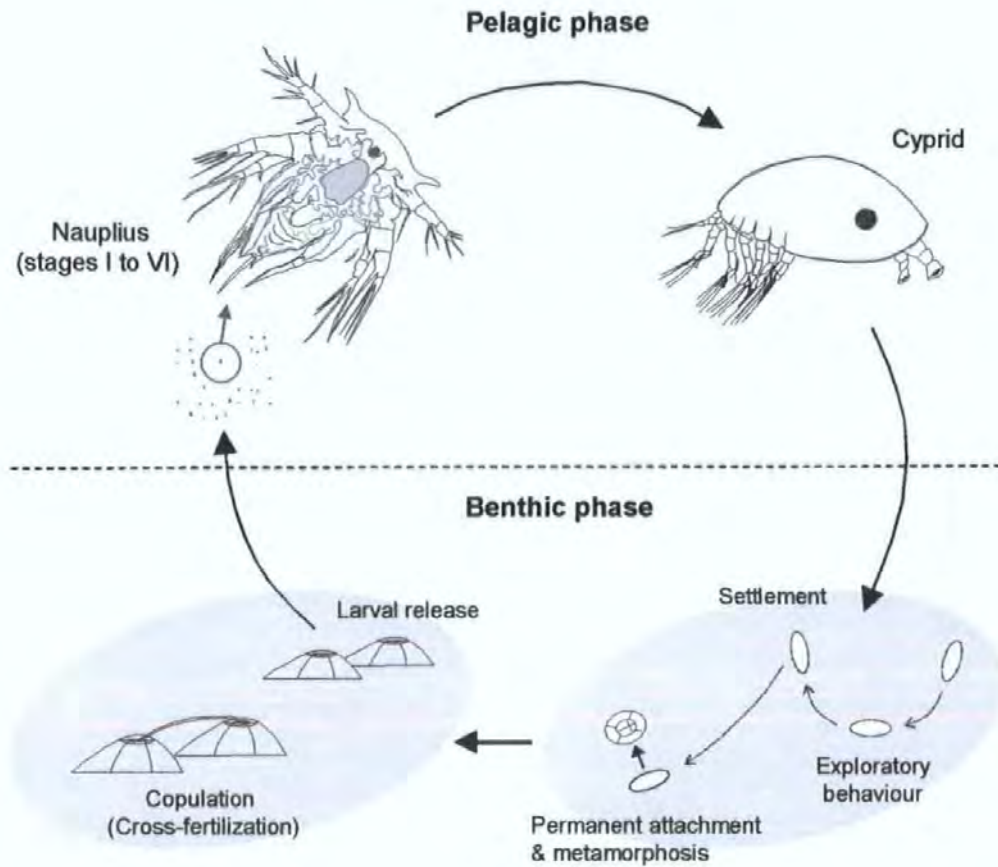
Fig. 1.1. The life-cycle of a barnacle.

1.6. Barnacle species in British estuaries

The main barnacle species that occur in British estuaries are *Elminius modestus* Darwin, *Semibalanus balanoides* Linneaus, *Chthamalus montagui* Southward, *Balanus improvisus* Darwin, *Balanus crenatus* Bruguière and *Verruca stroemia* (O. F. Müller) (Bassindale, 1964; Southward, 1976). *V. stroemia* and *B. crenatus* are subtidal species, although the latter is also occasionally found in the intertidal. *B. improvisus* inhabits sub and intertidal zones and is regarded as the barnacle species found furthest away from the

sea in estuaries (Foster, 1970). The distribution of this species in estuaries in the UK is patchy and subject to processes of population extinctions and re-colonization (Furman & Yule, 1991). Stable populations are restricted to large estuaries and this species is not common in estuaries in Southwest England (Furman & Yule, 1991). Among these species *E. modestus, S. balanoides* and *C. montagui* are the ones most commonly found on UK estuarine intertidal shores (Crisp, 1958; Southward & Crisp, 1952; 1959; Hiscock & Moore, 1986; Dixon, 1986; Moore, 1988; Hiscock, 1986). These three species were studied in this thesis (Fig. 1.2).
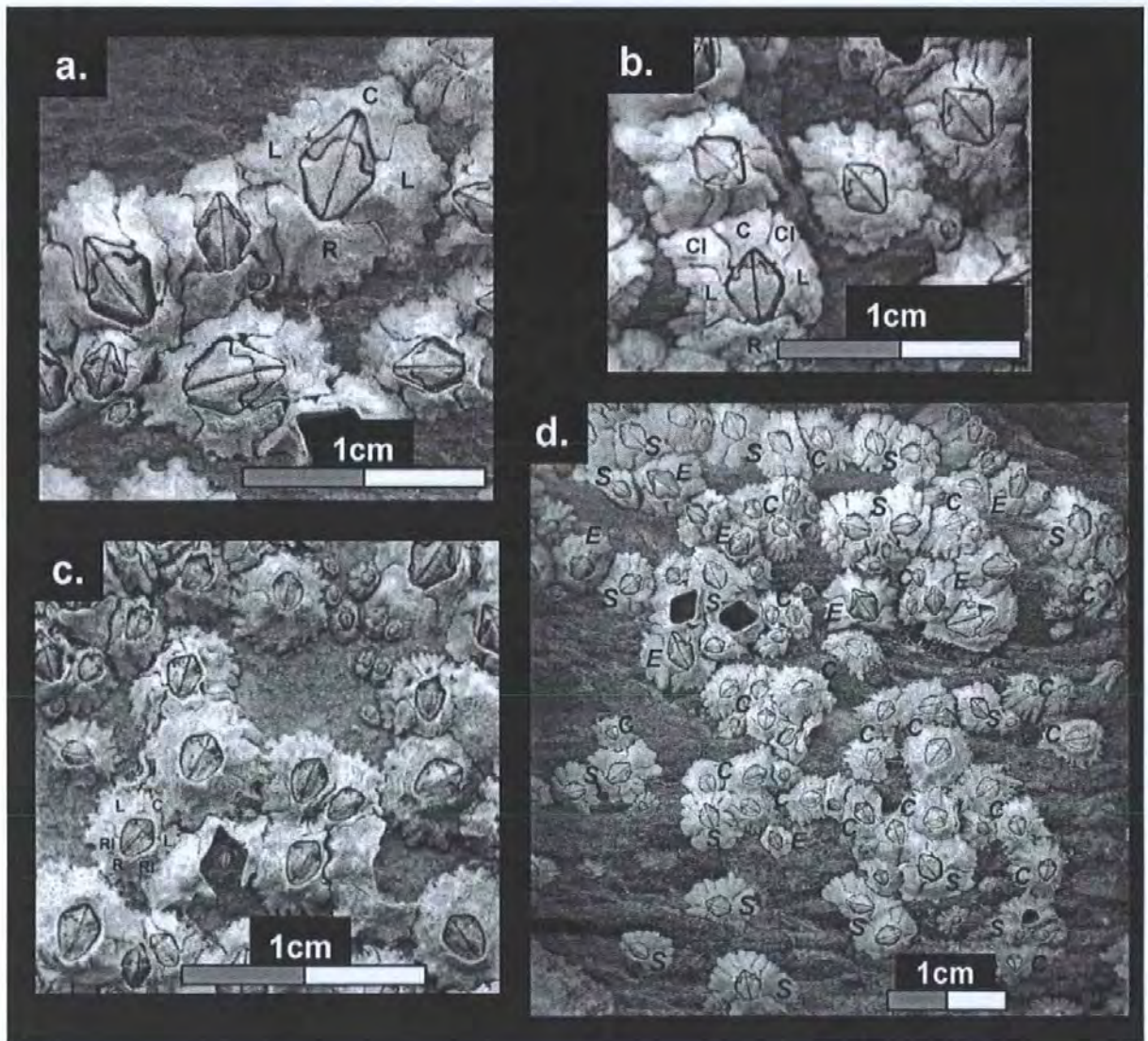
Fig. 1.2. Species utilized as model organisms in this thesis: a. *E. modestus*; b. *S. balanoides*; c. *C. montagui* (Wall plates: C: carinal, R: rostral, L: lateral, Cl: carino-lateral and Rl: rostro-lateral); and d. detail (5 x 5 cm) of the three species co-existing on an estuarine shore, *E*: *E. modestus*, *S*: *S. balanoides* and *C*: *C. montagui*.

E. modestus is an Australasian species, distinctively eurythermal and euryhaline, and typically found in estuarine and other sheltered marine areas (Southward and Crisp, 1956; Crisp and Southward, 1959; Barnes and Barnes, 1961, 1965; Crisp 1958; Foster, 1971, 1987; Harms, 1999). This species was introduced into British and European waters during the 1940s (Crisp, 1958) and since then has spread considerably. This species is now common on European coasts, from Shetland to northern Spain (Crisp, 1958; Crisp & Southward, 1959; Jones, 1961; Hiscock et al., 1978; King et al., 1997). There is an extensive literature on the introduction, spread and occurrence of *E. modestus* on European shores (Bishop, 1947; Boschma, 1948; Knight-Jones, 1948; Stubbings, 1950; Crisp, 1958, 1959, 1960; Crisp & Chipperfield, 1948; Beard, 1957; Bishop, 1954; Bishop & Crisp, 1958; Connell, 1955; Crisp & Southward, 1959; Jones, 1961; Den Hartog, 1953, 1956; Fischer-Piette, 1965; Fischer-Piette & Prenant, 1956, 1957; Barnes & Stone, 1972; Hiscock et al., 1978; Barnes & Barnes, 1960a, b, 1961, 1965, 1966, 1969; Barnes et al., 1972; Fischer-Piette & Forest, 1961; Evans, 1968; King et al., 1997; Flowerdew, 1984). *E. modestus* dominates estuarine intertidal shores in many British and European estuaries, where it can extend its distribution up to the riverine portions of the estuaries and reaches areas near to the estuarine limits of saltwater incursion and tidal influence. *E. modestus* has a broad range of vertical distribution (Foster, 1971; Crisp et al., 1981), occurring from the mean high water of neap tides (MHWN) to the subtidal (Foster, 1970).

S. balanoides is an Arctic-boreal species and is found on both sides of the North Atlantic and also on the Pacific coast of North America (Lewis, 1964). In the East Atlantic, the South-West of Britain is close to the southern limit of distribution of this species, which extends from Spitsbergen in the Arctic to Brittany and north-western Spain (Fischer-Piette and Prenant, 1956; Southward and Crisp, 1956; Crisp et al. 1981). This species is the major barnacle species found on intertidal shores in Britain, except

for some locations in the South-West, where it can be less abundant then chthamalids (Lewis, 1964; Crisp & Southward, 1958). *S. balanoides* can survive in estuarine areas, but is more common on the open coast (Lewis, 1964; Foster, 1970; Southward, 1976; Crisp et al. 1981). It is normally found between MHWN and MLWN, but occasionally extends its distribution to lower levels (Lewis, 1964; Foster, 1969, 1970). Its position is usually located just below the zone occupied by chthamalid species, although some overlap is typically observed (Lewis, 1964).

C. montagui is a warm-water species that occurs along the east coast of Great Britain, extends further South up to Mauritania and is also common in the Western Mediterranean (Crisp et al., 1981). The distribution of this species is very similar to the distribution of *C. stellatus* and in Britain the range of distribution of *C. montagui* and *C. stellatus* almost completely overlap. Despite this similarity in geographical range, it is possible to distinguish habitat preferences of *C. montagui* and *C. stellatus* that are consistent throughout the range of these species. *C. montagui* occupies upper vertical regions within the barnacle distribution zone as a whole (Southward, 1976) and is particularly successful in estuarine areas close to the sea; while *C. stellatus* is not found in estuarine areas, being more successful on open coasts exposed to strong wave action (Southward, 1976; Crisp et al., 1981). In estuaries, *C. montagui* is usually restricted to regions adjacent to the sea, showing less penetration into the estuary than *S. balanoides and E. modestus* (Lewis, 1964; Foster, 1970; Southward, 1976; Crisp et al. 1981). *Chthamalus montagui* is most common between mean high water spring tides (MHWS) and MHWN (Southward, 1976; Crisp et al., 1981).

The differing degrees of estuarine penetration of these three species (*E. modestus > S. balanoides > C. montagui*) and the dominance of *E. modestus* are commom features of the distribution of barnacles in British estuaries. Several physiological traits that differentiate *E. modestus* from *C. montagui* and *S. balanoides*

may contribute to these patterns, including: 1) higher tolerance to low salinity (Foster, 1970; Davenport, 1976; Cawthorne, 1979b; Cawthorne & Davenport, 1980) and siltation (Crisp, 1958); 2) higher cirral activities (Southward, 1955; Barnes & Barnes, 1962); 3) higher fecundity and multiple brooding (Crisp & Davies, 1955; Barnes & Barnes, 1968); and 4) shorter generation time (Crisp & Davies, 1955; Barnes, 1962, 1989). Although these have been frequently evoked as being responsible for patterns of distribution and abundance of *E. modestus* in comparison to native species, and also for the invasive success of *E. modestus*, few studies have attempted to test the ecological significance of some of these features in natural habitats (Barnes & Barnes, 1962 growth at differing shore heights; Moyse & Knight-Jones, 1967, O'Riordan & Murphy, 2000 reproductive output; Harms & Anger, 1989, Watson et al., 2005 recruitment). Therefore it is relevant to unravel the relative importance of some of these physiological traits and resulting ecological processess in determining the patterns of distribution of these species in estuaries.

1.7. Key identification features of the studied species

The identification and separation between *E. modestus, C. montagui* and *S. balanoides* is relatively easy at all stages of their life-cycle. Adults are easily recognised in the field by the number and position of the plates forming their external wall and also by their apertures' shape. Catalogues with descriptions of species, keys and notes for identification of barnacles can be found in Southward (1963), for species from European waters and in Bassindale (1964), for British barnacles. These guides include *E. modestus, S. balanoides* (as *Balanus balanoides*) and *C. stellatus*. Southward (1976) separated *C. stellatus* into *C. stellatus* Polli and *C. montagui* Southward and provided descriptions, discussion on the key identification features, as well as revised distribution

of these two species. A more updated introductory text on the biology of British

barnacles, including useful drawings of the external appearence and plate positions of

all British barnacles can be found in Rainbow (1984).

E. modestus is the only barnacle in British shores with the wall formed by four

plates. The limits between these plates are normally well defined in *E. modestus* and the

aperture is typically diamond shaped (Fig. 1.2.a). *C. montagui* and *S. balanoides* both

have six plates but the relative positions of these plates and also the shape of their

apertures differ in these two species. In *C. montagui* the rostral plate is overlapped by

the to rostrolateral plates (Fig. 1.2.c), while in *S. balanoides* the rostral plate is wider

and extends over the margins of the lateral plates (Fig. 1.2.b). Furthermore the aperture

in *C. montagui* is kite-shaped and the line formed by the articulations between the terga

and the scuta is straight and close to the carinal edge, less than one third the distance

down the rostrum. This latter feature is one of the most important for separation

between *C. montagui* and *C. stellatus* (Southward, 1976).

Identification of naupliar stages of British barnacles can be made based on Ross

et all (1999), which provided detailed discussion on identification features and two

identification keys, one for stages II and III of nauplii and one for stages IV, V and VI.

The most important features used for the separation between species are total length, the

relative sizes of the dorsal thoracic spine and the abdominal process, the size and

direction of the frontolateral horns, and also the shield length in stages IV to VI (see

Ross et al., 1999 for illustrations). *C. montagui* is readily separated from *E. modestus*

and *S. balanoides* at all stages by observation of the labrum, which is unilobed in *C.*

montagui and trilobed in the other two species. Chthamalid nauplii is also smaller than

those of *S. balanoides* and *E. modestus*. Complete descriptions of larval stages,

including setation formula can be found in Bassindale (1936) for *S. balanoides* and *C.*

stellatus; Crisp (1962) and Pyefinch (1948) for *S. balanoides*; Knight-Jones & Waugh (1949) for *E. modestus*; and Burrows et al. 1999 for *C. stellatus* and *C. montagui*.

Identification of cyprids is mainly based on sizes (ex. Power et al, 1999; O'Riordan et al., 2001), but the shape of the larvae is also utilized (ex. Jenkins, 2005). Identification of chathamalid cyprids can be made by length sizes, *C. montagui* being smaller (350 to 525μm) than those of *C. stellatus* (575 to 750μm) (Power et al, 1999; O'Riordan et al., 2001). Cyprids of *S. balanoides* are much bigger, with a minimum minimum length of 1000μm (Crisp, 1962; Pyefinch, 1948). The size range of the cyprids of *E. modestus*, is similar to that of the Chthamalids, but larvae can be recognised by its transparency, and its pointed anterior and posterior ends (Knight-Jones & Waugh, 1949). Chthamalids have distinctively round anterior ends and opaque brown colour. Early metamorphosed individuals are difficult to distinguish in the field due to its small size and the uncalcified nature of their carapace. Despite this, the species can be recognised in the laboratory with the use of an optic microscope, based on the number and position of their wall plates, which are similar to the adults.

1.8. Rationale, overall aims and specific objectives

Assuming availability of habitat of sufficient quality, two main models could explain the distribution of epibenthic organisms along estuarine gradients: 1. larval availability and ability to settle at different positions along estuarine gradients; and 2. tolerance of post-settlement stages to estuarine environmental conditions and consequent ability of this species to survive and establish adult populations.

In the first model, the origin of larvae that may potentially settle on estuarine shores (local production plus larvae transported from the sea or other estuarine area) and the predominance of import versus export of larvae from the estuary, which may be

influenced by patterns of water circulation and larval behaviour, must be considered. Models based on the tolerance of post-settlement stages need to take into account the nature of the environmental gradients found in a particular estuary, the potential of physico-chemical and ecological factors in causing stresses on organisms and the degree of spatial and temporal variability of these factors.

Possible patterns of horizontal distribution of marine species in estuaries and determinant factors of penetration are presented in Fig. 1.3. Availability of larvae may be responsible for limitations in settlement and consequently in the occurrence of post-settlement stages along estuarine gradients (Fig. 1.3.a). Alternatively, larvae may be present along the whole extension of the estuary, but limitations in settlement may restrict distribution (Fig. 1.3.b). It is also possible that larvae exhibit an extensive distribution in the estuary, which culminates in settlement along the whole estuary, but post-settlement mortality due to environmental factors limits species distribution (Fig. 1.3.c). In the final scenario, species occur from the entrance up to the riverine limit of the estuary, in which case limitations would appear to be absent throughout the life cycle of the species (Fig. 1.3.d).
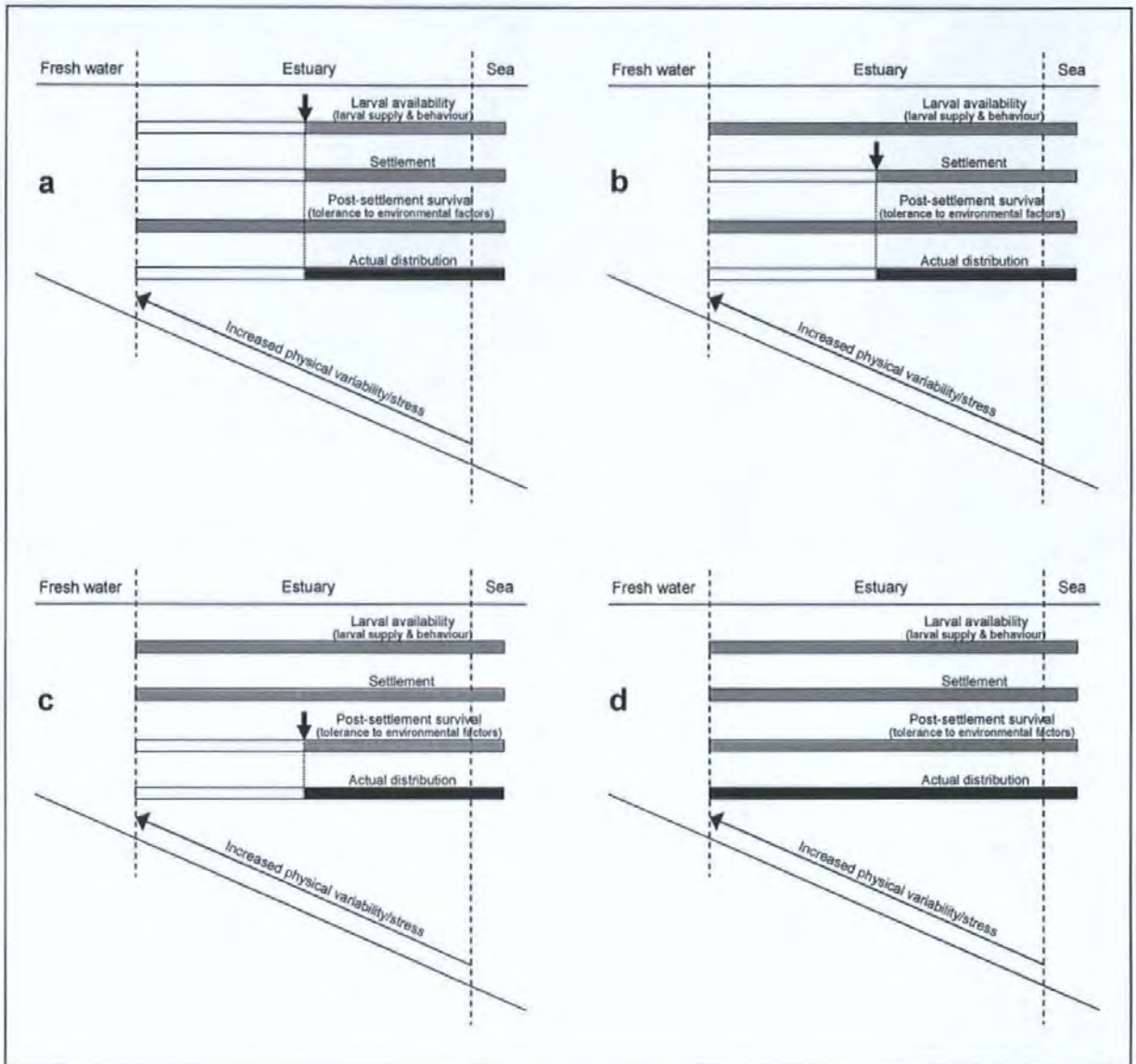
Fig. 1.3. Schematic representation of explanatory models for distribution of marine species in estuaries. a) larval supply limiting larval settlement and occurrence of post-settlement stages along the estuarine gradient; b) settlement-limited distribution; c) post-settlement mortality limiting species distribution; and d) distribution along the entire length.

The overall aim of this thesis is to examine the relative importance of factors that affect organisms along estuarine gradients, by testing the influence of larval supply, settlement and tolerance of post-settlement stages on patterns of distribution and abundance, using intertidal barnacles as model organisms. Mechanisms responsible for species dominance on estuarine intertidal rocky shores were also examined by the study

of the dominant non-native species *Elminius modestus*. The principles of two explanatory models for the ecological controlling of patterns of distribution of species in estuaries were examined. According to the two contrasting models, horizontal distribution of species in estuaries are dictated by: 1. tolerance of post-settlement stages to environmental conditions; or 2. processes that take place at pre-settlement and settlement stages of the life cycle of these species, namely distribution and abundance of planktonic larvae across estuaries and settlement on suitable substrata.

Patterns of distribution of intertidal barnacles in estuaries from the South-West UK were examined and surveys performed in two estuaries to provide detailed information on variations in the composition and abundance of barnacle populations along the marine-to-freshwater gradient (Chapter 2). The specific objectives of Chapter 2 were identification of the upper limits of penetration of each of the species in estuaries and to examine the degree of dominance of *E. modestus*.

Explanatory models for the distribution of organisms in estuaries based on the tolerance of species to environmental conditions were tested using transplant experiments between shores distributed along horizontal estuarine gradients in Chapter 3. This chapter assessed the relative ability of *C. montagui*, *S. balanoides* and *E. modestus* to survive conditions prevailing along horizontal environmental gradients in estuaries, to establish the correspondence between actual distributions of adults on the shore with the survival of specimens transplanted of each species and to test the correlation between survival and selected physico-chemical variables, namely salinity and siltation.

In Chapter 4, the influence of deposition of silt on each of the three species of barnacle was examined experimentally. Effects of burying *C. montagui*, *S. balanoides* and *E. modestus* by estuarine silt were compared using laboratory experiments, to

examine the relative tolerance to burial by estuarine muddy sediment and effects of burial on cirral activities on each species.

Results on the distribution of planktonic larval stages of barnacles along the estuarine gradients were not presented in this thesis, and the importance of pre-settlement processes was indirectly assessed by the study of temporal and spatial patterns of settlement. Plankton collections were made, but due to time restrictions processing could not be concluded. According to preliminary results, both in the Plym and the Yealm: 1. the diversity of species in the plankton decreased towards the riverine end; 2. All species tended to be more abundant at the mouth of the estuaries than at inner areas; 3. *E. modestus* and the subtidal species *V. stroemia* were the most abundant species, and together with *B. perforatus*, were the only species detected at all stations sampled along the length of the estuaries; 4. *C. montagui* was absent from samples taken at the sites located at the upper reaches of the estuaries, but was present at stations located at the seaward half of the estuaries. Although further work is needed for a more detailed and accurate description of the patterns of distribution of barnacle larvae in these estuaries, these results suggest that *E. modestus* is probably more abundant and dominant at planktonic stages and that larvae of *C. montagui* and other species may have a restricted degree of penetration up-estuary. These may be important for the determination of patterns observed at latter stages of development, in which case settlement would be influenced and reflect variations on the larval supply.

The patterns of settlement and recruitment and their influence on the distribution of adults were examined in Chapter 5. Settlement, defined as the attachment of a cyprid on experimental surfaces, and recruitment, defined as the survival of a post-metamorphosed individual to the time of sampling, were assessed in intertidal areas located at various distances from the sea along two estuaries, and compared to observed distribution of adults.

20

In Chapter 6 a synthesis of results is presented including an evaluation of models for distribution of epibenthic marine species in estuaries (Fig. 1.1) viewed in the light of my results.

CHAPTER 2
DISTRIBUTION OF BARNACLES IN ESTUARIES IN SOUTH-WEST ENGLAND

2.1. Introduction

South-West England is characterized by the occurrence of a series of ria-type estuaries distributed along the coasts of Devon and Cornwall (Dewey, 1948; Castaing & Guilcher, 1995). The main species of barnacles found in intertidal areas of these estuaries are *Elminius modestus*, *Semibalanus balanoides* and *Chthamalus montagui* (Little, 1988, 1989; Gill & Mercer, 1989; Rostron, 1987; Horsman, 1986; Moore, 1988; Frid, 1989; Dixon, 1986; Hiscock & Moore, 1986). *Balanus crenatus*, which is predominantly a subtidal species, is also found occasionally in intertidal estuarine habitats. *E. modestus* is dominant throughout the intertidal in most of these estuaries. *C. montagui* is typically restricted to lower seaward regions of estuaries, while the distribution of *S. balanoides* and *E. modestus* extends to mid and upper estuarine areas (Crisp et al., 1981; Little, 1988, 1989; Gill & Mercer, 1989; Rostron, 1987; Horsman, 1986; Moore, 1988; Frid, 1989; Dixon, 1986; Hiscock & Moore, 1986).

Elminius modestus is an Australasian species typically found in estuarine and other sheltered marine areas (Southward & Crisp, 1956; Crisp & Southward, 1959; Barnes & Barnes, 1961, 1965; Crisp. 1958; Foster, 1971, 1987, Harms, 1999). This species invaded British and European waters during the World War II, and is now well established (Bishop, 1947; Stubbings, 1950; Den Hartog, 1953, 1956; Crisp, 1958; Harms, 1999, Lawson et al., 2004). *S. balanoides* and *C. montagui* can also occur in sheltered areas but are more successful on the open coast (Lewis, 1964; Foster, 1970; Southward, 1976). The dominance of *E. modestus* in British and and other European estuaries is probably as a consequence of the interaction of several physiological and

reproductive characteristics of this species, which confer advantage over native species in estuarine environments (Crisp, 1958; Harms, 1999; Lawson et al., 2004; Watson et al., 2005).

The Yealm and the Plym are small estuaries with considerable extent of intertidal rocky shoreline as well as artificial hard substrata such as quays and jetties. These systems were chosen as models for the study of processes governing the distribution of intertidal barnacles in estuaries, and conclusions derived from this study are expected to enlighten our understanding of such processes in rias and estuaries in general. Intertidal fauna in these two estuaries have not been extensively investigated and information is restricted to a few positions scattered along the estuaries that have been examined previously (Cunningham et al., 1984; Cunningham & Hawkins, 1985; Hiscock & Moore, 1986).

Fluctuations in the abundance of *Chthamalus stellatus, Chthamalus montagui, Semibalanus balanoides* and *Elminius modestus* have been recorded for over forty years in an area located near the mouth of the Yealm Estuary (Cellar Beach) (Southward, 1991). At this location, *C. montagui* and *C. stellatus* were the most common species in the upper levels of the shore, *S. balanoides* occurred below *Chthamalus* species down to about MLWN and *E. modestus* was common only between MLWN and MLWS (Southward, 1991). *S. balanoides* and *C. montagui* showed fluctuations in abundance mainly related to the local annual sea temperature two years earlier, and at a decadal scale, were also correlated with long term climatic fluctuations in temperature. *E. modestus* showed strong annual fluctuations probably due to local availability of larvae (Southward, 1991). Although this work revealed detailed aspects of the dynamics of barnacle populations at the entrance of the Yealm, patterns of distribution and ecological processes in the inner regions of the estuary were not examined.

In areas further up the Yealm *E. modestus* is the dominant intertidal barnacle species, and it occurs at much higher levels on the shore (Hiscock & Moore, 1986). *E. modestus* and *S. balanoides* were previously recorded at lower and middle portions of the estuary (Hiscock & Moore, 1986), while *C. montagui* was found only on the lower estuary. All three species occurred at mid-shore positions, but only *S. balanoides* and *E. modestus* were present below mid shore level (Hiscock & Moore, 1986). In the Plym Estuary, only sites where conditions approximate to fully-marine, in the lower third of the estuary, have been surveyed previously (Hiscock & Moore, 1986); *E. modestus* and *S. balanoides* were recorded at these sites in the mid and low-shore zones.

Past surveys did not comprehensively examine the horizontal distribution of barnacles in these estuaries. Specifically, they did not locate the upper limits of distribution of these species or reveal subtle shifts in the composition of barnacle assemblages along the estuarine gradient. Therefore, the objectives of this Chapter were to identify patterns of abundance and distribution of intertidal barnacle species along the horizontal gradient of the Plym and the Yealm estuaries and to establish the location of the upper limits of distribution for each of the species under investigation. This Chapter informs the hypothesis testing Chapters (3, 4 and 5) in the reminder of this thesis.

2.2. Methods

2.2.1. Study Area

The Yealm and Plym Estuaries are located near Plymouth in South-West England (Fig. 2.1). They are macrotidal (5m tidal range) rias with low freshwater inflow and considerable protection from wave action. The Plym is located within Plymouth Sound, which is sheltered by the Plymouth Breakwater. The Yealm Estuary, located to

the east of Plymouth Sound, is protected by Wembury Reef and by a sandbar at its entrance. The coastlines of these estuaries are generally characterized by gentle slopes and large expanses of mud flats. In most intertidal areas mud covers the bedrock below mid-tide level, but above this level, outcrops of rock, boulders or cobbles occur. Artificial substrata are occasionally present as stone embankments and jetty walls, and these also contribute to the surfaces available for colonization by barnacles.
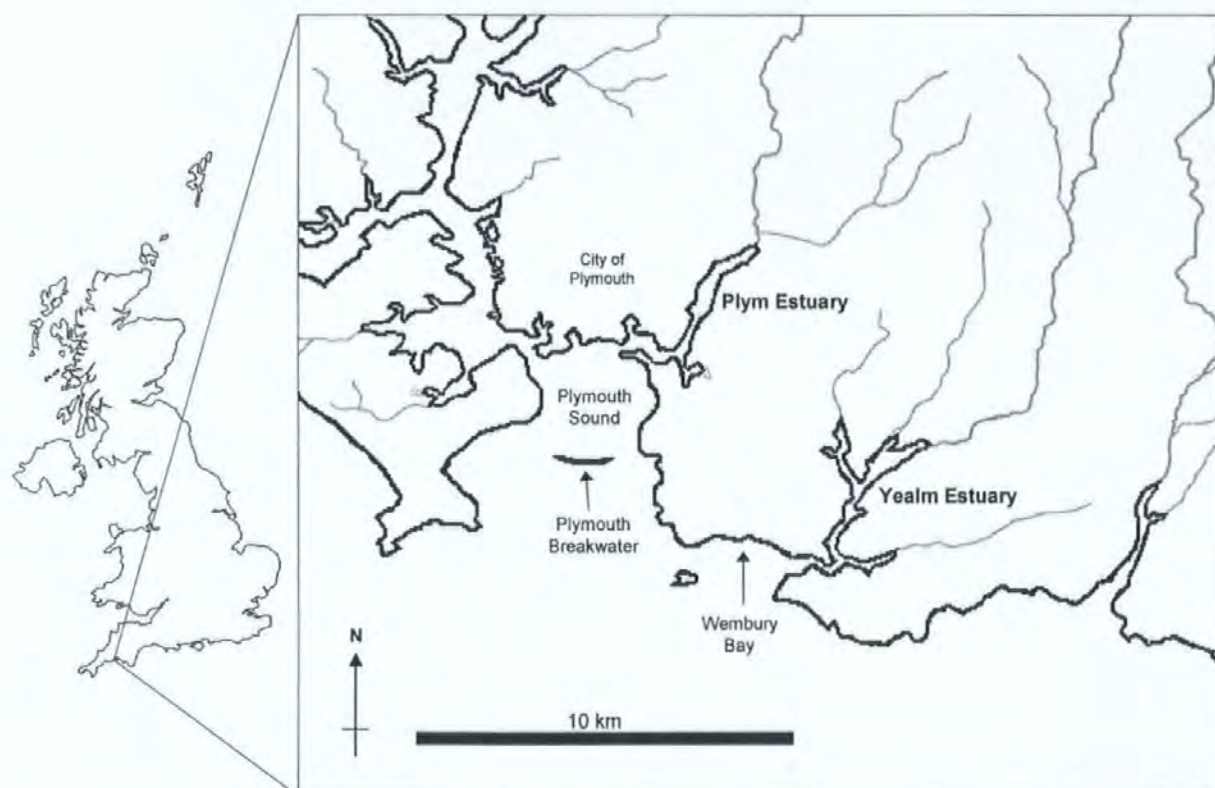
Figure 2.1. The Yealm and Plym Estuaries.

2.2.1.1. The Yealm Estuary

The River Yealm rises on Dartmoor and empties to the east of Plymouth Sound. The estuary is 6.5 km long, extending from Punslinch Bridge, near Yealmpton, to its seaward limit at Wembury Bay (Fig. 2.2). The main creeks present are Newton Creek, which extends eastwards for 1.5 km at the lower estuary; and Cofflete Creek, which extends for 2 km northwards from Steer Point (Fig. 2.2). Extensive yacht moorings are

present in the lower portion of the estuary, from Noss Mayo and Ferry Point up to the Heron's Reach area (Fig. 2.2). The predominant hard substrata bordering the Yealm Estuary is natural rock. Some narrow jetty walls occur at Newton Creek and Heron's Reach; and stone embankments extend on the west border of the Kitley Estate area, from Warren Point to near Punslinch (Fig. 2.2).
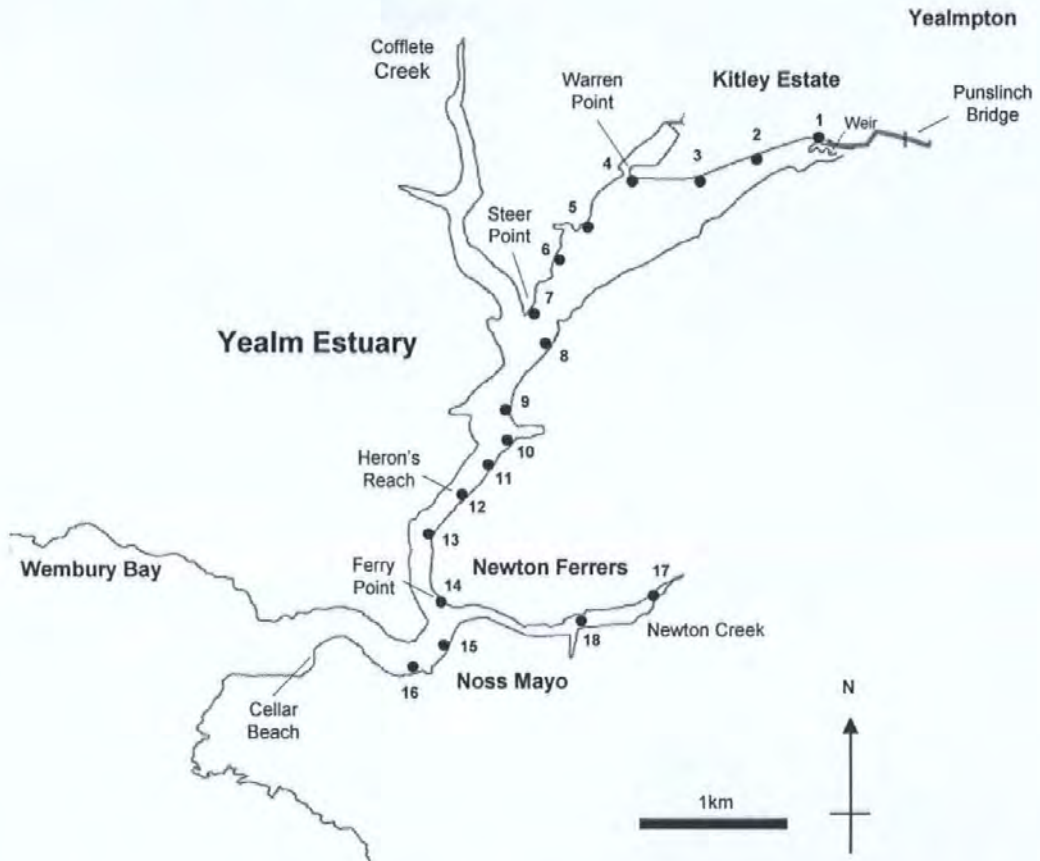
Fig. 2.2. The Yealm Estuary. Position of sites investigated in the survey and names of areas cited in the text. **1. Punslinch Bridge; 2. Quay/Kitley Estate; 3. Boat House/Kitley Estate; 4. Warren Point; 5. South Creek; 6. South Creek Quay; 7. Steer Point; 8. Hanaford Green; 9. Shortaflete Creek; 10. Newton Wood North; 11. Newton Wood South; 12. Heron's Reach; 13. Madge Point; 14. Ferry Point; 15. Ferry Cottage; 16. Passage House; 17. Newton Creek Top; 18. Newton Creek**

2.2.1.2. The Plym Estuary

The River Plym empties into the Plymouth Sound. The estuarine area extends for 5.5 km from Longbridge to its entrance to the sea at Mount Batten Point (Figs. 2.1 and 2.3). Cattewater, located at the entrance of the Plym Estuary, is an important area for commercial docking. Heavy mooring of recreational boats also takes place at this

area and extends up to Laira Bridge (Fig. 2.3). Wharfs and jetty walls border the estuary from Cattewater to Laira Bridge, followed by stone embankments up to Saltram Point, and are replaced by a natural rocky shoreline from Saltram Point towards the riverine end of the estuary (Fig. 2.3).
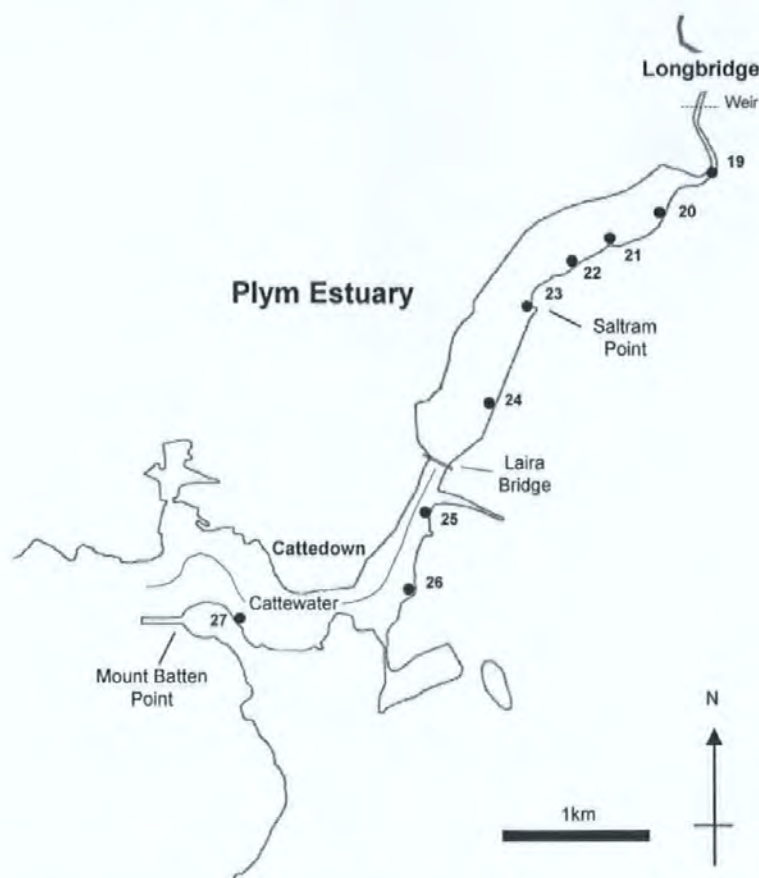
Fig. 2.3. The Plym Estuary. Position of sites investigated in the survey and names of areas cited in the text. **19. Blaxton Meadow North; 20. Blaxton Meadow South; 21. The Amphitheatre; 22. Saltram Wood; 23. Saltram Point; 24. Laira Bridge; 25. Yacht Haven Quay; 26. Oreston; 27. Mount Batten Centre.**

2.2.2. Surveys

A total of 18 sites in the Yealm Estuary and 9 sites in the Plym Estuary were sampled in autumn 2004 (Fig. 2.2 and 2.3). These sites were located along the length of these estuaries encompassing sites with considerable influence of freshwater, at the upper limits of the estuarine area, to sites where fully marine conditions prevail. The

surveys also included the whole range of barnacle distribution on these estuaries, as preliminary surveys indicated that barnacle populations were absent upstream site 1, in the Yealm and site 19, in the Plym.

Hard substrata were frequently limited to outcrops of rocks or groups of isolated boulders spread along shingle, sand or mud. Surveys were made in areas of the intertidal where barnacles were abundant, usually at mid and upper shore levels, as the lower shore was mainly mud-flats or bedrock covered by mud. Additional sampling was performed on the lower shore level, whenever hard substrata were available. This usually occurred at positions away from the riverine end of the estuaries, where the accumulation of mud on lower shores was less.

Surveys were performed using 10 x 10 cm quadrats. Ten quadrats were photographed at each site or vertical zone within a site. Barnacle species present in the photographs were subsequently identified and counted. The relative proportion of adults and recently metamorphosed individuals of *E. modestus*, *S. balanoides* and *C. montagui* were calculated for each site sampled. Densities were also calculated and expressed in number of individuals per 0.01 m^2.

2.3. Results

Elminius modestus was dominant on shores in both the Yealm and Plym. This species was the most abundant barnacle at all sites, except at one lower estuarine site in the Yealm (site 14, Fig. 2.4 and 2.5) and one in the Plym (site 27, Fig. 2.6 and 2.7). *E. modestus* was the only species for which recently metamorphosed individuals were observed in the samples (Fig. 2.8 and 2.9). *S. balanoides* and *C. montagui* were all adult and apparently more than one year old. The results also indicated differences in the distribution of the three species. *C. montagui* extended towards the riverine end of the

estuaries less than the other two species. *E. modestus* was found along the whole extension of both the Plym and the Yealm, while the limit of *S. balanoides* occurrence was between that of the *E. modestus* and *C. montagui*.

Chthamalus montagui was abundant in lower areas of the estuaries (Fig. 2.4 and 2.6) and was the most abundant species at only one location in the Yealm (site 14, Figs. 2.4 and 2.5) and one in the Plym (site 27, Figs. 2.6 and 2.7). These sites were both fully marine, being located close to the mouth of the estuaries (Fig. 2.5 and 2.7). The abundance of *S. balanoides* was greatest in the middle portions of the estuaries, but was only found at extremely low densities in the Plym (Fig. 2.6). *B. crenatus* was found at low abundance in some sites in the lower reaches of both estuaries. Further details on the distribution and abundance of these species along the horizontal gradient are presented for each estuary below.

2.3.1. Yealm Estuary

Along the upper third of the Yealm Estuary, from the tidal limit near Punslinch Bridge (site 1) to the entrance of South Creek (site 6), the barnacle cover was composed exclusively of *E. modestus* (Fig. 2.5). This species occupied considerably higher levels of the shore in these areas than at areas located further seawards. The lowest abundance of *E. modestus* was observed at site 1 (Fig. 2.4), where the lower shore was dominated by mudflats and outcrops of rock were restricted to the upper middle shore.

The middle third of the estuary, from Steer Point (site 7) to Heron's Reach (site 12), was characterized by the presence of all three species of barnacles (Fig. 2.4 and 2.5). The upper limit of *S. balanoides* occurred at Steer Point (site 7). This species reached peak abundances at the three sites located immediately seawards from Steer Point (sites 10, 11 and 12; Fig 2.4). *C. montagui* occurred from the south entrance of the

Shortaflete Creek (Newton Wood North, site 10) and at all subsequent seaward sites (Fig 2.4 and 2.5). This species was found at higher levels on the shore, just above the area populated exclusively by *E. modestus* and *S. balanoides* (Fig. 2.5).

In the lower third of the Yealm Estuary an increase in the relative abundance of *C. montagui* was observed, while *S. balanoides* was less abundant (Fig. 2.4). *Elminius modestus* was the only species recorded at the two sites located in Newton Creek (sites 17 and 18) (Fig. 2.5).
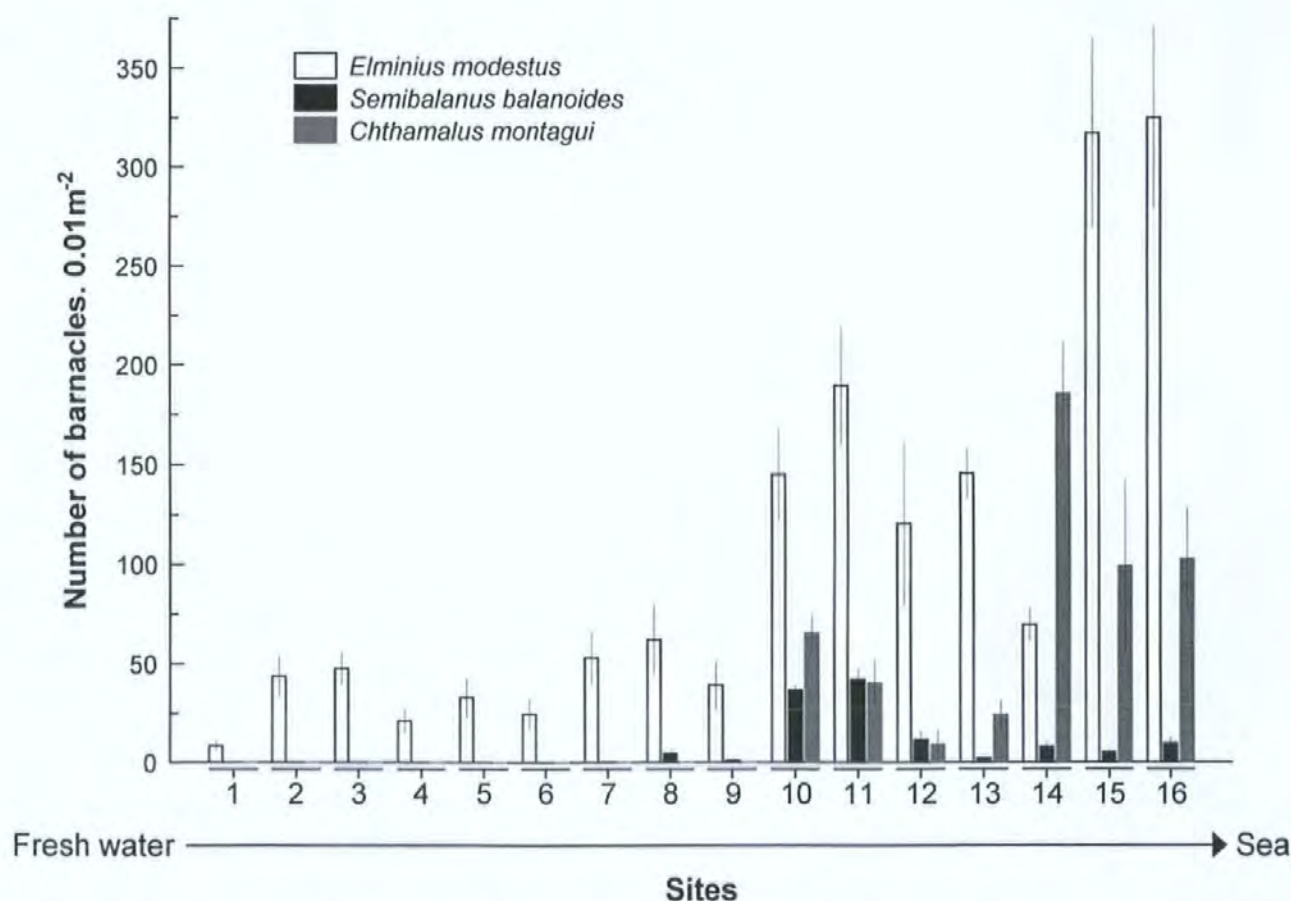
Fig. 2.4. Abundance of adult *Elminius modestus*, *Semibalanus balanoides* and *Chthamalus montagui* along the Yealm Estuary (Mean +/- SE). Arrow indicates the direction of the gradient from freshwater to the sea.
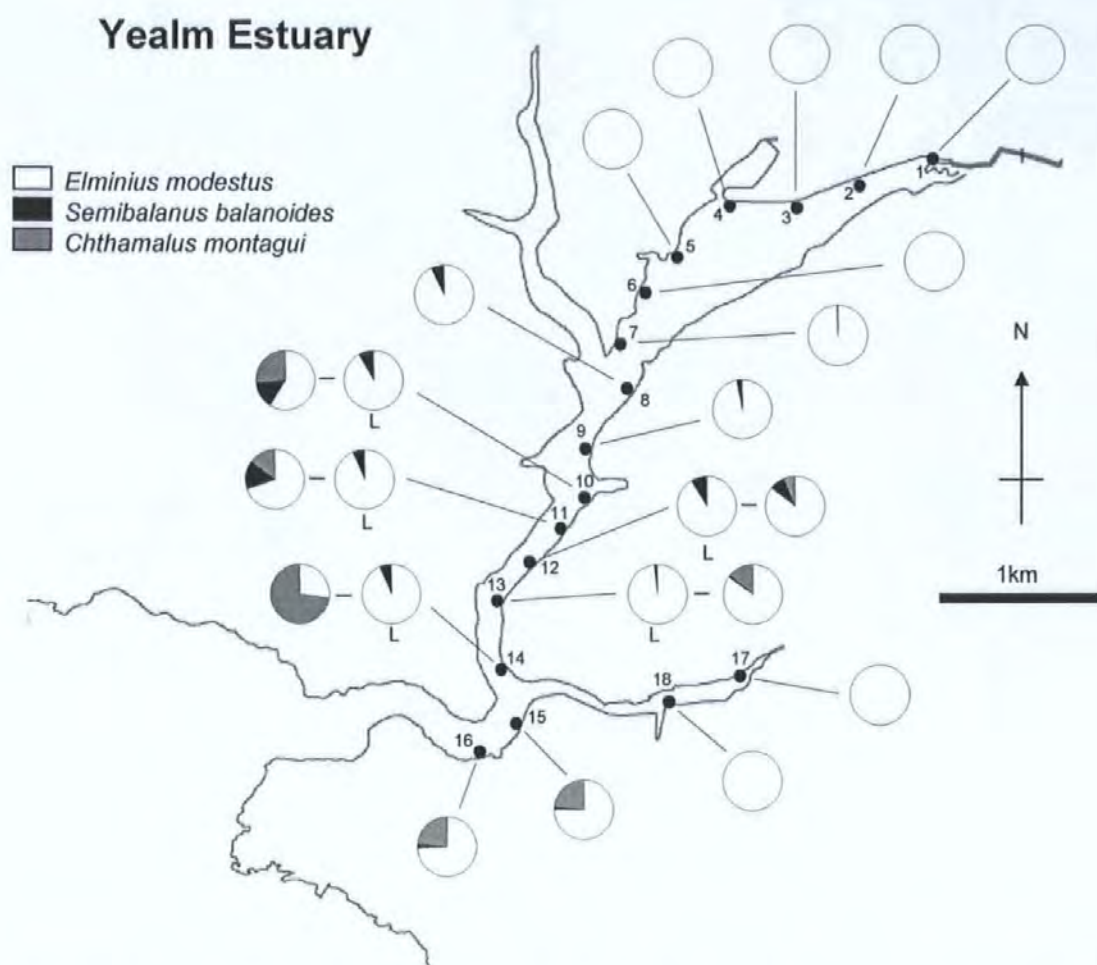
Fig. 2.5. Proportion of *Elminius modestus*, *Semibalanus balanoides* and *Chthamalus montagui* along the Yealm. Proportions representative of lower shore position are indicated by the letter (L) where sufficient substratum occurred for more than one tidal height to be surveyed.

2.3.2. Plym Estuary

The distribution and abundance of barnacles in the Plym Estuary differed from that in the Yealm. *S. balanoides* generally occurred in lower abundance than in the Yealm, but was found further up the estuary, and individuals were observed at the uppermost site (West of Blaxton Meadow, site 19), which also corresponded to the upper limit of *E. modestus* (Fig. 2.6 and 2.7). Although abundances of *S. balanoides* were much lower in the Plym Estuary, the highest abundance of this species was

31

recorded approximately at the mid point between the lower and upper limits of the estuary (Fig. 2.6). Contrary to the pattern observed for *S. balanoides*, *C. montagui* showed a less extensive distribution in the Plym that in the Yealm (Fig. 2.7). This species was absent in the upper and middle thirds of the Plym Estuary and was only recorded at the site closest to the sea (Mount Batten Centre, site 27) (Fig. 2.7). At the most seaward sites, in both the Plym and the Yealm, *C. montagui* was abundant in the higher portion of the intertidal, just above a zone exclusively inhabited by *E. modestus* and *S. balanoides* (Fig. 2.7).
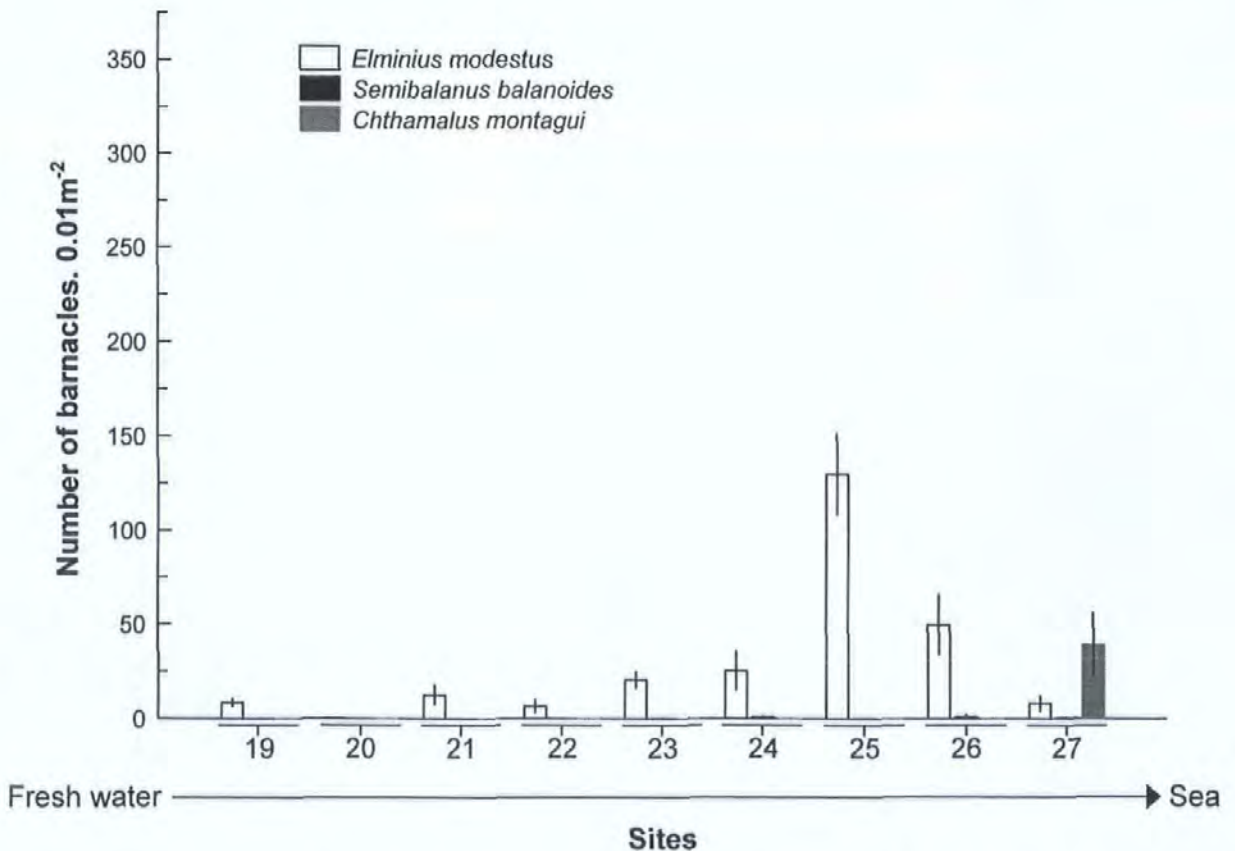
Fig. 2.6. Abundance of adult *Elminius modestus*, *Semibalanus balanoides* and *Chthamalus montagui* along the Plym Estuary (Mean +/- SE). Arrow indicates the direction of the gradient from freshwater to the sea.

Plym Estuary
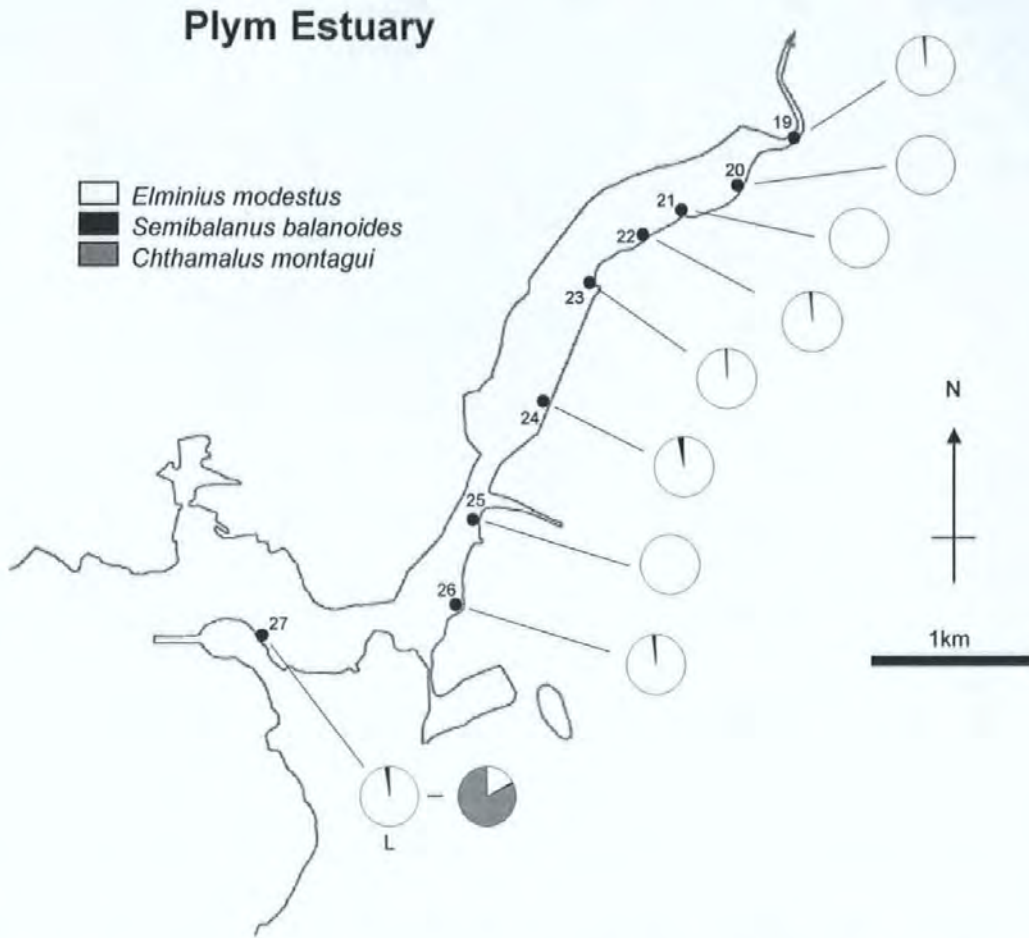
Fig. 2.7. Proportion of *Elminius modestus*, *Semibalanus balanoides* and *Chthamalus montagui* along the Plym. Proportions representative of lower shore position are indicated by (L) where sufficient substratum occurred for more than one tidal height to be surveyed.

2.3.3. Abundance of recently metamorphosed *E. modestus*

Recent settlement was evident for *E. modestus* when the survey was made in October 2004. Small individuals, which probably settled a few months before the surveys, were found at most sites, and settlement occurred along the whole length of the Yealm (Fig. 2.8). The lowest density of settlers at the Yealm was recorded at the uppermost estuarine site (site 1; Fig. 2.8), and the highest at the most marine site (site 16, Fig. 2.8). There was no clear pattern of abundance along the horizontal extension of the Yealm and densities commonly reached between 10 and 20 ind.cm^{-2} (Fig. 2.8). In

the Plym, settlers were absent in one site (site 20; fig. 2.9) and the highest densities

were observed in the first three sites seawards (sites 25, 26 and 27; Fig. 2.9).
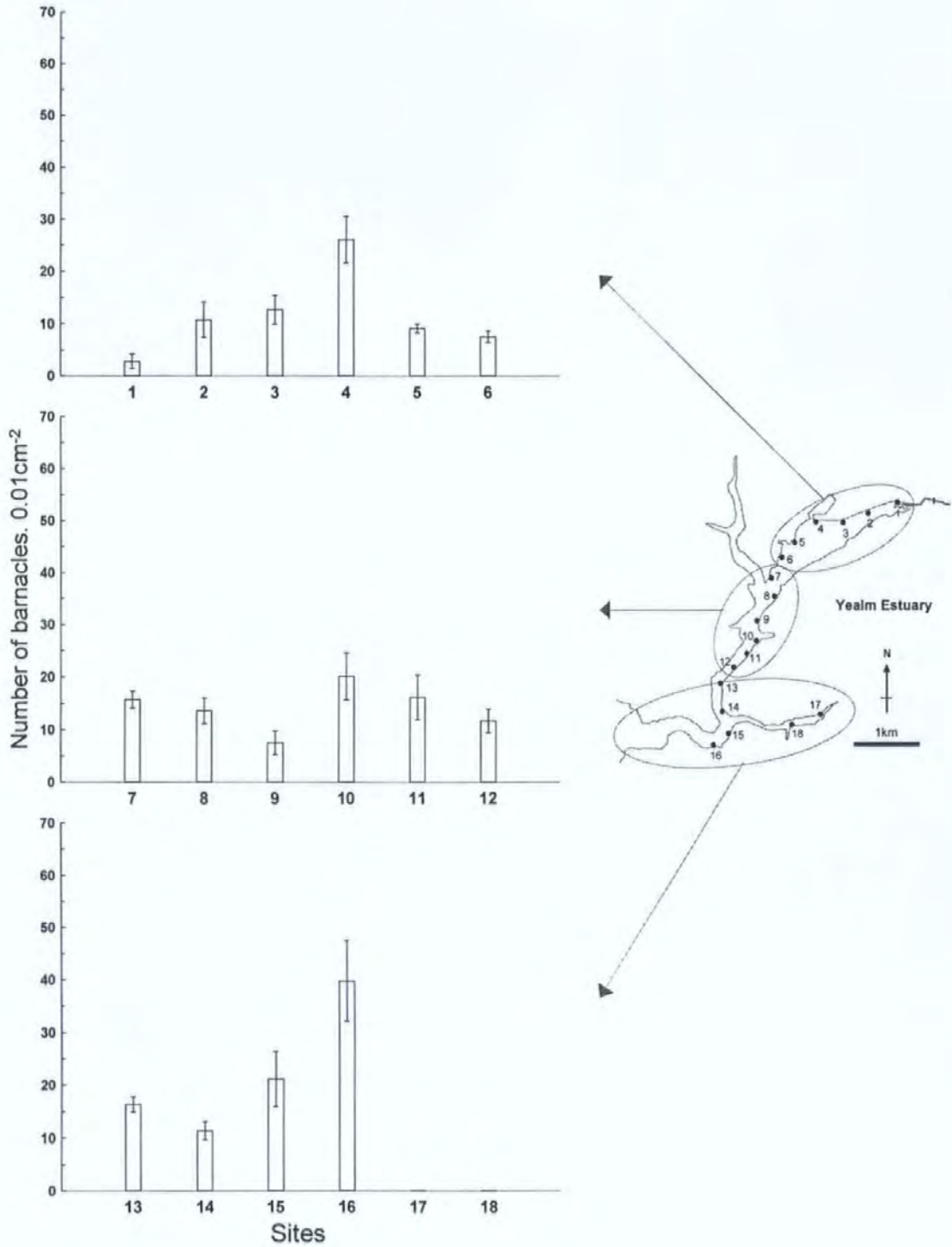
Fig. 2.8. Abundance of *Elminius modestus* recently methamorphosed individuals along the Yealm Estuary (Mean +/- SE).
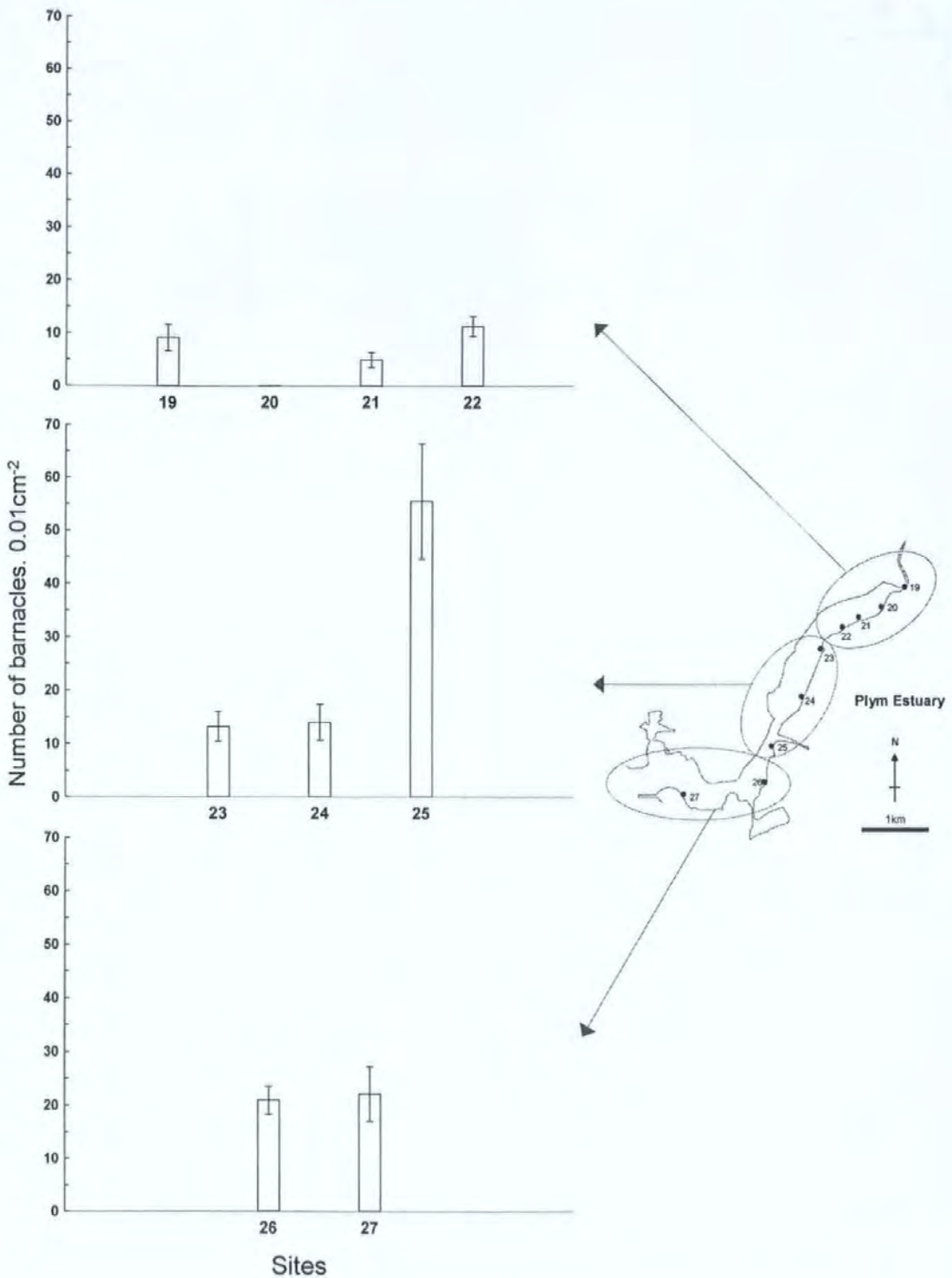
Fig. 2.9. Abundance of *Elminius modestus* recently methamorphosed individuals along the Plym Estuary (Mean +/- SE).

2.4. Discussion

The surveys undertaken in the Yealm and Plym Estuaries demonstrate that: 1. *E. modestus* was dominant in the intertidal areas of these estuaries; 2. Settlement of *E. modestus* took place in comparable densities along the horizontal extension of each of these estuaries; and 3. *E. modestus* was the species that occurred furthest up both estuaries, followed by *S. balanoides* and then *C. montagui*. The surveys also identified fine-scale spatial variations in the abundance of each species along the sea-to-freshwater gradient. This discussion highlights some aspects of the recorded distributions in relation to other estuaries. It also examines the implications of these findings for our understanding of ecological processes controlling the distribution of barnacles in estuaries.

In both estuaries, *E. modestus* was found along the whole extension of the estuarine gradient from fully marine conditions, to areas with high freshwater influence. *S. balanoides* extended up to mid portions in the Yealm and a few individuals occurred up to the limits of *E. modestus* penetration in the Plym. *C. montagui* showed a more restricted distribution than the other two species. The same relative order of estuarine penetration has previously been observed for these species in other estuaries, including the Bristol Channel and Severn Estuary (Boyden et al., 1977; Smith and Little, 1980; Mettam, 1994), the Rance Estuary in France (Little & Mettam, 1994) and several estuaries from the South-West of England (e.g. Dart Estuary, Horsman, 1986, Moore, 1988; Salcombe & Kingsbridge Estuary; Tamar Estuary, Hiscock & Moore, 1986; Looe Estuary, Little, 1988; Fal Estuary, Rostron, 1985; Helford Estuary, Rostron, 1987).

There is a general tendency of reduction on the number of marine epibenthic organisms towards the upper reaches of estuaries (Sanders, et al., 1965; Day, 1967; Boesch, 1977; Wilkinson, 1980), but variations in abundance differ among particular

species. For example, in the Great Bay Estuary System in New England it was observed that while some dominant species such as *S. balanoides, Mytilus edulis* and *Littorina littorea* decreased in abundance towards the inner estuary, others such as *Balanus eburneus, Littorina saxatilis* and *Fucus vesiculosus* var. *espiralis* increased (Hardwick-Witman & Mathieson, 1983). Patterns of distribution and abundance of any particular species along an estuarine gradient depend on the tolerance of different stages of its life cycle to the physical, chemical and biological conditions associated with this gradient. Consequently, there are numerous factors that may affect distributions and set limits to the penetration of species in estuaries.

Physical conditions become more variable, and consequently more stressful for most marine species, from the seaward to the upper regions of estuaries. Fluctuations in salinity, water turbidity, concentrations of dissolved sediment and particulate material, and sedimentation tend to increase towards the riverine end of estuaries. In many cases environmental extremes are known to determine distribution of estuarine species (Kinne, 1970, 1971). For example, tolerance to a major environmental variable such as salinity clearly sets the ranges of distribution of species in many estuaries where stable salinity regimes persist, in which case the salinities at upper limits of species penetration coincide with species tolerance limits.

The predominance of *E. modestus* over native barnacle species, as indicated by their relative abundances, decreased towards the seaward margins of the estuary. In the Plym, not only relative, but also absolute abundance of this species decreased towards the sea. Such reductions were expected, as *E. modestus* favours the more sheltered areas, both in its original geographical area in the Southern hemisphere (Moore, 1944; Foster, 1978, 1982) and in invaded environments (Fischer-Piette & Prenant, 1956, 1957; Fischer-Piette and Forest, 1961; Fischer-Piette, 1965; Crisp, 1958). On wave-exposed shores in Britain, *E. modestus* is not common and does not displace *S. balanoides* or *C.*

montagui at any vertical level (Crisp, 1958; Crisp & Southward, 1959; Foster, 1971; Southward, 1991). At a local level, previous work has shown that *E. modestus* was less frequent on wave-exposed shores than at more sheltered areas within the Plymouth Sound (Burrows, 1988; Hiscock & Moore, 1986); and that at the mouth of the Yealm (Cellar Beach), this species was not dominant and was restricted to lower levels of the shore (Southward, 1991).

Semibalanus balanoides and *C. montagui* are better adapted to life in areas with fully marine conditions (Lewis, 1964; Southward, 1976; Crisp et al. 1981) and restricted penetration towards the upper regions of the estuaries was expected for these species. In the Yealm, *S. balanoides* occurred up to Steer Point (site 7), a site where the species has previously been recorded (Hiscock & Moore, 1986). This position corresponds closely with a sharp shift in the prevailing salinity regime, between the mid and the upper third of the estuary, from which point much lower salinities and stronger salinity fluctuations occur (Data presented in detail in Chapter 3). Salinity, especially salinity fluctuations are important for the distribution of species in estuaries (Sanders et al., 1965; Carriker, 1967; Wolff, 1983; Attrill & Thomas, 1996) and it is possible that the observed limit of upper penetration of *S. balanoides* was related to its inability to cope with low salinity.

Elminius modestus is notably more tolerant to low salinity and salinity fluctuations than *S. balanoides* and *C. montagui* (Foster, 1970, Davenport, 1976; Cawthorne, 1978; Cawthorne & Davenport, 1980). This would help explain why *E. modestus* occupied areas where the salinity regime appeared stressful, and neither *C. montagui* nor *S. balanoides*, nor indeed any other intertidal barnacle species was found. This ability can be illustrated by a similar pattern of distribution observed at Lough Hyne, in Ireland, where *S. balanoides* and *C. montagui* dominated the shore up to 1991, but where more recently *E. modestus* is dominant (Little et al., 1988, 1992; Lawson et al., 2004). Although, in general, salinities in Lough Hyne are close to fully marine, in

certain inner sites they are influenced by freshwater inputs and dominance of *E. modestus* is even higher than at other sites and at some locations it is the only species present (Lawson et. al., 2004).

During the surveys in the Yealm and Plym it was common to find barnacles partially or completely covered by silt. It is possible that interference by silt may lead to mortality or sub-lethal detrimental effects in barnacles that affect their distribution in estuaries (Day, 1959, Carriker, 1961, Lewis, 1964; Silina, 2002). High siltation occurs in intertidal areas in both the Yealm and the Plym and portions of the rocky intertidal are commonly covered by a layer of silt. As observed for salinity, siltation levels were more stressful in the upper estuarine regions (Data presented in detail in Chapter 3). Hence siltation is another variable that may explain low abundances or absence of barnacle species observed in certain estuarine sites, fitting a model by which patterns of distribution and abundance in estuaries are linked to physiological tolerance of post-settlement stages to environmental factors. Predictions based on this model and the influence of salinity and siltation on survival of *E. modestus*, *S. balanoides* and *C. montagui* in the Yealm and the Plym are assessed in Chapter 3.

Chthamalus montagui was previously recorded at Madge Point (site 14), but not at Heron's Reach (site 7) (Hiscock & Moore, 1986), which indicated that the upstream limit of this species was located somewhere between these two positions. The current survey confirms this observation and established that this limit is located just south of Shortaflete Creek (site 11). In the Plym, *C. montagui* was also absent away from the upper third of the estuary, where the saline regime appears to be more stressful. This suggests that salinity may not be a key factor in setting absolute limits of penetration for this species.

An alternative explanation to post-settlement tolerance to physico-chemical and biological stresses as causes of the distribution patterns of these three species is that

limitations in settlement of larvae occur along the estuarine gradient. Distribution, abundance and settlement of larvae are undoubtedly crucial for the success of benthic populations and can influence adult patterns of distribution and abundance (Underwood & Denley, 1984; Gaines & Roughgarden, 1985; Connell, 1985; Raimondi, 1990, 1991; Minchinton & Scheibling, 1991). The distribution of *S. balanoides* and *B. glandula* in the Great Bay Estuary System in New England well illustrates some different mechanisms influencing larval supply and settlement in estuaries. While *S. balanoides* settled along the whole estuarine gradient its adult distribution in the estuary was restricted by differential post-settlement survival; *B. glandula* only settled at inner regions of the estuary where adults were found (Hardwick-Witman & Mathieson, 1983). There are other examples where distributions of barnacle larvae and adults are correlated in estuaries. For example, *Elminius covertus* showed positive correlations between densities of successive stages of development, from cyprids to adults, along the sea-to-freshwater gradient in a mangrove dominated estuary (Ross, 2001). Larval supply has also been used to explain the distributions of *C. montagui* and *S. balanoides* in the Severn, where arrival and settlement of larvae would be responsible for the limits of penetration of these species (Little & Smith, 1980; Mettam, 1994). Other epibenthic groups, such as macroalgae (e.g. Wilkinson, 1980; Hardwick-Witman & Mathieson, 1983; Zechman & Mathieson, 1985) and decapods (e.g. Dittel & Epifanio, 1990; Palma et al., 1999; Paula et al., 2003; Queiroga et al., 2006), also have their distribution influenced by availability and settlement of planktonic stages in estuaries.

Elminius modestus has a much higher reproductive output than *S. balanoides* and *C. montagui*, and this is certainly advantageous in estuarine and sheltered areas (Watson et al., 2005). The former species reaches reproductive maturity much faster than the two native species (Crisp & Davies, 1955) and reproduces almost all year round (Knight-Jones, 1948; O'Riordan & Murphy, 2000) by multiple broods (Crisp &

Davies, 1955). The role of high larval production, settlement and recruitment in *E. modestus* invasion and domination in sheltered coastal areas has been recently demonstrated in Lough Hyne (Watson et al., 2005). The high abundances of individuals and the presence of recently metamorphosed individuals along the whole extent of the Plym and the Yealm suggest that this species is extremely successful in producing larvae that are viable for settlement in these estuaries.

Settlement patterns of barnacles in the Yealm and the Plym are assessed in Chapter 5. The present surveys were not intended to quantify settlement in these estuaries and the timing was not appropriate to provide information on settlement of *S. balanoides* (which settles during spring). Dispite this, *C. montagui* individuals that settled during the previous summer were expected to be recognized by their smaller sizes (Southward, 1991). Individuals recorded appeared to be relatively old, and hence, it is possible that larval availability limits the distributions of these species. *S. balanoides*, appears to be at a disadvantage since it is less fecund than the other two species (Southward, 1991). Additionally, this species is not as common in the South-West as in other regions of Britain (Bassindale, 1964; Lewis, 1964; Newman & Ross, 1976; Crisp et al., 1981) and occurs at lower abundances than the other two species at the Plym and the Yealm. Poor local production of larvae is likely to happen both in the Plym and the Yealm , in which case, the settlement of *S. balanoides* would depend on dispersal of larvae from non-estuarine areas.

In the Plym, *S. balanoides* showed a more extended distribution relative to the upper limit of *E. modestus* occurrence. However, the abundance of this species was extremely low. This low abundance may be related to the more sheltered condition of the Plym Estuary in comparison to the Yealm. Despite the similarities in physico-chemical conditions along the estuarine gradient of these estuaries, the position of the Plym within the Plymouth Sound represents a more sheltered condition and may limit

larval dispersal. In the Plym, *C. montagui* was limited to the most marine site and as for *S. balanoides*, larval availability may be responsible. Temporal and spatial variability on settlement and recruitment in these estuaries are examined in greater detail in Chapter 5.

The results described above highlight the dominance of *E. modestus* in contrast to the relative restricted abundance and penetration of *C. montagui* and *S. balanoides* in the estuaries studied. The patterns of distribution and abundance of barnacles documented here, including the dominance of the alien species *E. modestus*, could be explained by differential: 1. availability of larvae and settlement success along the estuaries (see Chapter 5); 2. physiological tolerances to environmental factors (see Chapters 3 and 4).

CHAPTER 3
TOLERANCE OF ADULT BARNACLES TO ESTUARINE CONDITIONS

3.1. Introduction

Factors determining the distribution and driving the dynamics of barnacle populations may act at different stages of the life-cycle of these organisms, with events prior to and at settlement being particularly important (e.g. Hawkins & Hartnoll, 1982; Kendall et al., 1982; Caffey, 1985; Gaines & Roughgarden, 1985; Gaines et al. 1985; Menge, 2000; Minchinton & Scheibling, 1991). Prevailing physical conditions are known to be important determinants of the distribution of intertidal barnacles post-settlement (Connell 1961, 1969a, 1969b, 1970; Foster, 1969, 1971; Menge, 1976; Denley and Underwood, 1979; Wethey, 1983, 2001; Menge, 2000, Aveni-Deforge & Wethey, 2002). Physiological tolerance and behavioural responses to stresses caused by periods of emersion, such as exposure to high temperatures (Foster, 1969), desiccation (Barnes & Barnes, 1957; Barnes, Finlayson & Piatigorsky, 1963; Foster, 1971; Wethey, 1983) and salinity fluctuations (Foster, 1970), have been suggested as factors limiting the distribution of barnacle species on rocky shores. The importance of these physical factors is frequently amplified in estuaries, where greater spatial and temporal variability in physico-chemical conditions occurs in comparison to more stable open coast habitats.

Low salinity and salinity fluctuations are common features of estuaries which are particularly important in influencing the distribution of estuarine organisms (Sanders et. al, 1965; Carriker, 1976; Wolff, 1983; Attrill & Thomas, 1996). Most temperate estuaries have a salinity gradient, where the range of salinity fluctuations and the persistence of low salinity water are greater in the upper regions and decrease

43

towards the seaward end of the estuary (Milne, 1938; Sanders et al., 1965). Therefore, benthic marine organisms require a degree of tolerance to low salinity as well as mechanisms to help cope with salinity fluctuations to be able to live in estuaries. Such adaptations are likely to increase in their importance towards the upper regions of estuaries, where greater variability and more stressful conditions prevail.

Another important characteristic of estuaries that exerts considerable influence over organisms is that they are depositional environments (Van Straaten and Kuenen, 1958; Postma, 1967; Meade, 1969). There is a high sediment supply from rivers and sea to estuaries which, coupled with water movement, results in turbid water due to high concentrations of suspended particulate material (Dyer, 1997). This material tends to be deposited, generating high levels of sedimentation. In estuaries, benthic organisms, particularly suspension feeders, are strongly influenced by the detrimental effects of high fluxes of suspended sediment and accumulation of silt on both soft (Levinton & Bambach, 1970; Rhoads & Young, 1970; Aller & Dodge, 1974) and hard bottoms (Percival, 1929; Korringa, 1951; Day & Morgans, 1956; Day, 1959; Carriker, 1961; Saiz-Salinas & Urdangarin, 1994). On some occasions layers of silt accumulated on intertidal rocky surfaces in estuaries are thick enough to completely cover organisms, as observed in areas of the estuaries investigated in this work and elsewhere (Percival, 1929; Korringa, 1951; Day, 1959; Carriker, 1961).

Harms (1999) suggested that high rates of cirral activity by *E. modestus*, leading to more effective feeding, favoured this species in relation to native barnacles and was partly responsible for the species successful invasion of Europe. Evidence for this is supported by observations that *E. modestus* exhibits greater frequency of cirral beat than any indigenous species over a broad range of temperatures and geographical distributions (Southward, 1955), and has a greater ability to tolerate reduced submersion at high tidal shore levels (Barnes & Barnes, 1962). Advantages of highly effective

44

feeding are obvious, especially in habitats where food resources are scarce or where there are limitations in access to food, such as in the intertidal zone. Furthermore, greater ability to utilize food would be even more critical in estuarine intertidal habitats where feeding activity is restricted by tidal emersion, by submersion in low salinity water (Arnold, 1970; Foster, 1970), in response to rapid salinity fluctuations (Davenport, 1976; 1985; Cawthorne, 1979b, Wolcott & Wolcott, 2001) and possibly by obstruction due to the accumulation of silt (Day, 1959; Carriker, 1967).

Alternative explanations for the distribution of the *E. modestus, C. montagui* and *S. balanoides* across estuarine gradients are testable by experimental transplantations. Two possibilities appear more likely, the first that the ability of adults to tolerate environmental conditions restricts the distribution of these species, and the second, that limitation to the distribution is imposed by processes that take place at other stages of the life cycle of these species. *E. modestus* has a higher degree of penetration into estuaries than *S. balanoides* and *C. montagui*. Higher ability to survive in estuarine conditions by adult *E. modestus* in comparison to the other two species would indicate that adult tolerance plays an important role in the success of this species in estuaries. Failure of *S. balanoides* and *C. montagui* to survive when transplanted to areas beyond their actual distribution would indicate that these species are unable to inhabit those areas due to lack of tolerance to environmental conditions, as predicted by the first explanation. In contrast, survival of these species at areas beyond their actual distribution would indicate that tolerance of adults to the local conditions does not explain their distribution and would point to the alternative explanation. A progressive increase or decrease in adult survival of any of the species along the length of the estuaries would suggest gradual responses to estuarine stress gradients. Finally, correlations between survival and salinity or siltation could indicate the possible

influence of these variables on survival, and ultimately, on the distribution of the species under investigation.

Transplant experiments of marine animals along natural gradients have mainly focused on the study of genetic differentiation between populations (e.g. Crisp 1964; 1968; Bergeron & Bourget, 1986; Johannesson et al., 1990; Kautsky et al., 1990; Bertness et al., 1991; Bertness & Gaines, 1993; Brind'Amour et al. 2002); and on patterns of distribution and other biological attributes across gradients of tidal height (e.g. McQuaid, 1981; Petraitis, 1982; Chapman 1986; 1997; Menge, 2000) and wave exposure (e.g. Dewolf et al. 1997, Menge, 2000; Bertness et al. 2006). Apart from Berger et al. (2006), no other work has utilized transplants to investigate the performance of animal species along estuarine horizontal gradients.

Surveys of the intertidal had been conducted previously (Chapter 2) to assess the distribution of *C. montagui*, *S. balanoides* and *E. modestus* along the marine-to-freshwater gradient of the estuaries under examination. In order to test the ability of these species to survive the actual conditions prevailing in the estuaries, the survival of *C. montagui*, *S. balanoides* and *E. modestus*, transplanted from a marine location to different positions along the marine-to-freshwater gradient of estuaries, was examined. The objectives of this study were to investigate the importance of adult tolerance to environmental conditions in setting distribution patterns of barnacles in estuaries, and to examine the effects of salinity and siltation on the survival of these species. The experiments formally tested the hypotheses that: 1. survival of the three species varies horizontally in estuaries along the estuarine gradient, being less in more stressful areas at the riverine end of the estuaries and greater at more favourable habitats in fully marine conditions near the sea; 2. Mortality patterns reflect the observed distribution patterns (see Chapter 2), namely *E. modestus* is more tolerant of estuarine conditions than *S. balanoides* which in turn survive better than *C. montagui*; 3. survival limits the

boundaries of distribution for the species under investigation, in which case individuals transplanted to locations beyond their actual distribution do not survive; 4. salinity and/or siltation are correlated with survival of these species of barnacles.

3.2. Methods

3.2.1. Study area

Experiments were performed in the Yealm and Plym Estuaries, which are sheltered macrotidal rias with low freshwater inflow. Rocks and mudflats are the major intertidal habitats present in these estuaries. Artificial substrata are also present as stone embankments and jetty walls, and contribute to the surfaces available for colonization. A more detailed description of these estuaries is available in the previous chapter of this thesis (Chapter 2, pp. 24-27).

Surveys carried out in the Yealm and the Plym Estuary showed that *E. modestus* has the most extensive distribution in both estuaries (see Chapter 2). This species occurred from the mouth of the estuaries to the limits of tidal influence (Fig. 3.1). *S. balanoides* was present up to mid portions of the Yealm Estuary and was found further up the Plym Estuary, where it was recorded near the limit of *E. modestus* upper penetration (Fig. 3.1). *C. montagui* had a more restricted distribution than the other two species. The up-estuary limits of distribution of each species in relation to the sites utilized for transplantations are presented in Fig. 3.1. The up-estuary limits considered here refer to the absolute limits of each species.
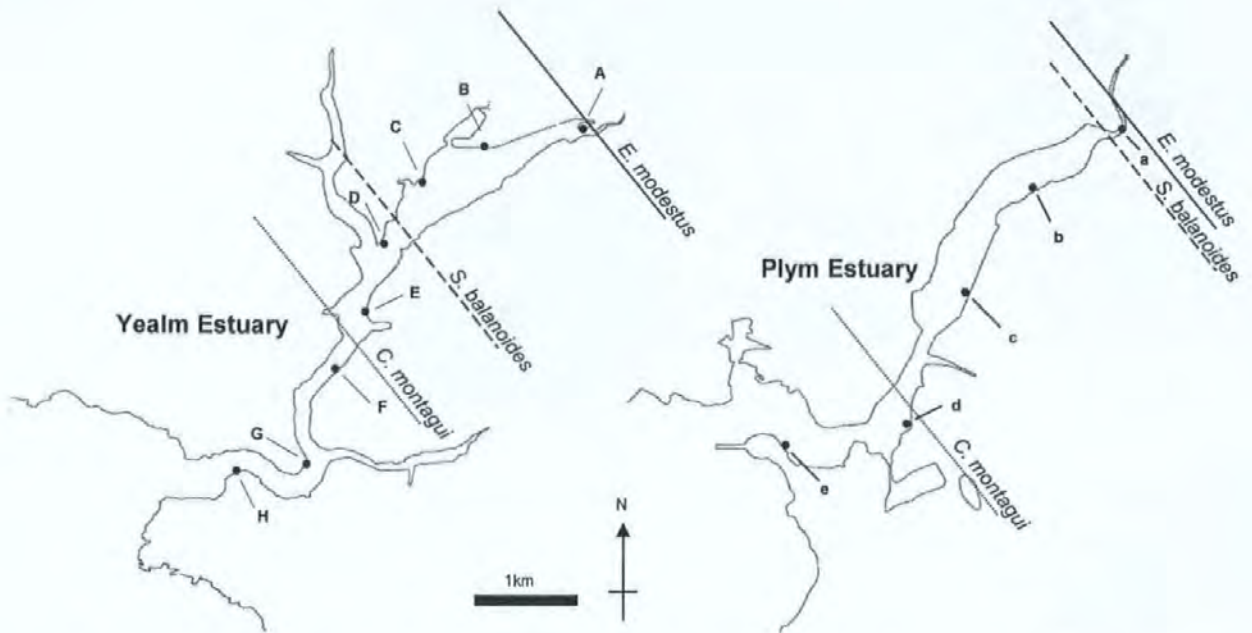
Fig. 3.1. Upper limits of penetration of *C. montagui*, *E. modestus* and *S. balanoides* in the Yealm and Plym Estuaries; and sites utilized for transplantations. Capital letters were utilized to designate sites in the Yealm, from A (uppermost site) to H (closest site to the sea); and low case letters to designate sites in the Plym, from a (uppermost site) to e (closest site to the sea). The geographic relationship between estuaries is shown on figure 2.1.

3.2.2. Transplant of barnacles along the estuarine gradient

3.2.2.1 *Elminius modestus* and *Chthamalus montagui*

Pieces of rock (approximately 10 x 15cm) with adult barnacles attached were collected at Batten Bay, a protected bay situated within Plymouth Sound (Fig. 3.1). The rocks were taken to circulating marine water tanks at the Marine Biological Association of UK, in Plymouth, where the composition and density of barnacles attached to the rocks were adjusted by killing some individuals with forceps. After this manipulation, each rock supported a single species. Individuals were distributed in an area of 8.0 x 8.0 cm and densities were between 0.5 to 1.5 individuals.cm^{-2}. Mean number of *C. montagui* per rock piece were 63.0 and for *E. modestus* 20.4. Photographs were taken to record initial numbers of barnacles on each rock.

The rock pieces were transplanted on 23 September 2002, ahead of the reduced salinity/higher turbidity winter period, to seven sites at approximately equal distances from each other along the horizontal axis of the Yealm Estuary (sites designated by capital letters: A, B, C, D, E, F, G; Fig. 3.1). A group of rocks was also back-transplanted to Batten Bay, as a control for the disturbance caused by manipulation. Four replicates were used at each site. The sites selected for the experiments encompassed a broad range of salinity regimes and are located at or within the distributional limits of the barnacle species found previously (Chapter 2). The closest site to the sea (site G; Fig. 3.1) displayed fully marine conditions and supported dense populations of both species. The uppermost site (site A; Fig. 3.1) was located near the limit of tidal excursion in the estuary and only *E. modestus* was present at this site at very low densities.

The rock pieces were attached to the shore using eyed-screws and cable-ties. They were sampled on four occasions, 10, 30, 60 and 120 days after transplant. A digital camera was used to record barnacles at these times. Dead individuals were recognized by the absence of the opercular valves (or complete absence of an individual that was present in a previous photograph).

3.2.2.2. *Semibalanus balanoides*

The survival of *S. balanoides* was assessed using a second transplant experiment starting in August 2003. As in 2002 there were few *S. balanoides* around due to settlement failure. A similar methodology to the experiment described for *C. montagui* and *E. modestus* was followed. Rocks supporting *S. balanoides* were transplanted to five sites along the gradient from sea to freshwater in both of the Yealm and the Plym estuaries (Yealm: A, B, D, F and H; Plym: a, b, c, d and e; Fig. 3.1). Four replicates were transplanted to each site and four fragments were also back-transplanted to Batten

Bay. The mean number of *S. balanoides* per rock was 20.0, and survival was assessed by sampling at 60, 90 and 120 days after the transplants.

3.2.3. Physico-chemical variables

The physico-chemical variables at each site were characterized on four occasions. Fluctuation in salinity during spring and neap tidal cycles was measured by deployment of loggers (CT Star-Oddi Iceland). Recordings were made over periods of fifteen days during spring, summer and winter in order to establish the effects of tidal and seasonal variations in salinity. In particular it was of interest to record salinity extremes, the range of salinity fluctuation and the duration of exposure to low and high salinities during periods of immersion.

Siltation was estimated at each experimental site using sediment traps. The traps consisted of a square of Astroturf mat of 100 cm^2 attached to a plastic base fixed on the shore by screws. The Astroturf mat (blades of 2 cm length) was used in an attempt to simulate a complex surface able to collect sediment, and provided an index of sedimentation allowing comparisons to be made among sites. Sediment collected by the Astroturf mat at the end of each sampling period was washed from the traps and dried to constant weight. Four traps (replicates) were attached to the shore for fifteen days during winter, spring and summer periods.

3.2.4. Statistical analyses

3.2.4.1 Assessment of Survival

Analyses of Variance were carried out using Statistica (version 6.0, Statsoft 2002). Separate one-way ANOVA's were conducted for each species, with position

within the sea-to-freshwater gradient (site) as a fixed factor, to test for differences in the percentage of barnacles surviving at the final sampling date (120 days after transplant). Data were arcsine transformed to ($2\text{Arcsin}\sqrt{x}$) when necessary to obtain homogeneity of variance. Post-hoc comparisons were made using SNK test ($p > 0.05$).

The median lethal time (time elapsed from the transplant to 50% mortality) was calculated graphically for each replicate from plots of the proportion of survival through time. Differences between median lethal times were examined using ANOVA (site as fixed factor) for each species. Replicates where mortality did not reach 50% after the experimental period had the median lethal time scored as 120 days.

3.2.4.2. Correlations between survival and physical chemical variables

Correlations between salinity and siltation parameters and survival of each species at the experimental sites were examined using Pearson's Correlation. Salinity parameters tested included average salinity, minimum salinity, average minimum salinity, and average salinity fluctuation. Correlation between survival and average siltation were also examined. Bonferroni correction was utilised to compensate the use of multiple comparisons made when testing correlation between survival and salinity plus siltation. The correction was applied by adjusting the alpha level of the tests to 0.01 (0.05 divided by 5).

The uppermost site utilized for transplants of *E. modestus* and *C. montagui* in the Yealm (site A) showed extreme physical conditions compared to the other sites, and as a consequence very high mortalities were recorded for both species. In some instances, this site alone was responsible for significant correlations when variables were analysed for the estuary as a whole. Correlations are therefore presented with and without the results from the uppermost site utilized for all experiments (Tables 3.6 and 3.7).

3.3. Results

3.3.1. Physico-chemical variables

3.3.1.1 Salinity

The ranges of salinity were similar along both the Yealm and Plym estuaries. In both estuaries a high degree of penetration of saltwater occurred with the tidal cycle and salinities close to 30 were recorded even at the upper estuarine sites investigated (Fig. 3.2). Horizontal salinity gradients in the Yealm and Plym estuaries were characterized by gradual and subtle attenuation of the saltwater influence, away from the mouth of the estuaries, up to two thirds of the way up each estuary (between sites C and B in the Yealm and sites c and b in the Plym), from which point this influence was markedly reduced. This is clearly shown by the values of average mean, maximum and minimum salinities for the periods of fifteen days sampled (Fig. 3.2) and also of absolute salinities during submergence times (Figs. 3.3 and 3.4). This major shift in salinity clearly differentiates the two up-estuary sites (A and B in the Yealm; and sites a and b in the Plym) from the remaining sites located towards the sea (C, D, E, F, G and H in the Yealm; and sites c, d and e in the Plym) in terms of salinity regimes.

Salinity fluctuations and occurrence of low salinities were much more apparent at the two up-estuary sites compared to other sites at all periods investigated (Figs. 3.3 and 3.4). Salinities below 20 were encountered at all sites (Figs. 3.3 and 3.4), but at most of the sites these events were occasional and occurred mainly during spring in the Yealm and summer in the Plym. The consistent occurrence of salinities below 20 was typical of the two up-estuary sites, indicating that greater stress for marine organisms must be found at these sites.

Salinity regimes observed at different periods of the year were similar in the Yealm and the Plym Estuaries (Figs. 3.2, 3.3 and 3.4). Both estuaries have low freshwater input, and this is reflected on the high penetration of saltwater during tidal cycles and also throughout the year.
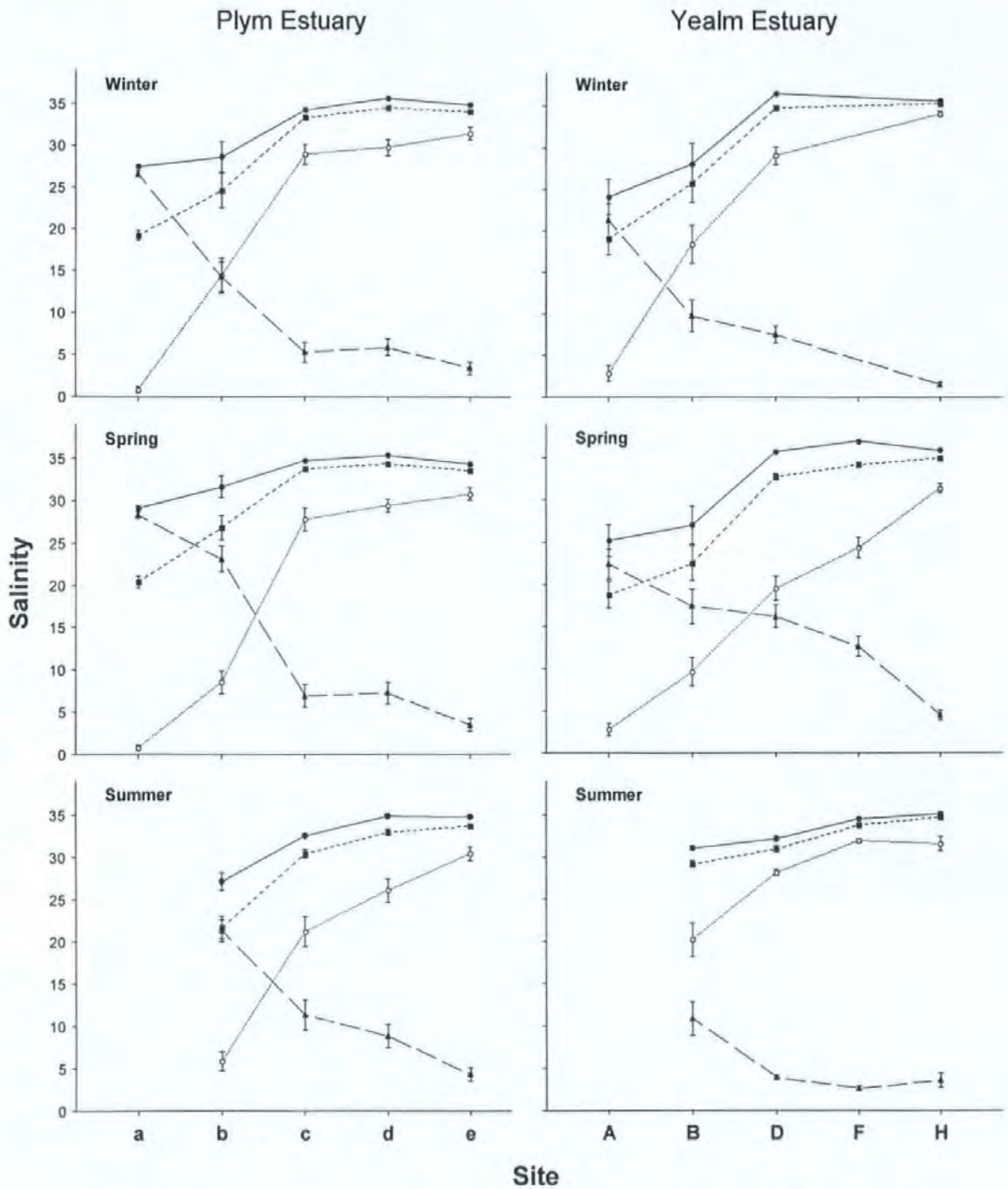
Fig. 3.2. Average, minimum and maximum salinities and salinity fluctuation during submergence for the fifteen day periods recorded during winter, spring and summer in the Plym and Yealm Estuaries. Each datum point represents the average of the variables from all submergence periods recorded. Bars represent standard errors of the mean. Letters represent sites (see Fig. 3.1).

-■- average salinity ··O·· minimum salinity -●- maximum salinity -▲· salinity fluctuation

Yealm Estuary
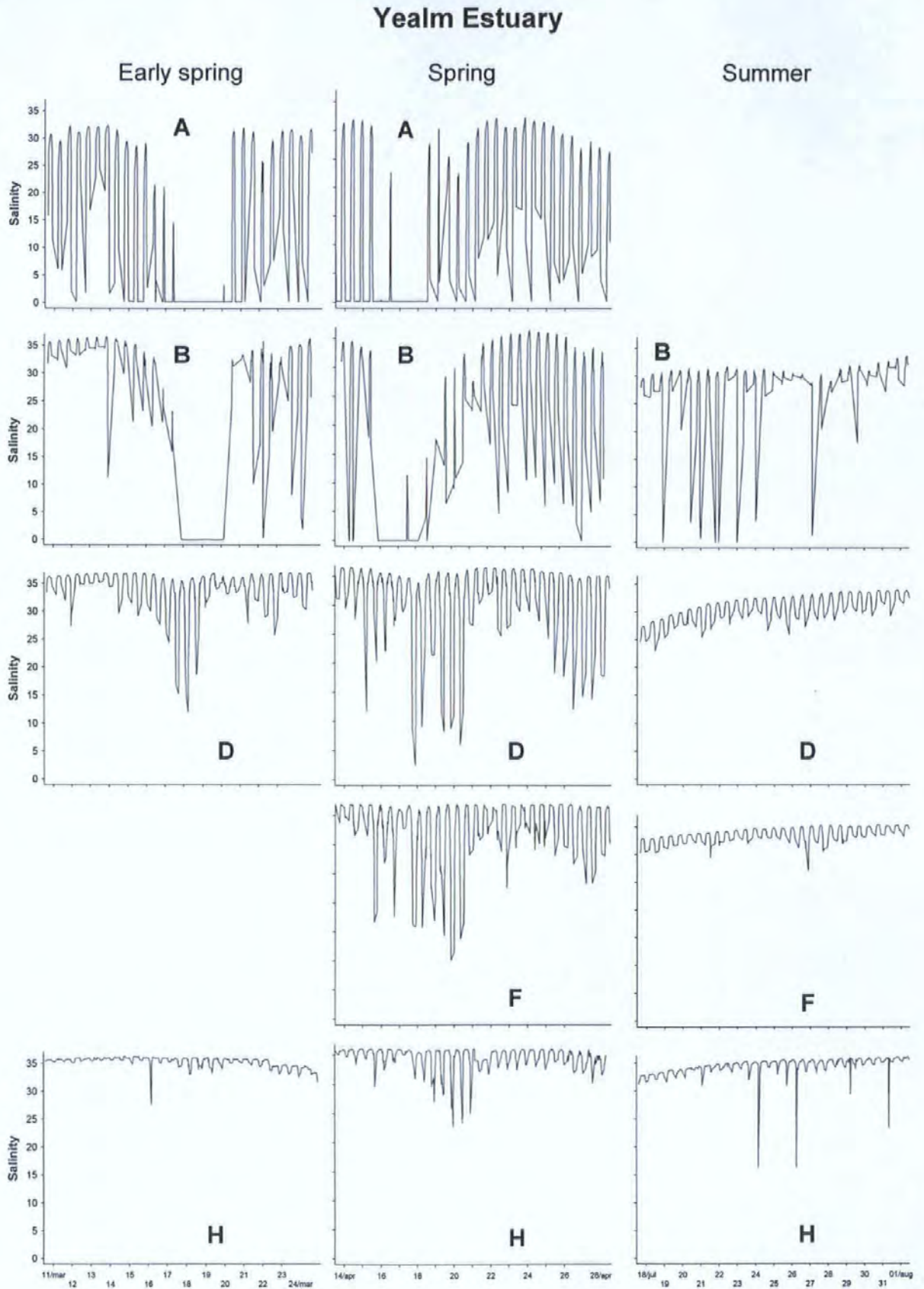
Fig. 3.3. Absolute values of salinity during submergence recorded at early spring (11th to 24th March 2004), spring (14th to 28th April 2004) and summer (18th July to 1st August 2004) in the five sites (A, B, D, F, H) utilized for transplantations along the estuarine gradient of the Yealm Estuary.

Plym Estuary
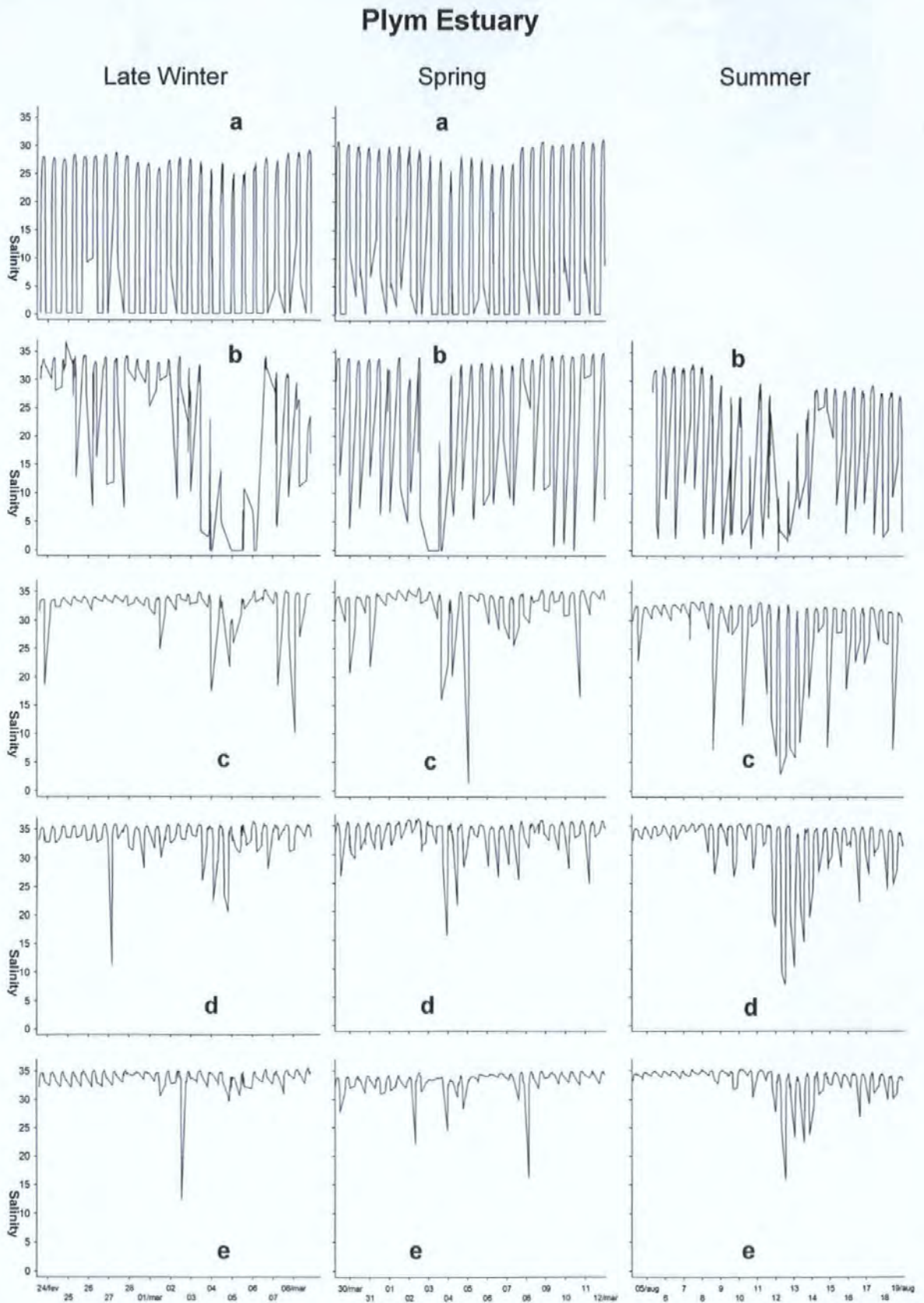
Fig. 3.4. Absolute values for salinity during submergence recorded at late winter (24th February to 8th March 2004, spring 30th to 12th March 2004) and summer (5th to 19th August 2004) in the five sites (a, b, c, d, e) utilized for transplantations along the estuarine gradient of the Plym Estuary. Letters represent sites (see Fig. 3.1).

3.3.1.2. Siltation

Siltation was high at all sites, except those located near the sea. At the closest site to the sea in both the Plym and the Yealm estuaries no silt was collected by the traps. Accumulation of silt tended to increase towards the riverine end of the estuaries and decreased towards the sea (figs. 3.5 and 3.6), although at both estuaries the mid sites (D, in the Yealm; and c in the Plym) showed the highest levels of siltation (figs. 3.5 and 3.6).

During the course of the experiments accumulation of sediment over rocks and other hard surfaces was also observed, particularly at mid and up-estuary regions. On many occasions the layer of sediment was thick enough to cover barnacles completely. At these locations removal of deposited sediment often revealed individuals of *E. modestus*, but not *S. balanoides* or *C. montagui*.
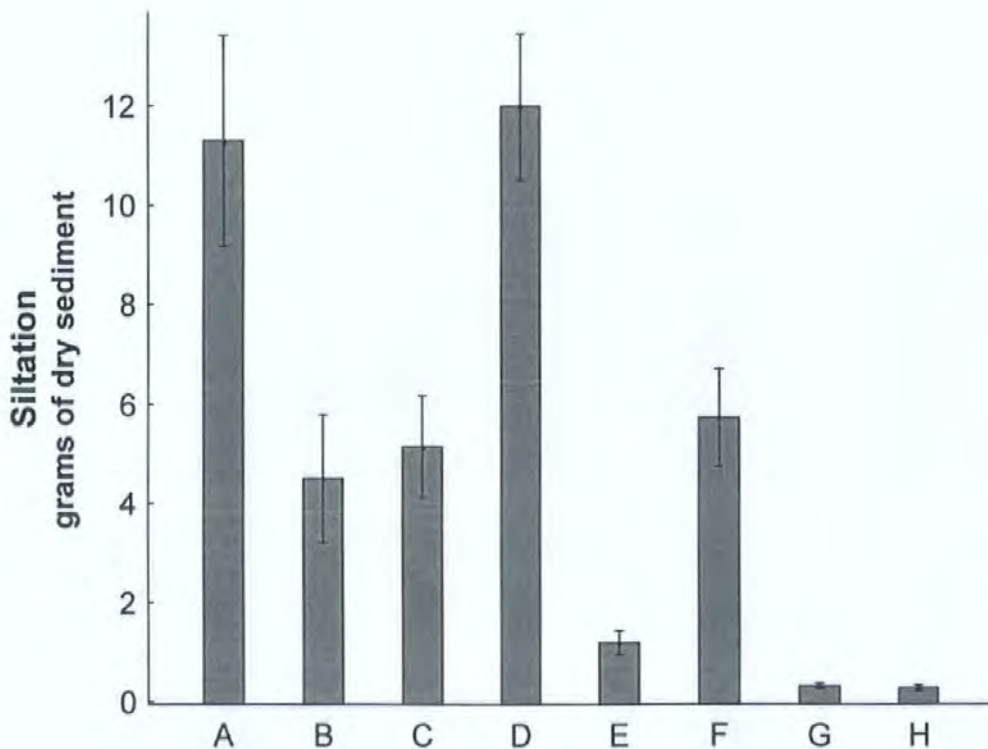
Fig. 3.5. Mean siltation at experimental sites utilized for transplants of barnacle species along the estuarine gradient of the Yealm Estuary. Columns represent mean siltation in four replicated sediment traps. Bars represent standard error of the mean. Letters represent sites (see Fig. 3.1).
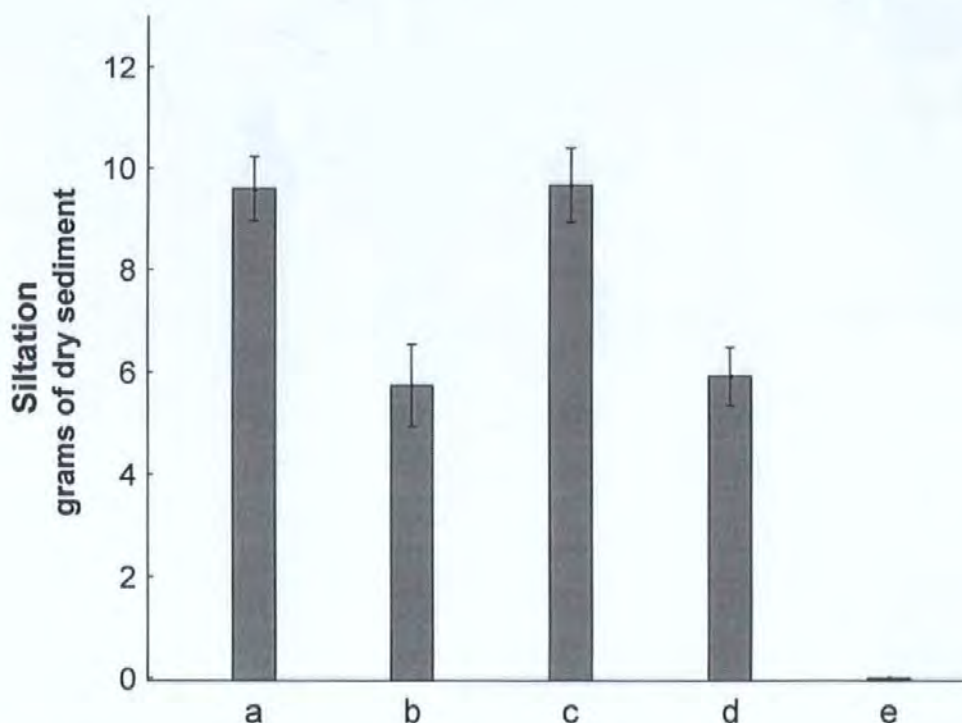
Fig. 3.6. Mean siltation at experimental sites utilized for transplants of barnacle species along the estuarine gradient of the Plym Estuary. Columns represent mean siltation in four replicated sediment traps. Bars represent standard error of the mean. Letters represent sites (see Fig. 3.1).

3.3.2. Survival across estuarine gradients

3.3.2.1. Proportion of survival

The survival of all the three barnacle species was affected by the horizontal position across the estuarine gradient. Following transplants, *C. montagui* and *S. balanoides* showed a progression in survivorship along the horizontal axes of the estuaries. Individuals of these species generally experienced higher mortalities at upper and mid-estuarine sites than at sites near the sea (Fig. 3.7, 3.8 and 3.9). This pattern contrasted with that observed for *E. modestus*, which showed higher survival at mid-estuary sites than at low-estuary and fully marine sites (Fig. 3.10).
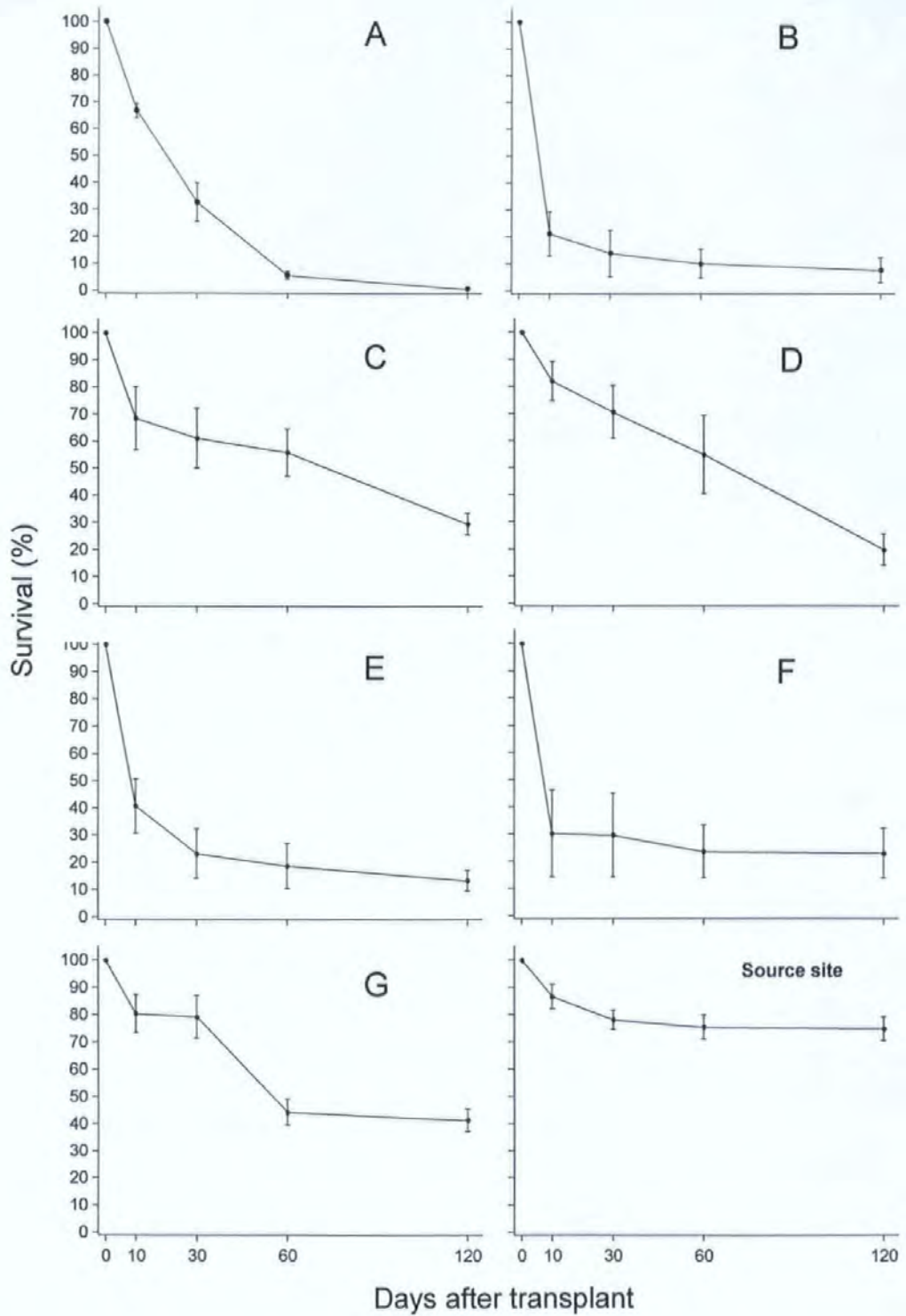
Fig. 3.7. Percentage survival of *C. montagui* transplanted to sites along the Yealm Estuary; from site A (uppermost site) to site G (closest site to the sea) and at the fully marine source site, Batten Bay (control). Each datum point represents the mean +/- SE (n=4). Letters represent sites (see Fig. 3.1).
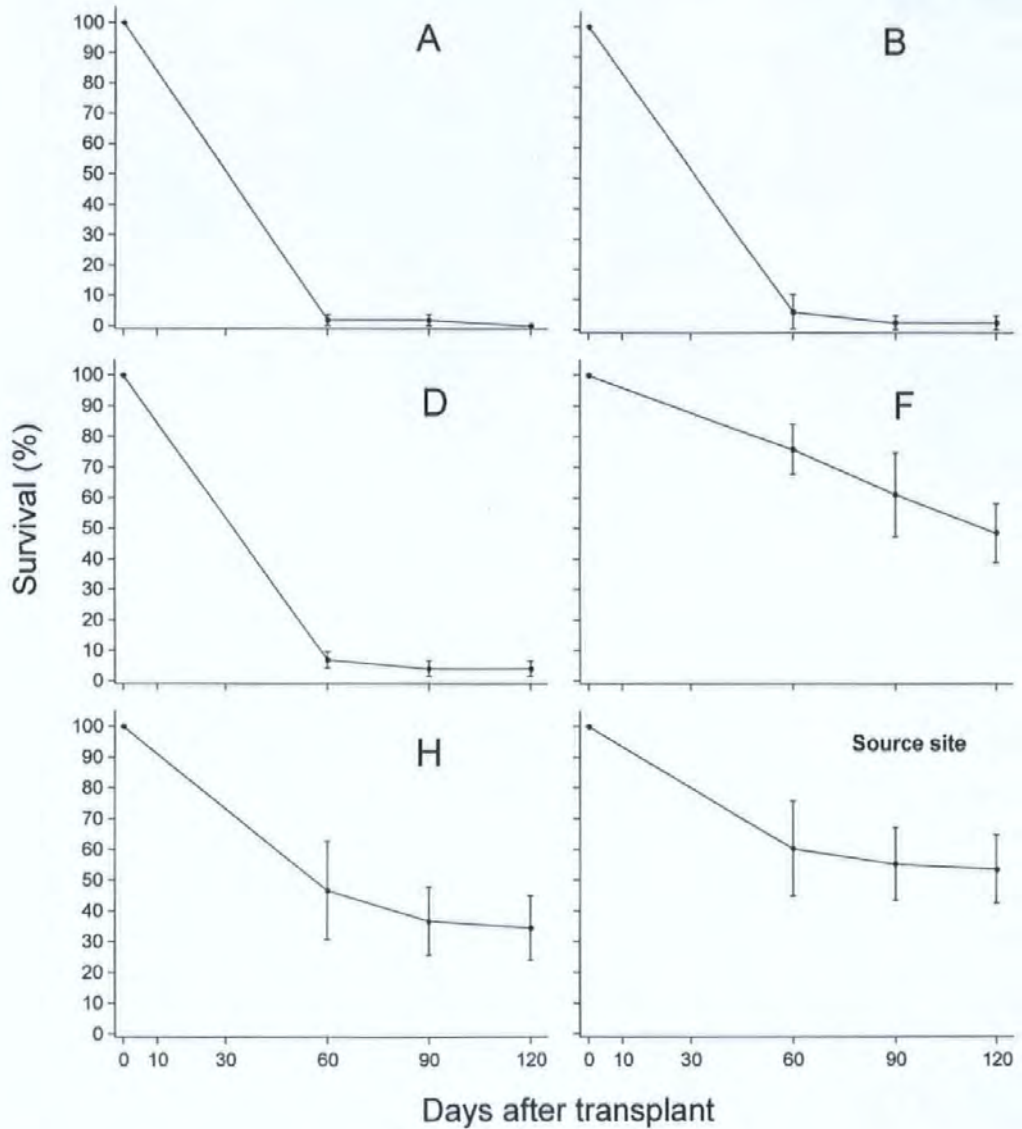
Fig. 3.8. Percentage survival of *S. balanoides* transplanted to sites along the Yealm Estuary; from site A (uppermost site) to site H (closest site to the sea) and at the fully marine source site, Batten Bay (control). Each datum point represents the mean +/- SE (n=4). Letters represent sites (see Fig. 3.1).

59
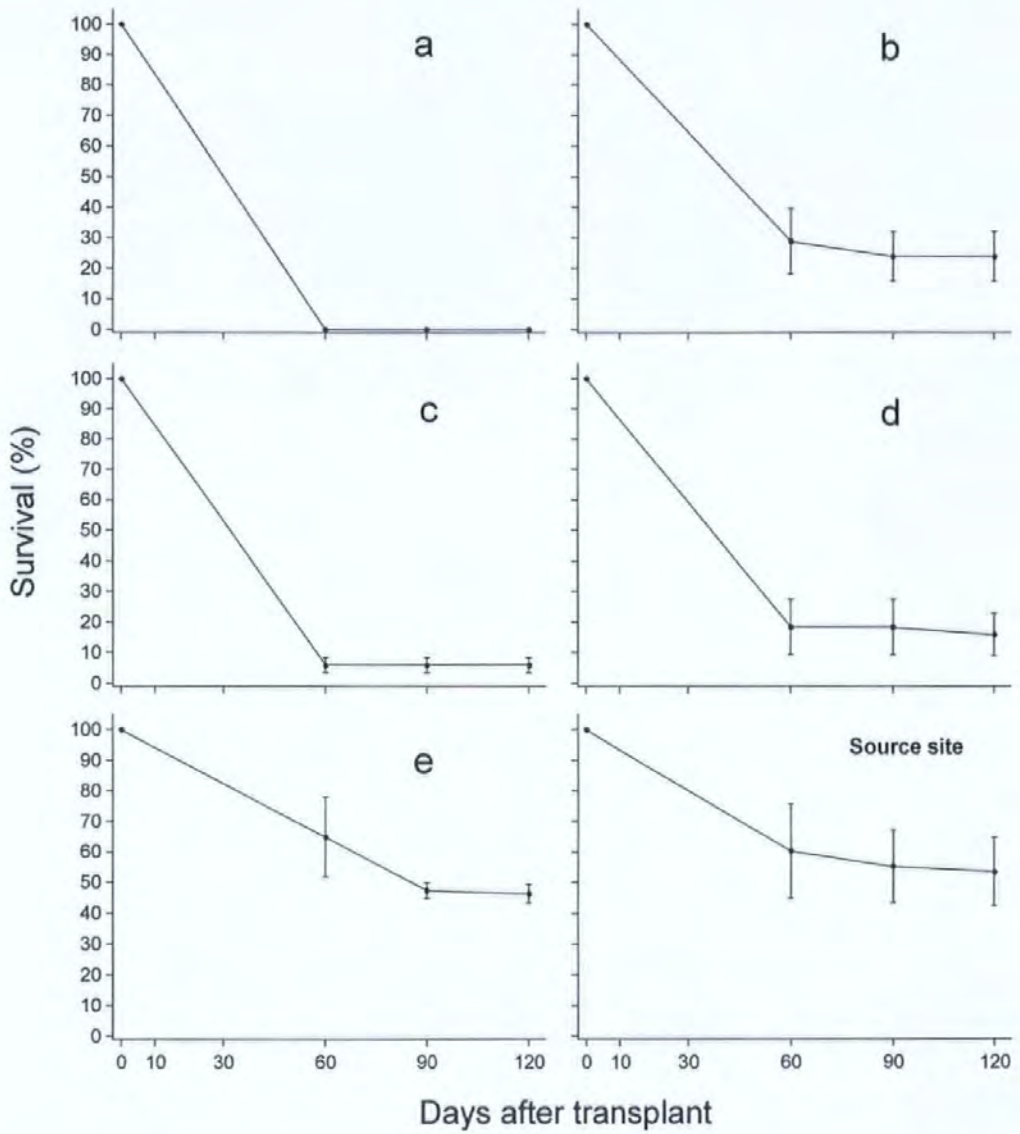
Fig. 3.9. Percentage survival of *S. balanoides* transplanted to sites along the Plym Estuary; from site a (uppermost site) to site e (closest site to the sea and at the fully marine source site, Batten Bay (control). Each datum point represents the mean +/- SE (n=4). Letters represent sites (see Fig. 3.1).
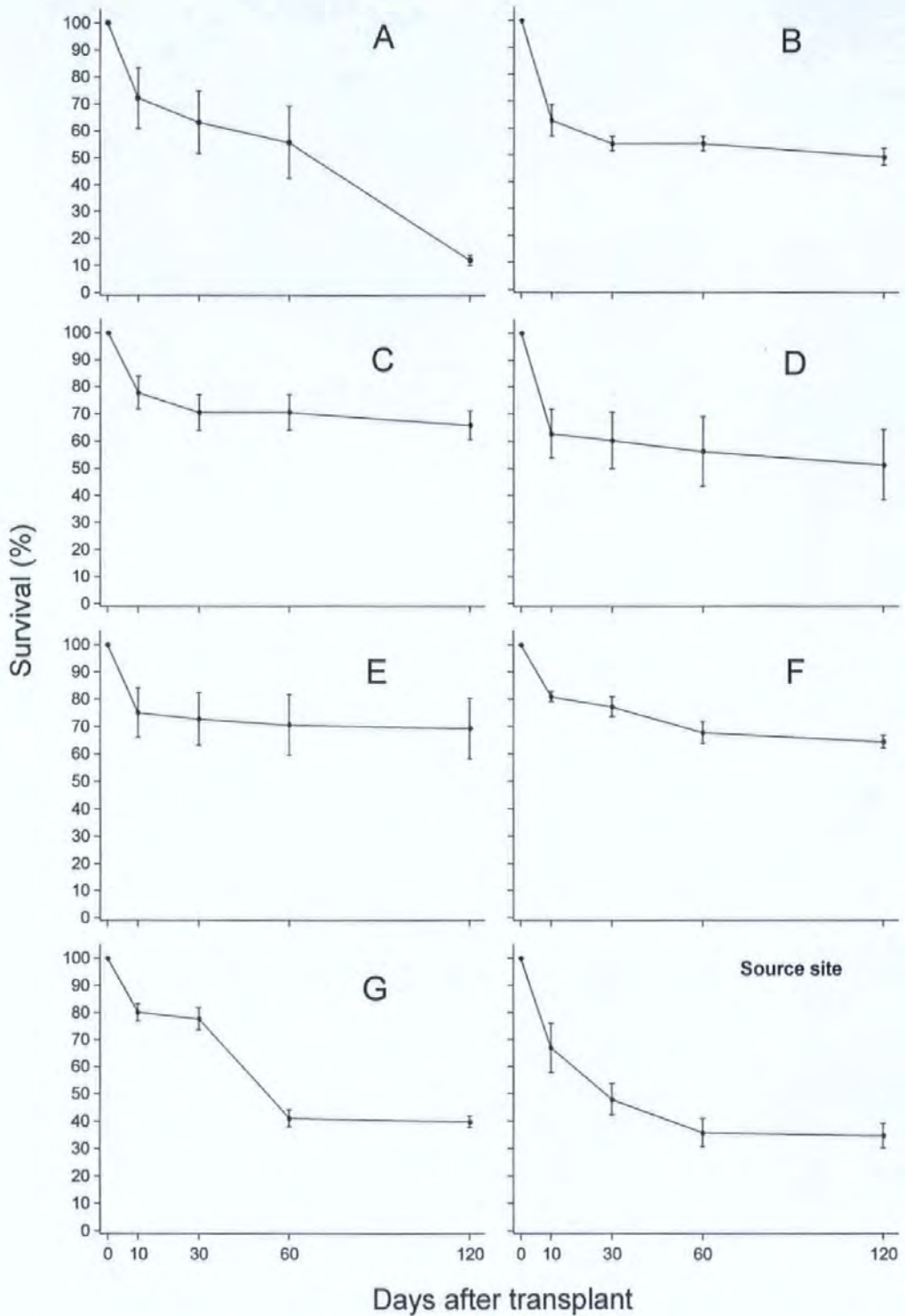
Fig. 3.10. Percentage survival of *E. modestus* transplanted to sites along the Yealm Estuary; from site A (uppermost site) to site G (closest site to the sea) and at the fully marine source site, Batten Bay (control). Each datum point represents the mean +/- SE (n=4). Letters represent sites (see Fig. 3.1).

After 120 days, *C. montagui* transplanted to the Yealm Estuary showed the lowest survival at the two uppermost sites (sites A and B; Fig. 3.10). Survival at these sites was significantly lower than at the other sites, except for site E. Survival at mid estuarine sites was relatively low and no significant differences in survival were observed between them. The highest survival of *C. montagui* was recorded at the most seaward site (site G). Survival at the source site was significantly higher than at any of the sites located in the estuary. (Fig. 3.11)
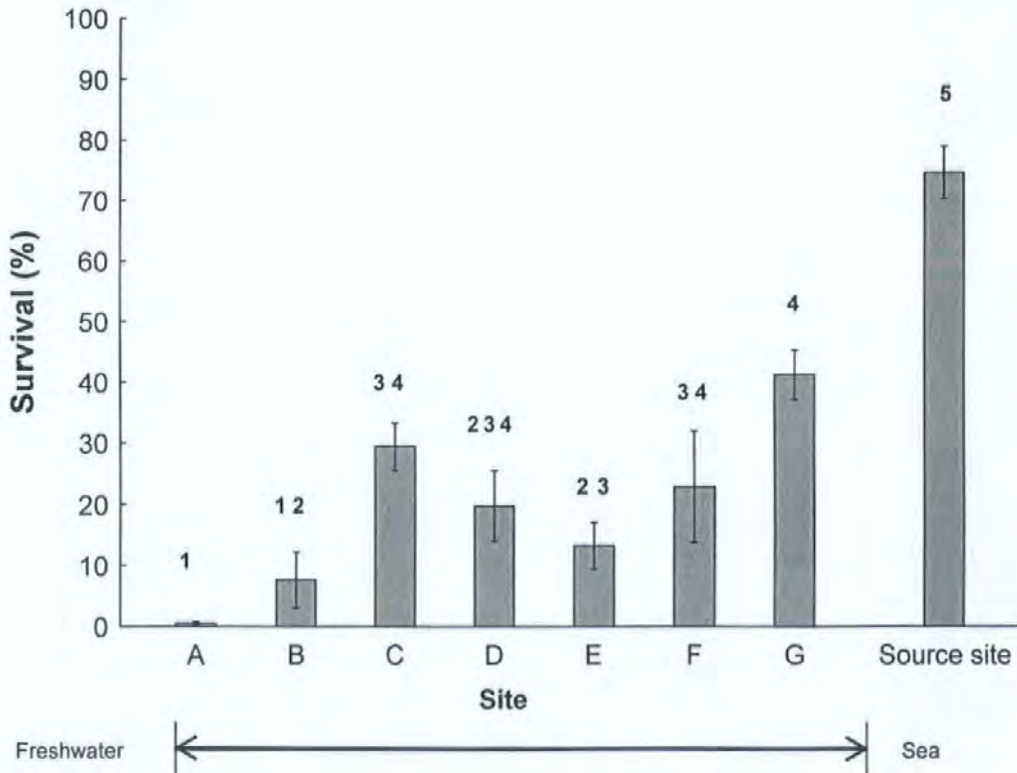
Fig. 3.11. Survival of *C. montagui* at experimental sites along the Yealm Estuary and at the fully marine source/control site (Batten Bay) 120 days after transplants. Bars represent mean proportion of survival +/- SE. Letters represent sites (see Fig. 3.1). Numbers over columns represent treatments (sites) that were not statistically different (homogeneous groups) according to ANOVA post-hoc test (SNK test, $p > 0.05$); e.g. all columns with number 1 above did not differ from each other but differed from columns with numbers 2, 3, 4, etc.

Table 3.1. One-way ANOVA (factor=site) on proportions of survival of *C. montagui* at experimental sites along the Yealm Estuary and at the source site (Batten Bay) 120 after transplants.

Time after Transplant	Source	Df	MS	F	P
120 days	Site	7	4926.6	19.4	< 0.001
	Error	23	253.9		

Semibalanus balanoides showed relatively high survival (similar to survival at the source site) in some estuarine areas (Fig 3.12). In the Yealm Estuary, mortality was extremely high at the three sites furthest from sea. No individuals survived at the uppermost site (A) and survival was very low at the next two sites (B and D). Survival at the other estuarine sites (F and H) and at the source was significantly higher than at the other three sites (A, B and D; Fig. 3.12).

In the Plym Estuary, very high mortality was observed at the uppermost site (a) where no individuals were alive 120 days after transplant. Survival was relatively low at mid-estuary (sites b, c and d) and no statistical differences were detected between these sites (Fig. 3.12). Survival at the source site was not statistically different from survival at the estuarine site closest to the sea (e), but was greater than at all other sites (Fig. 3.12).
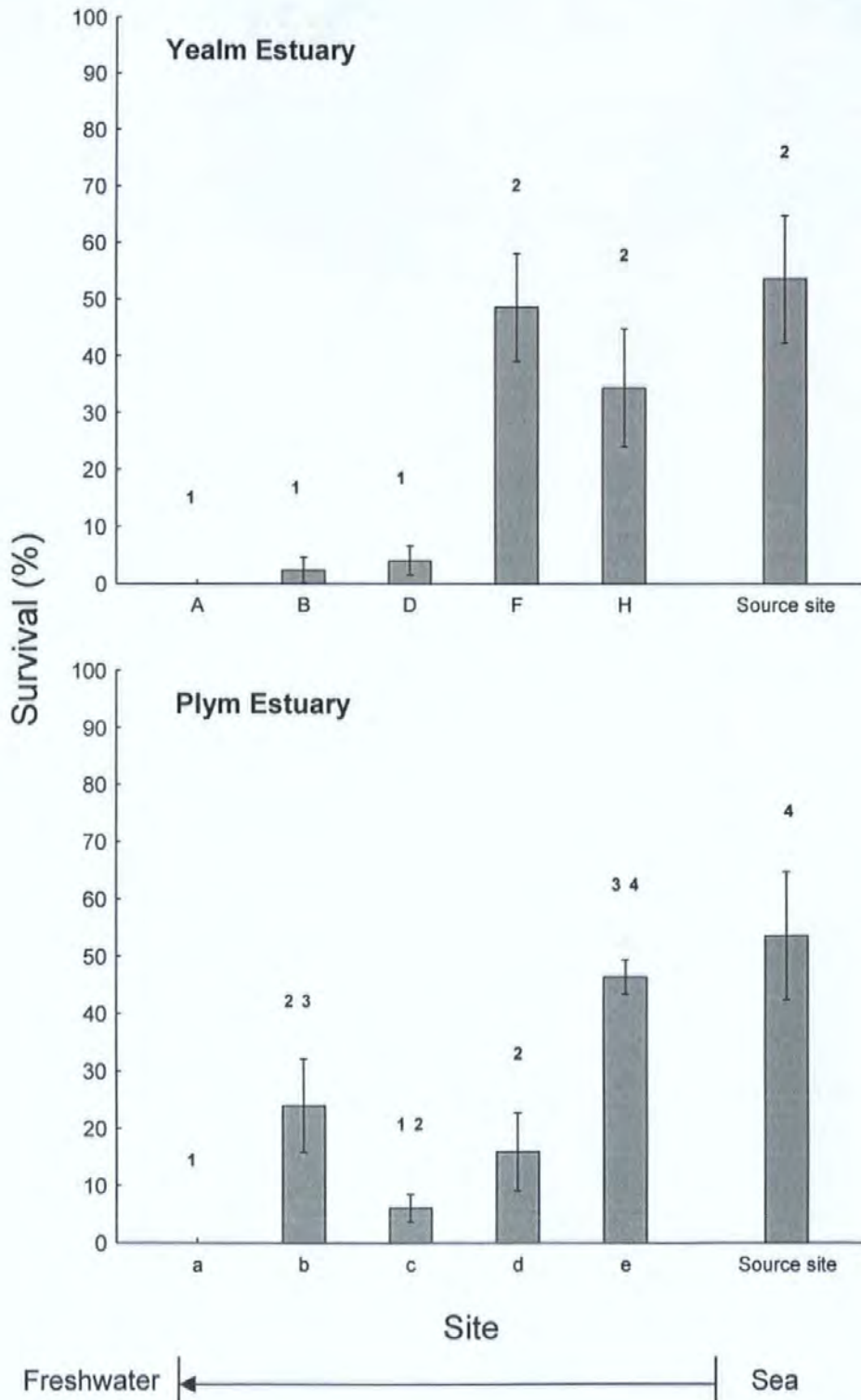
Fig. 3.12. Survival of *S. balanoides* at experimental sites along the Yealm and Plym Estuaries and at the fully marine source/control site (Batten Bay) 120 days after transplants. Bars represent mean proportion of survival +/- SE. Letters represent sites (see Fig. 3.1). Numbers over columns represent treatments (sites) that were not statistically different (homogeneous groups) according to ANOVA post-hoc test (SNK test, p > 0.05).

Table 3.2. One-way ANOVA (factor=site) on proportions of survival of *S. balanoides* at experimental sites along the Yealm Estuary and at the source site (Batten Bay) 120 days after transplants.

Time after Transplant	Source	df	MS	F	P
Yealm	Site	5	7147.7	16.3	< 0.001
	Error	17	439.9		

Table 3.3. One-way ANOVA (factor=site) on proportions of survival of *S. balanoides* at experimental sites along the Plym Estuary and at the source site (Batten Bay) 120 days after transplants.

Time after Transplant	Source	df	MS	F	P
Plym	Site	5	5257.3	11.9	< 0.001
	Error	18	441.3		

For *E. modestus*, in contrast to *C. montagui* and *S. balanoides*, optimum survival occurred at the mid-estuarine sites. Apart from the uppermost site (A), where survival was significantly lower than at any other site, survival was high at sites within the estuary and there were no statistical differences between these sites (Fig. 3.13). Survival at the source site was similar to survival at most of the other sites and the only significant difference was with site E, in which *E. modestus* had the highest survival (Fig. 3.13).
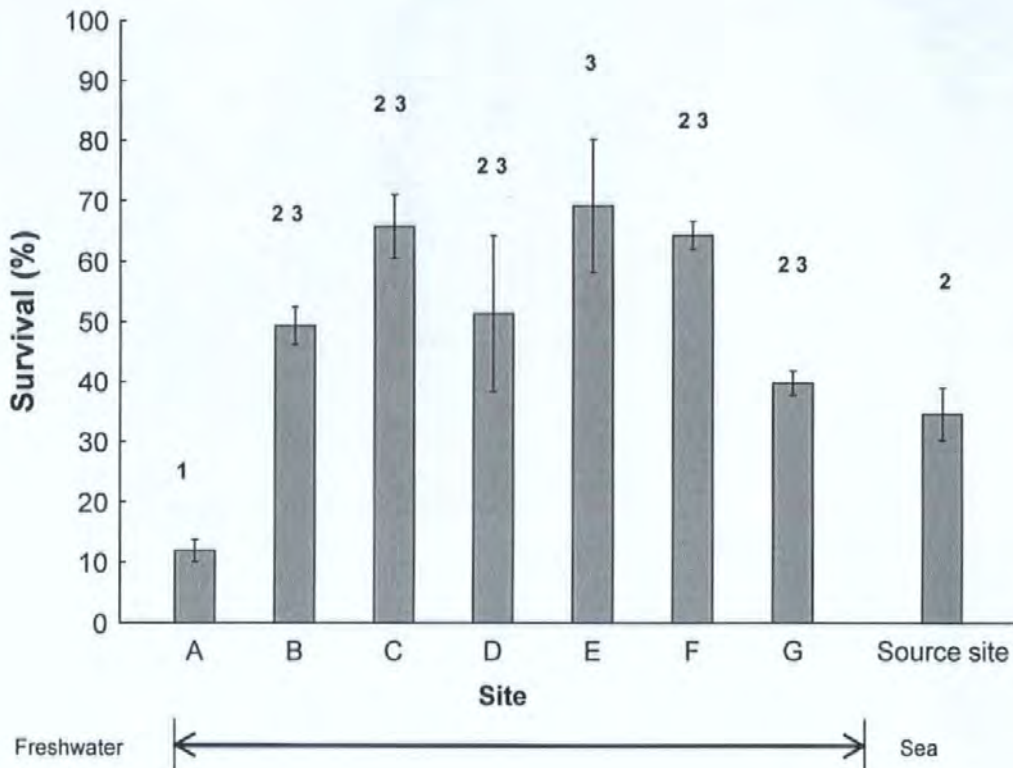
Fig. 3.13. Survival of *E. modestus* at experimental sites along the Yealm Estuary and at the fully marine source/control site (Batten Bay) 120 days after transplants. Bars represent mean proportion of survival +/- SE. Letters represent sites (see Fig. 3.1). Numbers over columns represent treatments (sites) that were not statistically different (homogeneous groups) according to ANOVA post-hoc test (SNK test, p > 0.05).

Table 3.4 One-way ANOVA (factor=site) on proportions of survival of *E. modestus* at experimental sites along the Yealm Estuary and at the source site (Batten Bay) 120 days after transplants.

Time after Transplant	Source	df	MS	F	P
120 days	Site	7	2573.8	6.17	< 0.001
	Error	24	417.4		

3.3.2.2. Median lethal times

Median lethal times obtained for the three species directly corresponded to their survival at each site. *C. montagui* died more quickly at inner and mid-estuary sites than at the source site and at the outermost estuarine site (G; Fig. 3.14). *S. balanoides*

showed higher median lethal times at the source site and at mid-estuary sites (Fig. 3.15).

Elminius modestus differed from the other two species and showed higher median lethal

times at mid and upper sites. (Fig. 3.14)
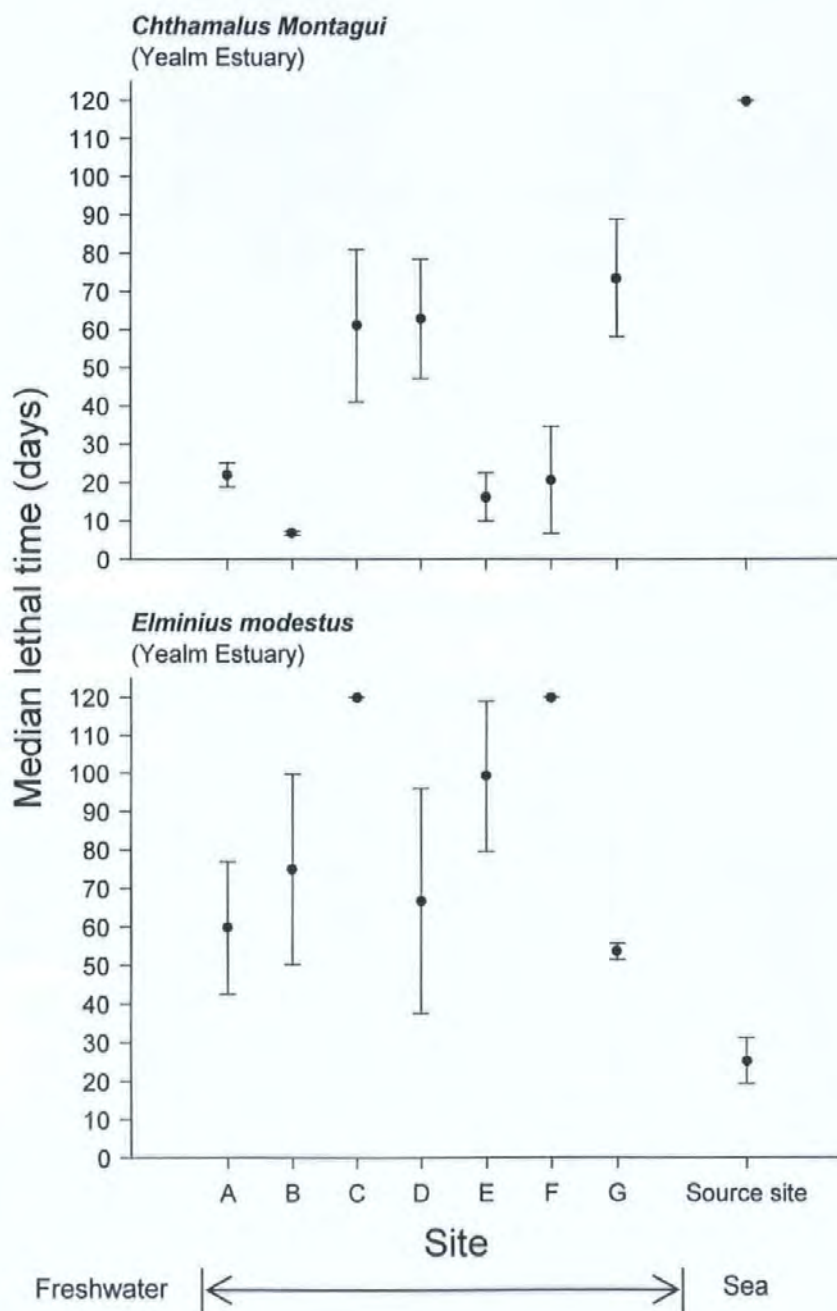
Fig. 3.14. Mean median lethal time (MLT) of *C. montagui* and *E. modestus* at experimental sites along the Yealm Estuary after transplants. Points represent mean MLT +/- SE (n=4). Letters represent sites (see Fig. 3.1).
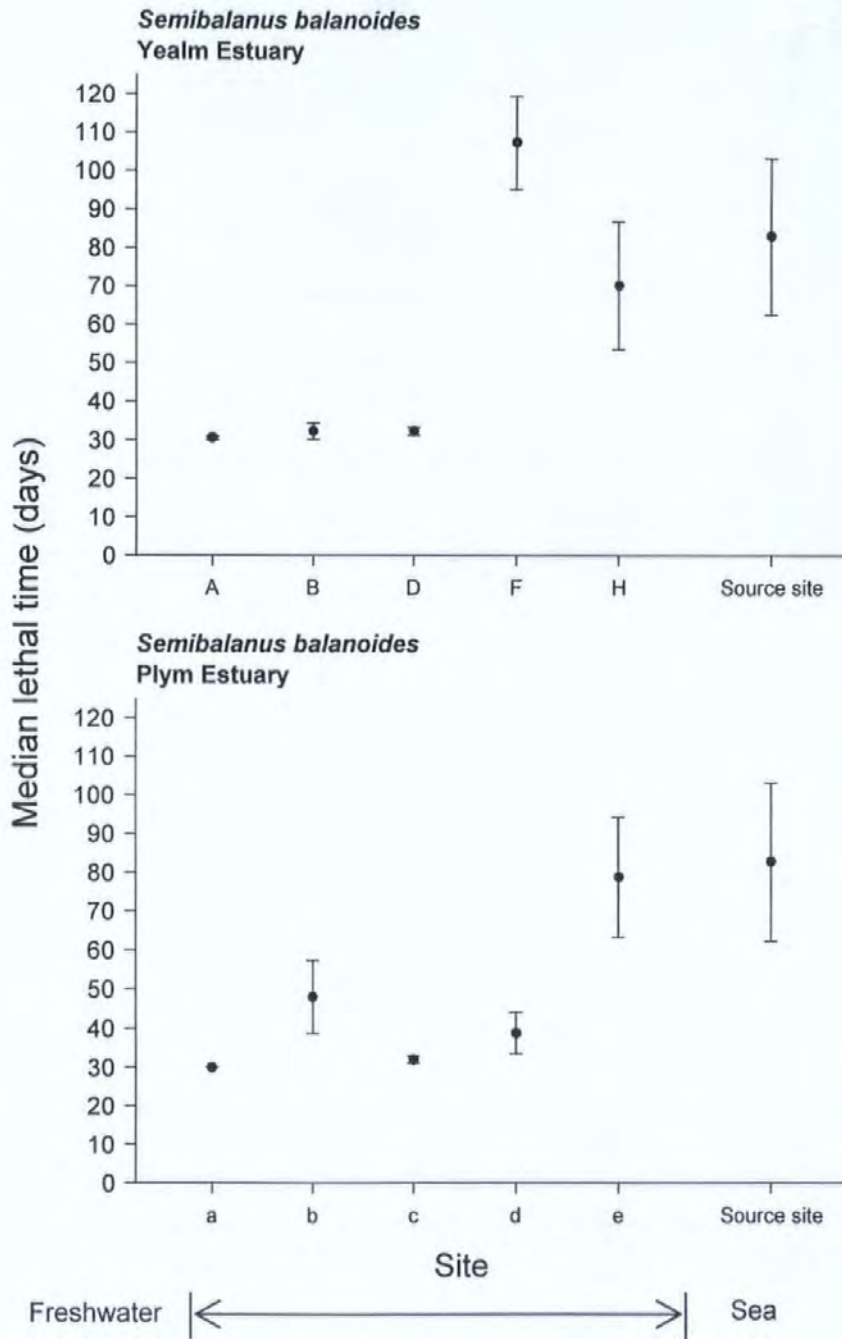
Fig. 3.15. Mean median lethal time (MLT) of *S. balanoides* at experimental sites along the Yealm and Plym estuaries after transplants. Points represent mean MLT +/- SE (n=4). Letters represent sites (see Fig. 3.1).

3.3.3. Correlation between survival and physico-chemical variables

There were some clear relationships between survival and physico-chemical variables. When the innermost site utilized for transplants is excluded from the tests, survival of *S. balanoides* was mainly correlated with siltation; survival of *C. montagui* was correlated with salinity parameters; and survival of *E. modestus* was not correlated with any of these factors. Survival of *Semibalanus balanoides* showed strong negative correlations with siltation in both the Yealm and the Plym estuaries (Table 3.6). In the Yealm, this species was also negatively correlated with minimum salinity and with average salinity fluctuation during submersion. Survival of *C. montagui* in the Yealm was not significantly correlated with siltation but was positively correlated with average and minimum salinity (Table 3.7).

Table 3.6. Pearson Correlation Coefficients (r) for correlation between survival of *S. balanoides* (120 days after transplants) and physico-chemical variables at the Yealm and Plym Estuaries. * above critical values at **0.01** alpha level; ** above critical values at **0.001** alpha level.

	Average salinity	Minimum salinity	Average minimum salinity	Average salinity fluctuation	Average siltation
S. balanoides Yealm Estuary[1]	0.5118	0.6345*	0.5752*	-0.6275*	-0.7262**
S. balanoides Yealm Estuary (excluding site A)[2]	0.6292	0.5436	0.6519*	-0.6811*	-0.7059*
S. balanoides Plym Estuary[3]	0.4223	0.5610	0.4710	-0.4738	-0.8296**
S. balanoides Yealm Estuary (excluding site a)[4]	0.0824	0.4019	0.1693	-0.1848	-0.7723**

[1] n = 19; [2] n = 15; [3] n = 20; [4] n = 16

Table 3.7. Pearson Correlation Coefficients (r) for correlation between survival of *C. montagui* and *E. modestus* (120 days after transplants) and physico-chemical variables at the Yealm Estuary. * above critical values at **0.01** alpha level; ** above critical values at **0.001** alpha level.

	Average salinity	Minimum salinity	Average minimum salinity	Average salinity fluctuation	Average siltation
C. montagui[1]	0.5856*	0.6936**	0.6626**	-0.6652**	-0.6248**
C. montagui (excluding site A)[2]	0.6006*	0.5519*	0.5262	-0.5035	-0.4331
E. modestus[3]	0.6854**	0.5835*	0.6359**	-0.5595*	-0.5433*
E. modestus (excluding site A)[4]	-0.0224	0.1203	0.0762	-0.1139	-0.0586

[1] n = 27; [2] n = 23; [3] n = 28; [4] n = 24

3.4. Discussion

My data in this chapter provided evidence that: 1. survivorship of *C. montagui*, *S. balanoides* and *E. modestus* varied along the sea-to-freshwater gradient, and while *C. montagui* and *S. balanoides* tended to survive better in the lower portions of the estuary, *E. modestus* survived more consistently along the length of the estuary and showed optimum survival at mid estuary locations; 2. although tolerance to estuarine conditions does not explain in full the distributions of these species, it would appear to be partly responsible for their success and patterns of distribution; 3. with the exception of *E. modestus*, there were correlations between the physico-chemical variables and survival. *S. balanoides* showed negative correlations with siltation and with salinity fluctuation, while *C. montagui* was positively correlated with salinity.

3.4.1. Survival across estuarine gradients

Proportions and rates of survival of the three species investigated here varied horizontally in estuaries and followed progressions along the estuarine gradient. Survival of *C. montagui* was higher at the marine source site than at any of the sites within the estuary. This was expected as the open coast is the primary habitat of *C. montagui* and, although this species favours sheltered and semi-estuarine habitats compared to its congener *C. stellatus*, it is not particularly successful in truly estuarine habitats (Southward, 1976; Crisp et al., 1981). Considering the estuarine sites alone, *C. montagui* experienced lower survival at the two innermost estuarine sites (A and B) than at the remaining sites. These results suggest that conditions experienced along the gradient became increasingly severe for *C. montagui* as locations approached the riverine end of the estuary.

Semibalanus balanoides also showed a general tendency of higher survival toward the sea, but conditions experienced within the estuaries were not as detrimental as for *C. montagui*. Although *S. balanoides* endured high mortalities at inner-estuary and also at a mid estuarine sites in the Yealm Estuary (site D), survival at the remaining mid and low estuarine areas were comparable to survival at the marine source site. These results provide evidence that *S. balanoides* is better adapted to estuarine conditions than *C. montagui*.

Elminius modestus performed best in the mid-estuary and this conforms to the observed patterns of abundance and distribution of this species, which is particular successful and dominant in estuarine areas than on the open coast (Crisp & Southward, 1959; Crisp, 1958; Foster, 1971, 1987; Lawson et al., 2004). Survival at the marine site and at the most seaward estuarine site was lower than survival at the other sites, and Median lethal times were much reduced here. This agrees with the known preference of

this species for estuarine areas (Moore, 1944; Fischer-Piette & Prenant, 1956, 1957; Fischer-Piette & Forest, 1961; Fischer-Piette, 1965; Crisp, 1958; Foster, 1978, 1982). *E. modestus* is able to survive in full-salinity clear water and there is no reason to suggest that chemical or nutritional limitations to survival exist on exposed shores (Crisp, 1958). One of the possible explanations for lower survival of *E. modestus* at the seaward sites lies on the fact that this species is known to have less resistance to mechanical damage than the other species that are more typical of wave-exposed shores. It is possible that this species suffers mortality due to mechanical damage caused either by wave action or by biological disturbance in these habitats. Predation, which may be more intense on wave-exposed shores than on less diverse estuarine shores, could also be responsible for higher mortalities of *E. modestus*. These results also agree with the observation that near the mouth of the Yealm estuary (Cellar Beach), *E. modestus* is an ephemeral component of the barnacle cover and is mostly represented by young individuals that rarely survived the year following settlement (Southward, 1991).

3.4.2. Physiological tolerance to estuarine conditions

Barnacles are osmoconformers and depend on behavioural mechanisms to avoid adverse conditions (Foster, 1970; Davenport, 1976). Additionally, as sessile species, avoidance of harmful conditions by migration is not possible. Barnacles respond to physiologically stressful salinities and other unfavourable conditions by closure of the opercular plates, which isolate the mantle cavity and soft body of the individual from the external environment (Barnes & Barnes, 1958; Foster, 1969, 1970, 1971). The success of a barnacle species in a variable environmental where adverse conditions are periodically encountered depends on: 1. the ability to feed efficiently during reduced periods of submergence; and 2. the capacity to avoid unsuitable conditions by closure of

the opercular valves; or 3. to tolerate them, when such conditions are persistent. In *C. montagui, S. balanoides* and *E. modestus* such abilities exist to different degrees and the present work provides evidence for the importance of physiological adaptations to the successful occupation of estuarine areas.

Individuals from a mixed *C. stellatus/C. montagui* population (experiments predated the separation of *C. stellatus* in *C. stellatus/C. montagui*, Southward, 1976) did not restrict contact with water at low salinity and did not prevent dilution of body fluids as efficiently as *S. balanoides* and *E. modestus* (Foster, 1970). Therefore, although *C. stellatus/C. montagui* restrict their activity in salinities below 25 (Foster, 1970) and are probably unaffected by immersion at low salinity for brief periods, specimens would experience negative effects when submersed in low salinities for extended periods as encountered in the upper reaches of estuaries. At the upper estuarine sites investigated here, salinities regularly reach values below 10 and persisted for a considerable proportion of the period when the organisms were submersed. *C. montagui* would clearly experience physiological problems in such areas. Firstly, individuals would be persistently inactive and retracted within the shell, which implies reduced feeding and potentially leads to starvation and metabolic deficits. Secondly, due to the species' inability to efficiently isolate the body, individuals would be directly affected and suffer dilution of body fluids that could lead to mortality or osmotic shock.

S. balanoides and *E. modestus* are more physiologically adapted to cope with fluctuating and low salinities than *C. montagui*. These species are not only more effective at avoiding low salinity water, but are also more tolerant and able to maintain cirral activity at lower salinities (Foster, 1970; Davenport, 1976). Additionally, these species have shown acclimation to salinity in controlled conditions and were able to adapt their body to low salinity regimes and keep activity at salinities down to 14 when gradually acclimated (Foster, 1970).

Although early laboratory experiments using constant salinities suggested similar tolerance to low salinities for both *S. balanoides* and *E. modestus* (Foster, 1970), subsequent experiments using fluctuating media demonstrated that *E. modestus* was more tolerant to fluctuation of salinity and that this species could remain active at lower salinity levels (Davenport, 1976; Cawthorne, 1979b). Moreover, these experiments showed that *S. balanoides* was sensitive to rates of salinity change, restricting its activity at higher salinities when salinity fluctuates at a faster rate (Davenport, 1976; Cawthorne, 1979b). Changes in salinity in the Plym and the Yealm occur rapidly and it is probable that this factor contributed to extend the period that this species were inactive.

E. modestus remained active at salinities down to 14 in experimental conditions and this limit was unaffected by differences in the rates of salinity change (Davenport, 1976; Cawthorne, 1979b). This species also had greater physiological tolerance to low constant salinity (Foster, 1970). It is obvious that such characteristics would be reflected in the performance of *E. modestus* in areas where conditions are stressful in terms of salinity. In other estuaries, *E. modestus* was successful, and in some cases was the only barnacle species present, in areas where salinity reaches 0 (Lawson et al., 2004). Furthermore, *E. modestus* apparently feeds more efficiently than the other two species, due to a greater frequency of cirral beat (Southward, 1955). This is believed to be one of the main adaptations responsible for the successful invasion of European shores by *E. modestus* (Crisp, 1958; Harms, 1999). Results obtained here suggest that this adaptation could, in a similar way, be considered to be largely accountable for the extensive distribution and dominance of *E. modestus* in estuaries.

Accumulation of silt in intertidal areas was another physical factor potentially stressful detected in the estuaries investigated. Deposition of silt on the boulders transplanted to the estuaries and on the adjacent areas of the shore was observed on

several occasions throughout the experiments. High fluxes of suspended sediment (Levinton & Bambach, 1970; Rhoads & Young, 1970; Aller & Dodge, 1974; Ellis et al, 2002) and deposition of sediment (Lohrer et al., 2004; Delapenna et al., 1998) are known to have adverse effects on epifauna and to affect their distribution in estuaries. During the transplant experiments presented here the main effect of siltation was the deposition of a layer of sediment over the barnacles which acted as a physical barrier to cirral activity. Such restriction in cirral activity was an additional limitation to periods of feeding, which as discussed before, already exists during submersion in low salinity water. Mortality by starvation and accumulation of toxic metabolites within the mantle cavity may have resulted from prolonged closure of the opercular plates, particularly in *S. balanoides* and *C. montagui*. Mortality due to burial by sediment and negative impacts of high deposition have previously been reported for barnacles (Menge et al., 1994; Seapy & Littler 1982; Rao & Sundaram, 1972-74; Silina, 2002), and it is possible that part of the mortality observed in the experiment conducted in the Plym and the Yealm result from this interference.

3.4.3. Association between survival and observed distribution in estuaries

Although *C. montagui* clearly faced physiological limitations in the upper reaches of both estuaries, the tolerance to the environmental conditions reflected in the survival of the transplanted adults did not fully explain the observed distribution of this species. The horizontal distribution of *C. montagui* in the Yealm Estuary decreased at positions located closer to the sea than positions where conditions appear to be physiologically intolerable. This species is found in areas where turbid waters, stretches of mud and moderate salinity fluctuations and silt deposition occur in other sheltered environments (Boyden et al., 1977; Crisp et al. 1981), and the observed survivorship is

in accordance with such records. Factors other than tolerance of adults to physico-chemical conditions are responsible for the limited upstream distribution of *C. montagui* in the Yealm.

Semibalanus balanoides extended further than *C. montagui* both in the Yealm and Plym. The upper limit of penetration of *S. balanoides* in the Yealm was site D. At this position and at other sites towards the riverine end of the estuary, survival after transplants was very poor. Similarly to that which was observed for *C. montagui*, physico-chemical conditions are probably limiting for *S. balanoides* in upper estuarine regions. At the Plym, this species occur in low abundance but some individuals were found near the upper distributional limit of *E. modestus*, which represents a more extended distribution than observed at the Yealm Estuary. This coincides with the occurrence of high survivorship further up estuary in the Plym than in the Yealm. It can be inferred that in the Plym suitable conditions for the occurrence of *S. balanoides* extended further up the estuary than in the Yealm. *S. balanoides* is relatively common in estuaries and can be a dominant form in lower and mid estuarine areas where suitable conditions are found (Hardwick-Witman & Mathieson, 1983; Little et al., 1988; Little et al., 1992).

Elminius modestus exhibited low levels of survival within the estuary at the upper estuarine site (site A). This position coincided with the upper limit of distribution of *E. modestus*, where this species was observed at lower densities than other estuarine areas. It was not to a surprise that *E. modestus* exhibited lower performance at this location compared to other estuarine sites. This position constitutes the limit of upper penetration of saltwater and a point where specimens may remain completely submerged in freshwater throughout the tidal cycle, including low-tide periods when freshwater flow is high. It is evident that conditions here were detrimental and

responsible for considerable effects on the physiology and performance of all three barnacle species investigated.

As mentioned earlier, in some particular cases, the tolerance to physico-chemical conditions did not offer a direct explanation for the observed patterns of distribution. Alternative explanations therefore deserve mention. It is possible that the effects of other environmental conditions influenced the distribution of these species indirectly affecting competition between them. Competition between these three species is known to play a role in determining their patterns of distribution on intertidal shores (den Hartog, 1953; Crisp, 1958; Southward and Crisp, 1956; Barnes and Barnes, 1965; Southward, 1991).

Larval supply may also account for the failure of *C. montagui* and *S. balanoides* to effectively colonize certain estuarine areas, as suggested for other estuaries (Little & Smith, 1980; Mettam, 1994). Consistent production and supply of larvae for settlement are required for the maintenance of sustainable populations. It is possible that the maintenance of populations of *C. montagui* and *S. balanoides* at mid and upper-estuarine locations depend on larval production and transport from marine or high saline estuarine areas, and that limitations to these processes exist. In contrast *E. modestus* would rely on local production of larvae and processes of larval retention, which undoubtedly would represent an advantage over the former species.

3.4.4. Correlations between survival and physico-chemical variables

Although correlation between survival and one of the physico-chemical variables tested does not imply a causal relationship, it does indicate the potential of these variables in influencing distributional patterns and permits some speculations. Very strong negative correlation between survival of *S. balanoides* and siltation was

observed both in the Plym and in the Yealm. The other species show no significant correlation with this variable. Siltation was not expected to be a problem for *E. modestus*, which is typically found in muddy habitats and appears well adapted to such conditions. As discussed previously, the main mechanism by which deposited silt could affect these barnacles was by limiting contact with the water column, and consequently reducing periods of feeding. This would probably be less detrimental for *E. modestus*, which has a much higher cirral activity and consequently feeds more efficiently than *S. balanoides* and *C. montagui*.

There has been no previous field evidence that suggests a higher tolerance to siltation in *C. montagui* than in *S. balanoides*. Despite this, the higher survival of *C. montagui* in comparison to *S. balanoides* in muddy areas of the Yealm and the absence of any correlation between survival of *C. montagui* and levels of siltation along this estuary suggest that this factor is not as important for this species as it is appears to be for *S. balanoides*. A clear physiological explanation for a higher tolerance to siltation and to extended periods of closure in *C. montagui* than in *S. balanoides* is not available here. Experimental evidence for a higher tolerance to this interference in *C. montagui* was obtained in Chapter 4, where further discussion of physiological mechanisms related in this tolerance are made.

Survival of *C. montagui* was positively correlated with average and absolute minimum salinity observed during submersion times at the experimental sites used for transplantations. The only variables associated with the salinity regime that correlated with survival of *S. balanoides* were the average minimum and average salinity fluctuation in the Yealm. Among these three species, *C. montagui* is less adapted to low salinity (Foster, 1970) and it is plausible that the correlations between survival of this species and salinity represent a consequence of this physiological disadvantage. The tolerance to salinity in *S. balanoides* is close to that of *E. modestus*, although the former

species is more susceptible in fluctuating salinity regimes. The absence of a significant correlation between *S. balanoides* and other parameters related to salinity (average and absolute minimum salinity) may be due to the relative high tolerance of this species or to a stronger influence of other factors such as siltation on the observed mortalities.

In conclusion, this work demonstrates that *E. modestus* is more adapted to estuarine conditions than *S. balanoides* and *C. montagui*, and is more able to cope with physico-chemical conditions prevailing across estuarine gradients. It also provided evidence that in some situations, notably in the extreme upper reaches of the estuaries, physico-chemical conditions prevent the successful occupation of shores by the latter two species.

CHAPTER 4
EFFECTS OF SEDIMENT BURIAL ON BARNACLES UNDER LABORATORY CONDITIONS

4.1. Introduction

Sedimentation is an important factor influencing the ecology of benthic communities (Ellison, 1998; Edgar & Barrett, 2000; Airoldi, 2003; Airoldi & Hawkins, 2007). Suspended sediment in the water and deposition of sediment influences a broad range of taxa and functional groups in virtually every known type of aquatic habitat. In the last few decades levels of sediment reaching the marine environment have been increasing due to anthropogenic activity and have become a recognisable threat to estuarine and other coastal habitats (Gray, 1997; GESAMP, 1994; Edgar & Barrett, 2000; Ellis et al., 2000; Norkko et al., 2002; Airoldi, 2003). Reviews on the effects of sedimentation are available for habitats as diverse as coral reefs (Dodge & Szmant-Froelich, 1985; Rogers, 1990; Richmond, 1993), mangroves (Ellison, 1998), seagrasses (Vermaat et al., 1997), rocky shores (Airoldi, 2003), lotic systems (Barko et al., 1991; Henley et al. 2000) and freshwater streams (Ryan, 1999). Information on the effects of sedimentation on biota is crucial, not only to understand ecological processes that control communities in habitats naturally influenced by sediments, but also to evaluate and predict impacts of particular depositional events or introduction of increased levels of sediment.

Estuaries receive sediments both from the sea and from land via freshwater runoff (Guilcher, 1967; Dyer, 1972; Meade, 1969) and are generally areas where considerable accumulation of sediment occurs (Postma, 1967; Meade, 1969, 1972; Dyer, 1986; 1997; Woodruff et al., 2003). In addition, due to their proximity to urban centres, the extensive use of adjacent land and estuarine waters themselves by man,

estuaries are regularly exposed to increased levels of or to activities that modify the dynamics of sediments. For these reasons estuaries tend to be highly influenced by sediments. In estuarine intertidal areas, which are normally characterized by low hydrodynamic flow, sediment deposition is common in natural conditions and can constitute a persistent influence on organisms living there (Lohrer et al., 2004; Delapenna et al., 1998). Regular patterns of deposition with short-term tidal or diurnal periodicity can result in accumulation of several centimetres of sediment in some estuaries (Dellapenna et al, 1998; Miller et al., 2002; Kniskern & Kuehl, 2003; Traykovski et al., 2004). It has long been noticed that hard substrata in estuaries are frequently covered by a layer of deposited sediment which on occasions is thick enough to bury organisms and have adverse effects on larval settlement and recruits (Percival, 1929; Korringa, 1951; Day & Morgans, 1956; Day, 1959; Carriker, 1961, Lewis, 1964; Silina, 2002).

Benthic organisms respond both to natural levels of sedimentation (e.g. Daly and Mathieson, 1977; Littler et al., 1983; D'Antonio, 1986; Dellapema et al., 2003; Anderson et al., 2004; Lohrer, 2006; Airoldi & Hawkins, 2007) and to increased sedimentation caused by human activities (e.g. Peterson et al. 2000; Smith & Kukert, 1996; Edgar & Barrett, 2000; Norkko, 2002). Epibenthic suspension feeders are particularly vulnerable to sedimentation because of their occurrence at the sediment-water interface, where depositional processes take place, and to the dependence of their feeding mechanisms on access to, and the quality of, suspended material in the water column. Negative effects of suspended sediment on feeding behaviour and efficiency are well documented (e.g. Loosanoff, 1962; Jorgensen, 1966, 1996; Rhoads & Young, 1970; McFarland & Peddicord, 1980; Bricelj & Malouf, 1984; Bricelj et al, 1984; Murphy, 1985; Ellis et al., 2000; Wilber & Clarke, 2001), and there are particular mechanisms by which deposited sediment affects epibenthic organisms. These effects

are summarized by Airoldi (2003) for hard-bottom organisms and include: 1. burial/smothering; 2. scour/abrasion by moving sediments; and 3. reduced stability and availability of substratum for settlement.

Burial of intertidal organisms by sediment may reduce the availability of light, oxygen and nutrients and cause metabolic waste products to accumulate. These alterations can be a major factor controlling species distribution and assemblage diversity, mainly by causing differential mortality or sublethal negative effects in species, which modify patterns of competition and dominance and favour opportunistic and sediment tolerant species (Daly & Mathieson, 1977; Littler et al., 1983; D'Antonio, 1986; Airoldi and Cinelli, 1997; Airoldi; 1998; Ellis, 2000; Cummings et al., 2003). A critical issue for organisms exposed to burial by sediment is mobility. Ability to move within sediments is clearly advantageous when buried and vertical or horizontal migration allows many species to escape (Kranz, 1974; Maurer et al., 1986; Chandrasekara & Frid, 1998; Cummings & Trush, 2004; Hinchey et al. 2006). In contrast to mobile species, sedentary infaunal and sessile epifaunal species are less adapted to survive burial events and their survival is primarily a function of species physiological responses to metabolic stress, such as anoxia, hypoxia and starvation (Hinchey et al. 2006).

Barnacles have limited mechanisms to reduce burial when sediments are deposited. Individuals that become physically isolated from water by a layer of sediment are unable to use their cirri, and consequently, to feed or to establish an adequate flow of oxygenated water through the mantle cavity for respiration. Mortality due to burial by sediment and negative impacts of high deposition have been reported for barnacles (Moore, 1977; Menge, 1994; Seapy & Littler 1982; Daly & Mathieson 1977; Rao & Sundaram, 1972-74; Silina, 2002), but limited information is available on the relative tolerance of species to such processes (Moore, 1977; Barnes, 1999), and the

82

influence of silt deposition on distribution patterns of barnacles due to differential mortality remains unknown.

The overall aim of my work was to test the tolerance to burial by estuarine muddy sediment of three barnacle species with differing patterns of distribution in estuaries (see Chapter 2). *E. modestus* extends along the whole estuarine gradient, inhabiting areas where high deposition of silt occurs and is frequently found under layers of silt; while *S. balanoides* and *C. montagui* are restricted to mid and lower regions of estuaries, where substrata are typically sediment-free. Hence patterns of distribution and survival of these three species correlate to spatial variation in levels of sediment deposition in estuaries (see Chapter 3; Crisp, 1958; Little and Smith, 1980; Mettam, 1994). It has been suggested that tolerance of silt deposition may be an important factor controlling the distribution and abundance of these and other barnacle species in estuaries (Crisp, 1958; Little & Smith, 1980; Mettam, 1994). In particular, the dominance of the invasive species *E. modestus* in estuarine areas has long been linked to its enhanced tolerance to silt deposition compared with native species (Crisp, 1958).

Considering that the response of barnacles that are experimentally buried by estuarine sediment will be related to their tolerance to metabolic stresses, particularly stresses related to respiration and feeding, differential responses are expected between the species tested here. Metabolic rates, oxygen demands and ability to undertake anaerobic respiration vary among barnacle species (Barnes & Barnes, 1959; Barnes et al., 1963a; Lopez et al., 2003). It has been suggested that *E. modestus*, which has higher cirral activity than the native species, is more efficient in acquiring food and tolerating periods of inactivity (Harms, 1999). If this is the case, it is predicted that *E. modestus* would better resist experimental periods of burial by sediment than *C. montagui* and *S. balanoides*. Such ability would benefit *E. modestus* in high depositional habitats in comparison to native barnacles and would contribute to mechanisms responsible for the

dominance of this species in estuaries. This chapter will specifically test the hypotheses that: 1. burial by sediment causes increased mortality in barnacles; 2. *C. montagui*, *S. balanoides* and *E. modestus* have different degrees of tolerance to burial by silt, in which case these species will show differences in mortality when subjected to similar burial periods; and 3. burial causes metabolic deficits in barnacles, leading to increased cirral activities following periods when the barnacles were buried.

4.2. Methods

4.2.1. Collection and preparation of barnacles and sediment

Pieces of rock supporting adult *E. modestus*, *S. balanoides* and *C. montagui* were removed from the shores at Mount Batten Bay, in the Plymouth Sound and Renney rocks, in Heybrook Bay. These locations support the typical fauna found on rocky-shores in South-West England. Sedimentation is low and virtually zero silt deposition occurs on these shores. The rocks were cut into pieces of about 8 x 5 cm and the density of barnacles attached manipulated so as to leave about 30 individuals of a single species on each piece of rock. The position of individual barnacles was recorded to assist later assessment of dead and surviving barnacles. Sediment was collected from an intertidal area in the upper region of the Yealm Estuary. Sediment was placed in plastic bags and kept frozen until used for the experiments.

Barnacles were placed in 1.5L tanks measuring 17.5cm (length) x 11.5cm (width) x 13 cm (height), with running seawater at the Marine Biological Association of the UK. All tanks contained three pieces of rock, each piece with one of the species under investigation. Barnacles were left to acclimate in these tanks for 7 days before the beginning of experiments.

4.2.2. Experimental design

To determine the effects of burial by deposited silt on *E. modestus*, *S. balanoides* and *C. montagui* two experiments were performed using a similar methodology. In the first, barnacles were buried by silt and left for 10 days. In the second, barnacles were submitted to 4 repeated 10 day periods of burial, alternating with 48 hour periods free of sediment.

Three treatments of sediment addition were used: 1. no sediment added (No sediment); 2. addition of 50 grams of sediment, which resulted in the deposition of a layer 2mm thick, but which left the apertures of the barnacles exposed (Sediment L1); 3. addition of 200 grams of sediment, which formed a layer of 8mm and buried all barnacles completely (Sediment L2). Each treatment was replicated in four tanks using a complete randomised block design.

Numbers of dead and live individuals were recorded prior to the addition of sediment. Any barnacles that were dead at the start of the experiment were discounted from subsequent observations. Sediment was added to tanks according to their respective treatments using the following procedure: 1. water flow was discontinued; 2. sediment was added and water was vigorously mixed (tanks where no sediment was added also had their water flow discontinued and water content mixed); 3. sediment was allowed to settle; 4. water flow was resumed after sediment had settled completely in all tanks; 5. condition of barnacles was checked (buried/not buried) in sediment addition treatments. All barnacles were completely covered by sediment in Sediment L2 tanks, while in Sediment L1 most of the barnacles had free opercula. Individuals covered in Sediment L1 tanks had their opercular plates gently freed from sediment with a small brush.

At the end of each 10 day period sediment was removed from the tanks by suction using a siphon. Water flow was continued to clear the tanks and enable the barnacles to remain submerged at all times. As a control, water was also pumped out of tanks without sediment.

4.2.3. Mortality and cirral activity

In the second experiment, cirral activities were monitored prior to the addition of sediment and during the first hour after sediment removals. Activity was recorded after addition of food (Liquifry Marine by Interpet Ltd.) as the number of active individuals and the frequency of cirral beating in individual barnacles. This was measured by counting the number of complete cycles of opening and closing of the valves accompanied by protrusion of the cirri within a 30 second period.

Dead individuals were recognised by the absence of opercular valves, the complete absence of an individual that had been alive at the beginning of the experiment, or failure to respond to mechanical stimulation of the opercular valves by withdrawal of cirri or closure of the opercular plates.

4.2.4. Statistical analyses

Differences in survival after a 10 day period in the first experiment and after 4 subsequent periods of burials in the second experiment were compared using two-way ANOVA with species and sediment treatment both considered as fixed factors. Variables were arcsine transformed (Arcsin$\sqrt{x}$) to achieve homocedasticity. For each species, Median lethal times (MLT) and the times to 10% mortality (L_{10}) were

estimated graphically for each replicate. Difference in the mean L_{10} between species was tested using a one-way ANOVA, followed by post-hoc SNK tests.

Differences in the proportion of active individuals between treatments in the second experiment were compared using one-way ANOVA. Tests were performed for each species separately on data obtained before the initial addition of sediment and after each period of burial. Significant differences between treatments indicate a rejection of H_0, namely that there were no increases in cirral/feeding activity in barnacles after burial periods. The initial data (before the addition of sediment in any of the tanks) constituted a control to which subsequent data were compared. To compensate the use of multiple ANOVA tests for each species, a Bonferroni correction was applied. The existence of differences between groups were only accepted when $p < 0.01$ (0.05 divided by 5).

4.3. Results

4.3.1. Effects of 10 day burial by silt

Semibalanus balanoides and *C. montagui* were both affected by burial from silt; survival after 10 days of burial was significantly lower than in treatments where no sediment had been added or where sediment was present, but did not obstruct opercular apertures (Fig. 4.1, Table 4.1). A strong interaction between species and treatment was detected (Table 4.1). In contrast, *E. modestus* was not affected by burial (Fig. 4.1). Survival of this species in burial treatments was slightly lower than at other treatments, but values were high (approximately 90% survival) and not statistically different (Fig. 4.1, Table 4.1).
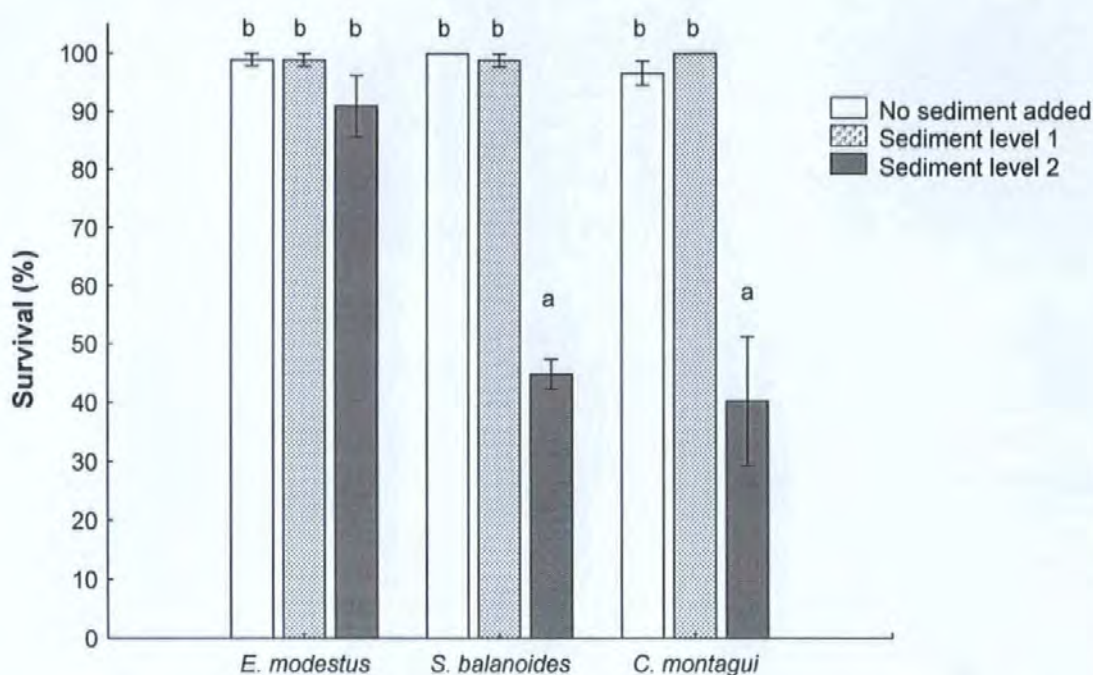
Fig. 4.1. Effect of 10 day period of burial by silt on survival of *E. modestus*, *S. balanoides* and *C. montagui*. Barnacles were exposed to 3 treatments of sediment addition: treatment 1. no sediment added; treatment 2. 50g.L^{-1} of sediment added, barnacles were surrounded by sediment but have free opercular apertures; and treatment 3, 200g.L^{-1} of sediment added, barnacles were completely covered by sediment. Values are mean ± SE. Each point represents the mean of 4 replicates. Letters above columns represent homogeneous groups according to ANOVA (SNK test, $p > 0.05$).

Table 4.1. Two-way ANOVA (factor 1: species, factor 2: sediment treatment) on proportions of survival of *E. modestus*, *S. balanoides* and *C. montagui* buried by sediment.

Source	Df	MS	F	P
Species	2	594.3	8.70	0.001
Treatment	2	4726.0	69.19	< 0.001
Interaction	4	649.1	9.50	< 0.001
Error	27	68.3		

4.3.2. Effects of successive burials by silt

Elminius modestus showed high tolerance to periods of burial by silt, in contrast to *S. balanoides* and *C. montagui*, which were both strongly affected by silt deposition. A reduction in survival of *S. balanoides* was noted after the first period of burial and further reductions in survival were observed after subsequent burials, which led to almost complete mortality at the end of the experiment (Fig. 4.2). Although *C. montagui* was also strongly affected by sediment, it showed a greater ability to survive burial than *S. balanoides*. Substantial mortality of *C. montagui* was only noted after the second burial period (Fig. 4.2) and final survival (Fig. 4.3 and Table 4.2), Median lethal time and time to 10% mortality (Fig. 4.4, Fig. 4.5 and Table 4.3) of this species were significantly higher than for *S. balanoides*.

The presence of deposited sediment at levels that do not obstruct the opercular plates did not have any detrimental effects in any of the species tested, as evidenced by the absence of significant differences between the first two treatments (1. No sediment and 2. Sediment L1) within, and between species (Fig. 4.3 and Table 4.2). Analyses of variance on final survival of the three species also showed a strong interaction between species and treatment. *E. modestus* showed no significant differences between the three treatments utilized, while *S. balanoides* and *C. montagui* showed significantly lower survival in the burial treatment. *S. balanoides* underwent more severe mortality, significantly lower, than mortality of *C. montagui* (Fig. 4.3 and Table 4.2).
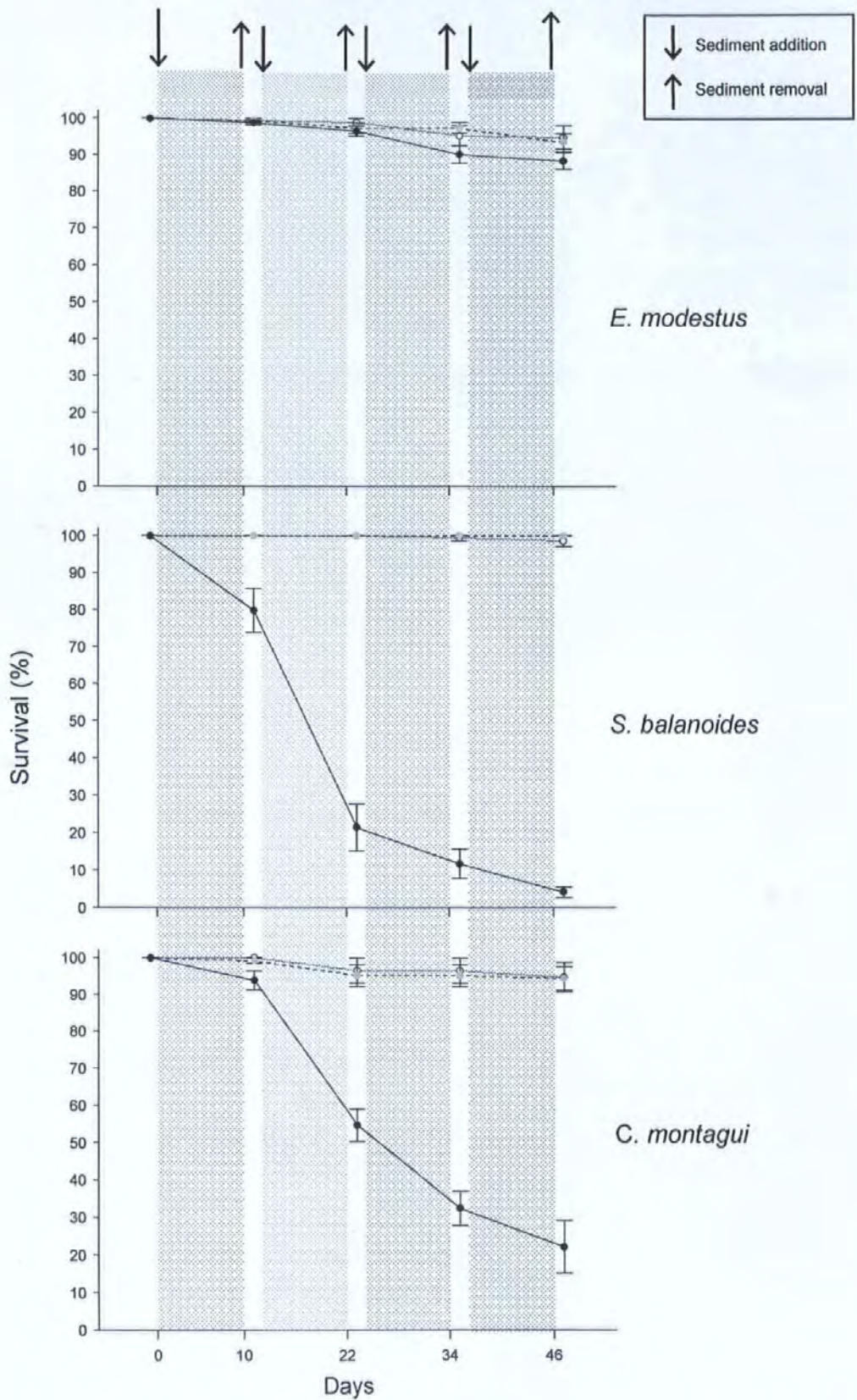
Fig. 4.2. Effect of repeated periods of burial by silt (indicated by shading) on survival of *E. modestus, S. balanoides* and *C. montagui*. Three treatments of sediment addition: 1. no sediment added; 2. 50g.L^{-1} of sediment effects added, barnacles were surrounded by sediment but had free opercular apertures; and 3. 200g.L^{-1} of sediment added, barnacles were completely covered by sediment. Each burial period lasted for 10 days and intervals between burials were of 48 hours. Values are mean ± SE. Each point represents the mean of 4 replicates.

··O·· No Sediment   -●- Sediment Level 1   ━●━ Sediment Level 2
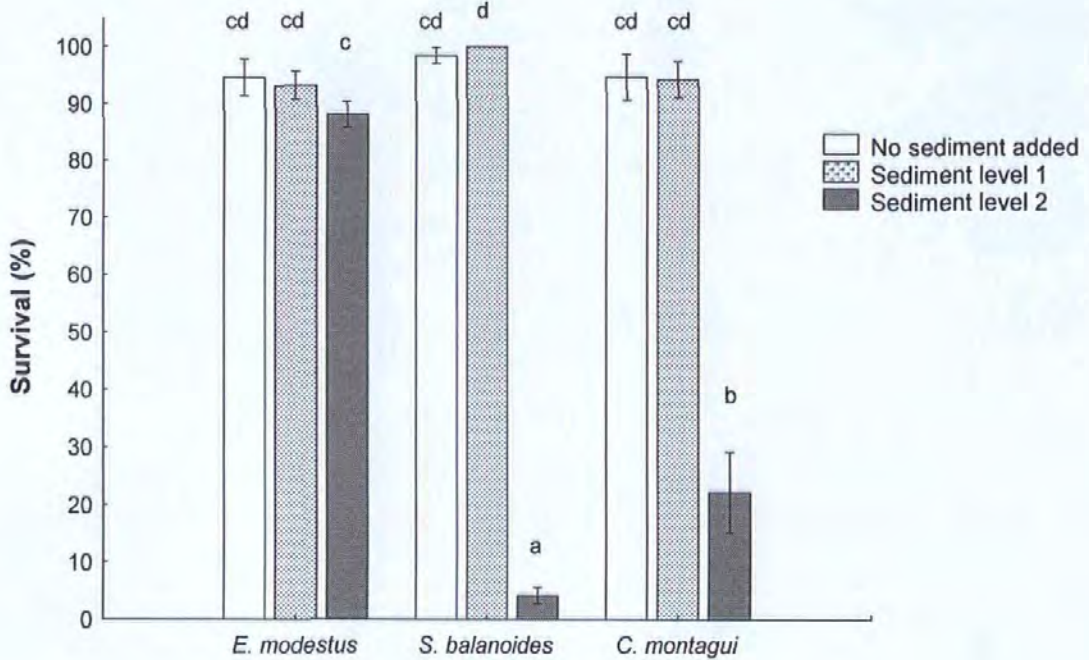
Fig. 4.3. Survival of *E. modestus*, *S. balanoides* and *C. montagui* after 4 subsequent periods of burial (10 days each). Barnacles were exposed to 3 treatments of sediment addition: 1. no sediment added; 2. 50g.L^{-1} of sediment added, barnacles were surrounded by sediment but have free opercular apertures; and 3. 200g.L^{-1} of sediment added, barnacles were completely covered by sediment. Values are mean ± SE. Each point represents the mean of 4 replicates. Letters above columns represent homogeneous groups according to ANOVA (SNK test, $p > 0.05$).

Table 4.2. Two-way ANOVA (factor 1: species, factor 2: sediment treatment) on proportions of survival of *E. modestus*, *S. balanoides* and *C. montagui*.

Source	df	MS	F	P
Species	2	674.5	9.18	< 0.001
Treatment	2	8631.5	117.47	< 0.001
Interaction	4	1701.9	23.16	< 0.001
Error	27	73.5		

4.3.3. Median lethal time (MLT) and times for 10% mortality

Survival curves for each replicate for each species were similar (Fig. 4.4). Mean MLT and mean L_{10} calculated from these curves were higher for *C. montagui* than *S. balanoides* (Fig. 4.4). Survival of *E. modestus* did not reach values below 50% in any of the replicates and only L_{10} were calculated (Fig. 4.4). Significant differences in L_{10} were detected between all three species according to ANOVA (Table 4.3). *E. modestus* showed the higher values of L_{10}, followed by *C. montagui* and *S. balanoides*, respectively.

4.3.4. Cirral activity

The proportion of active individuals was generally higher in barnacles exposed to burial than those in treatments where the opercular plates were free of sediment (Fig. 4.6). One-way ANOVA showed that cirral activity before addition of sediment was not significantly different between treatments for any of the species examined (Tables 4.5, 4.6 and 4.7). Comparison of activity after subsequent burial periods showed that in most cases the proportion of active individuals was higher in barnacles that underwent burial than in those that were not buried ($p < 0.01$). Exceptions occurred in *S. balanoides* and *C. montagui* after the second period of burial and in *C. montagui* after the last period of burial (Tables 4.5, 4.6 and 4.7).
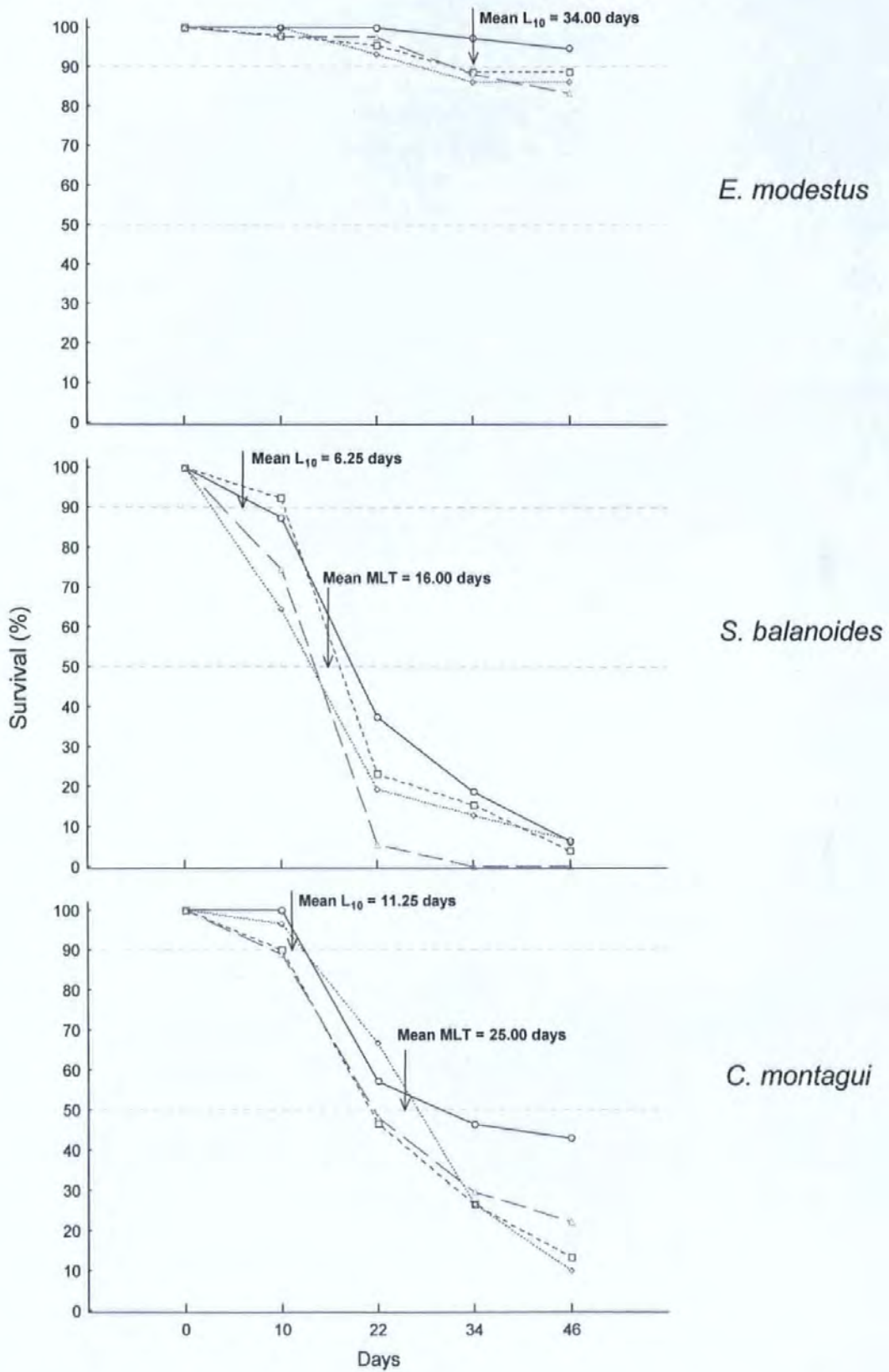
Fig. 4.4. Survival curves of a. *E. modestus*, b. *S. balanoides* and c. *C. montagui* for each replicate utilized in the treatment of complete burial by silt. Each line represents a replicated tank and values are percentage of individuals surviving. Each burial period lasted for 10 days and intervals between burials were of 48 hours.
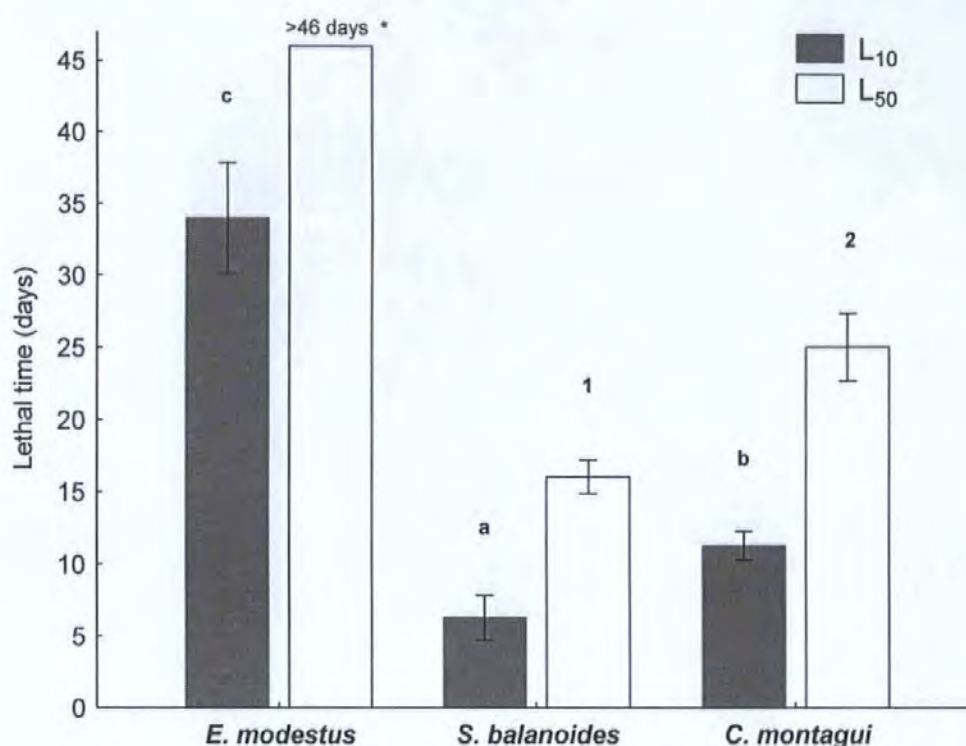
Fig. 4.5. Median lethal times (L_{50}) and time for 10% mortality (L_{10}) for *E. modestus*, *S. balanoides* and *C. montagui* during 4 subsequent periods of burial (10 days each). Values are mean ± SE. n = 4. Letters over columns indicate homogeneous groups according to ANOVA for comparison of L_{10} and numbers for comparison of L_{50} (SNK test, $p > 0.05$). * No mortality below 50% at the end of the experiment, not included in the ANOVA test.

Table 4.3. One-way ANOVA (factor=species) on 10% lethal times (L_{10}) of *S. balanoides, C. montagui and E. modestus* exposed to subsequent periods of burial by sediment.

Source	df	MS	F	P
Species	2	3.26	24.15	< 0.001
Error	9	0.13		

Table 4.4. One-way ANOVA (factor=species) on Median lethal times (L_{50}) of *S. balanoides* and *C. montagui* exposed to subsequent periods of burial by sediment.

Source	df	MS	F	P
Species	1	81.61	11.63	0.014
Error	6	7.02		
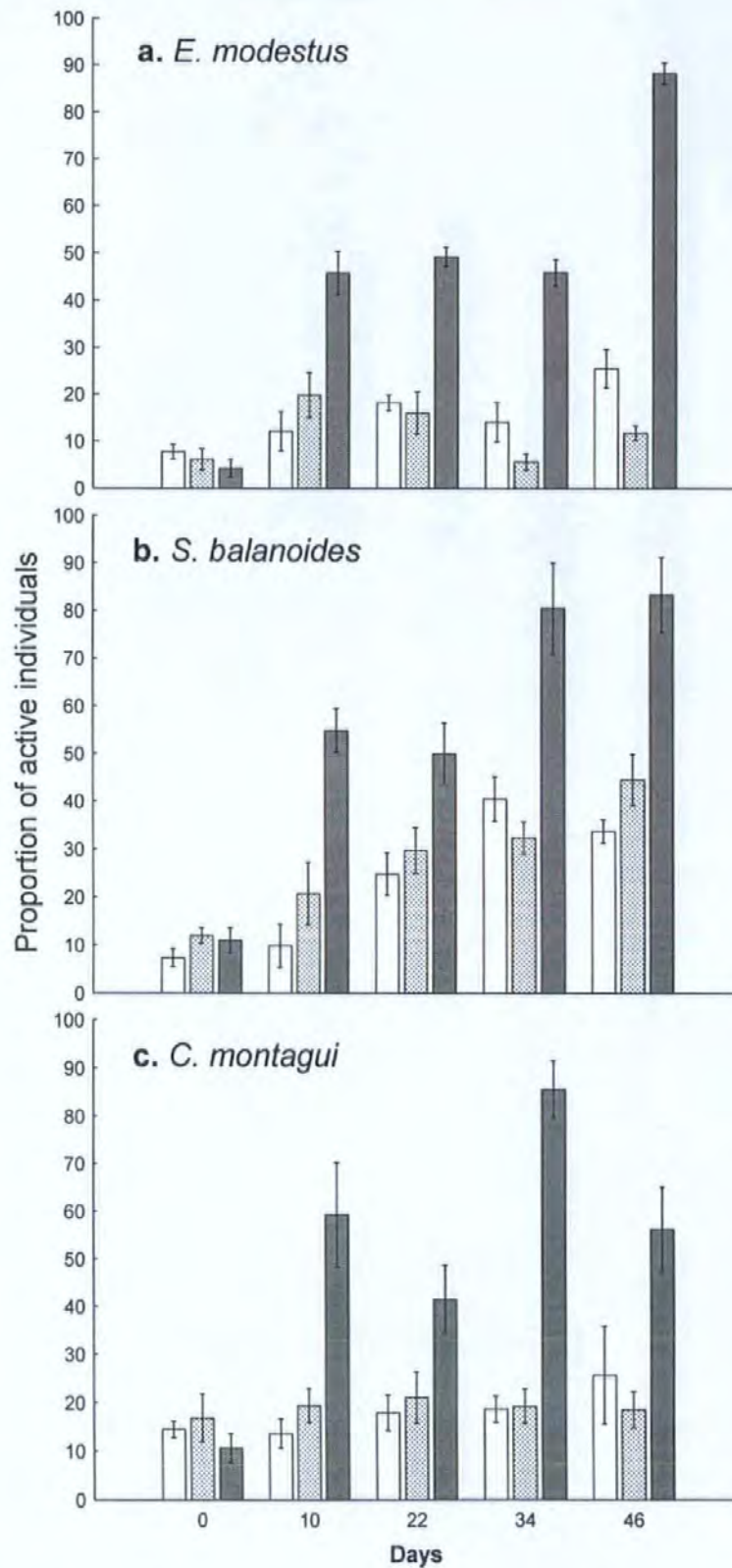
Fig. 4.6. Proportion of cirrally active individuals of a. *E. modestus*, b. *S. balanoides* and c. *C. montagui*, before (day 0), after (46 days) and between (10, 22 and 34 days) subsequent burials by silt. Barnacles were submitted to 3 treatments of sediment addition: treatment 1. no sediment added; treatment 2. 50g.L^{-1} of sediment added, barnacles were surrounded by sediment but had free opercular apertures; and treatment 3. 200g.L^{-1} of sediment added, barnacles were completely covered by sediment. Values are mean ± SE. Each bar represents the mean proportion of 4 replicates. Each burial period lasted for 10 days and intervals between burials were of 48 hours. ☐ No sediment ▨ Sediment level 1 ▓ Sediment level 2

Table 4.5. One-way ANOVAs (factor=SEDIMENT TREATMENT) on proportion of active individuals of *E. modestus* before addition of sediment (day 0); after exposed to one period of burial (day 10); after exposed to two periods of burial (day 22); after exposed to three periods of burial (day 34); and after exposed to four periods of burial (day 46). Significant effects (P < 0.01) are in bold.

		Source	df	MS	F	P
Initial Activity	(day 0)	Treatment	2	12.28	0.77	0.490
		Error	9	15.89		
After 1st Burial	(day 10)	Treatment	2	1243.73	13.71	**0.001**
		Error	9	90.74		
After 2nd Burial	(day 22)	Treatment	2	1380.09	34.98	**<0.001**
		Error	9	39.45		
After 3rd Burial	(day 34)	Treatment	2	1797.25	43.14	**<0.001**
		Error	9	41.66		
After 4th burial	(day 46)	Treatment	2	6646.68	183.89	**<0.001**
		Error	9	36.14		

Table 4.6. One-way ANOVAs (factor=SEDIMENT TREATMENT) on proportion of active individuals of *S. balanoides* before addition of sediment (day 0); after exposed to one period of burial (day 10); after exposed to two periods of burial (day 22); after exposed to three periods of burial (day 34); and after exposed to four periods of burial (day 46). Significant effects (P < 0.01) are in bold.

		Source	df	MS	F	P
Initial Activity	(day 0)	Treatment	2	23.54	1.23	0.336
		Error	9	19.10		
After 1st Burial	(day 10)	Treatment	2	2205.36	18.06	**<0.001**
		Error	9	122.09		
After 2nd Burial	(day 22)	Treatment	2	4.88	5.44	0.0283
		Error	9	0.88		
After 3rd Burial	(day 34)	Treatment	2	0.75	14.23	**0.002**
		Error	8	0.05		
After 4th burial	(day 46)	Treatment	2	9.82	20.06	**<0.001**
		Error	8	0.49		

Table 4.7. One-way ANOVAs (factor=SEDIMENT TREATMENT) on proportion of active individuals of *C. montagui* before addition of sediment (day 0); after exposed to one period of burial (day 10); after exposed to two periods of burial (day 22); after exposed to three periods of burial (day 34); and after exposed to four periods of burial (day 46). Significant effects (P < 0.01) are in bold.

		Source	df	MS	F	P
Initial Activity	(day 0)	Treatment	2	0.74	0.79	0.484
		Error	9	0.94		
After 1st Burial	(day 10)	Treatment	2	2.43	12.79	**0.002**
		Error	9	0.19		
After 2nd Burial	(day 22)	Treatment	2	5.75	4.73	0.039
		Error	9	1.22		
After 3rd Burial	(day 34)	Treatment	2	32.39	63.98	**<0.001**
		Error	9	0.51		
After 4th burial	(day 46)	Treatment	2	11.94	4.79	0.038
		Error	9	2.49		

4.4. Discussion

These experiments provided evidence that thin layers of deposited sediment have detrimental effects on intertidal barnacles and that differential tolerances to sediment deposition exist among barnacle species. *E. modestus* was not significantly affected by sediment and was clearly more tolerant to burial by silt than *S. balanoides* or *C. montagui*, both of which experienced high mortalities when exposed to single or to multiple periods of burial by sediment. *C. montagui* was more tolerant to burial than *S. balanoides*. Ability to withstand burial can be attributed to physiological tolerance to conditions imposed by the deposited sediment, rather than to any behavioural mechanism of burial escape. Increased cirral activity observed in barnacles of all three species after burial periods, indicated that metabolic deficits had probably occurred. The results suggest that tolerance to burial by silt benefits *E. modestus* and contributes to its success and dominance in estuarine intertidal areas, and potentially also in other habitats where high levels of sediment deposition may occur.

4.4.1. Behavioural avoidance of burial in barnacles

Barnacles exposed to 8mm thick sediment layers were completely buried. Cirral movements could not prevent deposition of sediment on opercular plates or remove sediment after depositions at this level of sedimentation. Partial avoidance of smothering by cirral beating has been observed in coral-dwelling barnacles (Pyrgomatidae) exposed to low levels of siltation, but this behaviour was ineffective in preventing smothering and clogging of the cirri (Fabricius & Wolanski, 2000).

Patterns of cirral activity were not monitored during deposition of sediment and it is not possible to speculate about cirral response to the settling particles in our

experiments. Nevertheless, observations of sediment layers and individual conditions (buried/not buried) after deposition indicated that specimens were unable to avoid burial when the surface of the deposited layers exceeded 2mm or more than their individual shell heights.

The observations made during my experiments suggest that barnacles are inefficient at escaping burial, even when compared to other sessile species. Although behavioural avoidance to burial by sediment in sessile or relatively sedentary species is not common, a few species can escape burial at low levels of deposition by deformation or expansion of their body parts. For example, anemones (*Anthopleura elegantissima, Actinothoe sphyrodeta, Cereus pedunculatus*, and others) can resist shallow sand burial by extending their column so that the oral disc and tentacles project above the sediment surface (Littler et al, 1983; Saiz-Salinas & Urdagarin, 1994; Hiscock, 1983); *Sabellaria vulgaris*, a reef building polychaete is able to emerge from sediment and escape depositions of sediment up to 1 cm (Miller, 2002); *Mytilus edulis* can escape up to 4 cm of burial by pulling up its byssus and siphonate bivalves can extend their siphons up to new sediment-water interfaces (Kranz, 1974).

4.4.2. Tolerance to burial by sediment

Differential physiological tolerances to respiratory stress and starvation were probably responsible for the greater survival observed in *E. modestus* than in *C. montagui* and in the even more susceptible *S. balanoides*. Correlation between physiological tolerance to anoxia/hypoxia and ability to survive burial by sediment in sessile and sedentary intertidal species has been demonstrated previously. For example, in laboratory conditions, Hinchey et al. (2006) showed that *Crassostrea virginica*, which is able to undergo anaerobic respiration and withstand anoxia, was tolerant to

burial for six days, while *Molgula manhattensis*, a tunicate, intolerant to anoxic conditions, was highly susceptible and died by suffocation. Similarly, Marshall & McQuaid (1989) showed that the limpet, *Siphonaria capensis*, which is capable of oxyregulation and anaerobic respiration, survived longer periods of burial than *Patella granularis*, which is more dependent on external oxygen supply and is apparently not capable of anaerobic respiration.

Field evidence also suggests that physiological tolerance is important for the ability to withstand periods of burial by sediment. For example, the mussel *Choromytilus meridionalis*, which withstands prolonged periods of hypoxia, is dominant on rocks associated with sand, while the less tolerant *Perna perna* occurs at higher shore levels, which are not usually influenced by sand deposition (Marshall & McQuaid, 1993a). Similarly, *S. capensis* is a higher shore species than *P. granularis* (Marshall & McQuaid, 1989; 1993b). Macroalgae are also examples of intertidal rocky shore organisms that have vertical zonation patterns correlated with their tolerances and physiological adaptations to sediment (Daly & Mathieson, 1977; Seapy & Littler, 1982; Taylor & Littler, 1982; Littler et al., 1983; review in Airoldi, 2003).

Several respiratory adaptations are required for successful life in the intertidal, including anaerobic and aerial respiration, and ability to reduce metabolism and respiration during periods of stress (Newell, 1973). Although these adaptations are primarily related to trade-offs between the supply of respiratory needs and avoidance of desiccation, they can provide advantages to help reduce the effects of sediment disturbance. *Semibalanus balanoides* and *Chthamalus* species undergo anaerobic respiration and lower their metabolic rates in anaerobic conditions (Barnes & Barnes, 1959; Barnes et al. 1963a, b). Similar information is not available for *E. modestus*, but it is very likely that this species also undergo anaerobic respiration. It was demonstrated recently that *S. balanoides*, *E. modestus* and also *C. stellatus* tend to live in hypoxia for

extended periods during submersion, apparently due to the inherent inefficiency of balanomorph ventilation systems (Davenport & Irwin, 2003). During periods of emersion, oxygen levels within the mantle cavity of these species are quickly lowered and species assume anaerobic or aerial respiration (Barnes et al., 1963a). *Chthamalus montagui* is the intertidal species which occupies the highest zones of the shore in comparison to any other barnacle on European shores (Crisp et al., 1981). This certainly requires greater ability to undergo anaerobic respiration.

In my experiments anaerobic conditions were certainly imposed for buried specimens. The oxygen available was limited to that dissolved in interstitial water. Interstitial water in sediments has reduced oxygen tension (Andersen & Helder, 1987), and even if levels were adequate for aerobic respiration, water would have to be pumped into the mantle cavity. Pumping water into the mantle cavity would require tergal movements, which are unlikely to have happened without some sediment disturbance. It is most probable that renewal or flow of water into the mantle cavity did not take place during burial, when the valves remained closed. This may have resulted in two main consequences which probably also affect barnacles during periods of burial in nature. Firstly, anaerobic respiration would result in the production of toxic metabolites, which would tend to accumulate within the mantle cavity and body tissues. In barnacles lactic acid, and possibly other toxic metabolites, are produced (Barnes & Barnes, 1963; Lopez et al., 2003). Secondly, anaerobic respiration utilizes carbohydrate reserves and these would be depleted in the absence of feeding.

Barnacles are very resilient to starvation and *S. balanoides*, for example, can survive under starvation for several months (Barnes, 1962; Barnes et al., 1963b). It is improbable that starvation alone was responsible for the mortality observed in our experiments, since starved barnacles utilize carbohydrate reserves before switching to the use of protein and lipids. Starvation induces a reduction in oxygen demand and

continuous closure of the opercular valves (Barnes et al., 1963a, b). This leads to the establishment of anaerobic conditions and use of anaerobic respiration, which would be similar to the effects of forced opercular closure by physical impediments, such as deposited sediment. The main difference between these two situations is that individuals induced to anaerobiosis due to starvation can respond to the accumulation of toxic metabolites by releasing those in the surrounding water, while in buried individuals this would not be possible. It is likely that the combination of production and inability to excrete metabolic end-products of anaerobic respiration was the ultimate cause of mortality during burial.

Barnes et al (1963a) demonstrated that in *S. balanoides* and *Chthamalus* species, lactic acid accumulated during periods of anoxia are rapidly excreted on return to aerobic conditions and that conversion of lactic acid back to carbohydrate is apparently low. It can be assumed that feeding during periods when conditions are suitable is sufficient to rebuild carbohydrate reserves necessary for survival in these species. In my experiments, however, feeding was restricted to periods between burials (48 hours between 10 days burials), and it was probably not sufficient to rebuild reserves necessary for anaerobic respiration. Deficits may have accumulated and culminated in mortalities observed throughout the successive periods of burial. *E. modestus* appears to be more efficient in acquiring food and accumulating reserves than *S. balanoides* and *C. montagui* (Southward, 1955; Barnes & Barnes 1962, Harms, 1999). This might have had a significant role on the tolerance to periods of burial exhibited by *E. modestus*. Chthamalids have lower oxygen demands and repay oxygen debts acquired during anaerobiosis more efficiently than *S. balanoides* (Barnes & Barnes, 1959; Barnes et al., 1963a). This may explain the higher lethal times and higher final survival observed in *C. montagui* than in *S. balanoides* subjected to repeated burials.

4.4.3. Role of tolerance to burial in the dominance of *E. modestus* in estuaries

Regardless of the mechanism by which *E. modestus* tolerates burial by sediment, there is no doubt that this would represent an advantage for this species in situations where accumulation of sediment takes place. The accumulation of silt would not enhance the performance of *E. modestus* directly, but the ability to resist periods of burial by mud would considerably increase competitive ability of *E. modestus* compared to native species in estuarine areas. In this sense, *E. modestus* would be ecologically similar to "sand-tolerant" species described for rocky shores impacted by sandy sediment and which are able to adjust to stress imposed by sediments and be indirectly benefited by reduced competition (e.g. Taylor & Littler, 1982: Littler et al. 1983; D'Antonio, 1986; Airoldi & Cinelli, 1997).

Higher tolerance to siltation is one of the characteristics believed to have contributed to the successful invasion of British and European estuaries by *E. modestus* (Crisp, 1958). Several field observations lead to proposals that sediment deposition has detrimental effects on the physiology of barnacles and influences their distribution (Purchon, 1937; Doochin & Smith, 1951; Crisp, 1958; Naylor, 1971; Daly & Mathieson 1977; Little & Smith, 1980; Seapy & Littler 1982; Mettam, 1994; Menge et al., 1994; Silina, 2002), but the results presented here provided the first direct experimental evidence for the physiological mechanisms involved in this process.

The impact of mud deposition along the horizontal extension of estuaries increases towards the riverine end of estuaries. In the estuaries investigated in this study, observations of barnacles (*E. modestus*) buried by mud were especially common at the upper reaches of the estuaries. Additionally, sediment traps and also boulders supporting barnacles transplanted to estuarine locations accumulated sediment, clearly

more so at experimental sites located in the upper reaches of the estuaries (see Chapter 3). This correlates with patterns of distribution and dominance of *E. modestus* in these estuaries. *E. modestus* is the only species found near the riverine end of the estuaries and the predominance of this species relative to *S. balanoides* and *C. montagui* increases progressively towards these areas (see Chapter 2). Obviously, this observation does not imply a causal relationship, but siltation and burial could potentially contribute to these patterns.

Lower levels of the shore tend to be more affected by sedimentation and subjected to excessive deposition leading to burial than higher levels on intertidal rocky shores (Taylor & Littler, 1982; Littler et al., 1983; Airoldi, 2003). On some occasions this may result in deviation from the general model of vertical distribution of intertidal assemblages by which upper limits of the shore are set by physical and lower by biological factors (Taylor & Littler, 1982; Littler et al, 1983). In a similar way, it is possible that in estuarine intertidal areas, especially at inner reaches of estuaries where sedimentation tends to be higher, siltation is the major physical factor influencing zonation and determining lower limits of species distribution. The results obtained here suggest that *E. modestus* is highly tolerant to accumulation of sediments and may benefit from this condition in natural habitats.

CHAPTER 5

RECRUITMENT OF BARNACLES IN ESTUARIES

5.1. Introduction

Patterns of settlement and recruitment can have considerable influence on dynamics of populations and community structure of marine species (Underwood & Denley, 1984; Gaines & Roughgarden, 1985; Gaines et al., 1985; Booth & Brosnan, 1995; Underwood & Keough, 2001; Jenkins, 2005). Recruitment can be defined as the survival of juveniles for a period of time after settlement (Connell, 1985). Thus, it is a variable defined by the observer to describe the entry of new individuals into a population, sometimes to a particular phase (e.g. the adult population). In the case of barnacles and other sessile species with pelagic larval stages, recruitment incorporates 1) settlement, which is the process through which an individual leaves the water column and permanently attaches to the substrata; 2) methamorphosis; and 3) initial post-settlement survival (Connell, 1985; Underwood & Denley, 1984).

Larval supply is one of the principal components that determines settlement, and in many cases, recruitment of marine invertebrates at a particular location (Hawkins & Hartnoll, 1982; Gaines et al., 1985; Bingham, 1992; Minchinton & Scheibling, 1993). Studies using intertidal barnacles have demonstrated that larval supply can be a major determinant of assemblage structure (Underwood & Denley, 1984; Caffey, 1985; Connell, 1985; Gaines & Roughgarden, 1985; Roughgarden & Iwasa, 1986; Raimondi, 1990; Sutherland, 1990). Post-settlement interactions have greater importance when settlement occurs at high densities, while larval supply tends to be more influential at lower settlement densities (Underwood & Denley, 1984; Caffey, 1985; Connell, 1985;

Gaines & Roughgarden, 1985; Roughgarden, 1986, Raimondi, 1990; Sutherland, 1990; Menge, 2000).

Extensive experimental studies on the ecology of intertidal barnacles have demonstrated the importance of settlement and recruitment in shaping adult populations. This occurs mainly by setting initial densities and distribution of individuals within and between shores, and consequently, determining the environmental conditions to which individuals are exposed and influencing post-settlement intraspecific and interspecific interactions (e.g. Connell 1961a, 1961b, 1970; Grosberg, 1982; Hawkins & Hartnoll, 1982; Underwood & Denley, 1984; Gaines & Roughgarden, 1985; Raimondi, 1990, 1991; Minchinton & Scheibling, 1991; Bertness et al., 1992; Gaines & Bertness, 1992; Jenkins et al, 1999). Therefore, understanding events that cause variations in settlement and recruitment of benthic organisms is a crucial step in explaining spatial patterns of adult distribution.

Invertebrate larvae are dispersed both by passive transport associated with hydrodynamic factors, especially at large spatial scales (Hawkins & Hartnoll, 1982; Shanks, 1983; Gaines et al., 1985 Bertness et al, 1992, 1996; Hyder et al, 1998, Queiroga et al., 2003); or by active transport originated by vertical and horizontal movements over small spatial scales (Grosberg, 1982, Raimondi, 1991; Young, 1995); or a mixture of both (e.g. Ross, 2001; Queiroga & Blanton, 2005). In estuaries, several mechanisms of active transport linked to tidal movements have been shown in barnacles and other invertebrates. These can produce patterns of distribution along estuarine gradients by controlling the direction of larval transport (seaward or landward) (e.g. Bousfield, 1955; Dittel & Epifanio, 1990; Hui & Moyse, 1987; Paula et al, 2003; Queiroga et al., 1998, 2006), which in turn influence settlement.

Recently the importance of larval supply and initial benthic stages of barnacle species in determining their distribution along estuarine gradients has been clearly

demonstrated in mangrove forests. For example, the density and availability of cyprids of *Elminius covertus* and *Hexaminius popeiana* at differing distances from the seaward edge of estuaries mirrored settlement patterns, recruitment and adult distributions, with post-settlement mortality having little influence (Satumanatpan et al., 1999; Satumanatpan & Keough, 2001; Ross, 2001). Alternatively, work on *S. balanoides* revealed that settlement was correlated with larval concentration in the water column, but factors affecting early juvenile mortality ultimately determined recruitment and distribution of this species (Leonard et al., 1999; Pineda et al., 2002).

It has long been recognized that *E. modestus* is particularly successful in protected and estuarine areas in its native geographic region of Australasia (Moore, 1944; Foster, 1978, 1982). This species is invasive in similar habitats in many other parts of the world (Fischer-Piette and Prenant, 1956, 1957; Fischer-Piette and Forest, 1961; Fischer-Piette, 1965; Southward and Crisp, 1956; Beard, 1957; Crisp and Southward, 1959; Barnes and Barnes, 1961, 1965; Crisp. 1958; Hiscock et al., 1978; King et al, 1997; Harms, 1999; Lawson et al., 2004). One of the main explanations for the success of *E. modestus* in invading and dominating estuarine areas lies in its high fecundity (Crisp, 1958; Harms, 1999; Lawson et al., 2004). *E. modestus* can produce much greater numbers of larvae per brood than any native European barnacle (Crisp & Davies, 1955), and produces multiple broods throughout much of the year (Knight-Jones, 1948; O'Riordan & Murphy, 2000). This is believed to result in high rates of settlement and recruitment which facilitate invasions and may ultimately lead to dominance (Den Hartog, 1953; Crisp, 1958; Harms, 1999; Lawson et al., 2004). Despite this, few studies have focused on settlement and recruitment of *E. modestus* (Harms & Anger, 1989; Watson et al., 2005).

In this Chapter, I use estuaries where patterns of distribution and abundance of barnacles along the estuarine gradient have been described (Chapter 2), to investigate

the role of settlement and recruitment in determining the distribution of marine species in estuaries. In addition, this study aims to further our understanding of the mechanisms that facilitate successful invasions by *E. modestus* and lead to its dominance in estuaries. Watson et al. (2005) demonstrated that *E. modestus* dominated intertidal recruitment at Lough Hyne and suggested that larval retention, which is promoted by the extremely sheltered condition of the Lough, played an important role in this dominance and on the process of invasion. Further investigations on the initial benthic stages of barnacles in estuaries where *E. modestus* dominates available surfaces are necessary to test the importance of larval retention and settlement, particularly in estuaries and other coastal areas with different hydrodynamics to Lough Hyne.

To achieve the aims described above, I tested the general hypothesis that patterns of distribution and abundance of adult barnacles in estuaries are determined by patterns of abundance of cyprids and recruitment along the estuarine gradient. Specifically, the following hypotheses relative to spatial (positions along the estuarine gradient), temporal (within months and years) and between-species variability in settlement and recruitment will be tested: 1. The relative abundance of cyprids among estuarine sites located at differing distances from the sea vary between species, with *E. modestus* showing a greater relative proportion of cyprids at the mid and upper sites than species with a more limited degree of penetration in the estuaries; 2. Recruitment of species varies at differential distances from the sea and corresponds to the adult pattern of distribution; and 3. There is no modification on the pattern set by settlement after a longer period of recruitment (7 months).

5.2. Methods

5.2.1. Recruitment

Unglazed ceramic tiles (10 x 10 cm) were utilised as substrata for barnacle settlement. These identical artificial panels were used to minimize surface heterogeneity caused by differing settlement cues related to natural biofilms and previous occupation of substrata by conspecifics. Panels were attached at mid-shore intertidal levels. At sites where *E. modestus*, *S. balanoides* and *C. montagui* were present, panels were attached to vertical areas where adults of the three species occurred. Panels were deployed in April 2003 and 2004 at three sites located at different distances from the mouths of the Yealm and Plym Estuaries (Fig. 5.1). These sites differed in salinity regime and levels of sedimentation as described in Chapter 3. Additional sets of tiles remained at each site for the entire periods of study (April to November in 2003 and 2004) in each site to assess patterns of recruitment over a greater temporal scale (7 months).

Ten replicate tiles were deployed at each site. Before deployment, tiles were seasoned by submergence for 24 hours in running seawater at the Marine Biological Association. Tiles were collected and replaced with new tiles every month from May to November. Attached post-metamorphosis individuals and cyprids were identified to species level and counted on each tile in the laboratory. Post-methamorphosis individuals represented recruitment that took place throughout the month, and hence incorporate a degree of post-settlement mortality. Counts of cyprids assessed the arrival of larvae during the period of submergence that immediately preceded collections. Only individuals in the inner area of 8 x 8 cm were analysed in order to minimise edge effects. *S. balanoides* were not observed on any of the tiles. *Balanus perforatus* and

Balanus crenatus were occasionaly found and are grouped in the analyses and graphics presented here. This group is hereby designated as *Balanus* species (*Balanus* spp.).
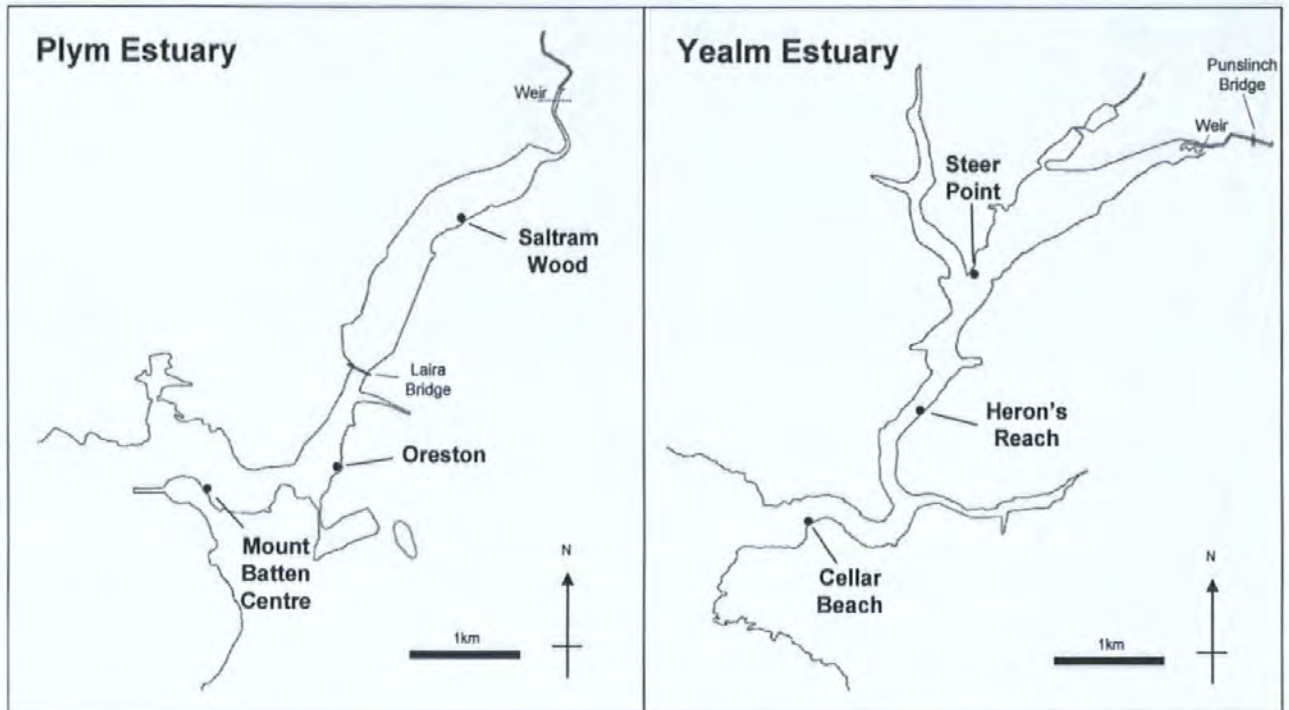
Fig. 5.1. Location of sites used to assess recruitment (●) in the Plym (Saltram Wood, Oreston and Mount Batten Centre) and the Yealm (Steer Point, Heron's Reach and Cellar Beach).

5.2.2. Statistical Analyses

Variations in monthly recruitment of *E. modestus*, *C. montagui* and *Balanus* species in each estuary were assessed by separate three-way factorial ANOVA tests with year, site and month as factors. Differences in the number of cyprids between sites within each estuary were compared using two-way ANOVA with date of collection and site as factors. Variations in longer-term recruitment (7 months) between sites and species were assessed by ANOVA tests with year, taxon (*E. modestus*, *C. montagui* and *Balanus* spp.) and sites as factors. Data utilised in all analysis were transformed to

square root to achieve requirements of ANOVA tests. Post-hoc tests (SNK test, p > 0.05) were performed to test for differences between means.

5.3. Results

5.3.1. Monthly Recruitment – 30 day panels

5.3.1.1. Plym Estuary

Recruitment of *C. montagui* was not detected at any site in the Plym in 2003 or 2004. *B. perforatus* was observed in August 2003 at Oreston, but only two recruits in total were detected on the 10 panels collected. Spatial (site/distance from the sea) and temporal factors (year and month) were all highly significant in explaining variability in recruitment of *E. modestus* (Table 5.1). Recruitment of this species varied for each year, at each site and for each month (Table 5.1). There was a 3-way interaction between year, site and month. However, most of the variability was associated with site and month as indicated by F values (Table 5.1).

In 2003, recruitment of *E. modestus* at Saltram Wood (site located further up estuary) was poor on all sampling occasions and was remarkably different from sites located in the lower parts of the estuary (Oreston and Mount Batten Centre) (Fig. 5.2). Most recruits in Saltram Wood were observed in September, but this was significantly less than recruitment peaks at Oreston and Mount Batten Centre. No significant differences existed between monthly recruitment of *E. modestus* at Oreston (intermediate site) and Mount Batten Centre (closest site to the sea) throughout the year. Recruitment at these two sites occurred from July to October with a peak in September.

Recruitment of *E. modestus* at the upper site (Saltram Wood) in 2004 was significantly higher than in 2003. The pattern of recruitment at Saltram Wood in 2004

was similar to recruitment in the intermediate site (Oreston) (Fig. 5.2) and no significant differences were detected between these sites in any of the months sampled. Recruitment at these sites took place from July to September, with maximum values in August. Recruitment at Oreston in July and August in 2004 was similar to recruitment in the same months in 2003. The main difference between years at Oreston was the strong peak observed in September 2003, which was not repeated in September 2004 (Fig. 5.2).

Recruitment at the Mount Batten Centre was greater in August and October 2004 than in the corresponding months in 2003 (Fig. 5.2), but there were no significant differences between the peaks of recruitment observed in September 2003 and 2004. In comparison to recruitment at other sites in 2004, there was a significantly greater recruitment at the Mount Batten Centre than at Oreston in September and October; and than at Saltram Wood in July, August and October (Fig. 5.2).

Table 5.1. Three-way ANOVA (factor 1: Year, factor 2: Site, factor 3: Month) on density of *E. modestus* recruits in panels deployed for 30 days in the Plym Estuary in 2003 and 2004.

Source	Df	MS	F	P
Year	1	4.11	17.28	< 0.001
Site	2	11.91	50.05	< 0.001
Month	6	18.91	79.48	< 0.001
Year*Site	2	2.33	9.80	< 0.001
Year*Month	6	2.21	9.27	< 0.001
Site*Month	12	2.29	9.64	< 0.001
Year*Site*Month	12	0.70	2.93	< 0.001
Error	355	0.24		
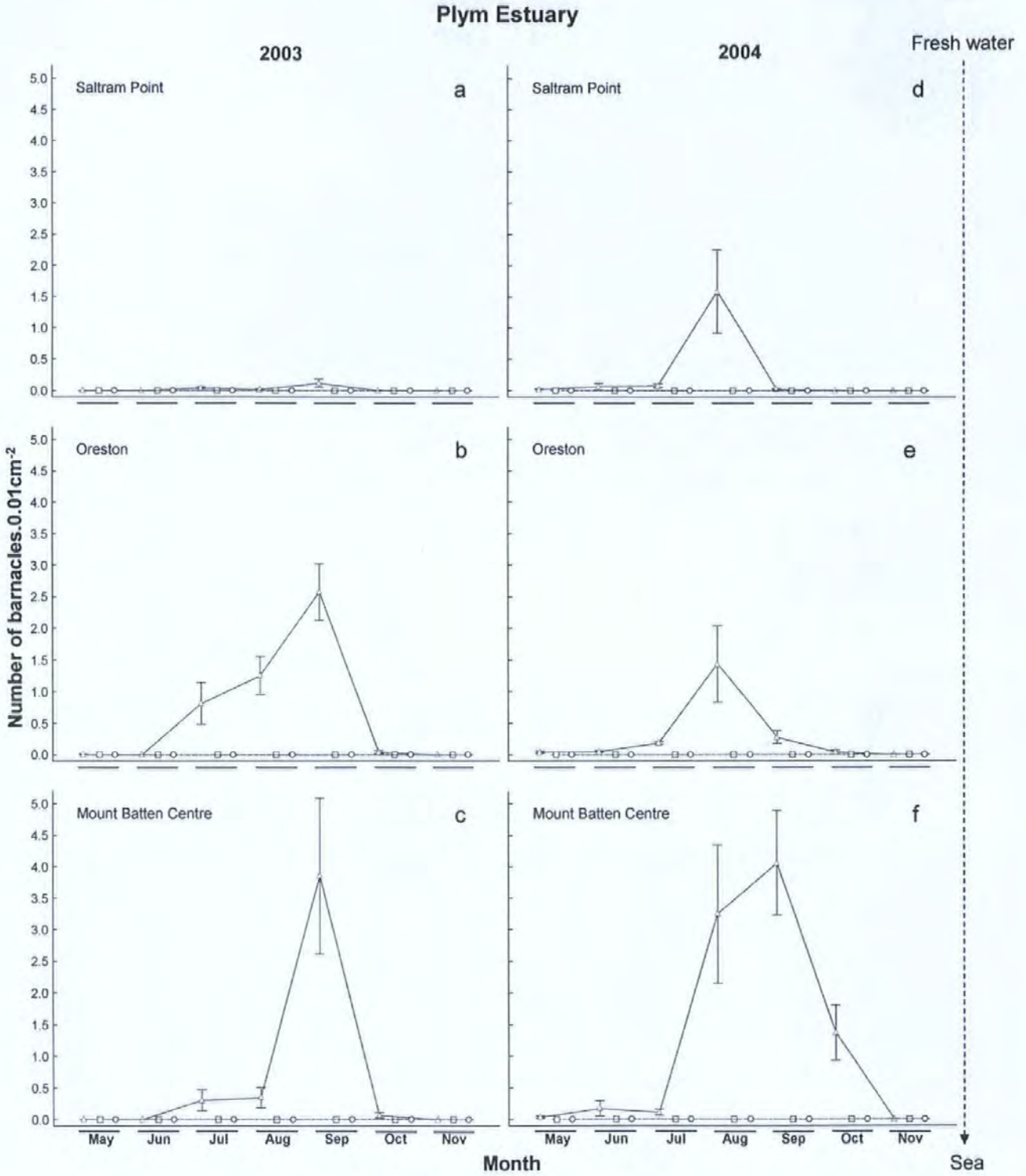
Plym Estuary

Fig. 5.2. Recruitment of *E. modestus, C. montagui* and *Balanus* species in the Plym Estuary during 2003 and 2004. Saltram Wood was the uppermost site and Mount Batten Centre the closest site to the sea. Each data point represents the mean of ten replicates. Bars represent standard error.

—△— *Elminius modestus*   - □- *Chthamalus montagui*   ···O·· *Balanus* spp.

5.3.1.2. Yealm Estuary

For *E. modestus*, there was significant interaction between year and site and month (Table 5.2). No significant differences occurred between years in corresponding months in 2003 and 2004 in the upper site (Steer Point). There were no statistical differences between the maximum monthly recruitment observed in each year (September in 2003; and August in 2004) (Fig. 5.3). No differences between years occurred at the midpoint site (Heron's Reach), except for recruitment in October, which was significantly higher in 2004 than in the previous year (Fig. 5.3).

At the mouth of the Yealm (Cellar Beach) recruitment was very high in September 2003 (Fig. 5.3), significantly higher than at any other month in 2003 or 2004. Apart from this month, recruitment was similar between corresponding months in 2003 and 2004. Most recruitment was observed from July to October in both years. Recruitment in Cellar Beach was higher than in both Heron's Reach and Steer Point from August to September in both years.

Table 5.2. Three-way ANOVA (factor 1: Year, factor 2: Site, factor 3: Month) on density of *E. modestus* recruits in panels deployed for 30 days in the Yealm Estuary in 2003 and 2004.

Source	df	MS	F	P
Year	1	0.17	0.42	0.517
Site	2	24.73	62.69	< 0.001
Month	6	19.74	50.04	< 0.001
Year*Site	2	6.59	16.70	< 0.001
Year*Month	6	3.74	9.47	< 0.001
Site*Month	12	1.91	4.85	< 0.001
Year*Site*Month	12	1.53	3.88	< 0.001
Error	322	0.39		

Yealm Estuary

Fig. 5.3. Recruitment of *E. modestus, C. montagui* and *Balanus* species in the Yealm Estuary during 2003 and 2004. Steer Point was the uppermost site and Cellar Beach the closest site to the sea. Note the different scale used for Cellar Beach. Each data point represents the mean of ten replicates. Bars represent standard error.

—△— *Elminius modestus*   -□- *Chthamalus montagui*   ··O·· *Balanus* spp.

For *C. montagui* there was a significant interaction between year, site and month. Apart from recruits observed in Cellar Beach, only one individual of *C. montagui* was found in the Yealm (Heron's Reach in September 2003) (Fig. 5.3). Recruitment of *C. montagui* in Cellar Beach varied between years and months (Table 5.3). In 2003, recruitment occurred in August and September; while in 2004, it was only detected in August (Fig. 5.3). Recruitment in both months in 2003 was significantly higher than in August 2004.

Table 5.3. Three-way ANOVA (factor 1: Year, factor 2: Site, factor 3: Month) on density of *C. montagui* recruits in panels deployed for 30 days in the Yealm Estuary in 2003 and 2004.

Source	Df	MS	F	P
Year	1	1.11	79.44	< 0.001
Site	2	4.63	330.62	< 0.001
Month	6	2.42	172.48	< 0.001
Year*Site	2	0.93	66.59	< 0.001
Year*Month	6	0.68	48.85	< 0.001
Site*Month	12	2.14	152.85	< 0.001
Year*Site*Month	12	0.56	39.99	< 0.001
Error	324	0.01		

For recruitment of *Balanus* spp. there was also a 3-way interaction between year, site and month (Table 5.4). Recruitment of this group varied considerably between months and reached considerable but differing values in August during both years (Fig. 5.3).

Table 5.4. Three-way ANOVA (factor 1: Year, factor 2: Site, factor 3: Month) on density of *Balanus* spp. recruits in panels deployed for 30 days in the Yealm Estuary in 2003 and 2004.

Source	Df	MS	F	P
Year	1	0.03	2.19	0.139
Site	2	0.87	57.27	< 0.001
Month	6	0.48	31.57	< 0.001
Year*Site	2	0.03	2.06	0.129
Year*Month	6	0.05	3.59	0.002
Site*Month	12	0.44	28.63	< 0.001
Year*Site*Month	12	0.05	3.38	< 0.001
Error	324	0.01		

5.3.2. Cyprids

5.3.2.1. Plym Estuary

Cyprids of *C. montagui* and *Balanus* species were found in very low numbers in the Plym, mainly in August and September (Fig. 5.4 and 5.5.). In 2003, cyprids of *Balanus* species settled at Oreston and the Mount Batten Centre in August (Fig. 5.4). *C. montagui* settled at Mount Batten Centre in August and at all sites in September (Fig. 5.4). In 2004, cyprids of these two groups were only detected at the site closest to the sea (Mount Batten Centre) in August (Fig. 5.4). However numbers of individuals were too low to permit formal testing.

E. modestus cyprids were found in higher numbers than the other barnacle species and were detected at all sites, at least on one of the sampled dates, both in 2003 and 2004 (Fig. 5.4 and 5.5). There was a significant interaction between site and month (Table 5.5). In 2003, settlement of cyprids was significantly higher in August and September than in the other months. In August, the number of settled cyprids was significantly higher in the mid site (Oreston) than in the upper site (Saltram Wood) and lower site (Mount Batten Centre) (Fig. 5.4.). In September, higher numbers of cyprids were detected in Mount Batten Centre than in the former month, and these densities were similar to those at Oreston (Fig. 5.4).

Table 5.5. Two-way ANOVA (factor 1: Site, factor 2: Month) on density of *E. modestus* cyprids in panels in the Plym Estuary in 2003.

Source	Df	MS	F	P
Site	2	10.75	43.53	< 0.001
Month	6	18.56	75.13	< 0.001
Site*month	12	5.06	20.50	< 0.001
Error	178	0.25		
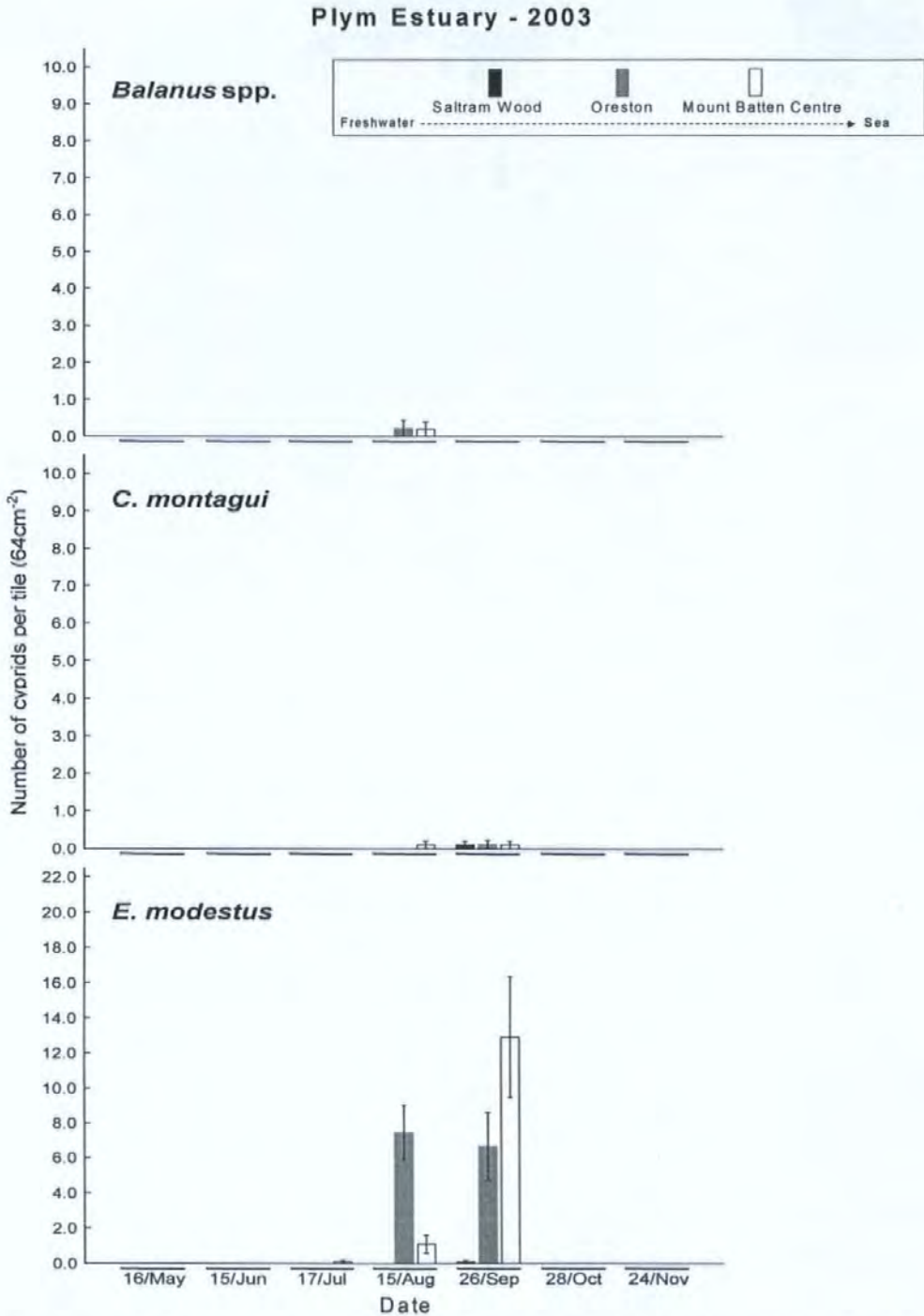
Plym Estuary - 2003

Fig. 5.4. Density of cyprids *Balanus* species, *C. montagui* and *E. modestus* in the Plym Estuary in sampling dates in 2003. Saltram Wood was the uppermost site and Mount Batten Centre the closest site to the sea. Each data point represents the mean of ten replicates. Bars represent standard error.

Settlement of cyprids of *E. modestus* was higher at Saltram Wood in 2004 than in 2003. There was a significant interaction between site and month (numbers of cyprids

at this site were comparable to those in the two lower sites in the July and August samples. In September, cyprid numbers at the Mount Batten Centre were significantly higher than at any other sampled site or date.
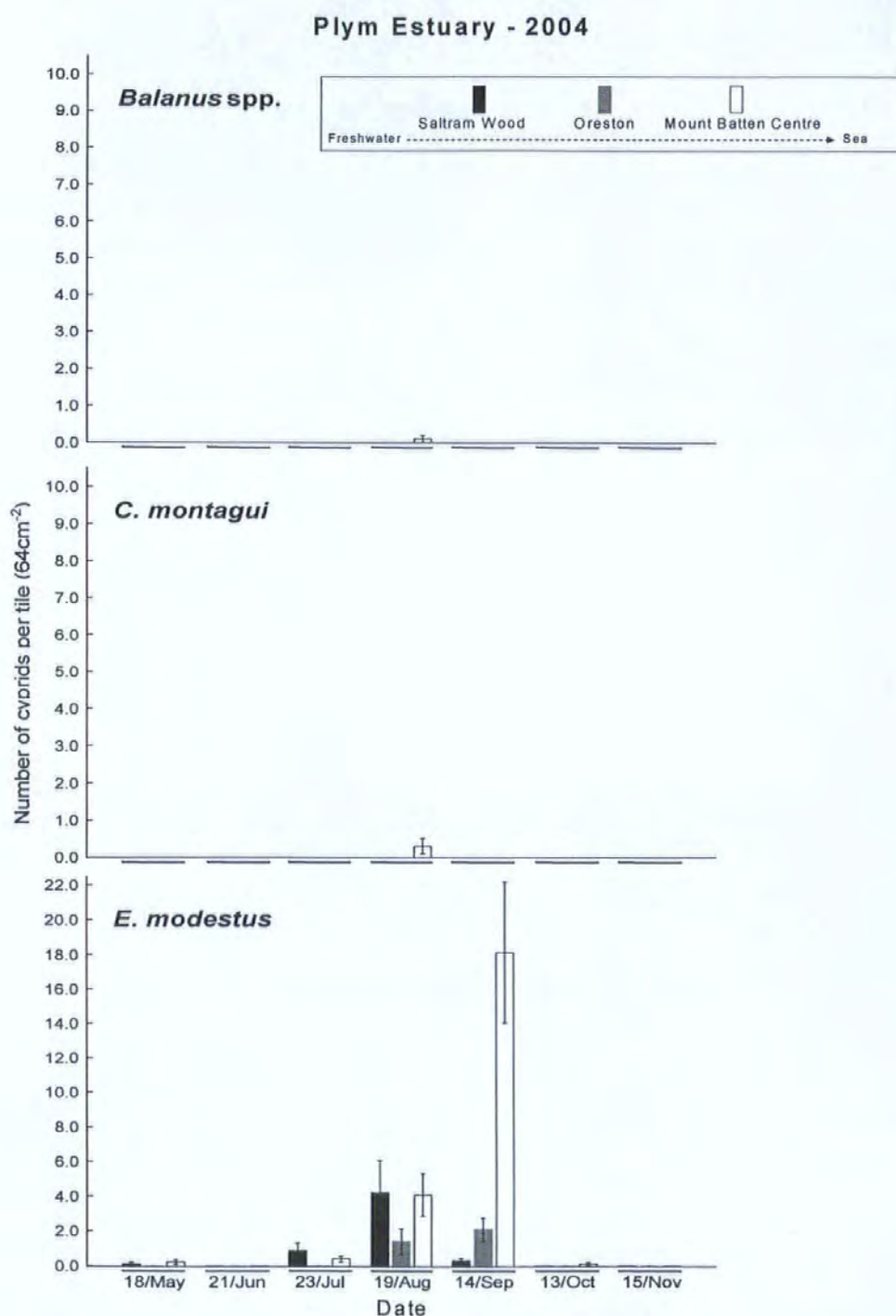
Fig. 5.5. Density of cyprids of *Balanus* species, *C. montagui* and *E. modestus* in the Plym for sampling dates in 2004. Saltram Wood was the uppermost site and Mount Batten Centre the closest site to the sea. Each data point represents the mean of ten replicates. Bars represent standard error.

Table 5.6. Two-way ANOVA (factor 1: **Site**, factor 2: **Month**) on **density of *E. modestus*** cyprids in panels in the **Yealm Estuary** in 2004.

Source	df	MS	F	P
Site	2	7.04	9.89	< 0.001
Month	6	16.08	22.58	< 0.001
Site*month	12	2.41	3.38	< 0.001
Error	177	0.71		

5.3.2.2. Yealm Estuary

In 2003, settlement of *C. montagui* and *Balanus* species at the mouth of the Yealm (Cellar Beach) reached higher values than in the mouth of the Plym either in 2003 or in 2004 (Fig. 5.6). In contrast to the Plym, cyprids were only found at this site and were absent from the sites located in the upper reaches of the estuary (Heron's Reach and Steer Point) (Fig. 5.6). In 2004 numbers of cyprids of these groups were extremely low at all sites (Fig. 5.6).

The number of cyprids of *E. modestus* sampled in the Yealm tended to be lower than in the Plym. In 2003, results were different from those obtained in the Plym, where the numbers of cyprids of *E. modestus* in mid and upper sites were comparable to numbers in the site located in the mouth of the estuary; cyprids in the Yealm were more abundant in Cellar Beach than at sites located in upper areas of the estuary. On some occasions this was the only site where cyprids were found (Fig 5.6). There was a significant interaction between site and month (Table 5.7).

Table 5.7. Two-way ANOVA (factor 1: **Site**, factor 2: **Month**) on **density of *E. modestus*** cyprids in panels in the **Yealm Estuary** in 2003.

Source	df	MS	F	P
Site	2	0.05	33.99	< 0.001
Month	6	0.05	40.14	< 0.001
site*month	12	0.03	21.11	< 0.001
Error	167	0.001		
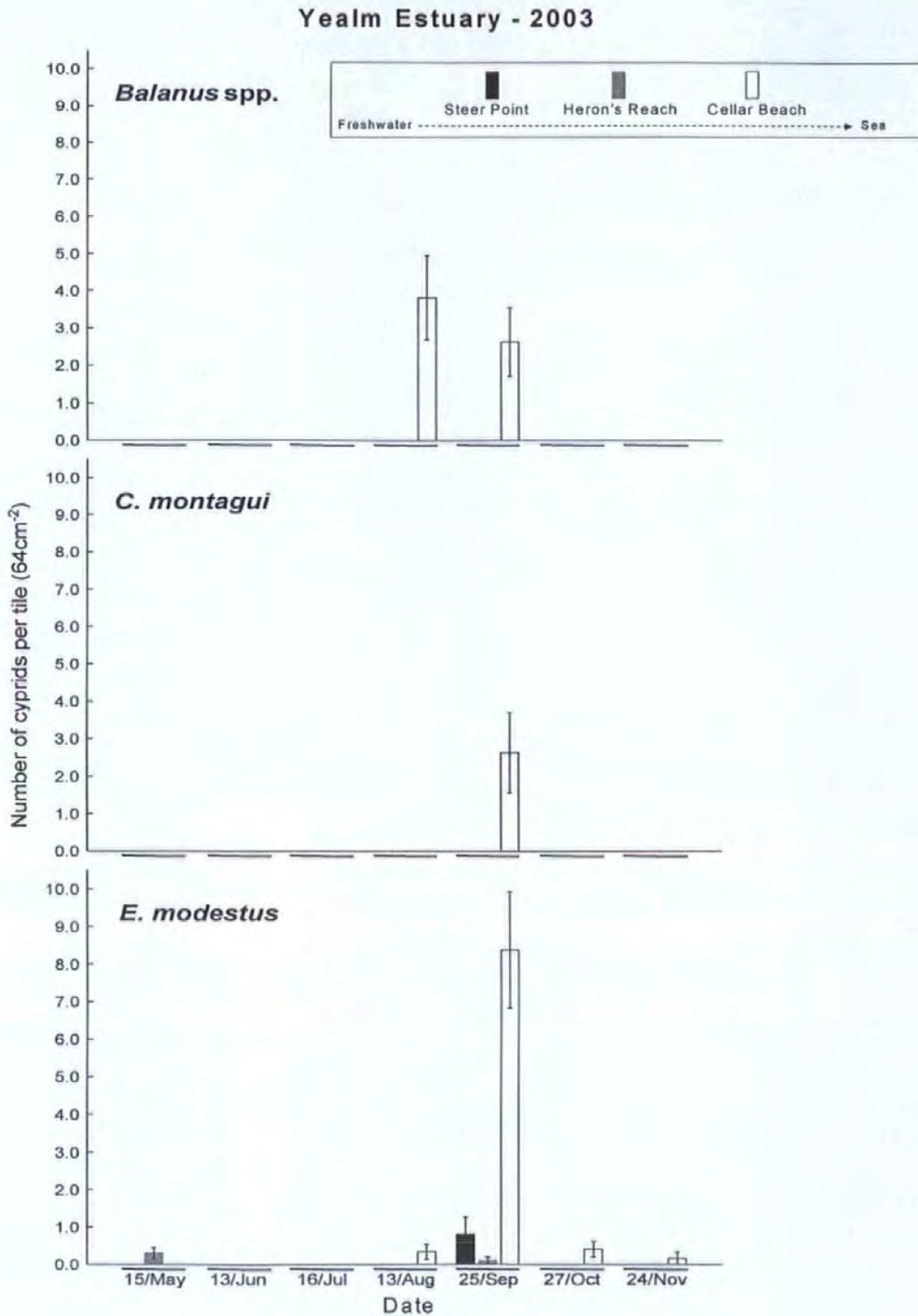
Fig. 5.6. Densities of cyprids of *Balanus* species, *C. montagui* and *E. modestus* in the Yealm Estuary for sampling dates in 2003. Steer Point was the uppermost site and Cellar Beach the closest site to the sea. Each datum point represents the mean of ten replicates. Bars represent standard error.

In 2004, the occurrence of *E. modestus* cyprids was more similar between sites (Fig 5.7) than in 2003, and no significant interaction existed between site and months (Table 5.8).
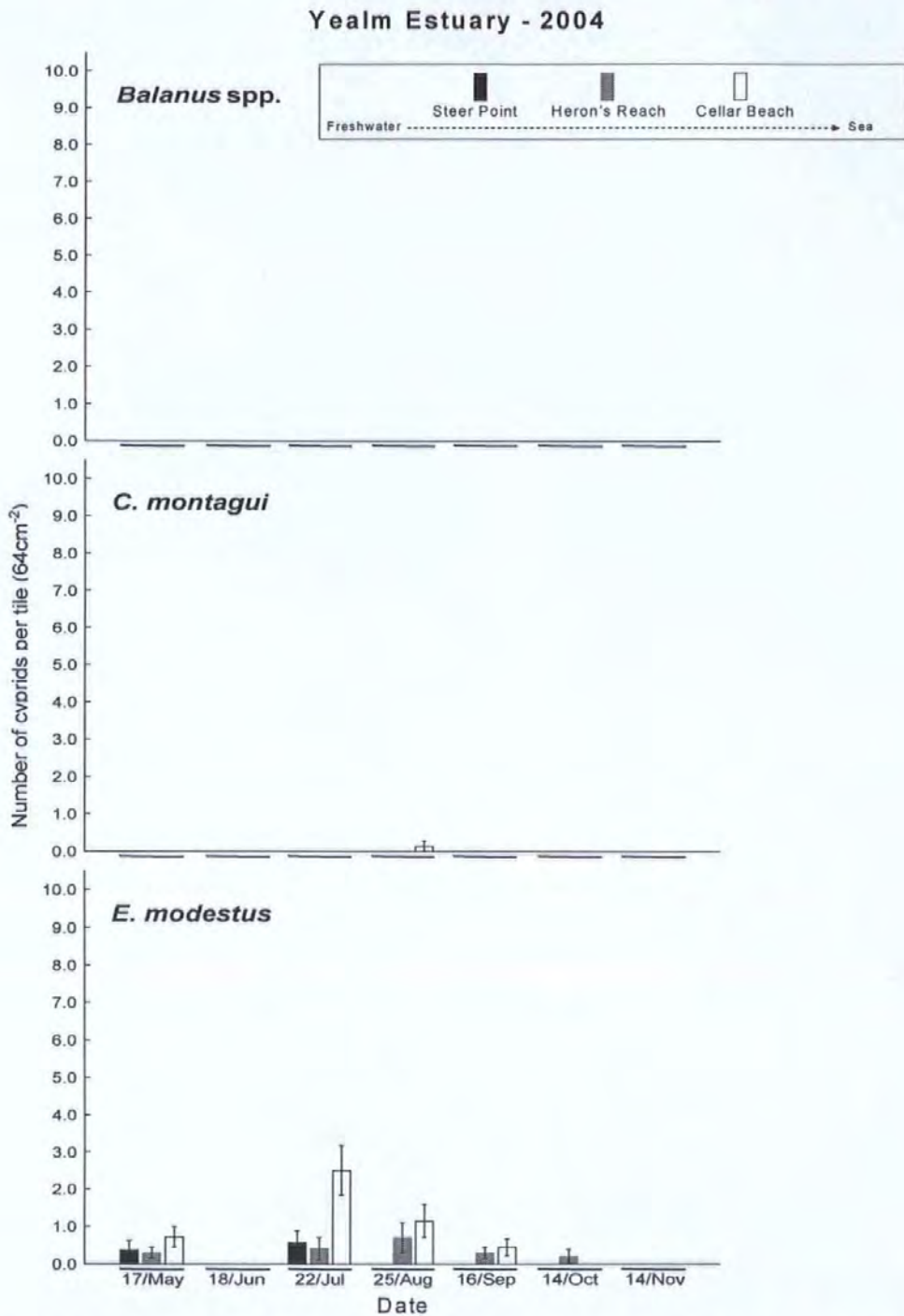
Yealm Estuary - 2004

Fig. 5.7. Densities of cyprids of *Balanus* species, *C. montagui* and *E. modestus* in the Yealm Estuary for sampling dates in 2004. Steer Point was the uppermost site and Cellar Beach the closest site to the sea. Each data point represents the mean of ten replicates. Bars represent standard error.

Table 5.8. Two-way ANOVA (factor 1: Site, factor 2: Month) on density of *E. modestus* cyprids in panels in the Yealm Estuary in 2004.

Source	df	MS	F	P
Site	2	9.04	8.10	< 0.001
Month	6	7.62	6.84	< 0.001
Site*month	12	1.76	1.58	0.103
Error	157	1.11		

5.3.1. Cumulative recruitment (7 months)

5.3.2.1. Plym Estuary

Patterns of cumulative recruitment over 7 months along the Plym estuary were similar between years (Fig. 5.8). Recruitment of *C. montagui* and *Balanus* species was virtually absent in 2003 and 2004 at all sites (Fig. 5.8). Results of ANOVA tests show that there were no significant difference between years, and no interactions between year or the other two factors (Taxon and Site) (Table 5.9). Distance from the sea (Site) is the factor that accounts for most of the variability in recruitment of *E. modestus*. There were no significant differences in recruitment of *E. modestus* between Mount Batten Centre and Oreston, and at both sites it was significantly greater than at Saltram Wood (Fig. 5.8).
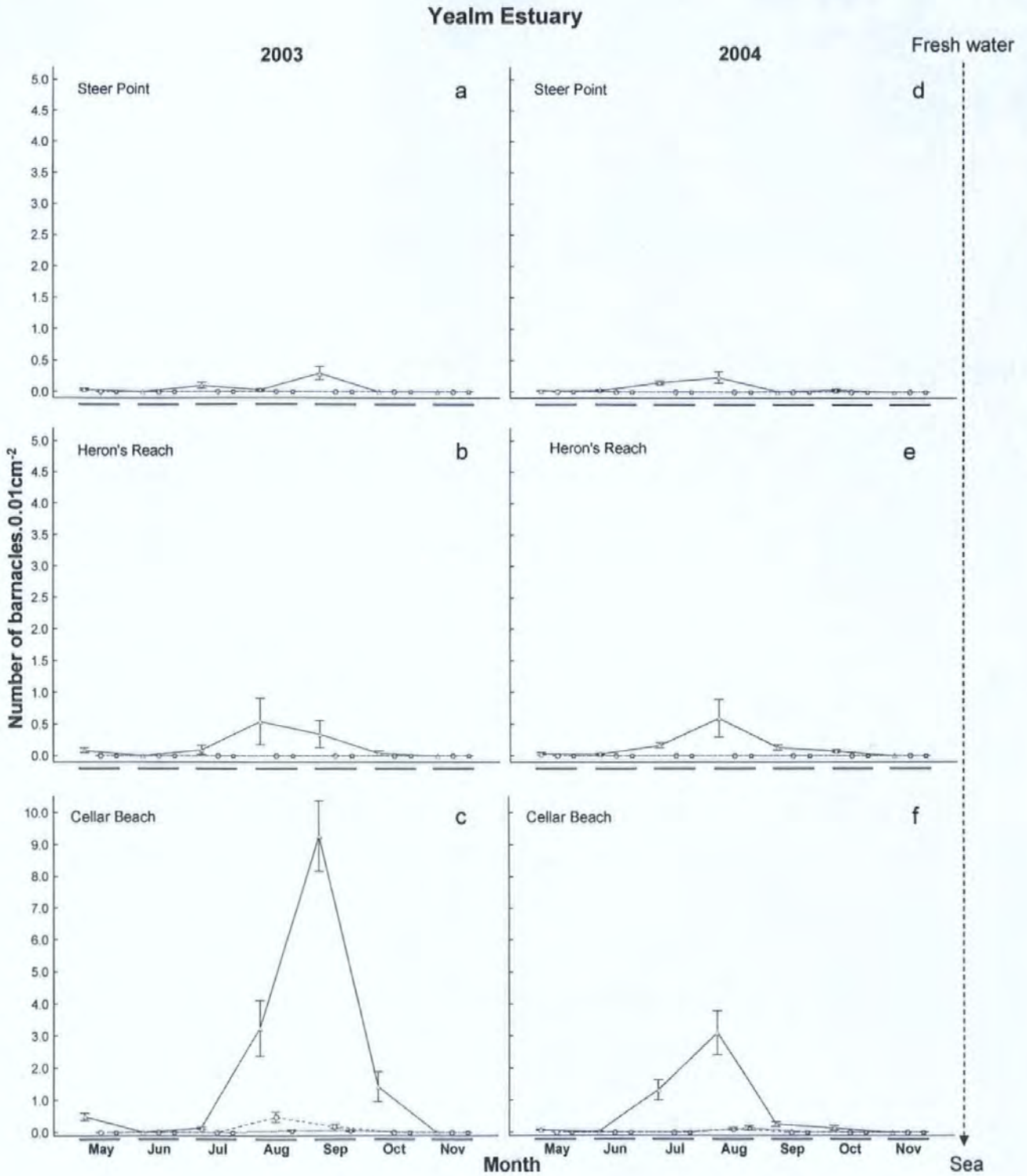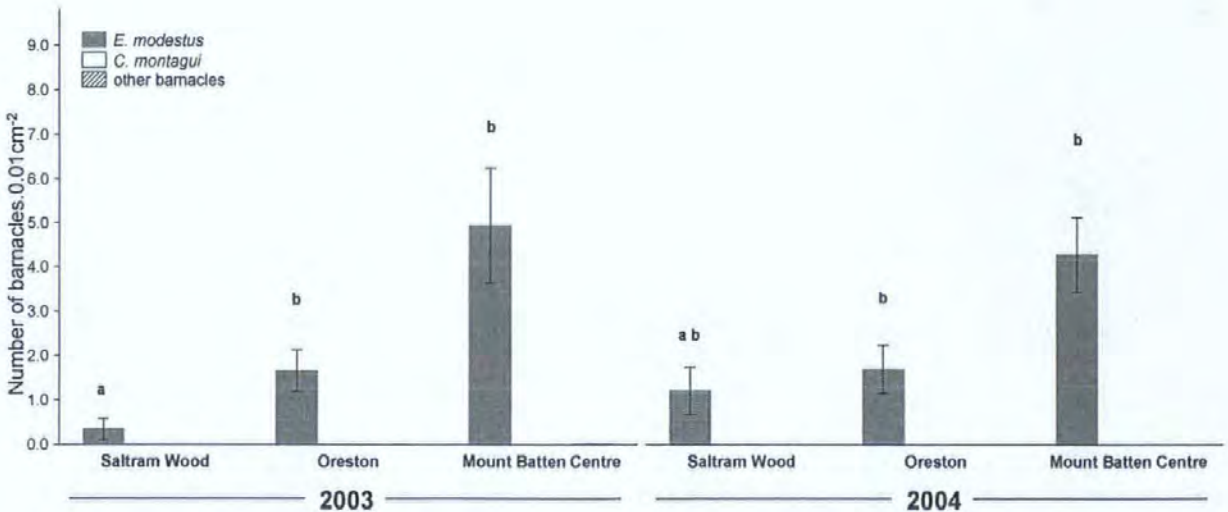

Fig. 5.8. 7-month recruitment of *E. modestus, C. montagui* and *Balanus* species in the Plym Estuary in 2003. Saltram Wood was the uppermost site and Mount Batten Centre the closest site to the sea. Each column represents the mean of ten replicates. Bars represent standard error. Letters above bars represent homogeneous groups according to ANOVA (SNK test, $p > 0.05$).

Table 5.9. Two-way ANOVA (factor 1: Year, factor 2: Site) on 7-month recruitment of *E. modestus* on panels deployed from May to November in the Plym Estuary in 2003 and 2004.

Source	df	MS	F	P
Year	1	1.05	1.68	0.201
Site	2	7.36	11.75	< 0.001
Year*Site	2	0.75	1.19	0.312
Error	48	0.63		

5.3.2.2. Yealm Estuary

As in the Plym, there were no differences between years and no interactions between years and other factors (Table 5.10). Relative position within the estuarine gradient (Site) was the factor explaining variability in recruitment. However, two important differences in 7-month recruitment existed between the two estuaries: 1. there was recruitment of *C. montagui* and *Balanus* species (Cellar Beach) (Fig. 5.9); and 2. the pattern of recruitment along the estuary was different, and recruitment at the mouth of the Yealm was significantly higher than recruitment at the two upper sites for all species (Fig. 5.9).
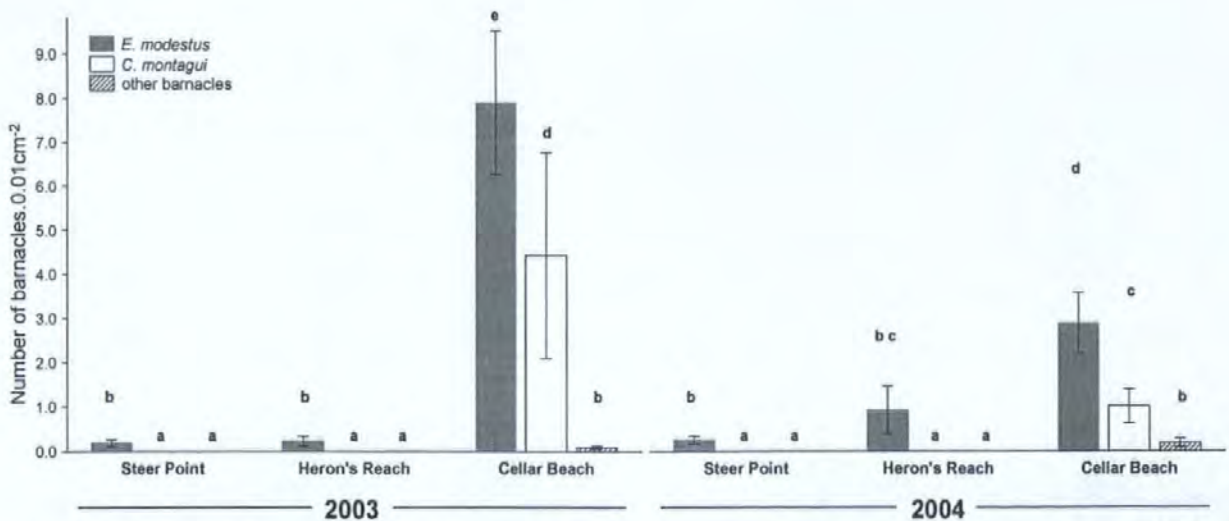
Fig. 5.9. 7-month recruitment of *E. modestus, C. montagui* and *Balanus* species in the Yealm Estuary in 2003. Saltram Wood was the uppermost site and Mount Batten Centre the closest site to the sea. Each column represents the mean of ten replicates. Bars represent standard error. Letters above bars represent homogeneous groups according to ANOVA (SNK test, p > 0.05).

Table 5.10. Three-way ANOVA (factor 1: Year, factor 2: Species, factor 3: Site) on 7-month recruitment of *E. modestus, C. montagui* and *Balanus* species on panels deployed from May to November in the Yealm Estuary in 2003 and 2004.

Source	df	MS	F	P
Year	1	0.10	0.49	0.485
Species	2	17.60	82.66	< 0.001
Site	2	25.24	118.57	< 0.001
Year*Taxon	2	0.15	0.72	0.488
Year*Site	2	0.63	2.94	0.056
Taxon*Site	4	1.25	5.86	< 0.001
Year*Taxon*Site	4	0.32	1.52	0.199
Error	132	0.21		

5.4. Discussion

The results clearly show that *E. modestus* dominated estuarine intertidal hard substrata at the settlement and recruitment stages. *E. modestus* was the only species with large numbers of cyprids and monthly recruitment at the inner sites of the estuaries investigated in this study. Recruitment over periods longer than a month (7 months) confirmed this dominance. Other barnacle species only recruited at the mouth of estuaries, wherer, in the case of *C. montagui*, comparable levels of recruitment to *E. modestus* were attained. These results highlight the importance of the initial stages in setting patterns of distribution of barnacles in estuaries. Patterns of distribution, abundance and settlement of larvae along the estuarine gradient are probably the main determinants of the observed recruitment patterns. There was temporal and spatial variability in settlement and recruitment. Temporal patterns of settlement throughout the year correlated well with the reproductive cycle of the species examined. Variability along the estuarine gradient was detected, with greater settlement and recruitment occurring at seaward locations and decreasing with increased distance from the sea for all species.

5.4.1. Settlement and larval supply

As distinct from the counts of post-methamorphosis individuals, which encompassed individuals that arrived throughout the month and survived to the time of collection of tiles, cyprid counts represented a snapshot in time, rather than a picture of the settlement throughout a particular month. Although this variable did not represent settlement intensity during the month, it did allow the comparison of settlement between sites at definite moments in time when sites were simultaneously sampled.

The distribution of cyprids in the estuaries suggests that patterns of recruitment are largely determined by settlement. No cyprids of *C. montagui* and *Balanus* species, or on some occasions very few, were observed at sites located in inner reaches of the estuaries. This contrasted with sites located at the mouth of the estuaries where greater numbers of cyprids settled. This pattern of settlement coincided with the general pattern of distribution of these species in the estuaries, which is characterized by lower abundance or absence of these groups in mid and upper reaches of the estuaries. The only deviation from this was observed for *C. montagui* at the midpoint of the Yealm. At this position (Heron's Reach) *C. montagui* was present during the surveys, although no evidence of recent settlement was detected. Settlement of *C. montagui* at this location may constitute an occasional event with settlement failure being the norm. In other estuaries, settlement and recruitment of this species in the proximity of its uppermost limits of occurrence within estuaries, also appears to be irregular. For example, in the Rance estuary, *C. montagui* populations found in the inner areas of the estuary consisted of old and weathered specimens (Little & Mettam, 1994); while in the Severn, monitoring of recruitment at transects where adults were found over three successive years revealed no settlement or recruitment (Mettam, 1994). This indicated that these populations are formed by individuals that settled in particular years but where there is

no consistent annual input of recruits. This may be the case for populations found in the Yealm and also in the Plym, and considering the similarities between these two estuaries and others in the region, settlement is possibly a widespread but occasional phenomenon in estuaries inhabited by this species.

Several studies have shown that adult distribution of barnacles can be strongly determined by settlement (e.g. Underwood & Denley, 1984; Connell, 1985; Gaines & Roughgarden, 1985; Gaines et al., 1985; Raimondi, 1990; Minchinton & Scheibling, 1991; Jenkins, 2005). The results here highlight the importance of settlement along the estuarine gradient. In other estuaries, variations in settlement were also shown to be responsible for differences in recruitment along the sea-to-freshwater gradient (Ross & Underwood, 1997; Ross, 2001; Satumanatpan et al., 1999). Across mangrove estuaries where density of *E. covertus* decreased towards the riverine end of the estuaries, horizontal settlement patterns were shown to mirror adult distribution, suggesting that settlement patterns were the main cause of the observed adult distribution (Ross & Underwood, 1997; Ross, 2001; Satumanatpan et al., 1999).

E. modestus also showed greater settlement at the mouth of the estuaries than at sites located in mid and upper reaches, but this was not a consistent pattern for this species. On many of the dates sampled *E. modestus* cyprids settled in comparable numbers at all sites. This species is found in great abundance from seaward areas up to the innermost limits of estuaries. In contrast to the other barnacle species studied here, populations within estuaries constitute the main source of competent larvae of *E. modestus* for settlement. Thus, the occurrence of heavy cyprid settlement in the mid and upper reaches of the estuaries was expected. On the other hand, this species is more abundant in inner regions than in the seaward limits of estuaries as demonstrated by surveys in the estuaries investigated here (see Chapter 2) and by work in other estuaries (e.g. Mettam, 1994; Hiscock & Moore, 1986). Particularly in the mouth of Yealm,

which is located at a more wave-exposed position outside the Plymouth Sound, *E. modestus* occurs at lower abundances than within the estuary and represents a much lower proportion of the total barnacle fauna (Southward, 1991). Despite this, settlement was heavy at this location and did not reflect adult abundances. It is probable that post-settlement processes assume a greater importance for *E. modestus* populations at this location, causing reductions at later stages of their development.

It is only possible to speculate about the pre-settlement processes that determined the patterns of settlement observed during the present study. Studies which focused on settlement along estuaries or other coastal horizontal gradients, demonstrated that patterns of settlement can result from larval supply (e.g. Hawkins & Hartnoll, 1982; Gaines et al. 1985; Gaines & Roughgarden, 1985; Gaines & Roughgarden, 1987; Ross, 2001; Satumanatpan & Keough, 2001; Jenkins & Hawkins, 2003) and/or larval behaviour (e.g. Boulsfield, 1955; Raimondi & Keough, 1990; Raimondi, 1991; Jenkins, 2005).

Gaines and colleagues (Gaines et al. 1985; Gaines & Roughgarden, 1985), compared cyprid supply at seaward and landward sites on rocky shores and demonstrated that differential densities of cyprids reached sites along this gradient due to settlement acting as a drain of cyprids and reducing availability of cyprids at more landward areas. The same phenomenon was observed controlling the densities of cyprids in the water column along the main axis of a mangrove forest for two barnacle species (*E. covertus* and *H. popeina*). In the latter, behaviour at settlement, with preferential settlement occurring in seaward areas due to cues on substrata intensified the drain of cyprids and reduced availability of cyprids in the upper reaches. Alternatively, work on *Chthamalus* species (*C. montagui* and *C. stellatus*) clearly demonstrated that active substratum selection by larvae can surpass the influence of larval supply and generate differential settlement between sheltered and wave-exposed

shores even when the supply of larvae is similar (Jenkins, 2005). The estuaries used in the present study differ considerably from mangrove forests, where settlement of barnacles occurs on the roots and branches of these trees which act as a filter for larvae passing along the estuary. Nevertheless it is possible that either preferential settlement at lower or upper reaches or differential larval supply along the estuary exist in the barnacle species investigated.

Differential larval supply may be expected, considering that *E. modestus* is much more abundant than other species in the estuaries. However, the maintenance of patterns of larval supply that emerge due to larval production depend greatly on the degree of openness of a particular system which is associated with the hydrodynamics and degree of exchange of water between the inlet or estuary and the open coast. A parallel can be made to patterns observed in Lough Hyne where *E. modestus* is also dominant at the adult and recruitment stages (Lawson et al. 2004; Watson et al., 2005). In this sea lough processes of larval retention have a major contribution to the observed patterns. Lough Hyne consists of an inner body of water with very low freshwater input linked to the sea by a narrow passage, which results in water being exchanged with the sea at low rates. In contrast, the estuaries used in the present study are small rias with relative short residence times, Plym 4 days and the Yealm 1.5 days (Uncles et al., 2002). Observations during fieldwork, revealed that these estuaries tended to drain substantially during low tides and in these occasions little water was present at the mid and upper reaches. The dominance of *E. modestus* in this case, requires a much more efficient mechanism of larval retention, or may depend on the production of large numbers of larvae, not only within the estuary, but also in other local estuaries and sheltered habitats.

It is also important to notice that in Lough Hyne the dominance of *E. modestus* occurs without loss of other barnacle species (Lawson et al. 2004). Larvae produced

inside the Lough by other species also tend to be retained regardless of their behaviour in the water column. In the estuaries studied here other species that are not as abundant and fecund as *E. modestus*, or that lack efficient mechanisms of larval retention, may endure severe loss of larvae from the estuary and the supply brought during flood tides may not reach the densities necessary for significant settlement on estuarine shorelines. This could explain extreme low settlement/recruitment at these areas.

5.4.2. Post-settlement patterns

Temporal variations in recruitment within the year occurred, as might be expected, considering the reproductive cycle of the species detected, which showed peaks during summer. *C. montagui*, which is a warm-water species, shows peak of developing embryos in July and August (Crisp. et al., 1981; Burrows et al., 1992, 1999) and previous work in the Plymouth Sound found abundance of early stage larvae throughout July to September with peak density in August (Jenkins, 2005). During the present study this species recruited mainly in August and September. Although *E. modestus* breeds throughout most of the year, it shows greater fecundity during spring and summer in British waters (Crisp & Davies, 1955; Barnes & Barnes 1968; O'Riordan & Murphy, 2000). This species showed a much more extensive period of recruitment (from May to October) than the other species.

Patterns of recruitment corresponded to patterns of cyprid settlement along the estuaries. This indicated that processes occurring during recruitment, such as mortality and biological interactions, did not produce considerable changes in patterns determined by settlement at the time scales investigated here (monthly and 7 months). As mentioned before, these patterns corresponded to general patterns of adult distribution of *C. montagui* and *Balanus* species, but not of *E. modestus*. These results provide

evidence that two different models can explain the distribution of these species along the estuarine gradient. In *C. montagui* and *Balanus* spp., post-settlement processes were not a strong influence, and settlement, due to variability in larval supply or to larval behaviour, controls the distribution of the adults.

Settlement of *E. modestus* was much higher than for the other intertidal barnacle species at all sites. Post-settlement processes would be expected to have a stronger influence on recruits and possibly change initial patterns determined by settlement. Differential mortality was expected for *E. modestus* along the estuarine gradient. Evidence suggests that this species is more successful and able to survive at sheltered estuarine habitats than in more wave-exposed conditions (Southward, 1991). In the transplant experiments performed during this study, this species showed better performance in inner estuarine areas than at sites located closer to the sea or outside estuaries (see Chapter 3). Despite this, considerable reductions in recruits in the seaward, relative to the estuarine sites, were not observed, either over the 30-day or over the 7-month periods. It is possible that these periods of time were not sufficient for a different pattern to emerge and that regulation takes place over longer time scales. Conditions during winter at these locations could be particularly important. As noted by Southward (1991) *E. modestus* is mostly represented on the mouth of the Yealm by young individuals, which do not survive through their first winter after settlement.

This Chapter demonstrates that *E. modestus* can dominate barnacle settlement and recruitment in estuaries. This species showed greater abundance of cyprids and greater subsequent recruitment than the other species. Settlement is a crucial stage determining patterns of adult distribution in these estuaries. Post-settlement processes are more relevant for *E. modestus* in the lower reaches of these estuaries where events causing winter mortality are the most plausible explanation for the lower abundance of adults of this species at the mouth of the estuaries.

CHAPTER 6
GENERAL DISCUSSION

In this discussion, I outline the limitations of my work before considering the relative importance of pre- and post-settlement processes in setting patterns of species distribution in estuaries. I also revisit the models introduced in the general introduction (Fig. 1.3), discuss some of the causes and consequences of *E. modestus* invasion and dominance in estuaries, and suggest further relevant work related to the topics studied in this thesis.

6.1. Limitations of this study

Semibalanus balanoides was not detected during the work on settlement and recruitment (Chapter 5). This species settles during spring, particularly in April and May, but shows considerable variability in the onset and duration of settlement between years (e.g. Hawkins & Hartnoll, 1982; Southward, 1967; 1980; 1991), with the onset of settlement being correlated to phytoplankton blooms (Barnes, 1956; 1957, 1962). A long-term study in the Yealm Estuary (Southward, 1991) demonstrated that peaks of settlement of *S. balanoides* occur typically in April and that this species exhibits periods of decline and years of settlement failure associated with warmer conditions (Southward, 1991). In the present study panels were deployed on the 4th and 5th of April in 2003 and 16th and 17th of April in 2004 and should have sampled *S. balanoides*. Hence, colonisation of tiles at times of deployment would have been likely if this species was present in any substantial numbers. This species has entered in a phase of decline since the beginning of the 1990s (Pannaciulli, 1995) associated with warmer local conditions, intensified by the influence of global climate change. Recruitment in

131

recent years has been low around Plymouth (S. J. Hawkins, pers. comm.) and it is therefore possible that *S. balanoides* was not present in sufficient densities to be detected.

It was hoped that the study of planktonic larval stages of *E. modestus* and native species along the estuarine gradients would provide valuable information on mechanisms generating patterns of settlement and distribution in estuaries. Plankton collections were made during the period when recruitment was monitored in my study, but processing could not be concluded and data have been not included in this thesis, but will be incorporated in subsequent publications. Briefly, plankton samples were collected every month at each station used for monitoring of recruitment during the periods when settlement tiles were deployed. The objectives of the work on plankton were to test the hypotheses that the relative abundance of species and ontogenetic stages of barnacle larvae differ horizontally along estuarine water masses and that recruitment densities correlate with the abundance of late larval stages (cyprids and late nauplii) along estuarine gradients. Although the absence of data on the planktonic larval stages along the estuarine gradient precludes a conclusive discussion on how pre-settlement processes operate, it does not disqualify considerations on how important they are, relative to post-settlement processes, in determining distributions.

6.2. Relative importance of pre and post-settlement processes on the distribution of barnacles in estuaries

My results indicate that both pre- and post-settlement processes influence patterns of distribution and abundance of barnacles along estuarine gradients. Post-settlement processes were probably important in leading to the decrease in abundance of *E. modestus* at seaward sites and in limiting the distribution of *S. balanoides* towards

upper reaches of the estuaries. Limitations on distribution caused by pre-settlement processes were especially important in setting the up-estuary limits of *C. montagui*, but also contribute to patterns of reduced abundance for *S. balanoides*. From the patterns of distribution and abundance described in Chapter 2, the results from transplant experiments along estuarine gradients presented in Chapter 3, the patterns of settlement and recruitment investigated in Chapter 5, and the evidence from laboratory experiments on the effects of silt from Chapter 4, it is possible to suggest how *E. modestus*, *S. balanoides* and *C. montagui* fit within the models proposed in the introduction of this thesis (Fig. 1.3).

Transplant experiments (Chapter 3) demonstrated that *C. montagui* was able to survive at sites beyond its up-estuary limit of distribution, although survival within the estuary was lower than at the marine source site. This suggests that pre-settlement factors rather than post-settlement tolerance to environmental conditions were responsible for setting absolute limits of its penetration up the estuaries investigated (Fig. 6.1 a). The poor settlement and recruitment observed for this species within the estuaries give additional support to this view. Within its range of distribution in the estuaries, this species was influenced by environmental factors, with salinity probably having a greater effect than silt deposition (Chapter 3 and 4).

The distribution and abundance of *S. balanoides* is known to be affected by low levels of settlement in the region (Southward, 1991), but despite this, adults occurred higher up the estuary than *C. montagui*. Periods of low recruitment of *S. balanoides* have been linked to climate, with warmer conditions having detrimental effects on settlement and abundances of this species (Southward & Crisp, 1952; Barnes & Barnes, 1966; Southward, 1991, Herbert et al., 2004). I suggest that low abundances observed for this species in the estuaries examined here follow the trend observed on the open coast, which is related to climatic conditions (Southward, 1991; Herbert et al., 2004). In

addition, this trend may have been amplified by considerable occupation of substrata by *E. modestus* in estuaries. Absolute limits of penetration in estuaries are related to the tolerance of *S. balanoides* environmental stresses typical of estuaries, with silt deposition being particularly important as evidence from Chapters 3 and 4 suggested (Fig. 6.1 b).

It is clear that larvae of *E. modestus* are normally available throughout the estuaries, as no limitation to settlement was detected (Chapter 5). It is not certain how larvae of this species achieved the necessary abundance and distribution along the estuarine gradient to reach the observed levels of settlement. After settlement, recruitment of this species tends to mirror its settlement (Chapter 5). However, there was evidence that post-settlement limitations occurred at the seaward extremity of the distribution range of *E. modestus*. Evidence for this comes from the comparison of the relationship between settlement and initial recruitment and adult populations (Chapter 2). Results from surveys performed in this study combined with results from other works (Southward, 1991, Pannaciulli, 1995, Hiscock & Moore, 1986) demonstrate that populations of *E. modestus* show lower abundance at the mouth of the estuaries than at inner estuarine areas. Considering that settlement and recruitment (up to 7 months) showed similar levels among these sites, limitations probably occur at a later stage in the development of the populations at seaward locations. This view was supported by results from transplants of adults along the estuaries, which demonstrated that *E. modestus* survived better at inner areas of the estuaries than at seaward areas or at the marine source site (Chapter 3). A model where larval availability is not limiting and post-settlement processes become paramount at the seaward limits of distribution of this species offers the best explanation for the observed patterns (Fig. 6.1 c).
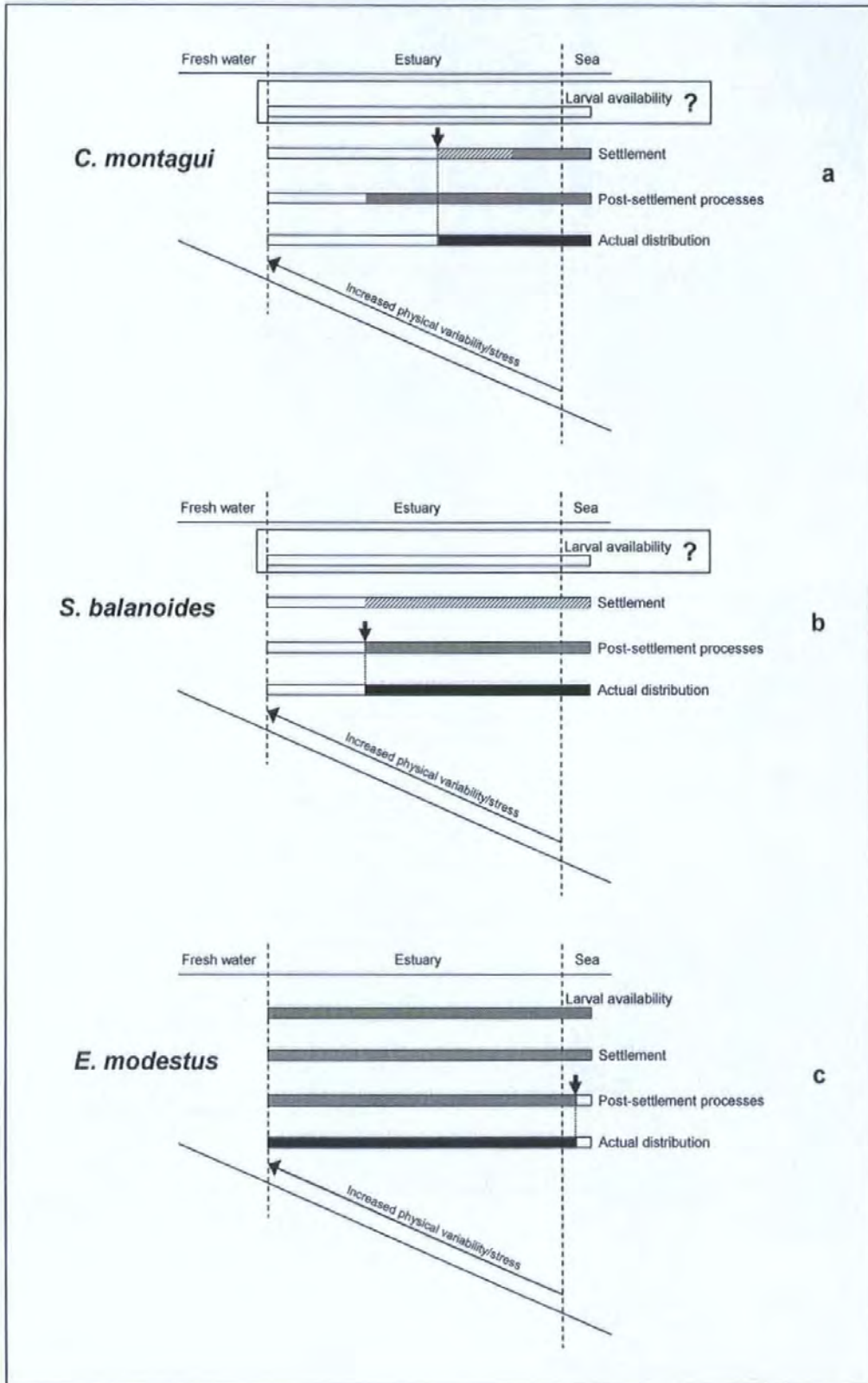
Fig. 6.1. Schematic representation of explanatory models for the distribution of barnacle species in estuaries. a) *C. montagui*; b) *S. balanoides*; and c) *E. modestus*. Hatched areas indicate areas with irregular settlement according to results from Chapter 5.

6.3. Dominance of *E. modestus* and consequences for native species

The invasion and current dominance of *E. modestus* is a consistent feature of many European estuaries (Crisp, 1958; Wolff, 1999; Nehring, 2006). Several of the characteristics of *E. modestus* believed to have facilitated its invasion of European estuaries were discussed in the previous chapters. However, it is convenient to synthesize this information in the view of results obtained here. Harms (1999) suggested that, besides the highly eurythermal and euryhaline larval stages and adults, the major attributes responsible for the successful invasion of European waters by *E. modestus* are: 1. the effective utilization of food by high cirral activity (Southward, 1955); 2. the high fecundity over much of the year (Crisp & Davies, 1955; Barnes & Barnes, 1968); and 3. the relative short generation time (Crisp & Davies, 1955). Crisp (1958), had previously considered the factors cited above, but also mentioned the observational deduction that greater tolerance to high levels of sedimentation and silt deposition would also be important. My work in Chapter 4 confirmed the importance of tolerance to sedimentation in allowing this species to thrive in estuaries. I believe that the considerations made by Crisp (1958) and by Harms (1999) are complementary in explaining the invasion potential of *E. modestus*, and that the features described above are also important in explaining the dominance of this species in estuaries.

My investigations corroborate Harms (1999) suggestion that greater effectiveness in utilizing food due to higher cirral activity gave *E. modestus* an advantage over native species. Direct effects of low salinities and salinity fluctuations on the osmotic balance of specimens was probably responsible for mortality at the most severe conditions found at the inner estuarine sites utilized for transplants, especially in *C. montagui*. However, barnacles are able to isolate themselves from adverse conditions by closing their opercular plates. The combination of periods of isolation from water,

enforced by low salinity, salinity fluctuations and deposition of silt, offered a much better explanation for the mortalities observed along the estuarine gradients (Chapter 3). Similarly, in my experiments on burial by silt (Chapter 4), which provided a demonstration that burial by layers of sediment can strongly affect the survival of these barnacles, the greater tolerance of *E. modestus* can be explained by its ability to withstand longer periods of isolation.

The introduction of a non-native species does not necessarily bring about harmful or large effects over native habitats and species (Ruiz et al, 1997; Reise et al., 2006). However, considering that *E. modestus* is highly dominant and shows a competitive superiority over native species in estuaries, the consequences of its invasion prompt concern. This species is not a strong competitor in fully marine conditions where it does not displace native species on rocky shores (Southward, 1991). However, *E. modestus* has largely displaced *S. balanoides* in estuaries, especially in the South-West. Estuaries are not the primary habitat for *S. balanoides*, which favours open shores (Lewis, 1964; Foster, 1970), and it could be expected that reductions of estuarine populations of *S. balanoides* would not affect this species at a larger scale. However, in combination with the effect of warmer weather conditions, the reduction of a previously available habitat found in estuaries may become of greater relevance. Estuarine areas which may have provided refuge for populations of *S. balanoides* in the past are now largely occupied by *E. modestus*, and this may have consequences for recruitment of *S. balanoides* to the open coast.

E. modestus is an important invasive species in European estuaries with potential effects on other estuarine biota. My results demonstrate that this species can achieve high levels of dominance along most of the estuarine gradient. The greater tolerance of post-settlement stages to conditions found at areas away from the seaward limits of estuaries, combined with high levels of settlement and early recruitment along

the whole estuarine gradient, probably explain this dominance. Post-settlement stages of *S. balanoides* and *C. montagui* were relatively more susceptible to environmental conditions experienced in inner areas of estuaries and low settlement and recruitment events probably contribute to the limited distribution and abundance of these species.

6.4. Conclusions and suggestions for further work

In conclusion this thesis has clearly shown that all species of barnacles examined experienced variations in abundance and survivability associated with estuarine gradients, *E. modestus* declining towards the sea and *C. montagui* and *S. balanoides* declining towards the riverine end of estuaries, and that *E. modestus* was the dominant species in estuaries most probably as a result of enhanced recruitment and physiological tolerance to salinity and sedimentation.

Further work is now required to examine the influence of larval supply on patterns of settlement observed in estuaries. This would contribute to our understanding of the ecology of the species examined here, including the dominance and invasive potential of *E. modestus*. Further study of the distribution of larval developmental stages along estuarine water masses could elucidate the coupling between local larval production and settlement, revealing the degree of openness of estuarine populations. Also, assessment of larval vertical and horizontal distributions and their correlation with physico-chemical parameters of the water body could help to determine the influence of larval behaviour and larval tolerance to salinity and other variables.

A further interesting outcome of this work was the decline in abundance and survival of *E. modestus* at seaward sites. This may be a result of differences in the relative importance of biological interactions such as predation and competition along estuarine gradients. More work is required to tease apart the relative importance of these

factors and experiments involving predator exclusions and examination of substrata pre-emption would be particularly useful.

Finally, the effects of sedimentation, and the mechanisms responsible for tolerance to this interference in barnacles, as suggested by my work deserve more attention. Further work on this subject using barnacles and other marine species is essential, especially taking into consideration that anthropogenic activity is now responsible for increasing levels of sedimentation in coastal habitats worldwide (Airoldi, 2003).

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