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Reproduction and Recruitment in Schleswig-Holstein Wadden Sea Edible Mussel (*Mytilus edulis* L.) Populations

von

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- To Andrew -
for patiently waiting so long

ABSTRACT

Populations of the edible mussel *Mytilus edulis* L. in the Schleswig-Holstein Wadden Sea have a relatively stable total biomass of some 200 000 t. In the late 1980s, successive years of poor spatfall and recruitment led to production losses in the mussel fishing and cultivation industries, and a need for increased information on the mechanisms affecting recruitment processes. Spawning of the adult population is extended throughout the year, with peaks in early summer and autumn. Spawning intensity and duration decreases with increasing height on the shore, as does mussel condition. Planktonic larval abundances peak 2 to 4 weeks after spawning maxima. Most larvae originate from local stocks, although imports from outside the area do occur. Annual abundances in larvae remained stable during this study, and regional abundance differences were insignificant. The location and intensity of larval attachment to filamentous substrates and artificial collectors, and subsequent settlement of spat, varied greatly. In the summer, peak attachment periods occur 6 - 8 weeks after spawning. Autumn spawned larvae tend to over-winter in deeper water, and recruit early in the year, contributing significantly to the annual mussel-seed production. Sporadic and intensive settlements are super-imposed on a constant rejuvenation of the wild beds throughout the year, and some recruitment is possible at any time of year. Hydrodynamic processes play a major role in determining mussel settlement pattens and subsequent colonization of available substrata. Spat are transported and deposited as passive particles in areas of reduced current velocities. This results in erratic distribution of settlement, and the subsequent distinctive, aggregated population structure. In most years, heavy predation on recruiting mussels in the Wadden Sea appears to prevent substantial natural restocking of mussel beds. The combination of highly variable distribution and concentration of larvae by winds and currents, high predation on larvae and early spat, and patchiness of suitable settlement substrata precludes effective prediction of timing, duration and location of initial settlements. Effective management procedures for this mussel fishery will therefore have to rely on the detection and quantitative assessment of post-settlement (1 mm - 5 mm) spat, and the implementation of fishery methods to optimize subsequent cultivation and harvest of successful settlements.

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INTRODUCTION

Successive years of failing spatfall and recruitment of the mussel *Mytilus edulis* L. (Bivalvia) during the late 1980s caused substantial production losses in the mussel fishing and cultivation industries in north-west Europe. The biological and economic problems arising from those recruitment failures (Dijkema, 1992; Ruth, 1994), led to the initiation of collaborative work in the European countries affected, to assess the status of spawning stocks of mussels and resultant spatfalls in successive years, and to investigate the influence of biotic and abiotic factors on recruitment in order to optimise cultivation and harvesting strategies.

Due to the high variability of environmental conditions of the Wadden Sea area, variations in biomass of mussel populations within and between years are to be expected. Aggregated distribution and spatial variation of mussel beds, caused by storms, dislocation by the commercial harvesting methods or erratic spatfall, make it difficult to estimate mussel biomass in a given area. The extent of littoral populations of mussels in the Wadden Sea have been well documented using aerial surveys and intertidal mapping (Munch-Petersen & Sand-Kristensen, 1987, 1989; Dijkema, 1992; Ruth, 1994). However, knowledge of the extent and location of subtidal mussel beds remains limited.

The unpredictability and irregularity of mussel recruitment in the North Sea have long been recognized (Kändler, 1926). Considerable variations occur in response to local conditions, without any apparent pattern. Whether these fluctuations arise mainly as a consequence of density dependent spawning of the parent stock, from differences in larval survival and settlement, from variation in post-settlement survival, or due to the variability of key abiotic factors, is largely unknown. However, high mortalities of eggs, larvae and newly settled spat are characteristic of temperate bivalve stocks, often limiting the establishment and maintenance of marine benthic communities of such species (Brousseau *et al.*, 1982).

Prolific spatfalls of mussels have been documented in many areas, particularly after severe winters (Savage, 1956; Reynolds, 1969; Dare, 1973, 1976; Beukema *et al.*, 1978; Meixner, 1985; Kleinsteuber *et al.*, 1988; Dijkema, 1992). However, the heavy recruitment in Schleswig-Holstein in 1990 after a mild winter, and the parallel recruitment failure in the adjacent Dutch and Danish Wadden Sea (Ruth, 1994), suggest that reproductive success is not governed by temperature alone. The mussel fishery in this area is dependent on good spatfall as a source of seed mussels, and the cultivation and exploitation of mussels is limited by settlement and recruitment to the natural stocks. In areas with a flourishing commercial fishery, successful prediction of time and place of recruitment would therefore facilitate optimal exploitation of the resource, while reducing the risk of overfishing in years of poor recruitment.

In Schleswig-Holstein, the demand for information on the population dynamics of Wadden Sea mollusc stocks came primarily from National Park management authorities. After the Schleswig-Holstein Wadden Sea area was given National Park status in 1985, a conflict of interests arose between conservation authorities and fishermen fishing in areas of the Park which were designated as exploitable areas. This resulted in motivations for the initiation of a large-scale Wadden Sea Ecosystem research program. Within this program, increasing pressure to manage the Wadden Sea mussel fishery in accordance with accepted fisheries management policies resulted in initiation of a study to investigate annual mussel recruitment, in order to propose management strategies to optimise harvesting of this annual recruitment without over-fishing the natural mussel stocks.

Colonization of a habitat by marine benthic organisms generally involves three phases: i) planktonic development, ii) attachment and settlement (metamorphosis) of the larvae, and iii) recruitment of juveniles into the population. Although these phases are differentially susceptible to biotic and abiotic influences, many studies of recruitment have not discriminated between phases, leading to an over- or under-estimation of the influence of certain factors in limiting the subsequent distribution and abundance of adults. In particular, many early studies made direct inferences about mussel spawning periods and larval settling behaviour from observed recruitment patterns of mussels, despite the highly migratory behaviour of mussel larvae, and their ability to repeatedly detach and attach to the substrate (reviewed in Gosling, 1992).

The teleplanic nature of mussel larvae may result in them being imported into a system far removed from the time or place of spawning (Scheltema, 1971). Direct methods of detecting spawning in adult mussels are necessary to provide information on the effect of local adult population structure on temporal and spatial variation in larval abundance. Subsequent assessment of larval densities will then allow comparison of the effects of these local spawning patterns with the effects of oceanographic conditions and long-range larval import. Finally, regular quantitative monitoring of settlement of plantigrades may enable prediction of actual recruitment to the adult stock.

As a result of the typically high variability of mussel spawning, it is important to use intensive sampling methods which are able to detect brief peaks in successive spawning events (Muus, 1973; Luckenbach, 1984). Inference of spawning events from plankton abundances, or of initial plantigrade settlement from final recruitment patterns, should be avoided. This study summarises the results of an intensive sampling program established to specifically investigate the following aspects of mussel recruitment in the Schleswig-Holstein Wadden Sea:

- Reproductive and gonad condition cycles.
- Periods of larval abundance.
- Larval attachment and settlement.
- Recruitment to established mussel beds.

Resultant improved understanding of the mechanisms effecting mussel recruitment processes, and of the location and extent of the vulnerable and ephemeral subtidal seed sources, should contribute substantially to the development of effective long-term management strategies for the Wadden Sea mussel resources.

1.

THE STUDY AREA

The Wadden Sea is a unique and highly productive area in the German Bight, stretching from the Netherlands to Denmark. With a total area of 6 000 km², it is sheltered from the open North Sea by a chain of islands parallel to the shore. Intertidal sandbanks and mudflats, bordered by shallow subtidal flats, flood bays, drainage gullies and deeper inlets and channels, extend in a zone of up to 30 km width (in Schleswig-Holstein) from the islands and sand reefs to the shore. The landward boundary between the mean high water mark and the shoreline dykes is dominated by saltmarshes and areas of land reclamation. The entire region is characterized by relatively high tidal amplitudes of 2 m to 3 m, reaching 3.5 m at Husum. Near the inlets, this results in strong tidal currents and high water turbulence. Due to its shallow nature, the Wadden Sea has a small water volume relative to its area, and there is little large-scale water transport and exchange, as the water body washes back and forth with every tide. A residual coastal current, however, results in small-scale exchange of Wadden Sea and North Sea water during each tide (Postma, 1982).

As a consequence of the local variability in hydrodynamic conditions, sediment characteristics are extremely variable (Korringa, 1976; Ragutzki, 1982). In general, the silt content of the sediment and the suspended solids content of the water decline with increasing distance from the mainland shore. Suspended solid values range from 7 mg - 278 mg suspended matter per litre (Gry, 1942; Postma, 1954), but may temporarily reach around 1 000 mg.l^{-1} during storms (Rickleffs, Forschungs- und Technologischeszentrum, Husum, pers. comm.). Salinity in tidal channels remains fairly constant at approximately 30 ‰ due to the strong currents and turbulent mixing. Substantial fluctuations in salinity due to fresh-water input and evaporation are, however, common on the intertidal flats. Temperatures are also highly variable. The intertidal flats may be covered by ice in severe winters, whereas during hot summer days temperatures may reach up to 32°C in tidal pools (Beukema, 1976).

Intensive remineralization processes occur in the study area (Postma, 1982). Together with the influx of large quantities of dissolved and particulate organic matter from the major rivers and the North Sea, this furthers the establishment of a highly productive benthic community, rich in biomass (Dankers *et al.*, 1981). The high temporal instability and low spatial variability of the Wadden Sea, however, results in low species diversity; 6 species account for more than 90% of the macrozoobenthic biomass (Beukema, 1976). The mean annual biomass of the intertidal macrozoobenthos, although subject to considerable annual fluctuations, is higher than in the adjacent subtidal regions (Beukema *et al.*, 1978; Dankers & Koelemaij, 1989; Dekker, 1989). The highly productive intertidal flats serve as nursery grounds for many species of North Sea fish and invertebrates, and are important feeding areas for large numbers of migratory sea birds (Wolff, 1983).

Of the species which contribute significantly to the total biomass, the bivalve *Mytilus edulis* L. is amongst the most dominant (Beukema *et al.*, 1978). This eurytopic species has a broad distribution pattern, occupying a wide variety of microhabitats in the northern hemisphere. Its upper distribution on the shore is governed by its physiological limits to temperature extremes and desiccation. The lower limits of its vertical distribution are influenced by biological factors, particularly predation (Seed & Suchanek, 1992).

In the Wadden Sea, mussels are primarily found in the intertidal zone, although ephemeral populations also occur in the deeper reaches of the subtidal zone, down to depths of 20 m - 25 m (Beukema, 1976; Dekker, 1989). Due to the lack of hard substrata in the area, the mussels exhibit gregarious clumping behaviour, attaching to shell fragments, larger grit particles, and to each other. The mussel patches generally lie upon a layer of pseudofaeces and mud collected between and beneath the mussels. This soft base renders the clumps susceptible to ice scouring and storm damage (Kleinsteuber *et al.*, 1988). It appears that the establishment and maintenance of temporally stable mussel beds is largely determined by localized hydrographic conditions, such as current speeds, availability of suitable substrata and food supply (Maas Geesteranus, 1942; Theisen, 1968; Seed, 1969b; Young, 1983).

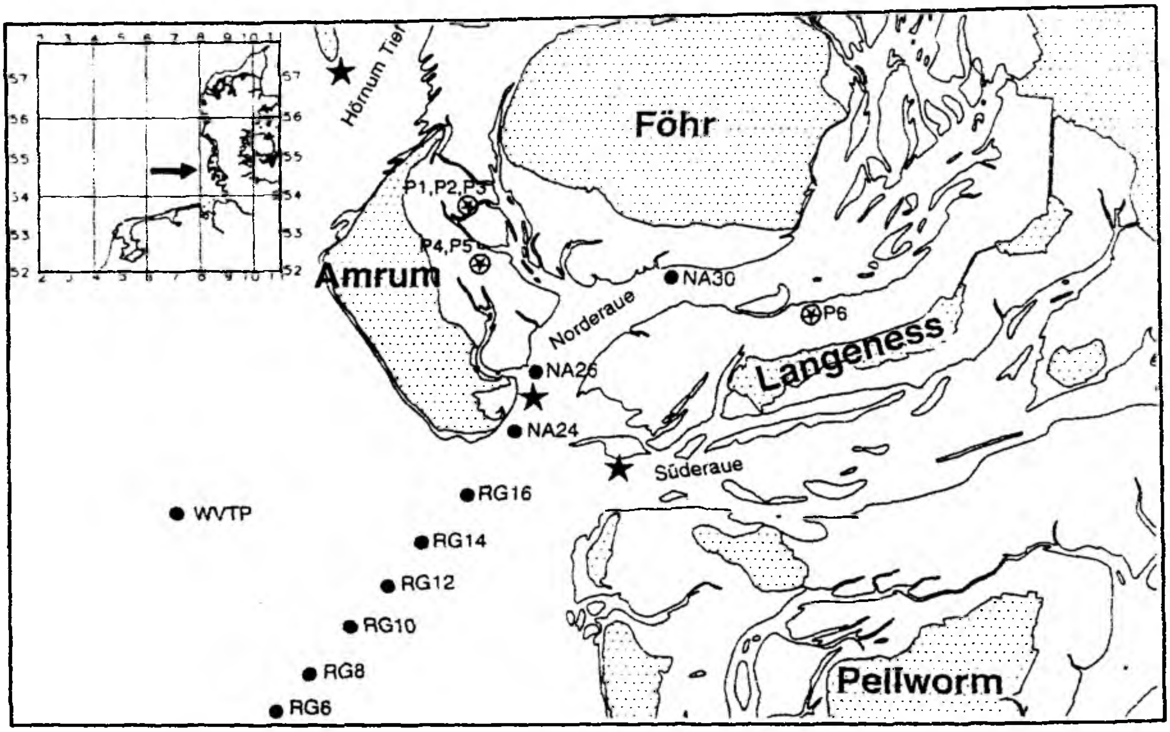

Figure 1.1 Map of the German Bight showing the Wadden Sea (insert) and an overview of the study area around Amrum showing the positions of the plankton stations (stars), the buoy row sampled (solid dots), and the mussel patches surveyed (circled stars).

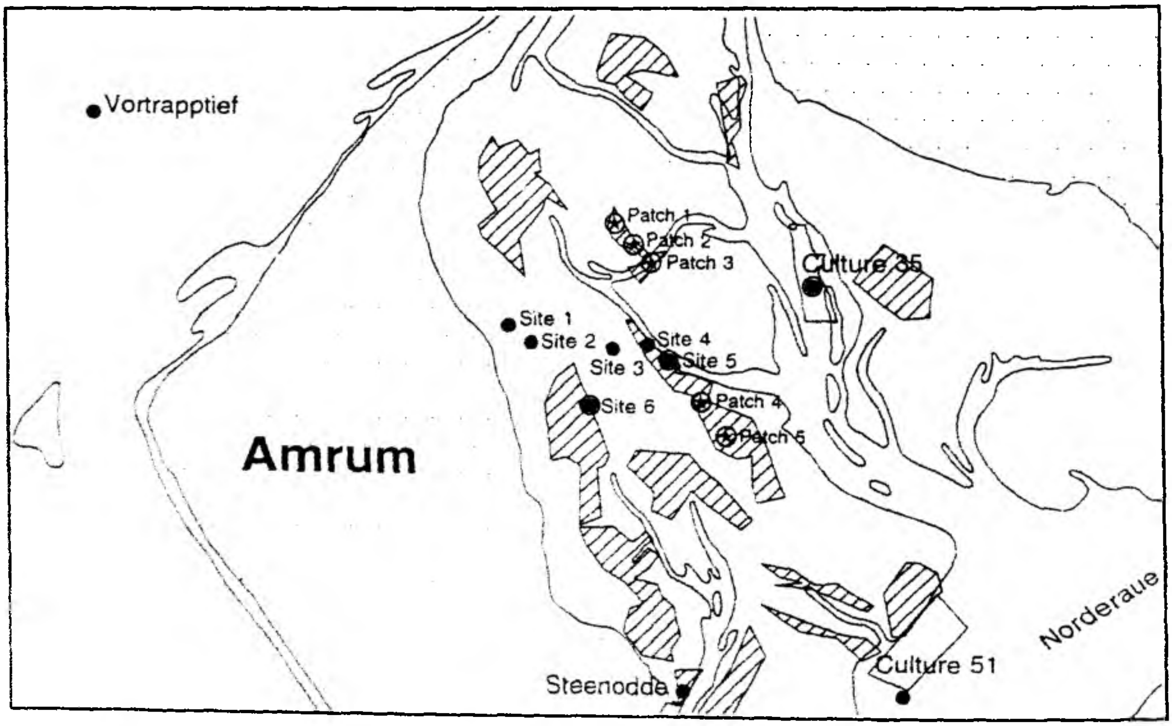

Figure 1.2 Map of the waddens east of Amrum, showing the extent of the intertidal wild mussel beds (hatched areas), the positions of the experimental sites (solid dots), regular sampling sites (circled dots), and the mussel patches surveyed (circled stars).

Although space is not limited *per se*, the frequent biological and physical disturbances of mussel patches do not allow the coverage to extend beyond a certain limit (Reusch *et al.*, 1994). Three basic types of mussel beds have been recognized and described by Ruth (1991), based on morphology and method of formation. These are: i) high elevation mussel beds located on the extensive tidal flats, ii) low elevation mussel beds on the edges of tidal gulleys, and iii) subtidal mussel beds. In comparison with the surrounding mudflats, these mussel beds are extremely productive biotopes, offering niches and substrates for a variety of algal and invertebrate species (Tsuchiya & Nishihira, 1985, 1986).

Intensified commercial culture of *M. edulis* on shallow subtidal plots has increased the total subtidal macrobenthos biomass in the Wadden Sea during the past few decades (Dankers & Koelemaij, 1989). Although not permanently occupied by mussels, the culture plots have fixed positions. The plots are stocked with seed mussels transplanted from both intertidal and subtidal wild beds, and sustain a biomass of up to 100 000 tonnes in Schleswig-Holstein. Once re-layed, the mussels are left on the plots for 1.5 - 2 years, until they have reached the marketable size of at least 50 mm (Theisen, 1968; Dankers & Koelemaij, 1989).

The Schleswig-Holstein Wadden Sea extends from the Danish border in the north, to the mouth of the Elbe estuary in the south, encompassing an area of 2 800 km^2. Although intertidal sand-flats constitute approximately two thirds of this area, the wild mussel beds, and consequently the fishery, are concentrated in the regions north of the Eiderstedt peninsula, sheltered from the prevailing westerly winds by the North Frisian islands and by offshore sand bars. In Schleswig-Holstein 3.4% of the subtidal area (28.5 km^2) is utilized for mussel culture, supporting a fishery with a mean annual landing of 20 000 tonnes. The tidal range in the area is about 2.7 m at spring tides and 1.7 m at neap tides. Larger tidal ranges are not infrequent during strong easterly or westerly winds.

The area around the island of Amrum in which this study was conducted is illustrated in Figure 1.1. At the start of this study in 1989, the Schleswig-Holstein mussel stocks were dominated by the strong year-class of 1987, after the extreme winter of 1986/87. Recruitment failure in subsequent years led to the virtual disappearance of a number of wild mussel beds, through natural mortality and commercial fishing. A relatively heavy spatfall in the spring of 1990 resulted in the re-establishment and rejuvenation of low intertidal mussel beds, and the formation of numerous isolated subtidal populations. The population structure in the intertidal zone was further altered by a second recruitment wave in autumn of the same year, spatfall occurring on the high elevation beds as well. Early in 1991, a moderate spatfall was again observed in the low intertidal and subtidal beds. Although small-scale settlement was observed continuously during the mild winter 1991/92, the recruitment during 1992 was weak and served only to replace losses due to natural mortality. In 1993, the spring spatfall was poor and moderate rejuvenation of the stocks was delayed until autumn of that year. Details of changes in the population structure of the mussel stocks in the Schleswig-Holstein Wadden Sea are discussed by Ruth (1994).

The intertidal flats on the eastern shores of the island of Amrum offer an easily accessible study area, with a diversity of sediment types and a number of established mussel beds (Fig. 1.2). On a transect across the flats from the shore to the tidal gulley, the sediment progresses from fine silt-mud (Site 1), through near-shore and off-shore *Arenicola* dominated sand flats (Sites 2 and 3, respectively), to a shell grit area and mussel bed near the edge of the tidal gulley (Sites 4 and 5, respectively).

The local hydrographic regime of the intertidal experimental sites is illustrated in three examples in Figure 1.3. Current strength and direction and submergence time were measured at 10 minute intervals over an 8 week period using Aanderaa RCM4 current meters set up on the tidal flats. The near-bottom flow measurements indicate that flows are primarily tidally driven and orientated NW-SE, there being little flow in the NE-SW direction. As expected for tidally driven flows, current speeds oscillate between an approximate minimum and maximum value twice daily. Although strong winds and the shallow nature of the area can cause these regular oscillations to deviate substantially, the intertidal flats are generally exposed for variable periods twice a day. On the transect measured, the duration is longer, and the current strength

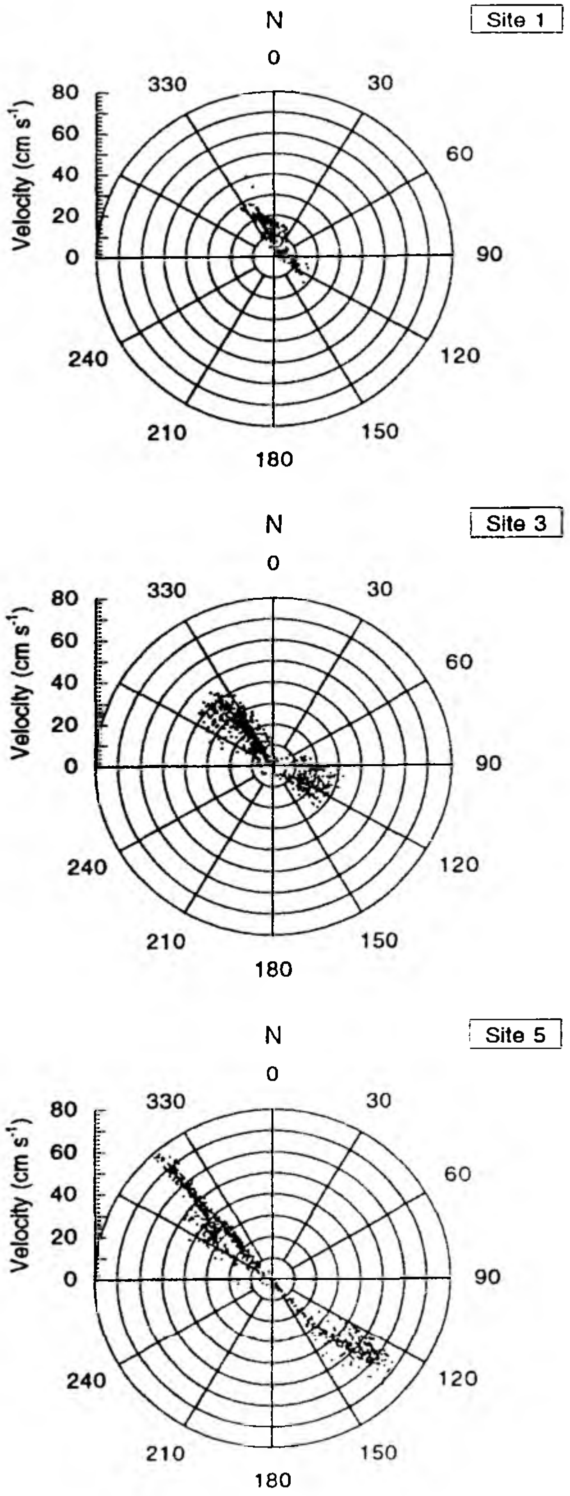

Figure 1.3 Current velocity and direction at three intertidal locations of different elevation (see Fig. 1.2 for identification of sites). Measurements were taken at 10 minute intervals over an eight week period. Each point represents an individual measurement.

larger, for the flooding current. The current vectors and submergence times increase with increased distance from the eastern shore of Amrum. Mean current vectors, tidal direction and tidal duration for the flood and ebb tides are summarized in Table 1.1.

The major tidal inlets around Amrum channel the tidal flux of three major water bodies. This facilitated the sampling of plankton from a wide area (Fig. 1.1). The water body between Sylt and Föhr drains through the Hörnum Tief, a channel having a steep northern bank and a depth of up to 35 m at the navigational buoy at Hörnum. The water between Föhr, Amrum and the Langeness island-chain enters just south of Amrum in the Norderaue. At the inlet, this channel is about 25 m deep, rising steeply towards the island. The Süderaue drains the area between Langeness and Pellworm. Near the inlet the channel has gently sloping banks and a depth of 10 m - 15 m. Maximum current velocities in the inlets range from 1.5 - 2 m.s^{-1}.

Table 1.1 Mean tidal duration, current velocity, current vector, and tidal direction for the flood (F) and ebb (E) tides at three intertidal locations (see Fig. 1.2 for identifications of sites).

		Site 1	Site 3	Site 5
Tidal duration (hr)		12.26	12.27	12.22
Flooding duration (hr)		3.23	4.25	6.35
Ebbing duration (hr)		0.47	1.43	3.57
Exposure time (hr)		8.15	6.19	1.50
Maximum velocity	- F	26.0	44.3	76.3
(cm.s^{-1})	- E	13.0	31.7	62.0
Current vector	- F	1.849	3.334	8.143
(km.tide^{-1})	- E	0.228	1.002	5.088
Current direction	- F	347	321	315
(degrees)	- E	109	112	124

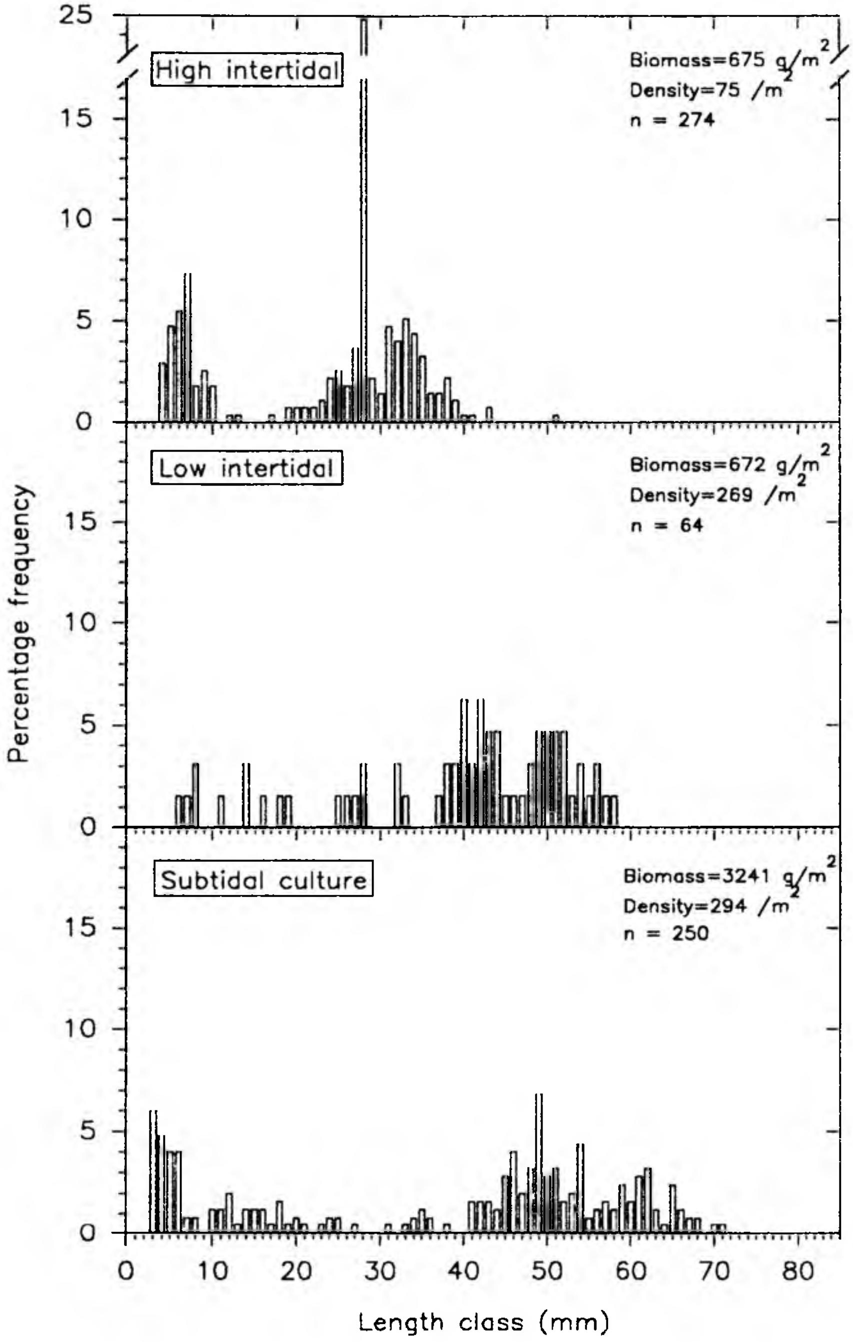

Figure 1.4 Length-frequency distributions of mussels on 8 June 1990 on the three mussel beds sampled regularly during the study (see Fig. 1.2 for identification of sites). n = number of observations.

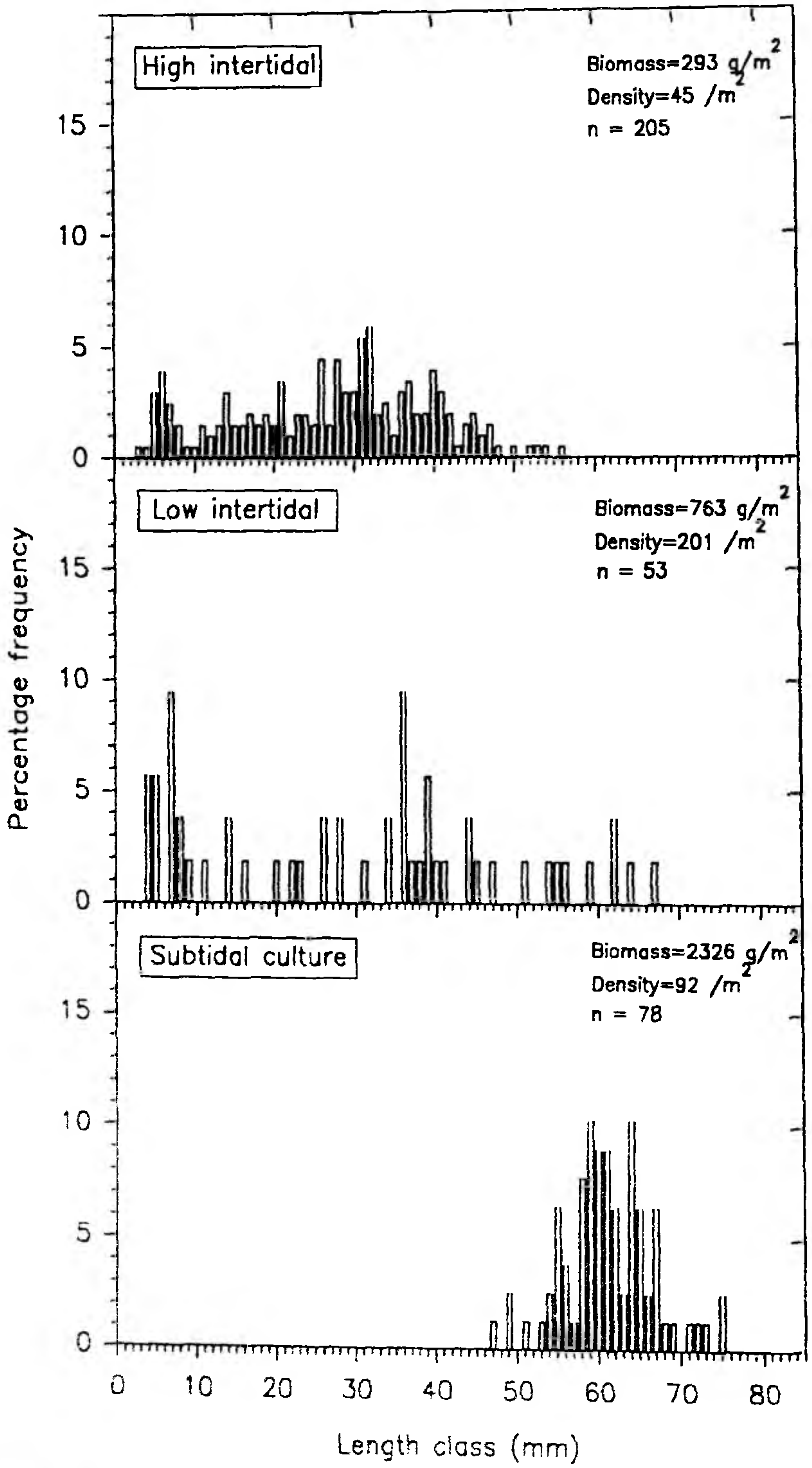

Figure 1.5 Length-frequency distributions of mussels on 4 October 1991 on the three mussel beds sampled regularly during the study (see Fig. 1.2 for identification of sites). n = number of observations.

The mussel populations studied were chosen from sites of different tidal elevation (Site 6, Site 5 and Culture 35 in Fig. 1.2), and represent the three types of mussel beds (high intertidal, low intertidal and subtidal, respectively) described by Ruth (1991) for the Wadden Sea. The high elevation site is situated close to the shore and characterized by fine sediments and mud. The mussels in the area constitute a small, scattered population which was strongly replenished during the strong recruitment in 1987. These mussels, which exhibit reduced growth and thickened shells, cover isolated banks of mussel shell and mud. The loose embyssment of the mussels and the dense epiphytic growth of *Fucus vesiculosus* makes these beds particularly vulnerable to destruction by storms and ice scour.

The low elevation site is situated on the edge of a tidal gulley. These beds are extensive, stable outcrops on ground composed of coarse sand and shell grit. The hummocky structure of these beds results in many large residual water bodies which provide a habitat for intertidal algal and hydroid communities. These mussels are tightly packed and strongly embyssed, and heavily covered by barnacles and *Fucus*.

A culture plot in a deeper tidal channel between the islands Amrum and Föhr provided samples from a subtidal population (Culture 35, see Fig. 1.2). This culture was stocked with mussels originating primarily from intertidal locations during 1988 and 1989, and was not fished during the study period. These mussels had a faster growth rate, and consequently a higher ratio of meat to shell weight, resembling mussels from natural subtidal habitats.

Figures 1.4 and 1.5 illustrate the length-frequency distributions of mussels at the three study sites on two sampling occasions. The seasonal appearance of mussel plantigrades on established beds and cultures in the study area results in a polymodal length-frequency distribution of the mussel populations. This poly-modality in *Mytilus* has been reported by many authors (Theisen, 1968; Seed, 1969b; Cerccherelli & Rossi, 1984; Commito, 1987). Successive age classes retain their identity in young populations with 2 - 3 conspicuous size groups. Although the size groups could result from differential growth of mussels originating from the same spatfall, they usually represent the result of seasonal spawning events. Due to extended spatfall periods and variable growth rates in some populations, distinct age classes may become difficult to discern. In any event, considerable overlap of generations occurs after 1.5 to 2 years, and the cohorts lose their separate identity in the length-frequency distributions.

A heavy settlement of spat, and subsequent establishment of a population on a gentle incline of pebbles and coarse shell grit in 3 m to 5 m depth in the Vortrapptief, directly seaward of Amrum (see Fig. 1.2), allowed for extended monitoring of a natural subtidal bed. The initial settlement of spat subtidally appeared to be confined to localized areas of suitable substrate and hydrographic regimes. Rapid growth and production of pseudofaeces and mussel-mud resulted in the mussels smothering the underlying biota and forming a dense, loosely embyssed carpet above the original attachment substrate. This renders them especially vulnerable to fishing and storm damage, although this looseness also allowed for the dispersal of seed mussels beyond their initial attachment sites, resulting in the development of extensive 'secondary' subtidal beds. This has the benefit of reducing density-dependent mortality, thereby leading to increased production. Higher subtidal predation pressure and intensive fishing of the valuable seed source usually cause such populations to be ephemeral, and they rarely persist for longer than a year. However, this Vorttrapptief site appears to be unusual in that local conditions seem to favour regular recruitment, maintaining a subtidal population which is annually renewed, despite heavy fishing.

2.

THE REPRODUCTIVE CYCLE

Although major spawning periods in populations of *Mytilus edulis* on the German North Sea coast could be inferred from indirect observations of the appearance of larvae in the plankton (Kändler, 1926; Werner, 1940; Rees, 1954; Heiber, 1988) or of spat settlement on the shore (Meixner, 1982, 1983), and on available artificial substrates (Duge, 1914), there is no assurance that such peaks reflect local spawning events. Larvae may be imported into the Wadden Sea from considerable distances, and it is thus important to include direct observations of gametogenesis, spawning behaviour and subsequent recession of the gonads of local mussel stocks. Gonad condition indices can further serve to illustrate the periods of accumulation of energy reserves required to fuel gametogenesis.

Although the cyclic nature of energy metabolism and the seasonality of gametogenesis in *M. edulis* have been well documented, most studies have dealt exclusively with rocky shore populations (reviewed in Gosling, 1992). In order to gain a specific understanding of recruitment processes of mussels in the Schleswig-Holstein Wadden Sea, particularly concerning the onset and duration of the breeding period, a detailed study of gametogenesis and condition index was therefore undertaken in the different mussel beds.

Improved understanding of mussel spawning and nutrient storage cycles should ultimately be of interest to the mussel culture industry. Geographical variation in condition, as well as the seasonality and intensity of spawning, may provide useful indicators of subsequent spat settlements. Such events have both immediate effects on the market value of the adult stock and long term effects on the permitted percentage of undersized mussels in the landed catch.

MATERIALS AND METHODS

Sampling

Variability in reproductive behaviour was investigated by comparing samples from the three chosen sampling localities: a subtidal mussel culture plot (Culture 35) and intertidal wild beds of both high and low tidal level (Sites 6 and 5, respectively; see Fig. 1.2). Sampling commenced in May 1991 and continued until February 1993. Samples of 100 - 150 mussels were taken at two-week intervals each spring and summer, and at monthly intervals each autumn and winter.

Gametogenesis

Twenty individuals of a selected size range from each sample (40 mm - 50 mm for the high intertidal site; 50 mm - 60 mm for the low intertidal site and subtidal culture) were stored at + 5°C and analysed for gonad stage within 24 h of collection. Individual shell lengths were measured to the nearest millimetre below, and the gonad tissue derived from the mantle was crushed on a glass slide, microscopically sexed and classified according a simplified scheme modified from Chipperfield (1953). This provides a simple, yet precise method for determining the onset and duration of the reproductive cycle using three main reproductive stages: resting, developing and ripe (Table 2.1).

Table 2.1 The three main gonad stages of *Mytilus edulis*, with their assigned ranks, showing subdivision into the seven recognised gonad stages (modified from Chipperfield (1953)).

GONAD STAGES	ASSIGNED RANKS
Resting (spent, inactive or immature)	0
Developing (developing or redeveloping)	1
Ripe (ripe or spawning)	2

A mean gonad index (GI) was determined for each sample by multiplying the number of gonads in each stage by the numerical ranking of the stage and dividing the sum of these products by the total number of individuals in the sample (Chipperfield, 1953; Seed, 1975). Values for males and females were combined. The resultant mean gonad index index varies from 0, when the entire population is resting, to 2 when all individuals are fully ripe or spawning. A steady increase in the GI indicates gonad development, while a sudden decrease indicates that spawning has commenced.

Condition Index

A subsample of 75 - 100 individuals, stratified to include similar numbers per 10 mm size class from 20 mm upwards, was selected from each sample (collected as described above) from each of the three locations. The mussels were cleaned of epiphytes, placed in a wire basket and immersed briefly in boiling water until the shell valves gaped open. Shells were dried and length and weight of each shell were recorded. The byssus threads were removed and the animals weighed after patting off excess moisture. The meat was transfered to numbered aluminium dishes, dried at 80°C for 48 h and the dry meat weight determined. The samples collected from the subtidal site were incinerated at 400°C for 24 h to obtain the ash-free dry weight of the meat.

Five condition indices were used to assess the seasonality of gametogenesis:

1) (Ash-free dry meat wt) / (Dry meat wt) x 100 (Seaman, 1991)
2) (Dry meat wt) / (Whole cooked wt - shell wt) x 100 (Crosby & Gale, 1990)
3) (Dry meat wt) / (Shell wt) x 100 (Walne & Mann, 1975)
4) (Whole cooked wt - shell wt) / (Shell wt) x 100 (Davenport & Chen, 1987)
5) (Whole cooked wt - shell wt) / (Whole cooked wt) x 100 (Davenport & Chen, 1987)

The dry and the cooked meat weights (DMW and CMW, respectively) were linearly regressed against length for each sample, after logarithmic transformation of the data. Obvious outliers were rejected and the predicted meat weights of a standard 55 mm individual for the subtidal and low intertidal site, and of a 45 mm individual for the high intertidal site, were determined from the linear equation and subsequently plotted against time to show seasonal changes in mean gonad condition. This technique has been widely used by Griffiths & King (1979), Bayne & Worrall (1980), Kautsky (1982) and Thompson (1984). Brinkman (1993), however, points out that back-transformation after estimation of both parameters of the length-weight formula is unreliable, as it assumes the relative errors in measured weights and lengths are equal for all data points. Estimation of the length-weight parameters was therefore additionally done using a non-linear Marquardt routine (Brinkman, 1993), and the predicted whole cooked weights (WCW) plotted against time, as described above. Fluctuations in body weight were assumed to be equal between the sexes, as was found for *Choromytilus meridionalis* by Griffiths (1977).

RESULTS

Sex Ratios and Gonad Index

Although during the peak breeding season it was sometimes possible to sex individuals by the colour and texture of the gonads, external signs of sexual dimorphism are usually not apparent. Sex was therefore determined whilst analysing gonad smears. However, during the non-breeding season and in the early stages of development, even microscopic examination proved unreliable in determining sex of certain individuals.

In *M. edulis* the sexes are separate and no evidence of hermaphroditism was observed in the course of this investigation. The percentage of individuals of indeterminable sex increased during summer and autumn, being highest at the high intertidal site and lowest at the subtidal site (Fig. 2.1). Although males appeared to be marginally more prevalent than females in the low elevation and subtidal sites (Table 2.2), male:female sex ratios did not differ significantly from 1:1 at the three sampling localities at the 95% confidence level (t-test for paired comparisons). On the low intertidal site and on the culture plot, some individuals attained sexual maturity within the first year of life (at 25 mm - 30 mm and 35 mm - 40 mm shell length, respectively). At the high intertidal site, growth is slowed and maturation occurs in the second year, when mussels have reached a size of 20 mm - 25 mm.

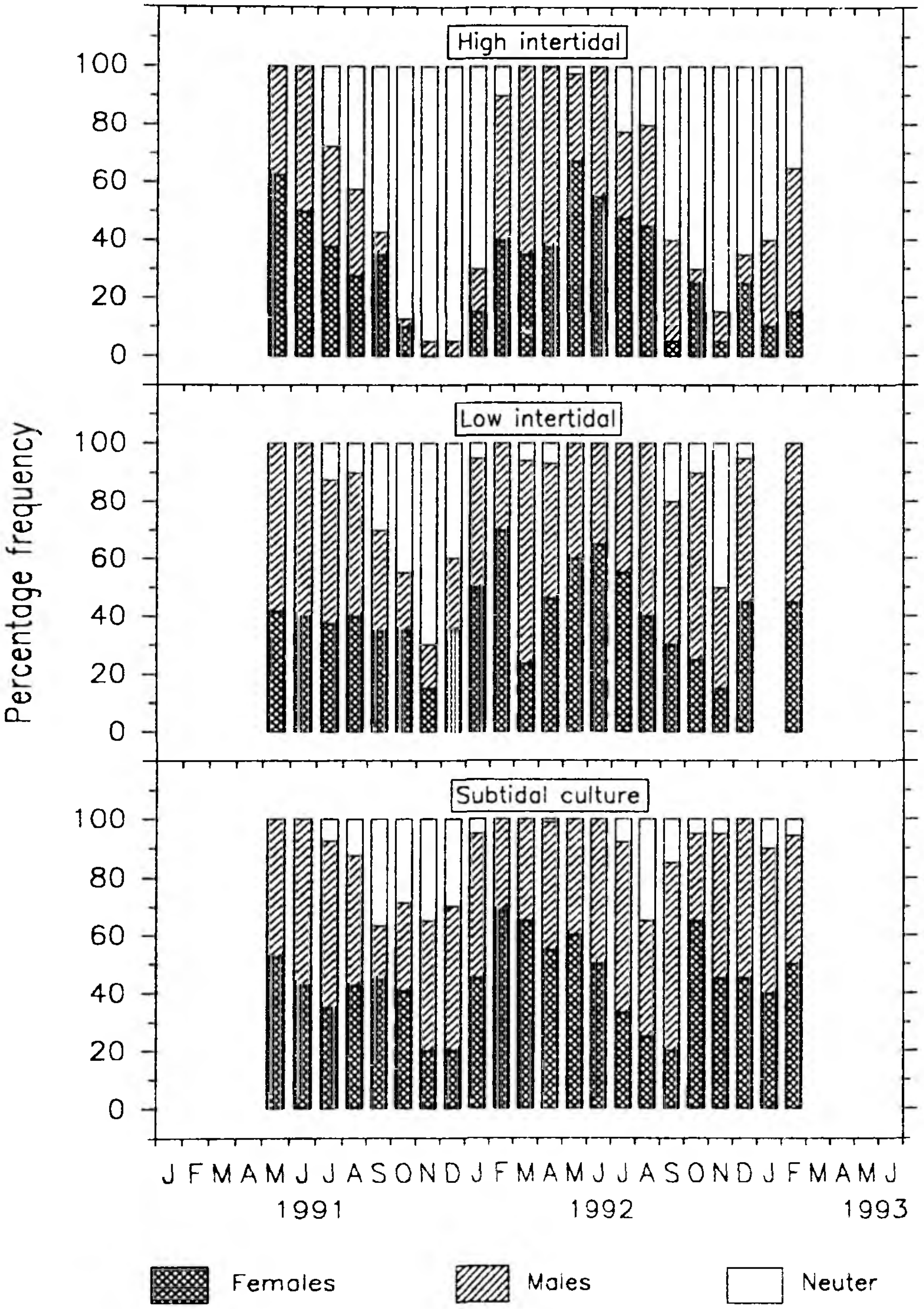

Figure 2.1 Temporal variations in mean monthly sex ratio of *Mytilus edulis* in three different habitats of different tidal elevation (see Fig. 1.2 and text for identification of sampling sites).

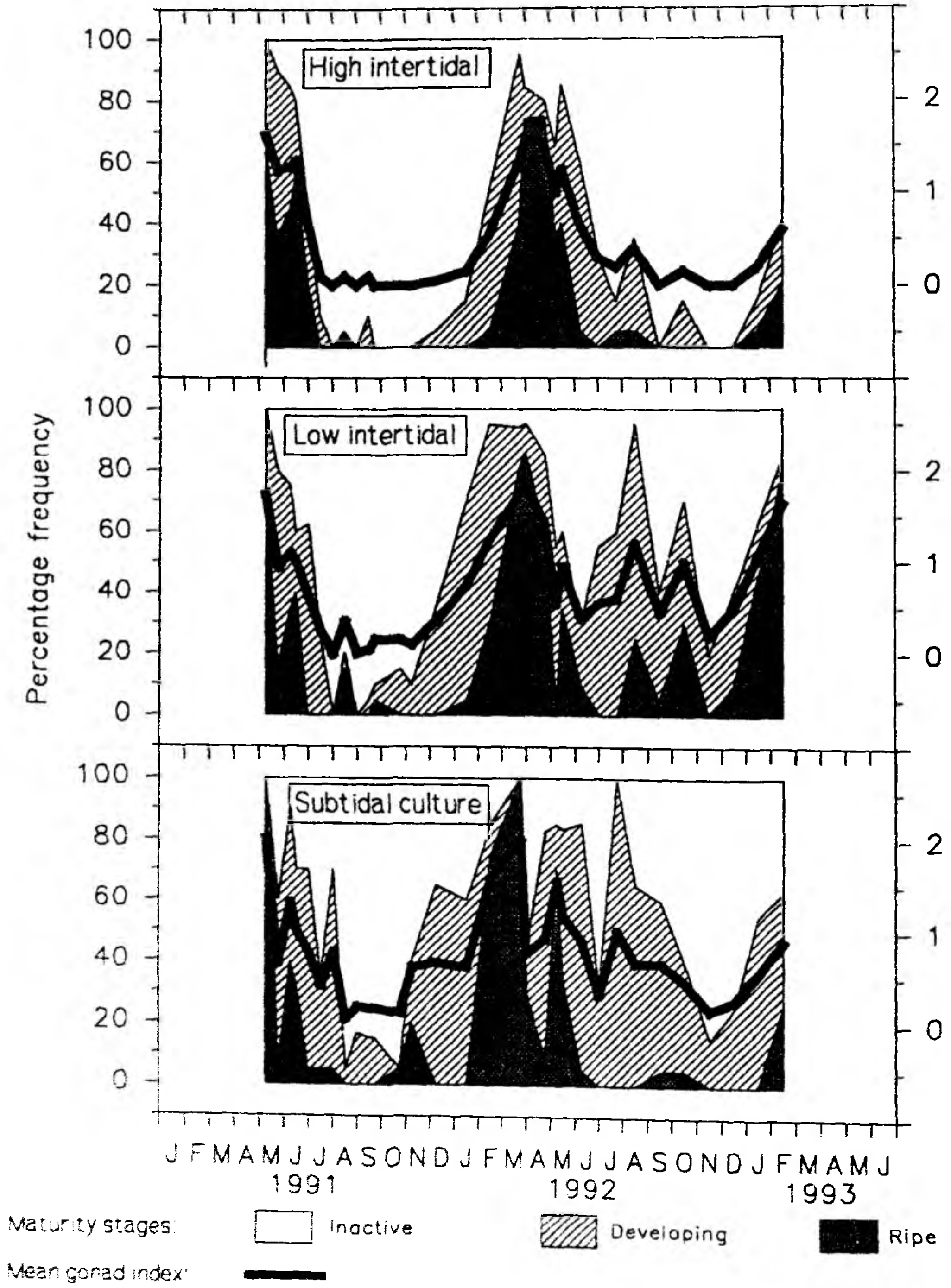

Figure 2.2 The reproductive cycle of *Mytilus edulis* from three habitats, showing the mean gonad index and the proportion of gonads in various maturity stages (see Fig. 1.2 and text for identification of sampling sites).

At all three sites, the highest proportion of ripe individuals was found during winter and spring, and the GI generally peaked in March (Fig. 2.2). Several discrete spawning periods, followed by phases of re-development, were evident at all locations. Re-development of the resting gonad began in November, followed by ripening as early as December/January, before the first spawning in late March/early April. This initial spawning appears to last from 2 to 4 weeks, with gonads regenerating rapidly before spawning again in May. The spring spawning lasts for an extended period of up to 4 months. An ANOVA found no significant differences in GI between the years sampled, or in annual variation at the three sampling locations (Scheffé range test, $p > 0.05$).

Table 2.2 Sex ratios of mussels for which sex could be determined at three sampling locations (see Fig. 1.2 for identification of sites).

LOCATION	FEMALES	MALES
High intertidal	52.3%	47.7%
Low intertidal	48.3%	51.7%
Subtidal culture	49.8%	50.2%

On the culture plot, gonad development was rapid and extensive, with the entire population exhibiting ripeness and spawning during the gonad activity peak. A large proportion of the population also exhibited gonad re-development and a subsequent second spawning. The mean GI during the second spring spawning attained a value comparable to that during first spawning. In comparison, in the intertidal populations some individuals always remained inactive, even during spawning maxima, re-development was not as intense and the GI failed to reach a second peak.

Complete release of gametes took place in all three populations in June/July. At the high intertidal site, the mussels re-develop their gonads to some extent immediately after spawning. In both 1991 and 1992 at the low intertidal and subtidal sites, re-development was postponed until August/September, when maturation peaked again.

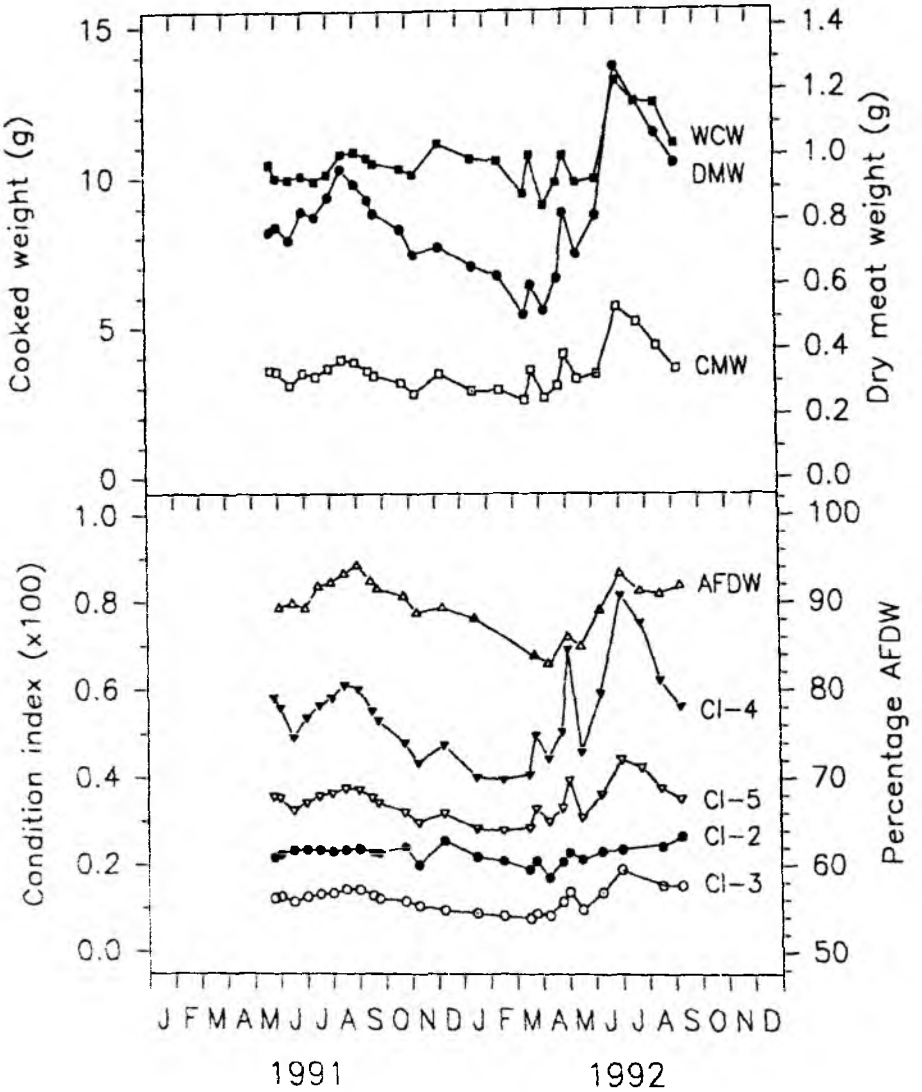

Figure 2.3 The annual cycle in various condition indices, whole cooked weight (WCW), and dry and cooked meat weights (DMW and CMW, respectively (see text for details) of *Mytilus edulis* from a subtidal culture plot (Culture 35, see Fig. 1.2).

At the latter two sites, ripe or developing individuals were found year-round. At the high intertidal site, however, the mussel population exhibited much shorter periods of gonad activity and less periodic spawning, with the majority of individuals remaining inactive throughout the year. The spawning season of high shore mussels appeared to occur slightly later than in low intertidal or subtidal populations.

Condition Cycle

The condition indices were found to be normally distributed, and the populations within each sampling location to be equally variable (Table 2.3a, 2.3b and 2.3c in Appendix I). This variability can be attributed to variations in the meat weight rather than in the shell weight. A comparison of the condition indices at the subtidal culture plot are given in Figure 2.3. The overall seasonal periodicity is similar for the different condition indices used, and a clearly defined annual cycle in gonad condition was shown by

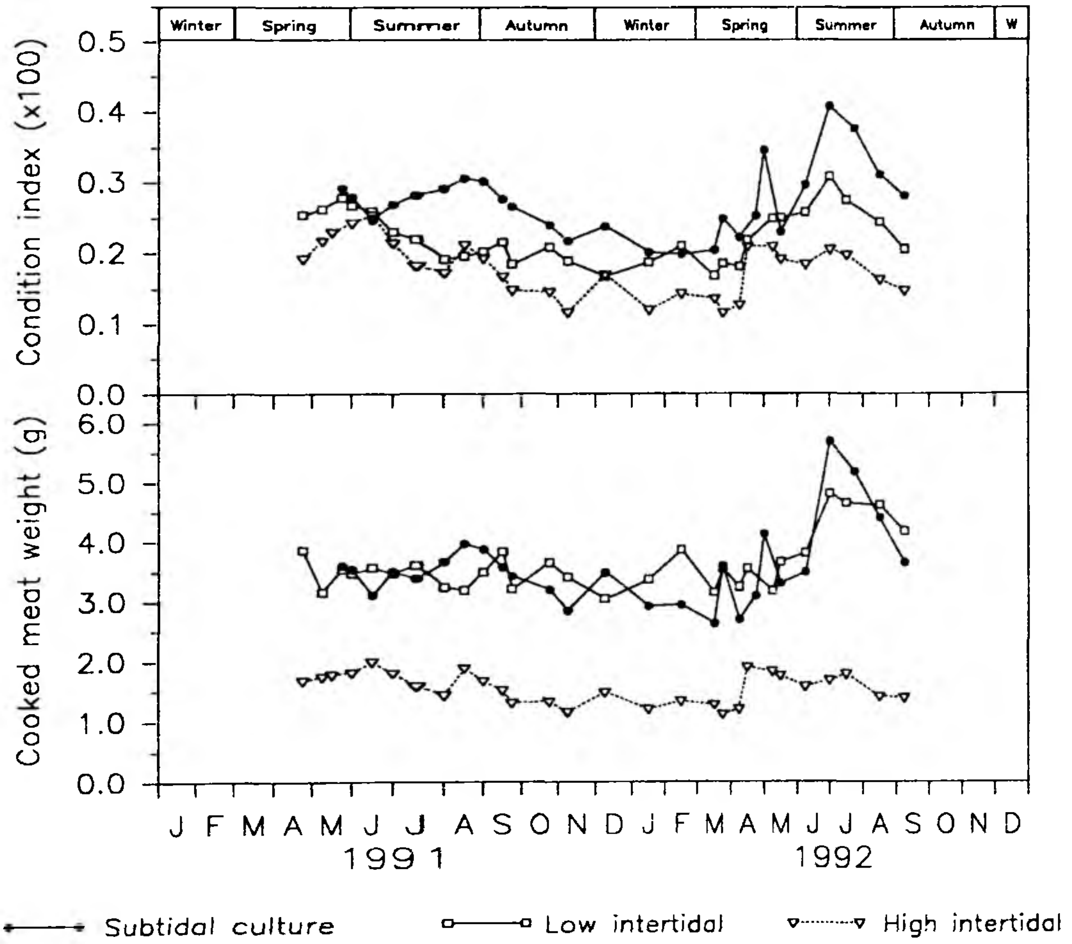

Figure 2.4 Annual cycles of cooked flesh/ whole cooked weight ratio (CI-5), and cooked meat weight (CMW) of *Mytilus edulis* from three habitats (see Fig. 1.2 for identification of sampling sites).

each method. The variation coefficients were lowest in condition index 5 (CI-5) and in whole cooked weight (see Tables 2.3a - c, 2.4a - b, and 2.5 in Appendix I). The CI-5, whole cooked weight (non-linear method) and cooked meat weight (linear method) indices were chosen for further investigation of geographic and temporal variation.

Although seasonality and amplitude of condition index cycles varied between 1991 and 1992, analysis of variance showed there to be no significant differences between mean annual condition (CI-5) and weight between these two years (Scheffé range test, p > 0.05). Condition index and weight data from both years were therefore pooled when testing for seasonality. Analysis of variance only found a significant difference between winter and summer cooked meat weights (Scheffé range test, p > 0.05) at all sampling sites. The spring and autumn values were intermediate between the winter and summer values.

The mussels at all three locations attained their highest meat weights and condition levels during the summer months (Fig. 2.4). The mussels started increasing in condition in March, when temperatures began increasing. Whereas condition dropped steadily in the subtidal areas during late summer and autumn, the mussels at intertidal sites displayed small periodic peaks in condition

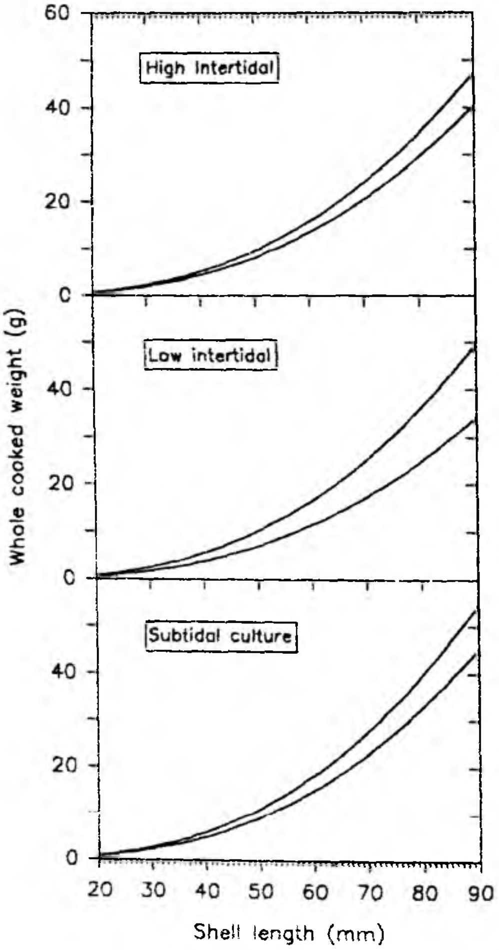

Figure 2.5 Variation in the ratio of length to whole cooked weight in *Mytilus edulis* from three habitats (see Fig. 1.2 for identification of sampling sites). The upper curves represent the relationship of whole cooked weight to shell length at maximum condition, while the lower curves represent the corresponding minimum.

on the low and high intertidal sites in August and September, respectively. Significant differences were found in condition between the three locations for each condition index (Scheffé range test, $p > 0.05$). Figure 2.5 shows the range within which whole body weight fluctuated annually at each location. The maximum weight varied by 15% between individuals of 55 mm shell length from different locations within a relatively small geographic area. Differences between minimum and maximum condition in a 55 mm mussel accounted for 34%, 21% and 17% of the body mass in the culture, high and low intertidal populations, respectively.

DISCUSSION

Condition indices can be useful indicators of the nutritional condition, reproductive status and commercial quality of bivalve populations. However, many of the indices described in the literature require cumbersome and arduous measurements, and are therefore inappropriate for routine, long-term monitoring studies. The principal aim of this study was to determine the overall cyclic nature of gonad activity, mussel recruitment and commercial quality, so an appropriate condition index was required that would reflect fluctuations in soft tissue weight, with adequate resolution to detect significant differences between the sampled populations.

Percentage ash-free dry weight (% AFDW) and percentage dry weight (% DW) ratios are good indicators of the true nutritive status of bivalve populations, the former being comparable to complex biochemical indices (Mann, 1978). In this study, the ratios including AFDW showed the least variability (see Table 2.3c in Appendix I), indicating that this parameter is more stable and less prone to measurement errors. Its determination is, however, time-ineffective. Whereas a tissue to shell ratio compares metabolism directed toward calcification vs. somatic and gametogenic processes, rather than being an index of nutritive status (Crosby & Gale, 1990), the close similarity between their cyclic patterns and those of the more arduous % AFDW method suggests that the latter is superfluous for an investigation concentrating on cyclic reproductive processes.

The reproductive tissue in *M. edulis* extends throughout most of the visceral mass, the gonads constituting a considerable part of the body weight prior to spawning. As the gonad cannot easily be separated from the body, the condition indices and gonad weight:shell length regressions assume minimal seasonal variation in weight of other meat components. Due to the difficulty in standardising the free water content, ratios incorporating wet meat weight have been criticised in the literature (Bodoy *et al.*, 1986; Seaman, 1991). However, in this study it was found that strict adherence to a standardised sample treatment technique minimizes errors in cooked weight determinations. This is shown by the lack of significant difference (ANOVA, $p>0.05$) between the coefficient of variation of index CI-5, and that of CI-2 (% DW ratio), which directly reflects the nutrient status. With the exception of the subtidal culture, differences between variability in CI-3 and CI-4 were similarly insignificant (see Table 2.3b and 2.3c in Appendix I). Differences between meat weight:shell weight ratios and CI-5 for the three populations studied were all significant. Davenport & Chen (1987) also report that freezing has little effect on the parameter measurements of cooked meats, further supporting the selection of CI-5 as the most appropriate, convenient and accurate measure of mussel condition, and indicator of spawning events. The combination of the CI-5 index and the non-linear regression method of Brinkman (1993), which provides a quantitative estimate of gonad production without necessitating the measurement of additional parameters, provides a practical and effective method for routine, long-term monitoring of reproductive status in mussel populations.

Condition index determinations should ideally be complemented by histological analysis to detect changes in gonad structure, and the extent to which loss of gametes represents complete or partial spawning. Squash-preparations tend to be more subjective, and do not give as high a quantitative resolution for gametogenic studies, as conventional histological techniques. However, histological descriptions of gonad maturation of *M. edulis* are provided in detail in the literature, making further investigation of this kind superfluous (reviewed in Seed & Suchanek, 1992). Furthermore, King *et al.* (1989), have concluded in a comparison of squash and histological techniques that, although the former may over-estimate the proportion of the resting stage, they proved reliable, more time and cost-effective and easier to use in the field. The frequent spawning peaks and rapid regeneration time of mussel gonads emphasize the importance of frequent sampling when monitoring the reproductive cycle of *M. edulis.* Brief spawning events may easily be missed as a result of infrequent sampling, making it more important to optimize sample processing time than histological resolution.

Decline in meat weight in *M. edulis* during winter has been well documented for populations from the United Kingdom (Baird, 1966; Bayne, 1975; Dare & Edwards, 1975; Seed, 1975), Ireland (Rodhouse *et al.*, 1984) and the Netherlands (De Zwaan & Zandee, 1972; Pieters *et al.*, 1980). This occurs primarily due to a loss of carbohydrate, although reduction of protein and lipid content also occurs, particularly during spawning events (Lubet, 1959; Williams, 1969; Dare & Edwards, 1975). Tidal elevation has also been shown to have a marked effect on mussel shell:meat weight ratios. Mussel populations from intertidal habitats generally have heavier, thicker shells, and correspondingly lower meat weights, than do subtidal ones, particularly raft-grown mussels (Hickman & Illingworth, 1980; Aldrich & Crowley, 1986; Raubenheimer & Cook, 1990). In the present study, the majority of the mussels on the subtidal study site were originally fished and transferred from intertidal wild beds. However, having been subtidally cultured for over two years, they developed an increased meat weight to shell weight ratio, resembling mussels originating from a subtidal habitat, rather than those from intertidal areas.

Differences between maximum and minimum mussel meat weight become more pronounced with increasing size and age, as a result of the transition from somatic growth to reproductive output (Bayne, 1976a; Thompson, 1979; Bayne & Worrall, 1980). The mussels in poorest condition are generally spawned individuals, as found by van Erkom Schurink & Griffiths (1991). However, in contrast to their study, the mussels in maximum condition in this study were not necessarily ripe individuals. Gonad indices show that mussels are capable of resting in prime condition, particularly in areas of poor food availability, such as the high intertidal zone. This delay between condition increase and spawning results from the offset between optimal feeding and

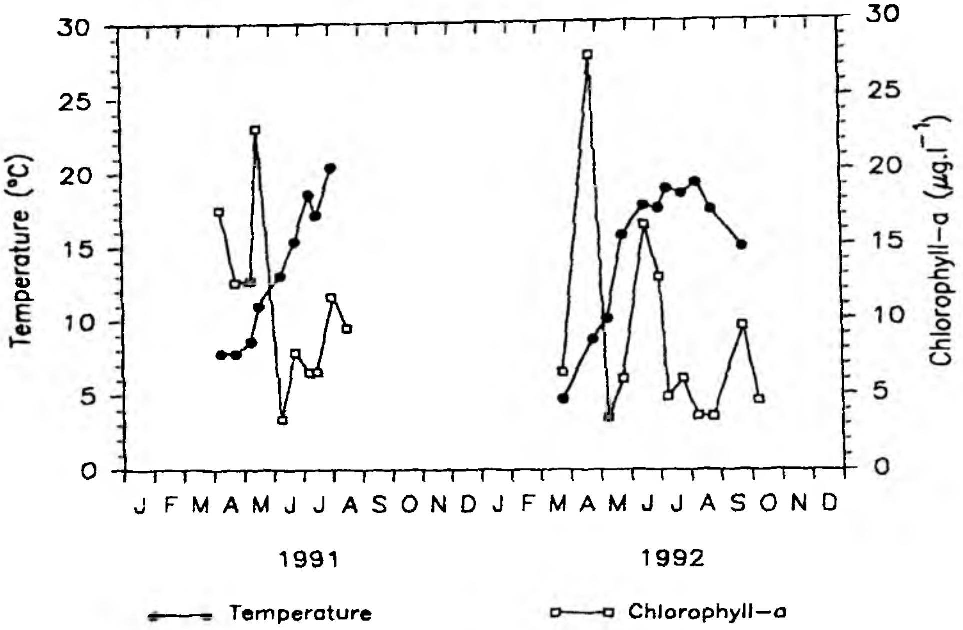

Figure 2.6 Mean sea surface temperatures and chlorophyll-*a* concentrations in the Norderaue tidal stream, in the vicinity of the three routine sampling locations shown in Figure 1.2. Data from regular aerial surveys to monitor phytoplankton development and blooms in the Wadden Sea (Göbel, in prep.).

spawning seasons in the Wadden Sea. Gonad maturity results further indicate that brief troughs in condition of the culture and low intertidal population resulted from spawning events, rather than from rapid changes in shell weight (Hilbish, 1986). Such periodic, sharp declines in body weight are therefore indicative of the quantities of gonad material released during a spawning event (Griffiths, 1977; van Erkom Schurink & Griffiths 1991).

The mean percentages body weight loss due to spawning were found to be 11.1%, 6.0% and 5.7% for the subtidal, low intertidal and high intertidal populations respectively. Using the non-linear Marquard routine, ranges between minimum and maximum condition of standard-sized mussels were found to be 34%, 21% and 17% for the subtidal, low intertidal and high intertidal sites, respectively. In comparison, the linear regression method yielded results of 74%, 53% and 73%, respectively. The latter correspond to figures given by Griffiths (1977), Thompson (1979), Kautsky

(1982) and Sprung (1983), also obtained using the linear regression method. The substantial difference between the linear and non-linear estimates confirms the estimation errors arising from back-transformation, as discussed by Brinkman (1993).

The role of phytoplankton blooms as spawning cues for *M. edulis* has been described by Starr *et al.* (1990), with increased food abundance ensuring greater reproductive success. During this study, a similar relationship between chlorophyll-*a* concentrations, periodic increases in condition index and spawning events was found (see Fig. 2.6). The condition of mussels began improving after the winter temperature minimum, when the first phytoplankton blooms occurred. Although an ANOVA (Scheffé range test, $p < 0.05$) found no significant difference between chlorophyll-*a* concentrations in 1991 and 1992, the phytoplankton in 1991 was dominated by *Phaeocystis* (Göbel, in prep.). This chain-forming diatom retards mussel filtration rate, limiting the recovery of gonads and nutrient reserves of *Mytilus* after spawning (Pieters *et al.*, 1980; Michaelis, 1991). This reduced food "quality" had a direct influence on mussel nutritive condition and gamete production, explaining the somewhat lower condition and the absence of significant spawning in the autumn of 1991.

Serial spawning in *M. edulis* has been well documented, and is subject to considerable variation, both annually and between habitats (reviewed in Seed & Suchanek, 1992). Seed (1975) described longer periods of gonad inactivity in high shore mussels, with evidence of only one spawning period in populations from higher latitudes. A single annual reproductive peak was similarly reported by Lowe *et al.* (1982), Emmett *et al.* (1987), and by Sprung (1983) working on rocky shore populations on Helgoland. Although it is unlikely that the cyclic nature of gametogenesis is governed by temperature alone, temperatures above 18°C do inhibit gonad development (Chipperfield, 1953; Lubet, 1959; Seed, 1969a). The elevated summer temperatures (>20°C) in the Wadden Sea could therefore account for the bi-annual spawning of *M. edulis*, as populations are exposed to optimum reproductive temperature ranges twice a year. As the onset of sexual maturity is a function of age rather than size (Seed, 1969a), the size of the smallest mature individuals will vary greatly with sampling location.

During periods of abundant food, seasonal increases in condition generally result from the direct utilization of available food (for either somatic or gonadal growth), or from accumulation of stored reserves. Development of the gonads in the winter months, when food is sparse and condition is at a minimum, confirms that gametogenesis and vitellogenesis can occur at the expense of limited energy reserves (Chipperfield, 1953). Following the scheme of Bayne (1976a), who classified the reproductive strategy of bivalves according to the relationship between their spawning and storage cycle, *Mytilus* stocks in the Schleswig-Holstein Wadden Sea exhibit both conservative and opportunistic strategies. The former is characterized by spawning early in the year, giving larvae the chance to utilize spring phytoplankton blooms. A second, opportunistic spawning in autumn utilizes resources accumulated during feeding concurrent with gametogenesis.

Mussel cultivation in the Schleswig-Holstein area occurs on sublittoral bottom-culture plots, and the culture and wild subtidal and intertidal populations feed on phytoplankton which is mixed with high levels of detritus re-suspended from the bottom. Compared with growth rates of mussels on navigational buoys or grown in suspended cultures, this food resource does not support maximal growth during spring and summer, but it does contribute to maintenance and gametogenesis in autumn and winter, and permits the mussels to maintain a more stable energy balance throughout the year (Rodhouse *et al.*, 1984).

Recent authors have ascertained that male and female mussels occur at a ratio of 1:1, independent of size and habitat (Lubet, 1959; Seed, 1969a; Sprung, 1983), and the results of this study also found no significant bias in the sex ratio. Observed monthly anomalies in sex ratio (Fig. 2.1) result from the variable percentage of reproductively inactive mussels. Increases in neuter individuals during late summer and autumn were also reported by Chipperfield (1953), Seed (1969a) and Seed & Brown (1977). The extremely high proportion of neuter individuals and gonad inactivity at the high intertidal site indicate that populations living under environmental stress invest energy available after spawning primarily in the synthesis and storage of nutrient reserves, with a resulting delay of gametogenesis (Bayne *et al.*, 1983).

3.

THE PLANKTONIC PHASE

A number of questions exist concerning the relationship between benthic mussel communities and planktonic distributions of mussel larvae in the Wadden Sea. For example, it is not clear to what extent peaks in planktonic larval abundance result from recent local spawning events, or from immigration of larvae from the North Sea. Larval abundances may further be suggestive of subsequent settlements. The relationship between planktonic larval abundance and subsequent spat settlements also appears to be complex. Detailed analysis of plankton samples in the study area was therefore conducted to provide insight into these questions, as well as other aspects of recruitment cycles of *Mytilus edulis* in the Schleswig-Holstein Wadden Sea.

In the majority of shallow-water bivalves, fertilization of large numbers of broadcast-spawned gametes occurs in the water column. The resulting trochophore larvae develop into planktotrophic shelled veligers. Species identification based on shell shape and structure becomes possible with the deposition of the final larval shell. After 2 to 3 weeks in the surface waters, the veliconcha larva develops a foot and the resulting pediveliger is capable of attachment to a substrate before metamorphosing into the sessile life form (Bayne, 1976b). Excellent reviews of the development, morphology and ecology of *M. edulis* larvae have been written by Widdows (1991) and Lutz & Kennish (1992).

The seasonal variation in occurrence of the larvae of bivalve species in the North Sea plankton has been documented by Kändler (1926), Werner (1940), Rees (1950) and Heiber (1988). As *M. edulis* was the specific subject of this study, investigations were restricted to this species, and only brief comparative references will be made to the various co-occurring bivalve species.

MATERIALS AND METHODS

To investigate temporal and geographic variations in the occurrence and abundance of planktonic *M. edulis* larvae, surface plankton samples were collected routinely during ebb tides, commencing in April 1990, from the seaward sections of each of three major tidal streams around the island of Amrum (Fig. 1.1 - station positions indicated by stars). In the Norderaue, samples were taken every two weeks during spring and summer, and every four weeks in autumn and winter (weather permitting). The Süderaue and Hörnum Tief were sampled at monthly intervals in spring and summer only. During 1991 the flood current in the Norderaue was additionally sampled to provide a comparison of the plankton composition in the flood and ebb tides. Occasional samples 10 km seaward of the regular sampling stations (Westvortrapptief, Fig. 1.1), were taken for comparison with the experimental samples.

Plankton samples were collected with paired 20 cm diameter, 150 µm mesh bongo-nets with centres 0.5 m apart. The nets were towed just below the surface against the current at approximately 3.5 to 4 knots (relative vessel speed), approximately 3 hr after high water during daylight hours. The irregularity of the channel bottoms made deep water tows impractical. Occasional oblique hauls (Hörnum Tief, Fig. 1.1) were, however, taken for comparison with the experimental surface samples. The water volume of each sample was determined using flow meters (General Oceanics) mounted in the mouths of the nets. Three successive tows were made at each location on each sampling occasion, providing six samples per station. The three locations were sampled in succession.

The content of each net was washed into the net bag, and the concentrated sample carefully transferred to 500 ml jars. Samples were preserved in a buffered 4% formalin-sea water solution, stained with Bengal Red and analysed within 4 months to avoid degradation of the larval shells. Staining of the material was necessary due to the large quantities of sand in the plankton samples. The sand particles made sorting of unstained samples especially tedious as the larvae are of similar size and colour to the sand grains. As preservation of the material results, in any event, in the disappearance of characteristic features such as shell colour, velum shape and eyespots, staining of the larvae did not further complicate identification. Samples which were too large for complete analysis were divided using a 10 division plankton splitter. Large planktonic species were excluded using a 300 µm mesh filter, the bivalve larvae being retained on a 150 µm sieve. The separated samples were assessed under a dissecting microscope, and a subsample of bivalve larvae taken for determination of species composition. The subsamples were photographed through a binocular photomicroscope and the species identified from the photographs by shell shape, prominence of the umbones and larval convexity. A selection of samples were further analysed in detail, with the assistance of Dr. K. Ocklemann (Marinebiologisk Laboratorium, Helsingør), for the construction of the species list.

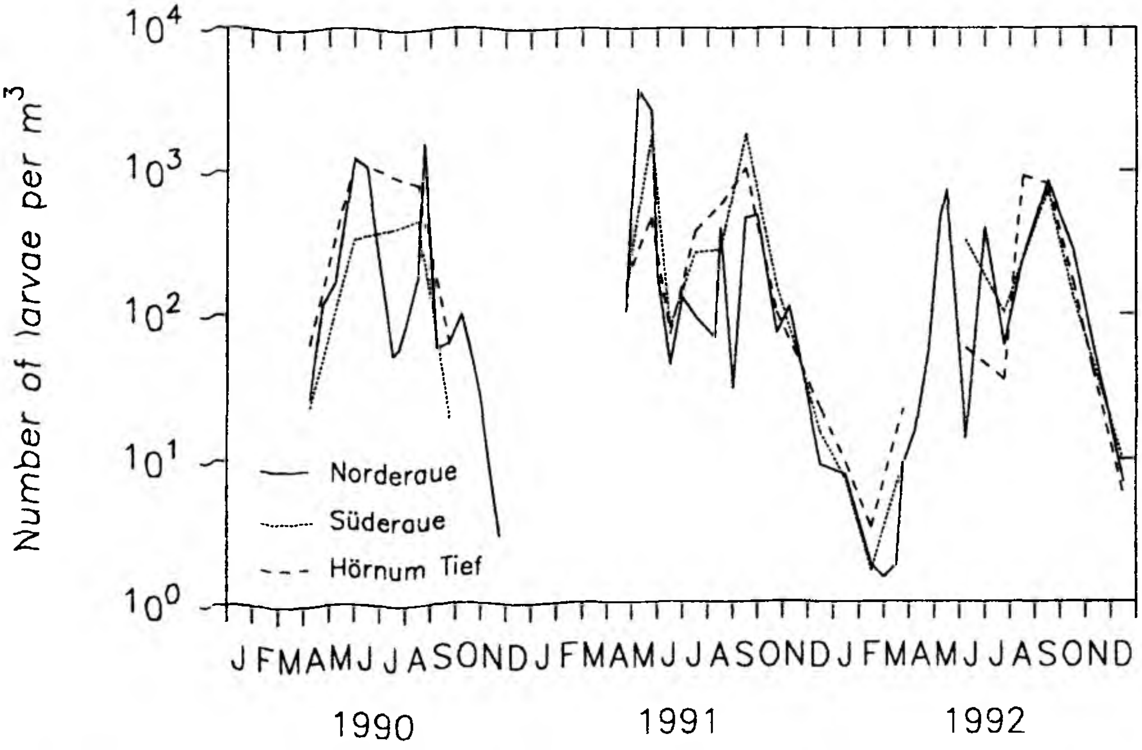

Figure 3.1 Temporal variations in mean number of bivalve larvae present in the plankton of three major tidal streams around the island of Amrum (see Fig. 1.1 for identification of sampling stations). Sampling was conducted in the Norderaue at fortnightly intervals, in the Hörnum Tief and Süderaue at monthly intervals. Number of observations per sampling interval = 6.

Samples were further analysed using a video camera attached to a binocular microscope. *M. edulis* larvae were measured from the video image using a computer-based image analysis system. Measurements were taken as the greatest dimension on a line parallel to the hinge (Bayne, 1976b). Successive cohorts in each normally distributed component of the bi-modal length-frequency distributions were separated using the Bhattacharya method (Bhattacharya, 1967) in the ELEFAN length-frequency analysis package (Gayanilo *et al.*, 1988).

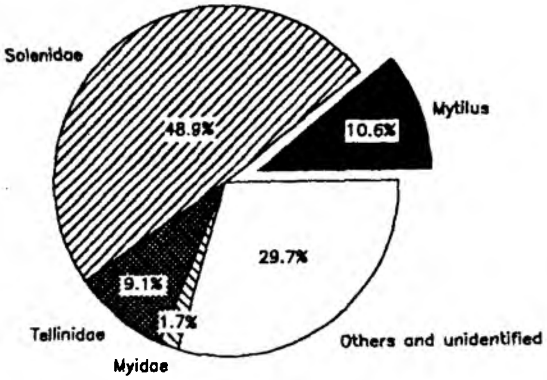

Figure 3.2 Percentage larval composition of the major bivalve groups represented in the plankton of the tidal streams around the island of Amrum, (number of samples = 660).

Although bivalves >300 µm were present in the plankton in small numbers, these were found to be post-larval drifters and were only considered in size-frequency analyses. Data were analysed after log transformation by analysis of variance, using the Scheffé range test at a 95% significance level.

RESULTS

Temporal variability in the mean numbers of bivalve larvae in three major tidal streams from 1990 to 1992 was considerable (Fig. 3.1). Although coefficients of variation between localities and sampling periods were variable (Table 3.1 in Appendix II), differences in total plankton abundance between the three sampling locations were insignificant. At least two distinct periods of maximum larval density occurred, in late May and June, and again in the autumn (August/September). In the Norderaue where sampling was more frequent, intermediate peaks were also apparent.

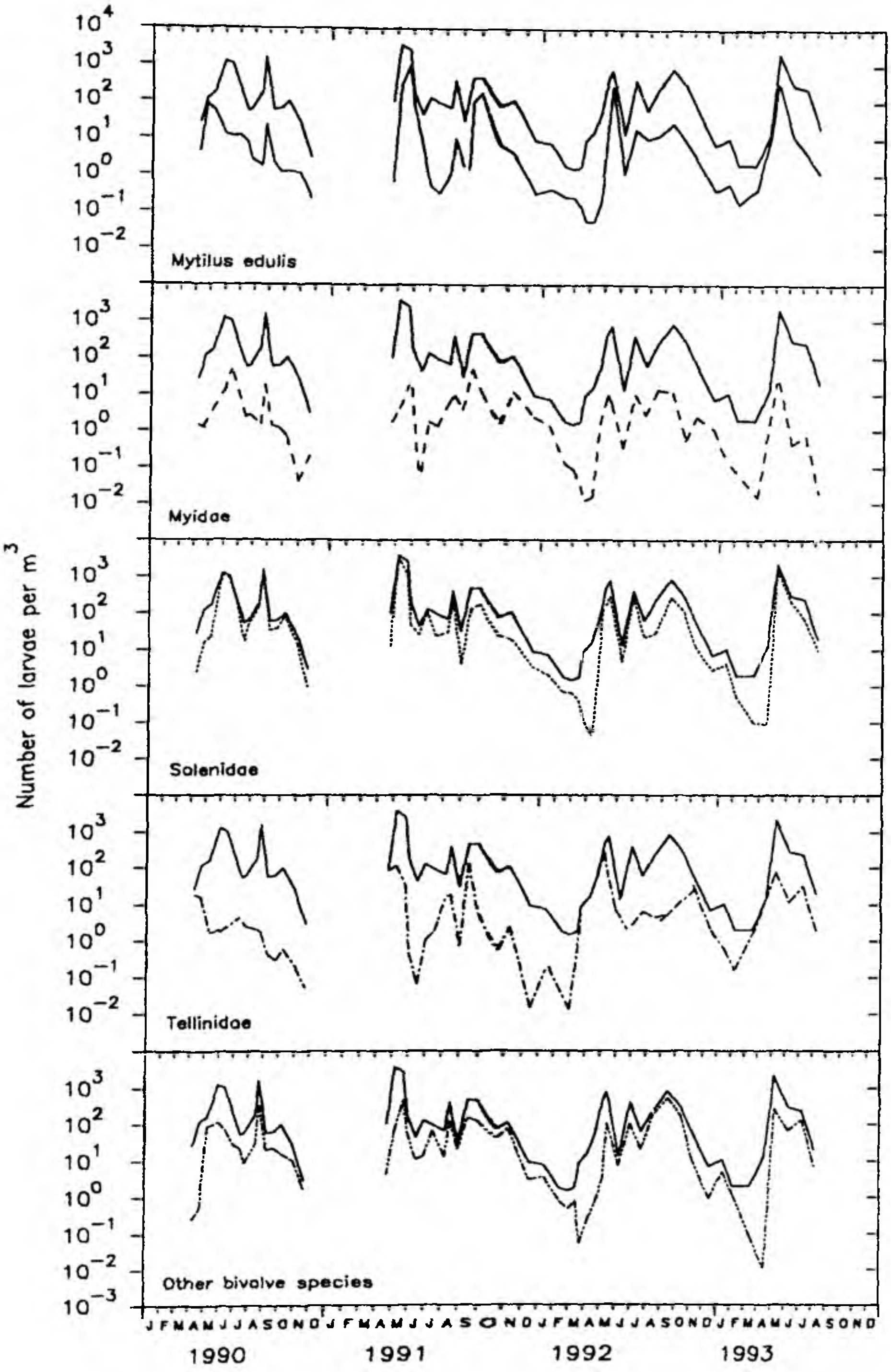

Figure 3.3 Temporal variation in the total number of bivalve larvae (upper solid lines) and the larval densities of the major bivalve groups (dashed lines) in the Norderaue plankton. Each data point is the mean of 6 observations taken at fortnightly intervals during summer, and monthly intervals during winter.

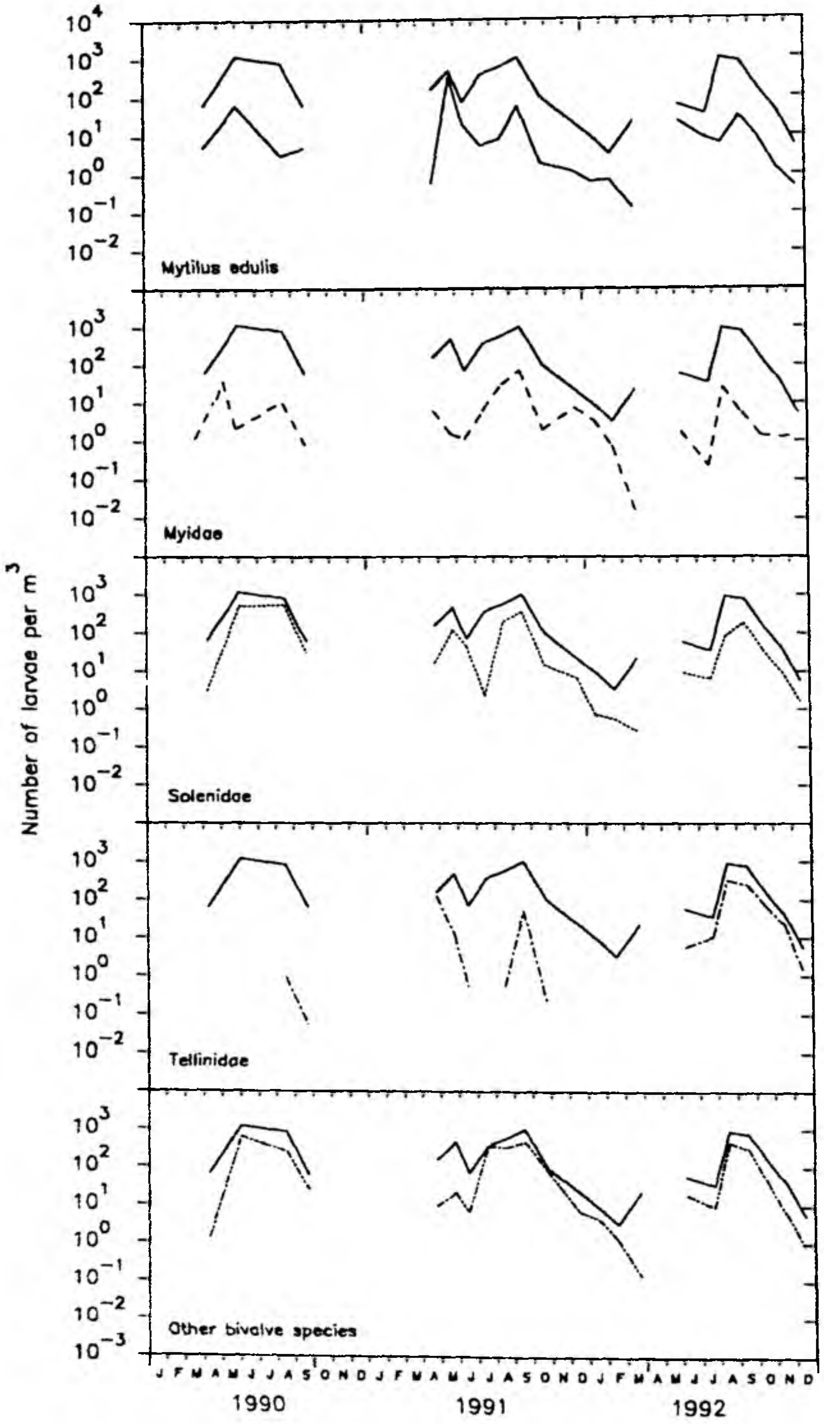

Figure 3.4 Temporal variations in the total number of bivalve larvae (upper solid lines) and the larval densities of the major bivalve groups (dashed lines) in the Hörnum Tief plankton. Each data point is the mean of 6 observations taken at monthly intervals.

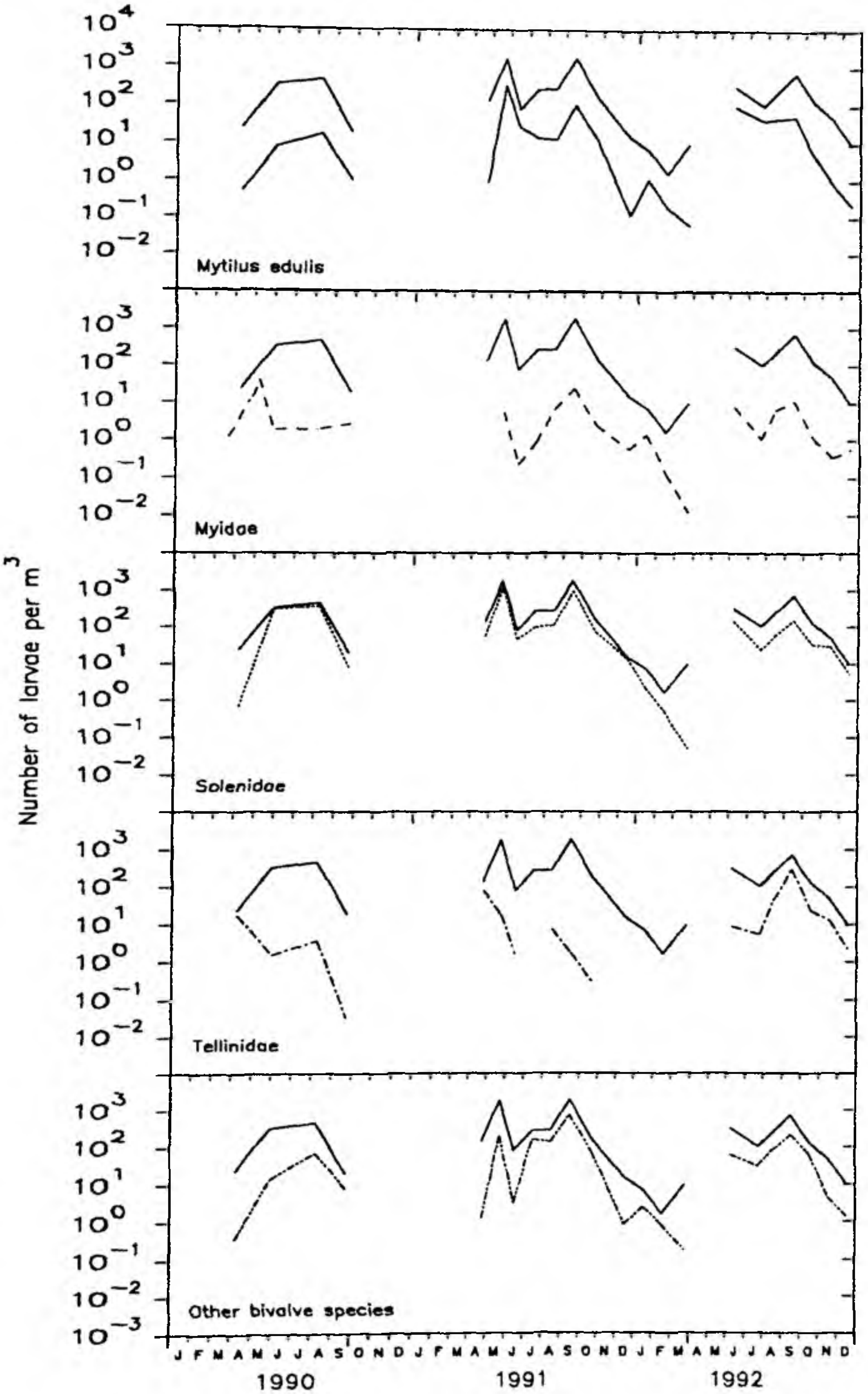

Figure 3.5 Temporal variations in the total number of bivalve larvae (solid lines) and the larval densities of the major bivalve groups (dashed lines) in the Süderaue plankton. Each data point is the mean of 6 observations taken at monthly intervals.

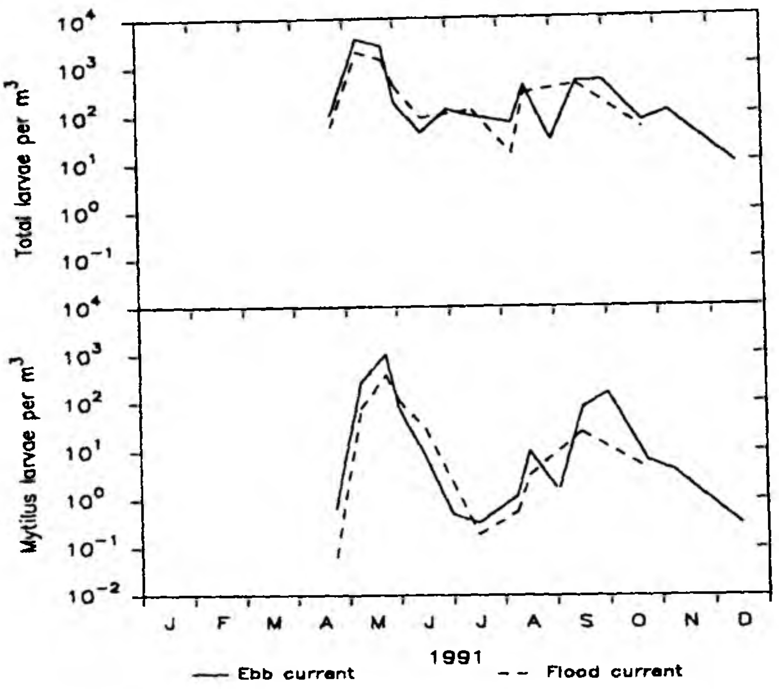

Figure 3.6 Total number of bivalve larvae and mean numbers of *Mytilus edulis* larvae per unit volume in the ebb and flood currents in the Norderaue during 1991. Each data point is based on 6 observations taken at fortnightly intervals.

The high diversity of bivalve larvae in the plankton (Table 3.2 in Appendix II) necessitated the grouping of allied species into their respective families for further analysis. Figure 3.2. shows that the Solenidae, which are almost exclusively represented by *Ensis americanus (=directus)*, dominated the bivalve component of the plankton, with *M. edulis* being the second most abundant species.

The temporal variations of the five major bivalve groups represented in the plankton of the Norderaue, Hörnum Tief and Süderaue are illustrated in Figures 3.3, 3.4 and 3.5, respectively. Although variations in the timing and amplitude of total larval densities occurred, no significant differences were found between years. The overall seasonal periodicity between the groups was isomorphous, although slight temporal shifts in abundance maxima were apparent. Thus, whereas in 1990 in the Norderaue the first peaks in total abundance occurred slighly later than in successive years, the spring maximum of *M. edulis* larvae had already passed by April. In 1991, however, the *Mytilus* peak was observed in late May, a fortnight after the maximum in total bivalve larvae. These nuances were not detected at Hörnum Tief and Süderaue due to the less frequent sampling. When plankton sampling was conducted throughout the winter, small numbers of mussel larvae were found, even in winter.

Occasional comparative oblique hauls found slightly higher larval concentrations (total bivalves and mussels) in subsurface samples. These differences were, however, not significant at the 95% level.

Although insignificant, larval abundance in the ebb current in the Norderaue was, on average, higher than on the rising tide (Fig. 3.6). A slight influx of *M. edulis* larvae was only observed in the period May to July, the densities being higher in the flood tide than the ebb tide. Amongst the other families, only the Tellinidae showed a marked difference in abundance between rising and falling tides, there being a significant export of larvae throughout the year.

The largest proportion of larvae measured during 1991 and 1992 were 200 - 300 µm in size (Fig. 3.7). Successive cohorts were recognizable in the majority of the samples measured. Increases in mean length over a 2 - 4 week period represent growth of the respective cohort during its pelagic residence (Table 3.3 in Appendix II). In 1991, an increase in the mean length and an increase in the length-frequency range occurred between 9 and 24 May. In early June this cohort was still recognizable at a mean size of 294 µm, prior to leaving the plankton and settling in the benthos, and a succeeding cohort (mean = 209 µm) appeared. The dominant second mode in late June may represent bysso-pelagic post-larvae undergoing migration in the plankton between successive attachments. Similar patterns were noted in the length distributions for October, representing larvae from the autumn abundance, and in length distributions the following year.

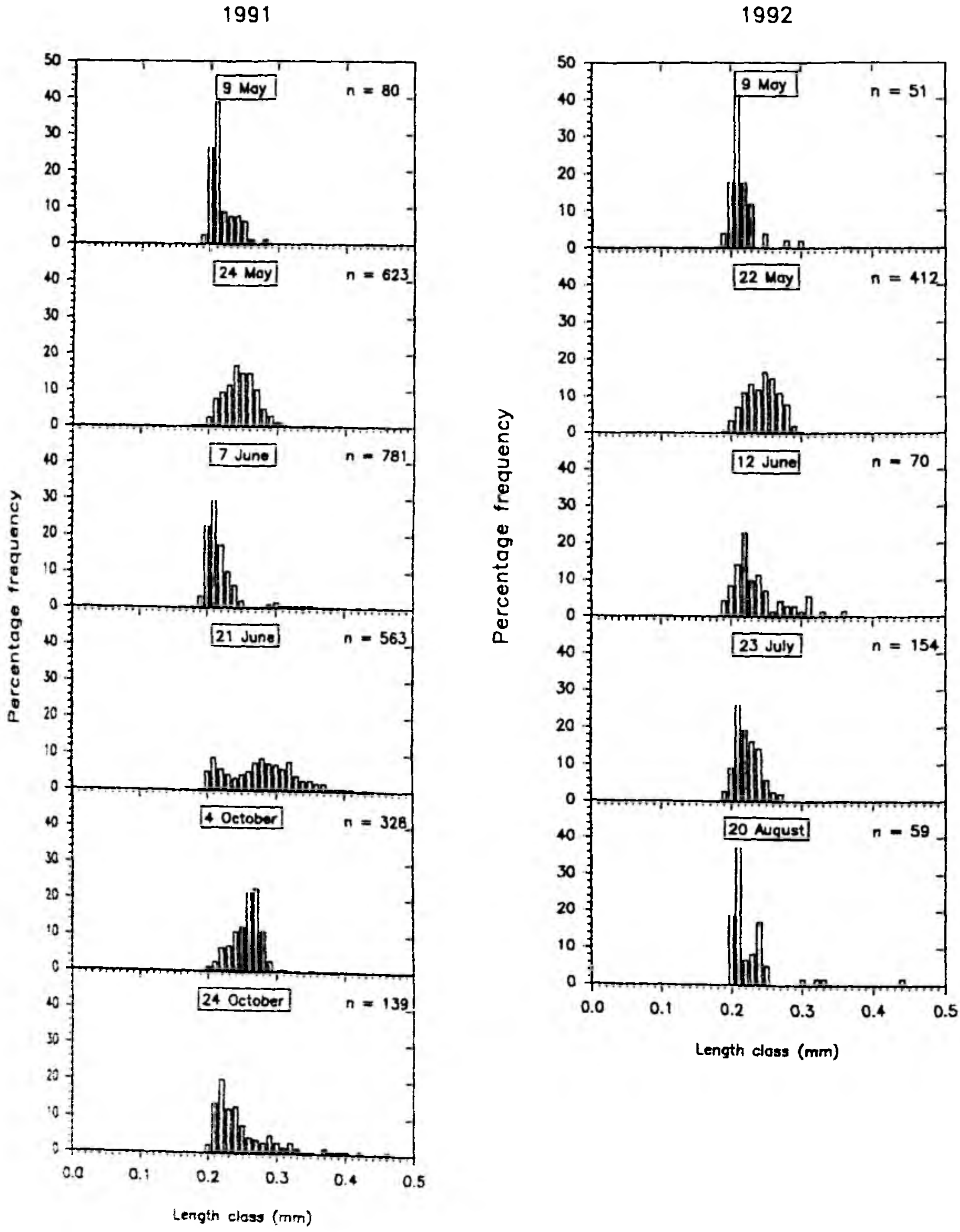

Figure 3.7 Size-frequency distributions of *Mytilus edulis* larvae at intervals during 1991 and 1992 from the Norderaue plankton (n = number of larvae measured; class widths = 0.01 mm).

DISCUSSION

The planktonic species diversity and temporal occurrence of bivalves found in this study are similar to descriptions of North Sea plankton by Kändler (1926), Werner (1949), Rees (1954) and Heiber (1988). However, whereas these authors reported a dominance of *M. edulis* larvae throughout the year, *Ensis americanus* was found to be the most abundant of the bivalve larvae encountered in the Schleswig-Holstein Wadden Sea. Heiber (1988) found *Ensis* to be sub-dominant in the plankton of the Weser estuary, and its dominance over the entire period of this study suggests a possible increase in this species in the Wadden Sea fauna.

In contrast to the almost total absence of *Cerastoderma* in the present study, Heiber (1988) also found up to 1 300 cockle larvae per m^3 in the Lower Saxony Wadden Sea. Adult *C. edule* cockles have the highest biomass of the Wadden Sea bivalves, followed by *M. edulis* and *E. americanus* (Ruth, Institut für Meereskunde, Kiel, pers.comm.). The low abundance of cockle larvae in the Schleswig-Holstein samples is therefore strange. The strong turbulent currents at maximal tidal exchange (mid-way between high and low tides) in the Wadden Sea tidal channels appear to cause complete mixing of the water column within these channels. Turbulent eddies, carrying large quantities of bottom sediment and detritus, were often observed reaching the surface during sampling. Surface plankton samples also contained large quantities of sand particles (up to 300 µm diameter), indicating homogeneous mixing of tidally suspended bottom sediments. Samples taken at the surface during the maximal ebb current are therefore probably representative of the distribution of bivalve larvae in the entire tidal stream and associated water masses. Reliance on surface sampling was additionally justified by the insignificant difference in larval abundances between the surface and oblique-haul samples.

It is, however, possible that *C. edule* larvae specifically shelter in areas unavailable to the bongo-net sampling techniques used, such as in calmer seabed eddies, or a seabed boundary layer. For example, Jonsson *et al.* (1991) found that, when water velocities exceed >5 $cm.s^{-1}$, cockle larvae become confined to a slowly drifting seabed boundary layer, and are unable to enter the water column above. Alternately, cockle larval abundance may have been under-estimated due to difficulties with identification. Problems with the laboratory culture of cockle larvae (Seaman, Institut für Meereskunde, Kiel, pers. comm.) have resulted in a lack of reliable larval descriptions in the literature, complicating identification. Resolution of these questions requires further work on cockle larval identification and distribution.

Mileikovsky (1973) reported the ability of the larvae of many bivalve taxa to regulate heir position in the water column by means of active vertical movement. Although arval densities in oblique hauls in this study were not significantly different from surface samples, there were indications that limited accumulation of *M. edulis* larvae may persist near the surface in strong flowing ebb currents, provided turbulence is not strong enough to mix the water column. For example, Verwey (1966) and Buyanovskii & Kulinova (1984) reported concentrations of larger larvae (195 - 235 µm) in the upper water layers at high current velocities, when smaller veliger larvae (<185 µm) were evenly distributed throughout the water column. However, strong vertical turbulence, uch as occurs during maximal tidal exchange in the Wadden Sea, results in mixing f even the larger larvae.

he temporal relationship between *M. edulis* larval abundance peaks and parent-stock spawning events appears to be relatively consistent (Bayne, 1964; Seed, 1969a; eiber, 1988). However, larval abundance itself is highly variable. Maximum reported densities of 7 000 individuals per m^3 in the Dutch Wadden Sea (Binsbergen, RIN-DLO, npubl.) and 9 000 larvae per m^3 in Lower Saxony plankton (Heiber, 1988) differ by early an order of magnitude from the range of numbers found in this study, even hen averaged over the period of highest occurrence (May - September). Bayne 964), working in Wales, obtained larval counts similar to those presented here. Such gnificant annual variations in larval densities are thought to result primarily from uctuations in spawning duration and intensity, rather than from variations in biomass the adult populations.

uch fluctuations appear to result mainly from environmental conditions (Jørgensen, 81). Severe winter temperatures cause a marked decrease in basal metabolism,

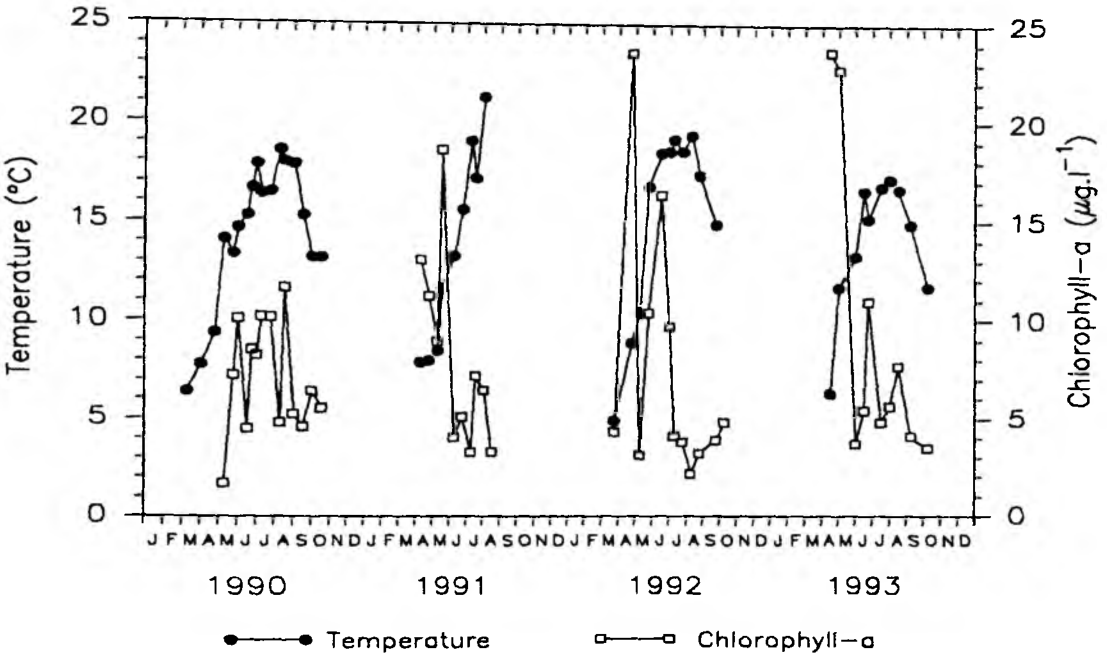

Figure 3.8 Mean sea surface temperature and chlorophyll-*a* concentrations in the Norderaue tidal stream. Data from regular aerial surveys to monitor phytoplankton development and blooms in the Wadden Sea (Göbel, in prep.).

resulting in reduced depletion of energy reserves and an increase in gamete production when temperatures increase. Temperature increases in spring are more rapid after such winters, resulting in synchronous and more intense spawning of the stocks. For example, meteorological records show that the winters 1975/76 and 1981/82, preceeding the studies of Binsbergen (RIN-DLO, unpubl.) and Heiber (1988) respectively, were characterized by below average winter temperatures (Amtsblatt des Deutschen Wetterdienstes, 1975 - 1982), which was not the case in the present study. Limited sample numbers and patchy plankton distributions may, however, also lead to increased variability between localities and sampling periods (Table 3.1 in Appendix II).

The continuous presence of *M. edulis* larvae in the plankton indicates the occurrence of spawning throughout the year. In comparison with cycles in gonad index and condition index (Figs 2.2 and 2.4, respectively), the larval abundance peaks occur somewhat later than spawning events. In the spring, peak larval densities occur 1 - 2 weeks after spawning, corresponding to the normal time for development from the veliger to the velichoncha (Loosanoff & Davis, 1963). Larval development after the autumn spawning appears to take slightly longer, presumably as a result of the declining water temperatures and reduced phytoplankton concentrations. Gonad activity observed in August was only reflected in larval abundance 4 weeks later.

The spawning event shown in gonad indices in the low intertidal and subtidal populations during October/November were also not well represented in the plankton samples. Similarly, increased larval densities during January/February were not associated with any local spawning event. As mussel egg cleavage does not occur below 5°C (Bayne, 1965), and winter water temperatures in the study area are typically below this, these abundance peaks are thought to represent the appearance in the plankton of larvae with a prolonged pediveliger stage. Delay in metamorphosis is characterized by a cessation of feeding and growth for periods of up to 6 months (Lane *et al.*, 1985), and is triggered by reduced temperature, rather than reduced food availability (Bayne, 1965).

The temperature and chlorophyll-*a* concentrations measured near the Norderaue plankton station (Göbel, in prep.) (Fig. 3.8), show the close relationship between larval abundance maxima and phytoplankton blooms during summer. The correlation between periods of gamete release and subsequent larval abundances in the plankton suggests that the majority of mussel larvae encountered in the plankton in this area result from local spawning. However, the larval abundance peaks observed in July 1991 and August 1992 (Fig. 3.3), did not appear to result from local spawning. These larvae were observed too early to result from local spawning events (Fig. 2.2), and the larval densities were too high to result from low-level, year-round spawning of a small proportion of the stock. These larvae therefore seem to have been imported from adjacent regions in the North Sea.

Planktonic larval abundances generally decline with increasing distance offshore (Werner, 1940; Mileikovsky, 1968). A series of plankton samples taken 10 km seaward of the Norderaue station during the larval peak in June 1990 (Westvortrapptief, Fig. 1.1) showed that the density of bivalve larvae in the offshore waters was only 12% as high as at the inshore stations. In contrast, Rees (1954) reported large concentrations of *M. edulis* larvae in the middle of the North Sea. Those larvae were in advanced stages of development, confirming their teleplanic nature and their ability to disperse over large distances in ocean currents (Scheltema, 1971).

The fortnightly sampling interval used in this study was adequate for identifying larval cohorts. Monthly samples gave a picture of the overall cyclic patterns of plankton abundance, but the mussel larval developmental period of 3 - 4 weeks at 16 - 20 °C can result in abundance peaks being missed, or in poor estimates of larval densities. The higher resolution of fortnightly samples was needed to follow successive spawning events from appearance of bivalve veliconcha to their disappearance as pediveligers, and to allow for detection of incursion of cohorts from other habitats. Such incursion of plankton into the Schleswig-Holstein Wadden Sea does appear to occur, as local larval densities do not relate entirely to local spawning events. The proportion of larvae imported into the region is difficult to determine, but could be investigated by comparison of daily shell increments with spawning events in local populations.

4.

ATTACHMENT AND SETTLEMENT

Having established the periodicity and duration of spawning of *Mytilus edulis* in the Schleswig-Holstein Wadden Sea, and the timing and abundance of subsequent larval densities in the plankton, the subsequent attachment and settlement of larvae on locally available substrates was investigated. After an obligate developmental period in the plankton, *M. edulis* larvae respond to specific environmental cues, and the presence of suitable substrata, and leave the water column to attach and settle. Although attachment is a pre-requisite for metamorphosis, it is reversible. The post-larvae, termed "plantigrades" by Bayne (1964), retain the ability to undergo repeated attachment to filiform algae and hydroids before finally settling on creviced surfaces or between established conspecific adults. A knowledge of mussel larval substrate preferences, and of their behaviour before and after attachment, should therefore assist in explaining some of the reasons for recruitment success or failure.

Past investigations into spatfall of mussels have resulted in the development of a variety of spat collectors. These include grooved or roughened panels of various materials (de Blok & Geelen, 1958; Seed, 1969a) and free or bound oyster/mussel shell cultch (Engle & Loosanoff, 1944; Young, 1946; Reynolds, 1969; Ceccherelli & Rossi, 1984) which offer sheltered niches for settlement. Despite their abundance, early plantigrades (200 - 500 µm; primary settlers) have proved difficult to collect and retain on artificial hard substrates, largely as a result of their dispersive nature. Successful colonization of such substrates, primarily by older plantigrades (secondary settlers >500 µm) occurs only after previous fouling by other benthic organisms. Preferential attachment of mussel spat to fibrous and filamentous substrates, including hydroids and filiform algae, has been observed and confirmed by many workers (reviewed in Lutz & Kennish, 1992). This has prompted the use of various threads, coir ropes and rubberized fibrous matting as artificial attachment surfaces (de Blok & Geelen, 1958; Davies, 1974; Dare, 1976). As they simulate the filamentous nature of some of the primary colonizing organisms, these substrates have proved sufficiently attractive to young spat to induce settlement.

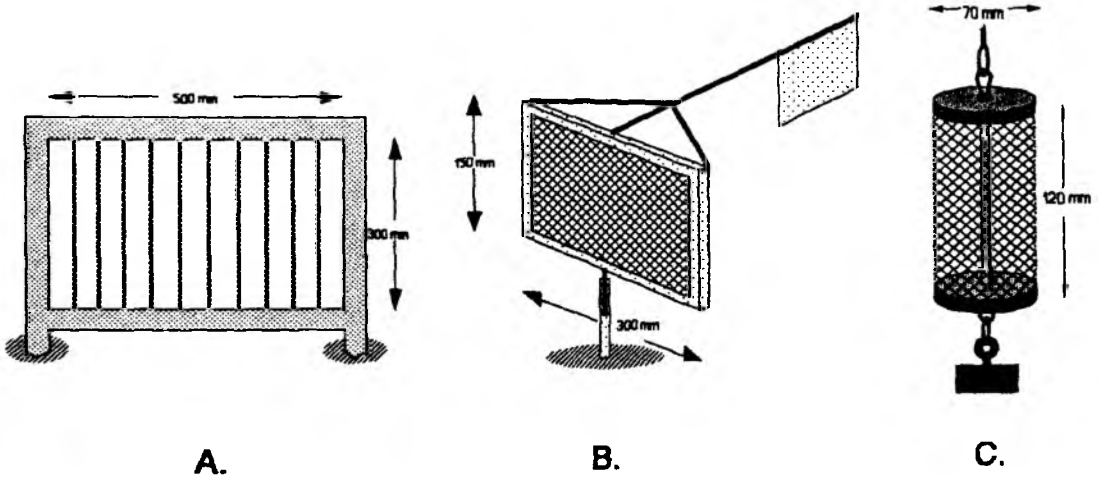

Figure 4.1 Experimental mussel spat collectors used in test trials during this study. A)Type 1 fixed rope collector (distance between ropes = 50 mm), B)Type 2 rotatable collector with continuous direct current exposure of the panel during submergence (mesh size = 5 mm), and C)Type 3 vertical profile collector (mesh size = 5 mm).

MATERIALS AND METHODS

Spat Collectors

In the present study, various spat collectors were designed and tested. The success of the various designs was evaluated by comparison with samples from adjacent natural substrates, providing information on settlement behaviour on natural substrates. The high catch efficiencies of intertidal rope collectors reported by Dare *et al.* (1983) and the "bouchots" (rope-wound poles) used as seed collectors and mussel cultures in France (Field, 1922), prompted the design of the Type 1 rope collectors. Initial trials in spring 1990 were conducted with woven sisal ropes (8 mm Ø) strung vertically in wooden collector frames 300 x 500 mm (Fig. 4.1 A). The frames were staked into the ground 50 mm or more above the sediment. Two frames, one perpendicular and one parallel to the flood current, were set up at five intertidal elevations in a transect across different benthic types, from the shore to the edge of a tidal gulley (Site 1 - Site 5; see Chapter 1 and Fig. 1.2).

The marked effect of tidal direction on the settlement success of the Type 1 collectors led to the development of rotatable (Type 2) collectors which oriented a settlement surface perpendicular to the current direction (Fig 4.1 B). These collectors consisted of a 300 x 150 mm stainless steel frame pivoting 200 mm above the substrate on a stake inserted into the ground. For collection in tidal streams, the collector was suspended from an anchored buoy. The settlement frame was kept perpendicular to the current by a vane, and held polyester gauze strips (each 50 mm x 120 mm), used successfully in the Netherlands as an artificial settlement surface during similar studies (Binsbergen, RIN-DLO, pers. comm.). The total gauze settlement area of the Type 2 rotatable collector was 600 cm^2.

In the spring of 1991, Type 2 spat collectors (Fig. 4.1 B) were set up at 3 elevations across the intertidal flats (Sites 1I, 3I and 5I) and subtidally in a tidal gulley (Site 5S) and tidal stream (Site 51S) (see Fig. 1.2). During initial trials, settlement rates on 5 different gauze types differing in mesh size and shape, were compared by simultaneous deployment on collectors. The resultant mean settlement rates were found to be not significantly different on the different gauze types (ANOVA, Scheffé range test, 95%-level), so subsequent deployments were done using only a 5 mm diamond mesh gauze, which most closely resembled that used in the Netherlands, and which had mesh angles and a thread diameter most similar to hydroids in the area. In late 1992 and during 1993, an additional collector was staked horizontally in an intertidal residual water body beside a tidal gulley (Site 5H; horizontal collector), to simulate the filamentous substrates occurring in such habitats.

Although not shown by the vertical plankton hauls in this study, reports by Verwey (1966), Mileikovsky (1973) and Buyanovskii & Kulinova (1984), suggest that mussel larvae have the ability to regulate their vertical position in the water column, despite strong currents. This prompted the design of Type 3 collectors to investigate the vertical distribution of spat in the water column. These collectors consisted of a cylinder of the same polyester gauze, clamped to plywood disks (70 mm Ø) held 120 mm appart by a central stainless steel rod (Fig. 4.1 C). The total gauze settlement area of the Type 3 collector was 290 cm^2. The effects of current direction were catered for by the cylindrical design and these collectors were deployed in roped groups of three: one attached to an anchor weight (± 6 m depth), another in midwater (± 3 m depth) and the third at the surface, just below a supporting buoy. These Type 3 collectors were deployed at three locations in the Vortrapptief tidal channel during the 1993 settlement period (see Fig. 1.2).

At fortnightly intervals during 1991 and 1992, samples of a wide variety of algae, hydroids, polychaete tubes and barnacle-covered stones were collected to determine substrate preferences of mussel spat, and to monitor settlement on natural substrata for comparison with the collectors. Samples generally consisted of the entire plant or clump of the species concerned. A total of 153 samples were randomly collected by hand from the intertidal flats and residual water bodies east of Amrum, and by dredge from the Vortrapptief, which contains a high diversity of benthic species (see Fig. 1.2). Plantigrades were removed quantitatively from the samples, and the substrates identified to species where possible. Algae, hydroids and polychaete tubes were dried to constant weight at 80°C for subsequent estimation of number of settled mussel spat per gram dry weight of substrate. Encrusting organisms such as barnacles were not used for determination of settlement densities, due to the difficulty of removing and quantifying these substrata.

Treatment of Substrate Material

Due to rapid fouling by marine organisms and drifting macroalgae, Type 1 collectors had to be checked and cleaned weekly, and the ropes replaced every 4 weeks. The gauze strips on the Type 2 and Type 3 collectors were replaced every 7 - 10 days. In a control experiment, the gauze strips and sisal ropes showed no visible deterioration after 6 and 12 weeks submergence, respectively. The collector substrates were nevertheless replaced with new material when changing collectors. All artificial and natural substrate samples were stored frozen in polyethylene bags for later analysis.

The plantigrades were detached from their respective substrates by dissolving the byssal threads with diluted bleach (Davies, 1974). Spot checks of the material were made to ensure that no spat remained on the substrate after removal. Plantigrades

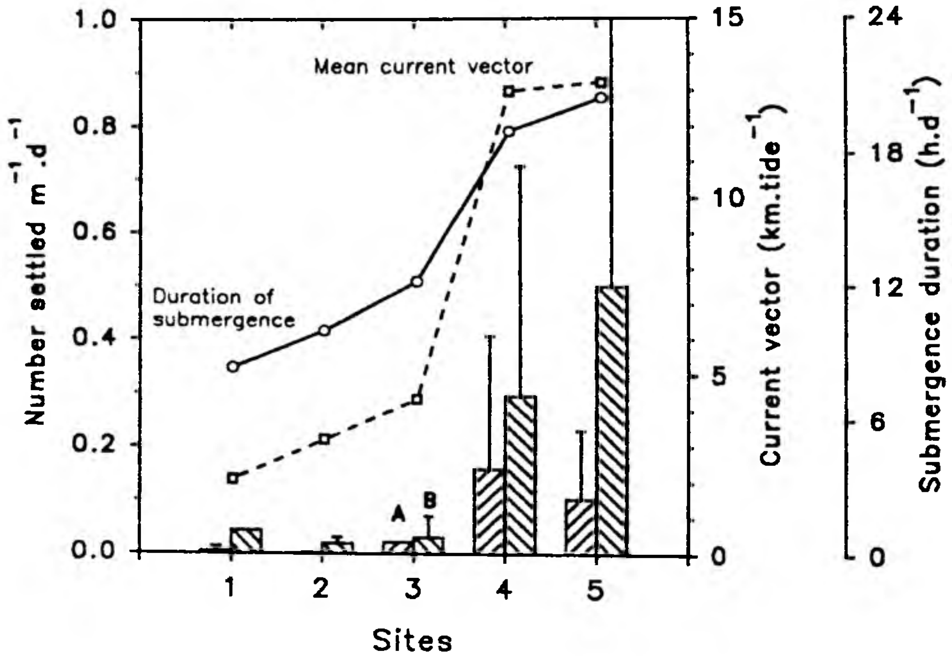

Figure 4.2 Catch efficiency of the Type 1 rope collectors, set parallel to (A) and across (B) the tidal stream. Standard errors of the means, based on 7 observations for (A) and 6 observations for (B) collectors, are given.

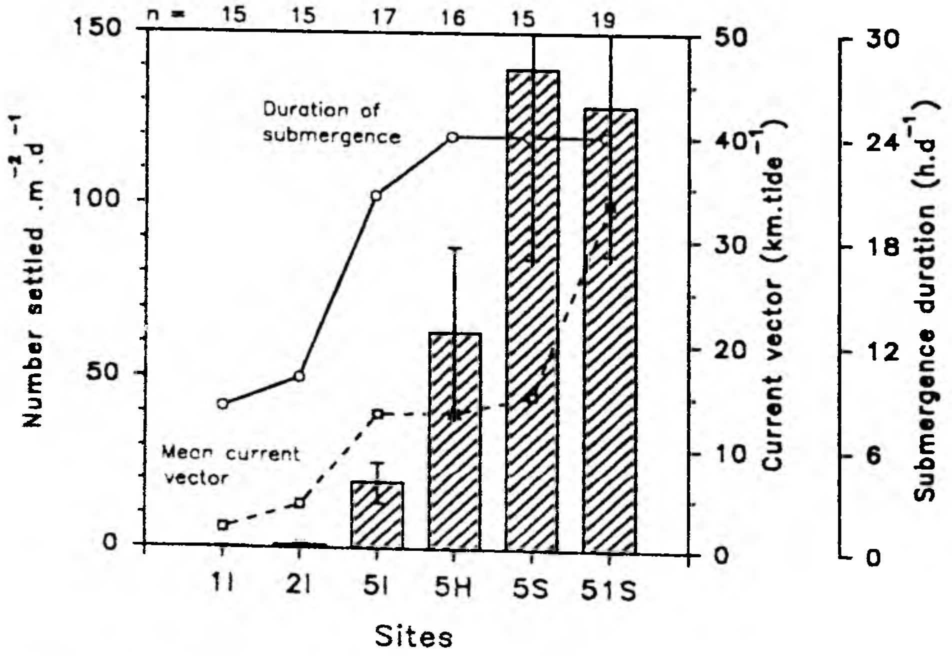

Figure 4.3 Catch efficiency of Type 2 rotatable collectors. Standard errors of means are given; n = number of observations (I - intertidal ; H - horizontal ; S - subtidal collectors).

were counted and, where possible, the shell lengths of at least 200 individuals were measured from microscope video image using a computer image analysis system. In order to enable quantitative comparison between settlement rates on the Type 2 and Type 3 collectors, spat counts were standardized to counts per m^2 of gauze per day deployed.

Data Analysis

The length-frequency distributions of settled plantigrades were analysed with the ELEFAN length-frequency analysis program (Gayanilo *et al.*, 1989), and successive cohorts in multimodal distributions were separated using the Bhattacharya method (Bhattacharya, 1967) in order to determine growth from modal progressions.

A Kruskal-Wallis non-parametric ANOVA (95% confidence level) was used to test the effect of tidal elevation and orientation of Type 1 and aerial exposure of Type 2 collectors. As attachment rates were low, all samples for each collector site were pooled. In comparing temporal settlement trends, low attachment rates per collector and site also necessitated the pooling of data across collector sites. Vertical distribution preferences and settling densities on natural substrates were also analysed with a Kruskal-Wallis non-parametric ANOVA at the 95%-level. Size-frequency distributions of plantigrades attached to different substrates were compared with a paired two-sample test (significance; $z < 0.05$).

RESULTS

Effect of Collector Orientation on Settlement

Although a slight gyre was noted in the current direction and velocity data from the current meters (see Fig. 1.3), the direction of the flood and ebb currents is primarily uni-directional. Figure 4.2 shows how collectors set across the main current flow caught significantly more larvae than those set parallel to the current. After submergence times longer than 18 h and current vectors above 10 km.tide^{-1} the differences were remarkable. The total settlement levels were, however, low.

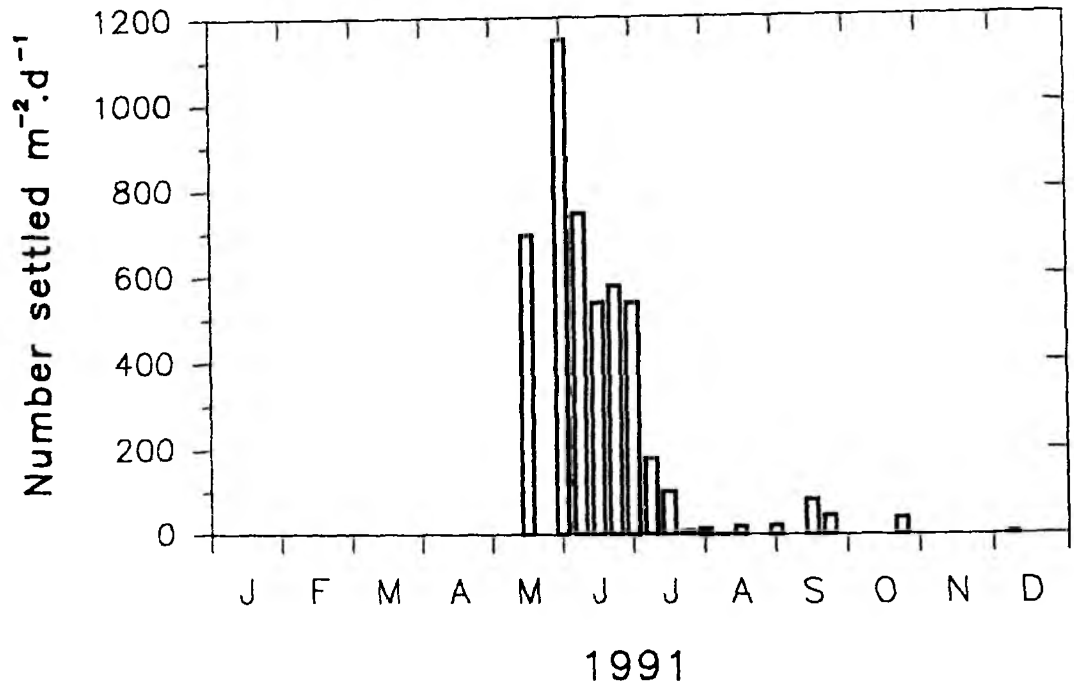

Figure 4.4 Temporal variations in plantigrade settlement on Type 2 rotatable collectors during 1991. Sampling commenced in May and continued until December.

Duration of Submergence

The effect of tidal elevation on spat settlement rates is shown in Figures 4.2 and 4.3. Type 1 collectors set close to a tidal gulley (Site 4 and Site 5), with a submergence time >12 h per day, show a significantly higher settlement rate than those higher on the shore. Similar results were obtained on Type 2 collectors the following year; catch rates of aerially exposed intertidal collectors, submerged intertidal collectors and subtidal collectors were significantly different. More detailed analysis of settlement on the three Type 2 collectors at Site 5 revealed differences in settlement rates between the subtidal, horizontal and intertidal collectors (Fig. 4.3). These three collectors were set within 20 m of each other, and were exposed to similar current vectors and exposure times. The differences in catch rates, although insignificant, suggest that desiccation and filtered water volume may influence settlement success. The slightly reduced attachment to the collector exposed to the largest current vector in the tidal stream (51S), however, implies that current velocity and/or position in the water

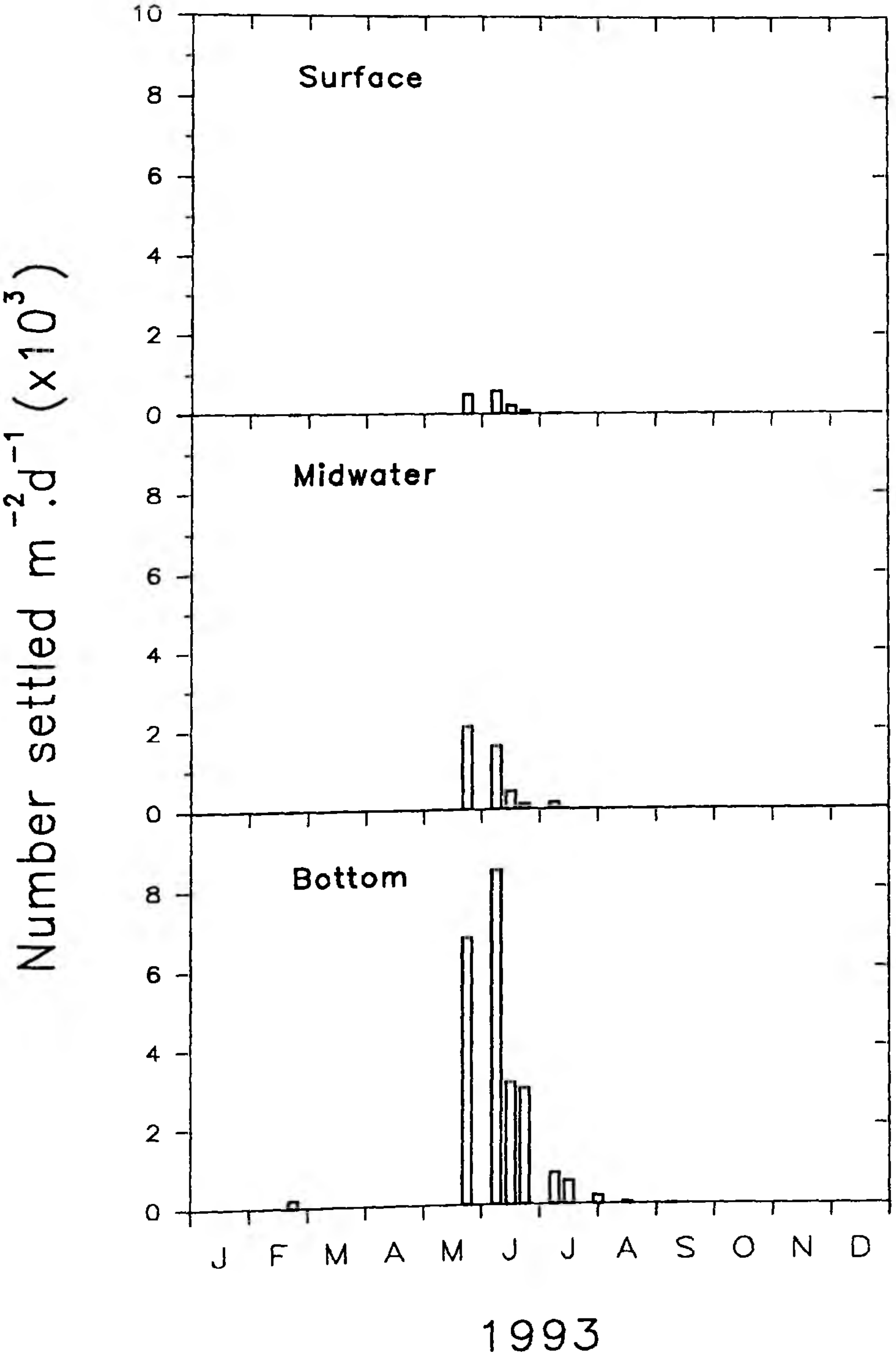

Figure 4.5 Temporal variations in plantigrades settlement at three depths on the Type 3 vertical profile collectors. Sampling commenced in late February and continued until early August.

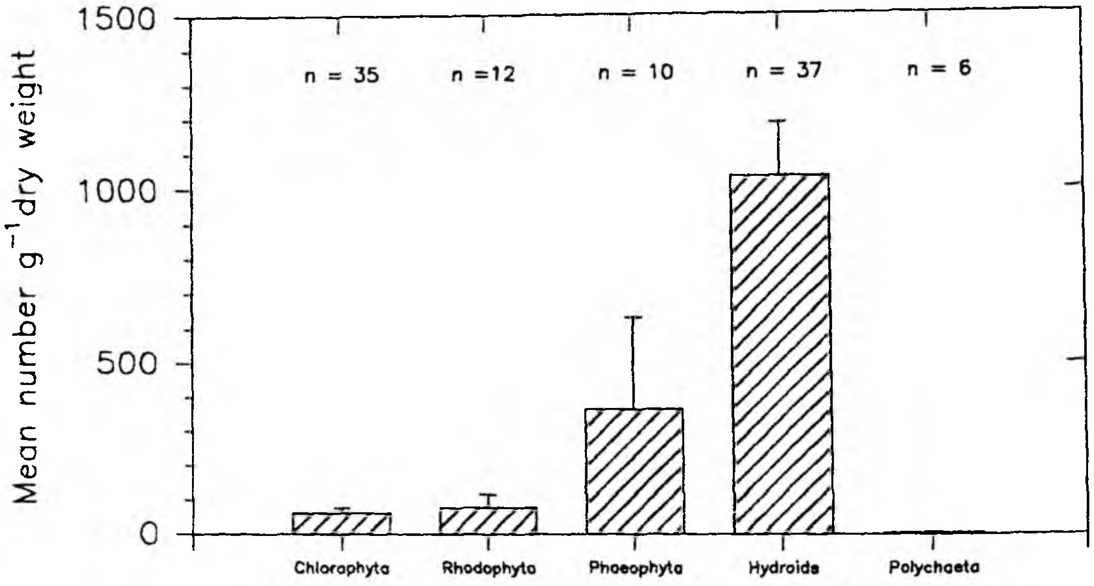

Figure 4.6 Mean number of plantigrades attached to various natural substrates. Standard errors of the means are given; n = number of observations.

column may play an additional role. This was confirmed by the Type 3 vertical profile collectors, on which differences in settling intensity at the three depths were remarkable. The percentage occurrence of plantigrades settled at the three depths are shown in Table 4.1, the collector units attached to the anchor-weights having caught considerably more spat than those higher in the water column (see also Fig. 4.5).

Table 4.1 Percentage occurrence of plantigrades settled on the vertical profile collectors (see Fig.4.1c).

BOTTOM	MIDWATER	SURFACE
72.4%	20.9%	6.7%

Seasonality of Settlement

Despite low settlement rates, pooled data were adequate to monitor settlement seasonality. Primary settlement appears to be abrupt and intensive, the major larval settlement in the study area occurring from mid-May to mid-July. This settlement period may be followed by a second, shorter and much lower settlement in late September and October. The temporal variations in settlement recorded on the Type 2 and Type 3 collectors are presented in Figures 4.4 and 4.5, respectively. Figures 4.4a and 4.4b (in Appendix III) show the temporal settlement patterns observed on the Type 1 collectors during 1990, and on the horizontal collector during 1992 and 1993.

Natural Substrates

Although settled plantigrades were found on a wide variety of substrata (Table 4.2 in Appendix III), clear preferences were shown for hydroids, followed by algae (Fig. 4.6). Within the algae, filiform species were preferred to those with smooth, flat thalli, unless the latter were already hosts to epizooic hydroids. Plantigrades were observed to attach gregariously in filament axils, the smaller spat (200 - 500 µm) settling on the finer, terminal ramifications and the larger ones (>500 µm) on the thicker branches

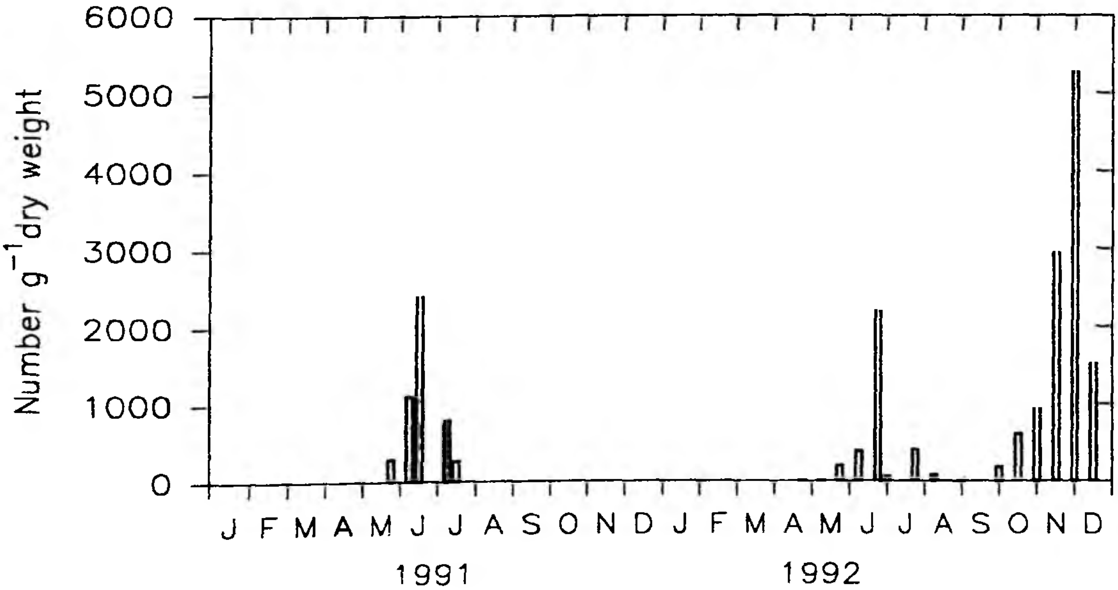

Figure 4.7 Temporal variations in the number of plantigrades attached per gram dry weight of hydroids. Sampling from April to August 1991 and from April to December 1992.

and stems. The temporal occurrence of plantigrades on hydroids is shown in Figure 4.7. Although peaks in attachment were evident from May to July in 1991 and 1992 (corresponding to those observed on the collectors), more extensive sampling during 1992 revealed even higher spat numbers on subtidal hydroids during winter.

Subtidal, benthic samples taken during the year contained large numbers of spat in the crevices of barnacles, or in small pits in shells and pebbles. Spat persisted on these substrates throughout the winter, beyond the settlement period observed on algae and hydroids. Plantigrades (both primary and secondary) were also relatively common between the byssal threads of intertidal and subtidal adult mussels. Such settlement occurred to some degree throughout the year, but spat were most abundant in mussel beds in autumn, when filamentous primary substrates in the tidal pools were scarce. However, it was noted that these spat did not attach to the byssal threads of the adults, but continued to creep actively between them.

Length-frequency of Plantigrades

Length-frequency analyses of the larvae and spat on the collectors showed that both the primary (200 µm - 500 µm) and secondary settlement stages (>500 µm) were represented on all collector types (Fig. 4.8 and Figs 4.8a - c in Appendix III). The length-frequency distributions of larvae and spat did not differ with collector depth. Sporadic brief peaks in settlement of small plantigrades (± 200 µm) on collectors, resulting from direct attachment of larvae from the plankton, coincided with periods of increased settlement on natural substrates, confirming the effectiveness of the gauze in simulating natural filamentous primary attachment surfaces. For example, the settling cohort appearing on spat collectors in May/June 1991 (Figs 4.4 and 4.8) also appeared on hydroid samples (Fig 4.7). Similarly, the length-frequency distributions of plantigrades which settled on hydroids and algae in May and September 1991 (Fig. 4.9a in Appendix III), were similar to those on spat collectors over these periods.

Figure 4.9 shows the length-frequencies of plantigrades attached to filiform algae and hydroids collected subtidally during 1992. Similar data for 1991 and 1993 are shown in Figs 4.9a and 4.9b in Appendix III. As these length-frequency distributions were

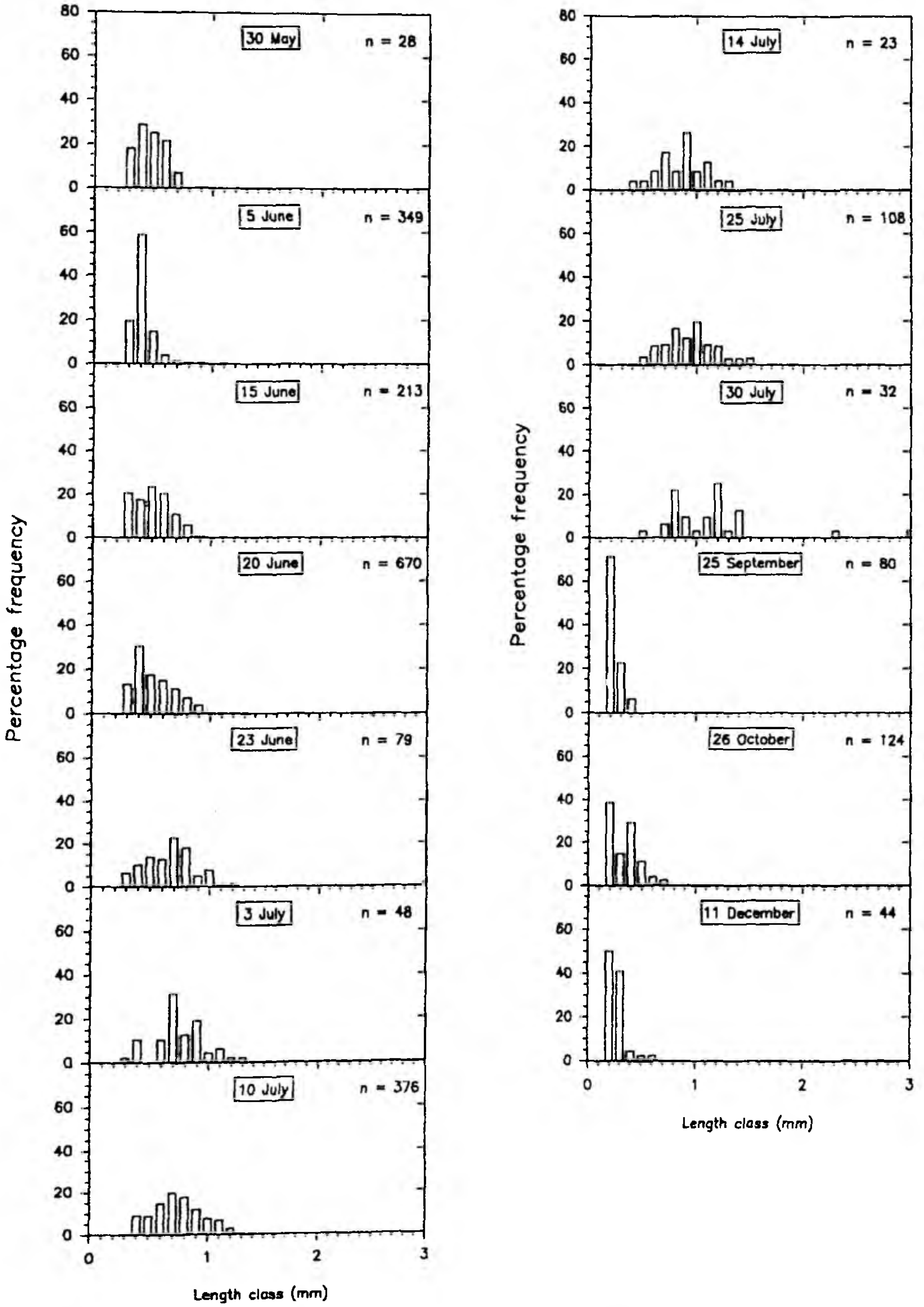

Figure 4.8 Size-frequency distribution of plantigrades attached to the Type 2 rotatable collectors during 1991 (n = number of specimens measured; class width = 0.1 mm).

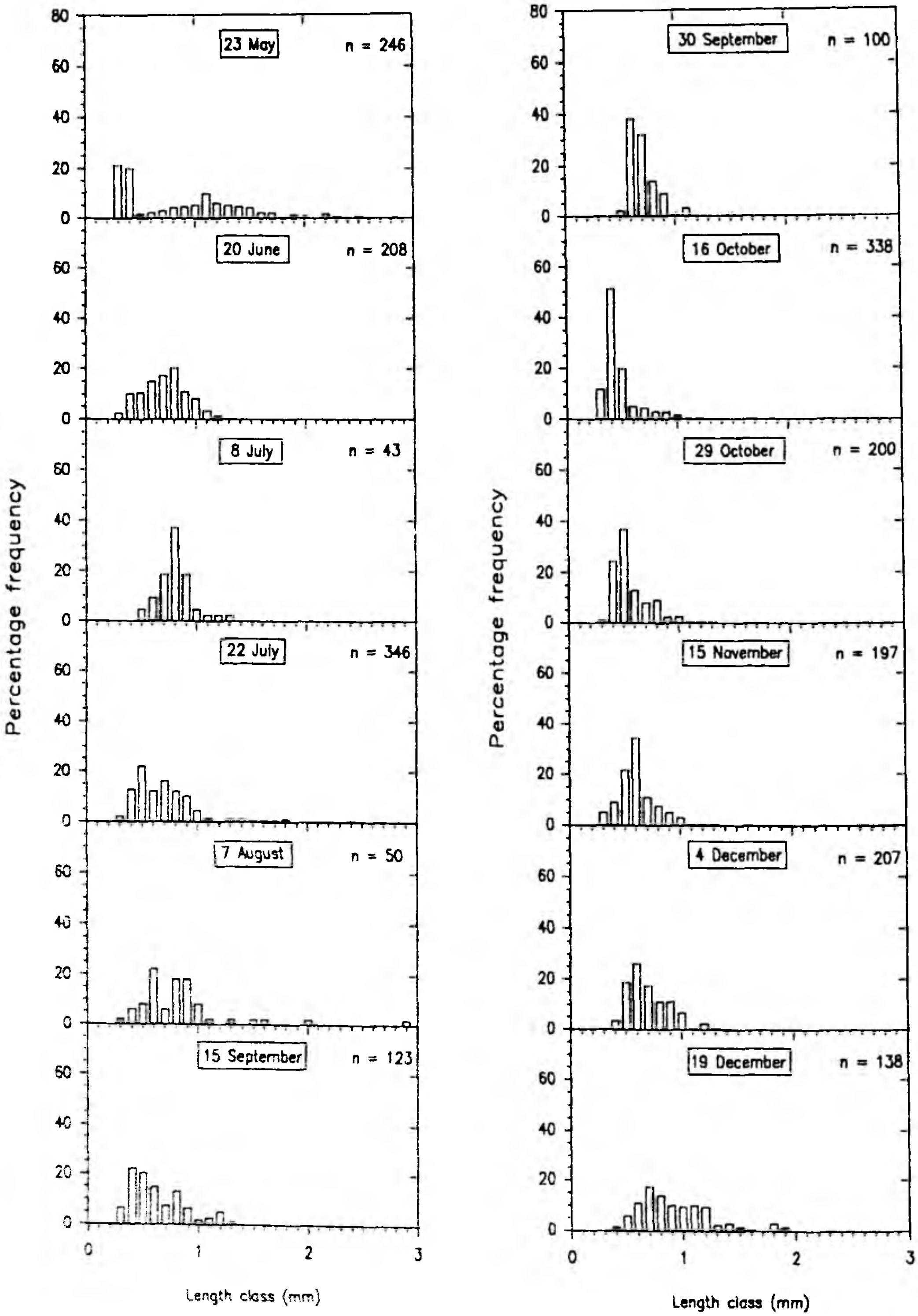

Figure 4.9 Size-frequency distribution of plantigrades attached to subtidal hydroids and filamentous algae during 1992 (n = number of specimens measured; class widths = 0.1 mm).

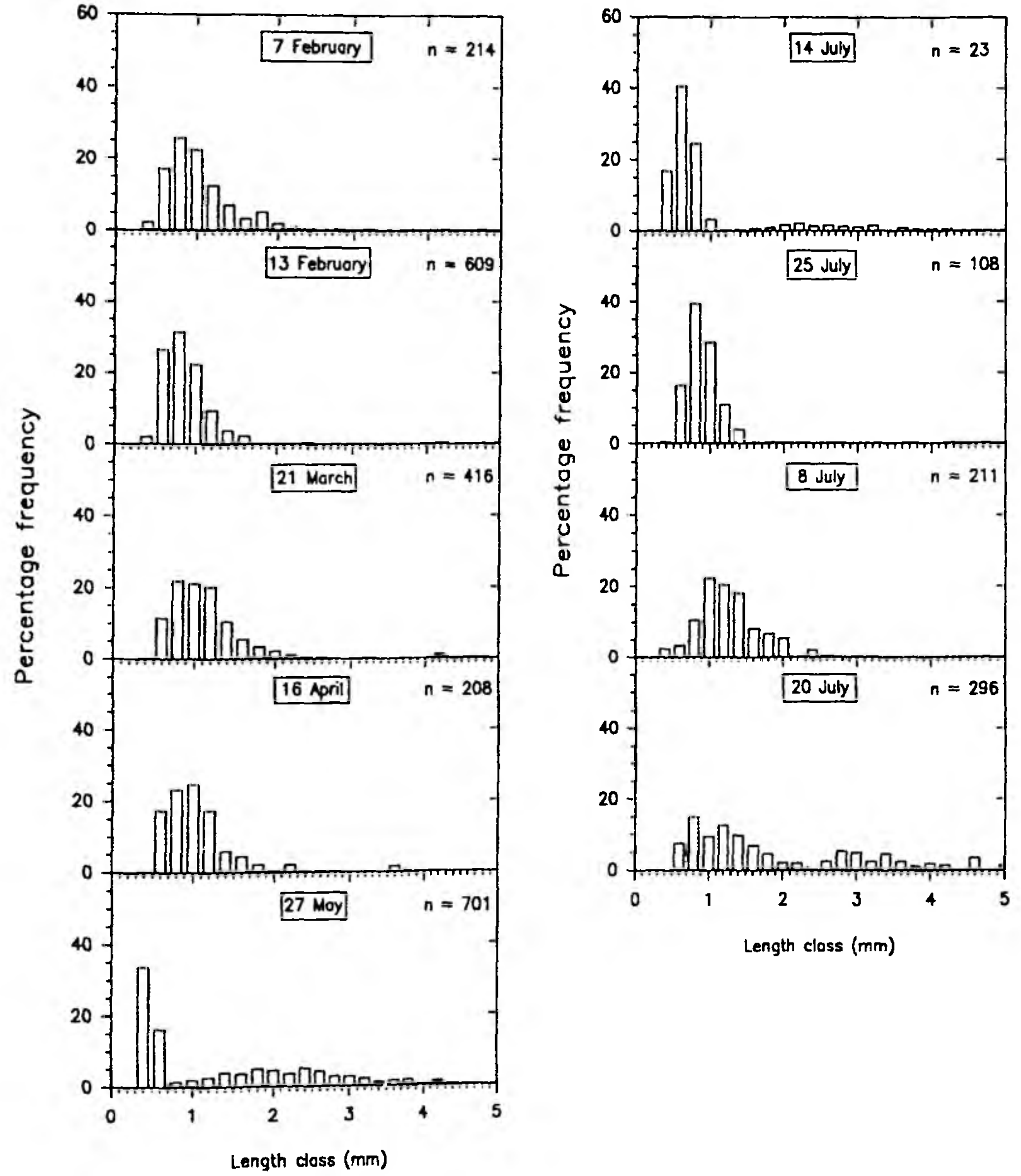

Figure 4.10 Size-frequency distribution of plantigrades attached to subtidal barnacle during 1993 (n = number of specimens measured; class widths = 0.1 mm).

usually multi-modal, identification of cohorts undergoing primary and secondary attachment is possible. Tables 4.3 - 4.9 in Appendix III show the mean size of the first two or three cohorts present in the length-frequency distribution data, determined with the Bhattacharya method (Bhattacharya, 1967) in the ELEFAN length-frequency analysis program (Gayanilo *et al.*, 1989).

Whereas the majority of spat found on natural and artificial filamentous substrates were <1 mm in length, plantigrades attached to barnacles (Fig. 4.10 and Table 4.10 in Appendix III) were generally >1 mm (range: 0.2 - 10.0 mm), with larger length classes being more abundant. Comparison of four samples taken within 3 days of each other in the same subtidal habitat, found significant differences between the length distributions of plantigrades attached to barnacles and those attached to filamentous substrates (Paired two-sample test, $z < 0.05$). Settlers on *Lanice* tubes were similarly significantly larger than those on hydroids (range: 0.3 - 2.6 mm).

DISCUSSION

The importance of tidal orientation of spat collectors was evident from settlement on Type 1 collectors. This is expected, as a surface perpendicular to the current flow will offer a larger surface area for attachment to drifting larvae or migrating plantigrades. Davies (1974) and Gabaev (1981) also observed higher catch success in collectors set across the main current stream. This suggests that larval settlement would be increased by the presence of dense assemblages of filamentous and fibrous substrates, with stands of algae or hydroids serving as effective filters, concentrating even low pelagic abundances of larvae and post-larvae.

The different settlement rates on collectors set at various levels on the shore indicate that the settlement success of the young plantigrades is determined to some extent by tidal elevation. Low settlement success on aerially exposed artificial substrates set above the mean low water mark suggests that the upper limit to settlement is determined by post-settlement mortality, rather than by the abundance of planktonic larvae (Engle & Loosanoff, 1944; Reynolds, 1969; Seed, 1969a; Dare, 1973; Dare *et* *al.*, 1983; Connel, 1985). The time required for secure attachment of mussel larvae is 4.5 - 6 h (Chipperfield 1953), so recently settled plantigrades cannot persist intertidally unless sufficient time has elapsed for the newly secreted byssus material to harden, or they are sheltered in a moist position. Although the crevices of the plaited ropes in the Type 1 collectors would offer some shelter to vulnerable spat, high predation during extended exposure periods probably caused high mortality of settled spat on these collectors. Numerous juvenile *Carcinus maenas* were found on the Type 1 collectors, seeking refuge in the moist rope-holes of the wooden frames. Dare *et al.* (1983) similarly report low settlement success on ropes exposed for longer periods. Despite the much shorter sampling intervals for the Type 2 and Type 3 collectors, the gauze used dries rapidly once exposed. Desiccation of both the substratum and the settled larvae could therefore have resulted in low survival on the intertidal collectors.

Immersion does not, however, appear to guarantee attachment success. The single horizontal collector was permanently submerged in an intertidal pool. Although exposed to a current vector similar to the neighbouring subtidal collector, this collector received fewer spat than the collector in the tidal gulley. This confirms that availability of suitable filamentous substrates alone is inadequate to ensure settlement success, and that settlement is also influenced by water movement. Eyster & Pechenik (1987) found that water movement enhanced attachment of spat in the laboratory. Active water flow also leads to improved larval growth (Seaman *et al.*, 1991), mainly as a result of increased food availability. Active selection of attachment surfaces exposed to water movement should therefore ensure greater spat survival.

Higher densities and prolonged settlement of plantigrades on near-bottom collectors were also noted by Engle & Loosanoff (1944) in the northwest Atlantic Ocean, and Jørgensen (1981) and Kautsky (1982) in the Baltic Sea. This suggests that attachment of *Mytilus* larvae is not random. Some studies have found that mussel larvae of primary settling size (190 - 250 µm) tend to concentrate near the water surface during flood tides, and settle out during the high slack and ebb tides (Verwey, 1966; Mileikovsky, 1973; Buyanovskii & Kulinova, 1984). Seaman (Institut für Meereskunde, Kiel, pers. comm.) furthermore found that *M. edulis* larvae gather at the bottom of rearing vessels in the absence of water movement. Such behaviour would favour initiation of primary attachment and metamorphosis in calm water. However, if the required settlement cues are not present, secretion of a gas bubble (Nelson, 1928) or drifting thread (de Blok & Geelen 1958; Sigurdsson *et al.*, 1976; de Blok & Tan-Maas, 1977; Board, 1983), allows for resuspension and redistribution of the plantigrades.

Investigations by Lane *et al.* (1985) and Eckman (1990) into the vertical distributions of suspended particles in regions with weak vertical density stratification, and characterized by strong tidal mixing or by wind mixing (as is the case in the Wadden Sea), found that older plantigrades (> 500 µm) have the tendency to concentrate nearer the sea bed, in the benthic boundary-layer. Higher densities of older bivalve post-larvae near the bottom at maximum current speeds, and during the ebb tide, have also been reported by Carriker (1951), Kunkel (1957), Verwey (1966), Wood & Hargis (1971), and Beukema & de Vlas (1989). The higher abundances of plantigrades, and prolonged settlement period on near-bottom collectors in the Schleswig-Holstein Wadden Sea, confirms these tendencies. Spat settling on the midwater and subsurface collectors are also exposed to strong turbulences and bombardment by sand and silt particles. De Blok & Geelen (1958) reported that larval settling rates were lower in areas with a higher silt load in the water. In the absence of protective niches offering shelter from such forces, attachment may be impared.

The appearance and attachment of plantigrades is abrupt and seasonal. The settlement periods observed in the Schleswig-Holstein Wadden Sea agree with those described for populations of *M. edulis* from Great Britain (Chipperfield 1953; Bayne 1964; Seed 1969a; Dare 1973, 1976; Dare *et al.*, 1983), Ireland (King *et al.*, 1989), the Netherlands (de Blok & Geelen 1958) and the Baltic Sea (Kautsky, 1982). The appearance of spat on collectors and filamentous substrates can generally be predicted from the breeding cycle and the incidence of mature larvae in the plankton. However, the ability of the larvae to delay metamorphosis and migrate makes it difficult to determine the time lapse between larval abundance in the plankton and subsequent recruitment. In the summer, this period of temporary attachment may be only 3 - 4 weeks long, whereas it can extend over 3 - 4 months during the winter.

The duration of settlement is also, to some extent, influenced by the seasonal availability of potential substrates for primary attachment. Algae and hydroids growing intertidally in residual water bodies offer suitable settlement surfaces from spring to autumn only. Whereas settlement was found to be high during autumn and winter on perennial subtidal hydroids, it was poor on the collectors and on degenerating intertidal filiform substrates. King *et al.* (1983) reported similar lower plantigrade densities on intertidal algae in winter. This explains why attachment to filamentous substrates during the winter months occurs primarily in subtidal regions.

The substrate choices shown by potential settlers during this study confirm that *M. edulis* plantigrades preferentially attach to filamentous surfaces (reviewed in Lutz & Kennish, 1992), and subsequently migrate onto pitted and creviced hard surfaces. Due to the high water turbidity in the Wadden Sea, macroalgae are primarily confined to the intertidal areas. Other than *Zostera* and *Fucus* (which form dense stands in the higher intertidal zones and on mussel beds, respectively), distribution and occurrence of other macroalgae is scattered and isolated. Although Ruth (1991) reported a complete smothering of intertidal eelgrass meadows by mussel spat, settlement on *Zostera* during the course of this study was rare. Utilization of eelgrass as a settlement substrate therefore only appears to occur in years of exceptionally high recruitment. Hydroids, on the other hand, grow prolifically on macroalgae, bivalves, shell fragments and pebbles in intertidal pools during the summer. Subtidally, the large hydroid species *Sertularia* forms perennial 'forests' in suitable areas, dense enough to once support a selective hydroid fishery for use in decorations. This fishery has ceased, and these hydroids now provide a permanently available subtidal filiform substrate for primary attachment of mussels (Reitzenstein, 1913; Heidrich, 1927).

Reports on to the effect of dense assemblages of adult filter feeders on the success of larval settlement are somewhat contradictory (reviewed in Widdows *et al.*, in prep.). Thorson (1957) discusses the competitive difficulties encountered by larvae and plantigrades settling between conspecific adults, concluding that primary attachment away from the adult population enhances survival. However, primary settlement of mussel spat in parent beds is not uncommon (Petersen, 1984a; McGrath *et al.*, 1988;

King *et al.*, 1989; Cáceres-Martínez *et al.*, 1993), and cannot always be explained by decreased substrate discrimination following delayed metamorphosis (Bayne, 1965). Widdows *et al.* (in prep.) recently found that mussel larvae may settle preferentially in the proximity of conspecific adults, and determined that ingested larvae are capable of attaching and settling after excretion in the pseudofaeces of adult mussels (Mileikovsky, 1974). Bayne (1964) suggested that mussel larvae are able to liberate themselves from faeces, but not from pseudofaeces. However, Seaman (Institut für Meereskunde, Kiel, pers. comm.), observed that injestion by the adults is almost always fatal, and that larvae are usually unable to liberate themselves from either faeces or pseudofaeces. Larvae which survive ingestion and remain in suitable protective niches amongst the adults, could possibly supplement the rejuvenation of adult beds by secondary settlers. Although primary attachment to filamentous substrates is usually a natural prelude to permanent settlement eslewhere, it seems that this is not a pre-requisite to final settlement.

The gauze used on the collectors appears to be effective in simulating natural filamentous substrates, providing similar and sufficient axes for attachment. The thread diameter of the gauze used was also similar to natural hydroid diameters, and within the range in which de Blok & Geelen (1958) found no differences in catching ability. The length frequency distributions of spat found on the collectors covered the entire larval size range, from larvae leaving the plankton at ± 200 µm, to spat recruiting into the adult population at 1000 - 1500 µm. The length distributions of plantigrades on the collectors were also similar to those found on algae and hydroids during the same periods. In contrast, Davies (1974), Dare (1976), Kautsky (1982), and Dare *et al.* (1983), who recorded exceptionally high monthly catch rates on coir and split-film polypropylene ropes, and on "Hairlock" matting, captured mainly secondary plantigrades (>500 µm).

The occurrence of small plantigrades (<500 µm) on Type 2 collectors in mid-December 1991, and on subtidal hydroids in the same period the following year, was not correlated with the mussel breeding cycle or planktonic larval abundances, and probably resulted from larvae which delayed metamorphosis and/or reduced growth during unfavourable conditions in winter. These spat initially attached to hydroids before crawling onto barnacles and established parent beds in February/March, after a short planktonic dispersal period in January/February (see Figs 3.3, 3.4 and 3.5). Direct attachment to creviced surfaces at this time also occurred. The continuous presence of these larvae during winter, and subsequent and decreased substrate discrimination, provides clear field evidence for the natural occurrence of "delay-larvae" described by Bayne (1965) from laboratory observations. As large-scale settlement of these larvae is not simultaneously induced, they constitute an extensive reservoir of potential settlers, capable of delaying metamorphosis and undertaking repeated pelagic migrations between temporary settlements. This accounts for the continuous, small scale recruitment observed intertidally and subtidally in the Wadden Sea area, and reported from other regions (Seed, 1969a and Dare, 1976: United Kingdom; Kautsky, 1982: Baltic Sea; Cáceres-Martínez *et al.*, 1993: Spain).

As with planktonic larvae, densities of plantigrades decline rapidly between primary attachment and establishment on mussel beds, irrespective of initial abundances. The value of spat collectors in ecological investigations depends primarily on how reliably they reflect the numbers and size distributions of potential settlers in an area, and on their capacity to catch sufficient numbers to yield meaningful results. Even considering the annual and spatial variability in mussel larval settlement, overall catch rates for all collector designs used in this study were unexpectedly low when compared with results reported from other studies. The limited settlement recorded on Type 1 collectors probably resulted mainly from predation during the extended deployment periods. Nonetheless, it was decided not to use predator excluding meshes or envelopes on any of the collectors, due to the increased siltation and fouling problems caused by such covers. Davies (1974) suggested that, in fact, such protection is only necessary for long deployment experiments. Predation is a natural phenomenon contributing to the natural mortality of vulnerable, small mussels, and should not be excluded in field investigations of mussel settlement. Exceptionally high settlement rates recorded on permanently submerged Type 2 and Type 3 collectors in recruitment studies in the Baltic Sea, where predation pressure by crabs and starfish is high (Reusch, 1994), indicate that reduced catch rates in the Wadden Sea correctly reflect lower absolute abundances of larvae, rather than collector design.

5.

RECRUITMENT TO ADULT MUSSEL BEDS

Mussel plantigrades finally settle in established beds of adult mussels, either after release from initial attachment to filamentous substrates, or through direct settle-ment between conspecific adults. Although newly settled plantigrades in adult beds face severe competition for food and space, established mussel beds appear to be attractive to gregarious juveniles because they offer protective niches amongst community members (Maas Geesteranus, 1942; Thorson, 1957; Seed, 1969b; Petersen, 1984a, 1984b). Adult mussel patches increase in size as a result of this immigration, and this final settlement, together with subsequent post-settlement survival and growth, therefore constitutes the actual process of recruitment.

While large-scale dispersal of planktonic larvae is primarily a passive process controlled by hydrography, the ability of mussel larvae to regulate their vertical position in the water column, and to attach preferentially to certain substrates, suggests that final settlement in specific small areas (often of the order of a few square metres or cm) is active. In particular, there is consensus in the literature that larvae respond to specific cues indicating substrate suitability before settling (Meadows & Campbell, 1972; Doyle, 1975; Petraitis, 1978).

As a result of the non-random nature of final settlement, differences in recruitment density typically occur, often apparently related to factors such as height on the shore, microhabitat and pre-existing adult patch size. In the absence of *in situ* observations of the behaviour of plantigrades at settlement, specific responses to settlement cues have to be inferred from the final distribution of settled juveniles. However, variations in recruitment patterns result from a combination of active larval settlement preferences and variable post-settlement mortality in different habitats. The hazards of inferring settlement patterns from distributions of early-stage juveniles (recruitment) alone, is discussed by Keough & Downes (1982) and Luckenbach (1984). For example, selective predation on juveniles may markedly alter the abundance, spatial distribution or size distribution of the population (Thorson, 1966; Peterson, 1986). It is therefore necessary to distinguish between initial spat settlement, and final establishment of juveniles in adult mussel beds, or true recruitment.

Recent investigations into settlement patterns of invertebrate larvae have shown that larval settlement may be strongly affected by hydrodynamic influences, and that such processes may produce distinct recruitment patterns (Eckman, 1979, 1983, 1990; Butman, 1987,1989; Eckman *et al.*, 1990). Hydrodynamic processes that control sediment transport and deposition may therefore also determine initial depositional sites for larvae. Changes in the boundary-layer flow environment can create small-scale environmental heterogeneity, affecting both initial attachment and subsequent distribution of biological assemblages. Physical and biological factors therefore interact closely in controlling larval settlement processes and recruitment patterns.

It has long been recognized that mussel recruitment rates vary temporally and geographically. However, observation of juvenile distribution patterns suggest that recruitment cannot be explained solely the hypotheses of Keough & Downes (1982), which propose that settlement patterns result principally from accidental substrate encounter rates. Variations in initial settlement affect the abundance and distribution of juveniles and, ultimately, of adult mussels.

Encounters with suitable substrata, and subsequent patterns and densities of recruitment, appear to result from a complex combination of substrate characteristics and abundance, larval behaviour, surface morphology and hydrographic influences. Investigations into recruitment of juvenile mussels should therefore consider the relative roles of initial settlement patterns, interactions with established conspecifics and differential post-settlement mortality rates on the distribution and abundances of juveniles, in order to determine the effect of these factors on the distribution of established communities.

MATERIALS AND METHODS

Sampling Strategy and Treatment of Samples

The occurrence of a heavy spatfall in the spring of 1990 was initially reported by commercial mussel fishermen in the Schleswig-Holstein area. Dredging confirmed the settlement of a substantial juvenile subtidal population, and sampling of the establishing subtidal bed was immediately initiated. To follow temporal recruitment patterns, benthic samples were taken from both a low elevation intertidal mussel bank at Steenodde, on the eastern shore of Amrum, and from a subtidal wild mussel population in the Vortrapptief, seaward of the island (see Fig. 1.2). Samples were collected with a boat-towed dredge specifically designed to quantitatively dredge the seabed down to a depth of approximately 5 cm, and to close automatically after sampling 0.17 m^2 seabed area (Ruth, 1994). The intertidal area was relatively sheltered in the lee of Amrum, and samples were collected there every 2 - 4 weeks. In contrast, the subtidal site was exposed to wave action, making sampling there impossible during adverse weather conditions. However, It was usually possible to obtain at least one set of samples from the subtidal site per month. On each sampling occasion, 6 to 8 dredge samples of ± 0.17 m^2 were collected at each site. Samples were individually frozen and subsequently analysed in the laboratory.

From 10 km seaward of Amrum, a series of ten navigational buoys mark the course of the Rüttergat and Norderaue navigation channels. The buoys, which are fairly regularly spaced in towards the shore, and are typically 1 - 3 m in diameter and penetrate the water to a depth of several metres, provided a transect of artificial settlement surfaces from deep water to the shore. In late June 1992, mussels fouling these navigational buoys were sampled by scraping a single, non-quantitative sample of mussels from the most dense area of mussel growth on each buoy. The depth and position of each sample in relation to current direction were also recorded,. As for the dredge samples, all samples were separatrely frozen and subsequently analysed in the laboratory.

In late summer 1991, small-scale settlement patterns of plantigrades on established mussel beds was investigated by sampling along three transects across a mussel patch, or hummock. The transects were conducted parallel to the direction of the flood current, and mussels were sampled at regular 0.5 m intervals along each transect, from edge to edge across the hummock, using a 10 cm diameter PVC tube corer. In September 1991, three patches at different tidal elevations in an extensive bed on the banks of a tidal gulley were similarly sampled to determine the effects of current exposure and patch topography on colonization patterns. Patch 1 was situated furthest up the gulley, with the highest elevation. Patch 2 and Patch 3 were situated progressively further down the gully, into the flood current. Each patch was randomly chosen from a number of patches in the area and the three-dimensional topography of each patch above the surrounding mudflats was measured using a 25 cm x 25 cm survey grid. Core samples were then taken every 0.5 m in a 2.5 x 3.5 m grid laid over the patch, for subsequent length-frequency analysis in the laboratory.

Three additional patches in the study area were surveyed one year later, to determine whether settlement patterns noted in the 1991 samples were repeated the following year. Patches 4 and 5 were situated at a high elevation, a considerable distance from a tidal gulley, whereas Patch 6 was at mid-elevation beside a tidal gulley. However, specific position was unimportant as these patches were selected to investigate the effect of patch topography on settlement patterns, and not for comparisons of settlement intensity in relation to tidal elevation.

Data Analysis

Mussel larvae were followed through the plankton samples, and subsequent spat settlement was monitored on collectors. Length-frequency distributions of mussels in the dredge samples were analysed to track resultant recruitment into established mussel beds. The lengths of all mussels in the dredge samples > 3 mm, were measured to the nearest millimetre below to determine length-frequency distributions. The number of 3 mm - 5 mm plantigrades per sample were counted, and the mean number per 0.17 m^2 sample calculated and plotted against time to show seasonal recruitment patterns. Mussels in the navigational buoy samples were similarly measured to provide comparative length-frequency distributions, and to investigate the effect of distance offshore, permanent immersion and current direction on recruitment.

The mussel-patch core samples were analysed to provide high resolution data on the relationship between juvenile settlement patterns and tidal elevation, current direction and patch topography. To achieve accurate separation of juveniles from established adults, the youngest cohort in each sample was separated from the multimodal length-frequency distribution using the Bhattacharya method (Bhattacharya, 1967) in the ELEFAN length-frequency analysis program (Gayanilo *et al.*, 1989). The topographical distribution of numbers of juvenile mussels per core sample in the six sampled patches were plotted using the SURFER (® Golden Software Inc., Colorado, USA) three-dimensional surface-plot and contouring program.

General linear modelling techniques were used to investigate the relationship between abundance of juvenile mussels, and position within each patch. A general linear model (GLM) (Model 5.1 in Appendix IV) was fitted using the SAS Statistical Analysis System (SAS Institute Inc., NC, USA), and used to test whether the proportion of age-class 0 mussels in the samples taken in the flood-tide lee of the hummock apex was significantly higher (95%-level) than in the upstream region of each patch. The extent of turbulent water flow created by a mussel patch depends to some extent on patch size. However, only the effects on settlement within each patch, and not the extent of patch influence, were of specific interest. In specifying the GLM, it was therefore assumed that the composition of the patches, and the dynamic interactions that produce patch composition, are not related to patch size, but rather to patch topography, particularly height and apex position.

It was also necessary to set data limits to avoid excessively high variances resulting from inclusion of edge samples. Peripheral samples were characterized by extreme variability, resulting from edge effects such as differential growth, survival or predation (Tsuchiya & Nishihira, 1985, 1986; Wildish & Kristmanson, 1984; Okamura, 1986a; Newell, 1990), or from low mussels numbers in such samples. Limits were set with consideration of the flood-tide current direction, to ensure inclusion of samples possibly affected by turbulence created by the patch apex (see Table 5.4 in Appendix IV). The GLM was then specified to investigate influences of both absolute position, and position in relation to the patch apex, on proportion of juvenile mussels in each sample. Another GLM was specified to investigate the effect of tidal elevation on the number and size of mussels in each patch (Model 5.2 in Appendix IV), and to conduct multiple ANOVA (MANOVA) comparisons of mussel numbers and sizes in patches at different tidal elevations.

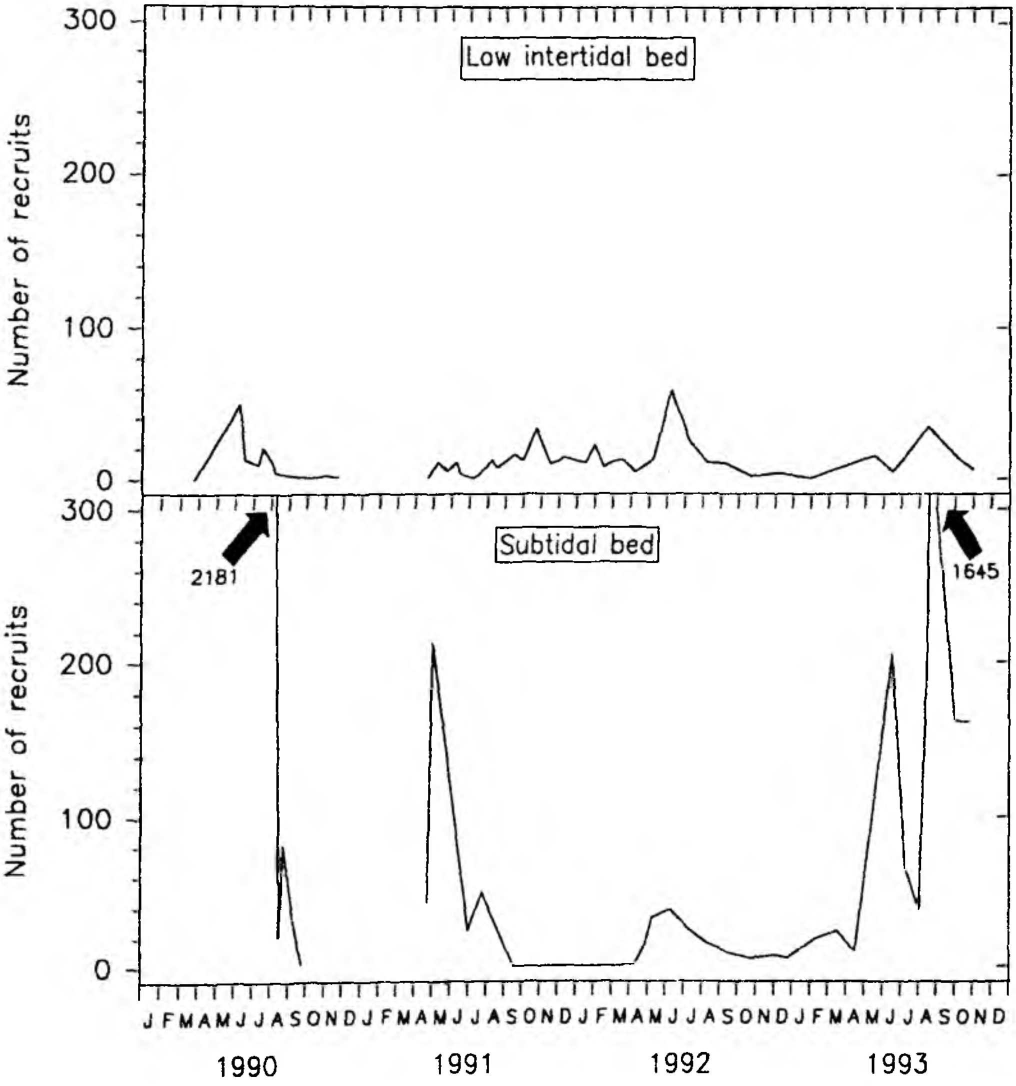

Figure 5.1 Temporal variations in the mean numbers of *Mytilus edulis* recruits 3 mm - 5 mm in length, per 0.17 m^2 sample on a low intertidal mussel bed (Steenodde), and a subtidal mussel bed (Vortrapptief). For identification of sampling locations see Figure 1.2.

RESULTS

Recruitment onto Mussel Beds

A marked rejuvenation of the intertidal mussel bed occurred in late May and June of 1990, followed by a second, less pronounced, recruitment in July (Fig. 5.1). In the summer of the same year, a massive recruitment resulted in the establishment of the new subtidal bed in the Vortrapptief. During 1991, recruitment on the subtidal bed was again pronounced, following a similar pattern to the previous year. Intertidal settlement was more or less continuous during spring and summer of 1991. A heavy recruitment in autumn, however, led to the strong recovery of the established intertidal bed (see Fig. 5.1). During winter, the intertidal spat population remained relatively stable. However, the winter seed fishery on the subtidal bed almost totally depleted the juvenile mussels in that area.

Table 5.1 Maximum length of mussels fouling navigational buoys in the Rüttergat and Norderaue, sampled on 25 June 1992. Refer to Figure 1.1 for location of buoys.

BUOY	DATE DEPLOYED	EXPOSURE (days)	MAX. LENGTH (mm)
WVTP	8 April '92	78	13
RG4	27 March '92	90	18
RG6	27 February '92	119	19
RG8	27 February '92	119	19
RG10	28 October '91	241	19
RG12	15 March '90	833	55
RG14	9 March '92	108	19
NA24	2 April '91	450	57
NA26	11 March '92	106	18
NA30	3 April '91	449	54

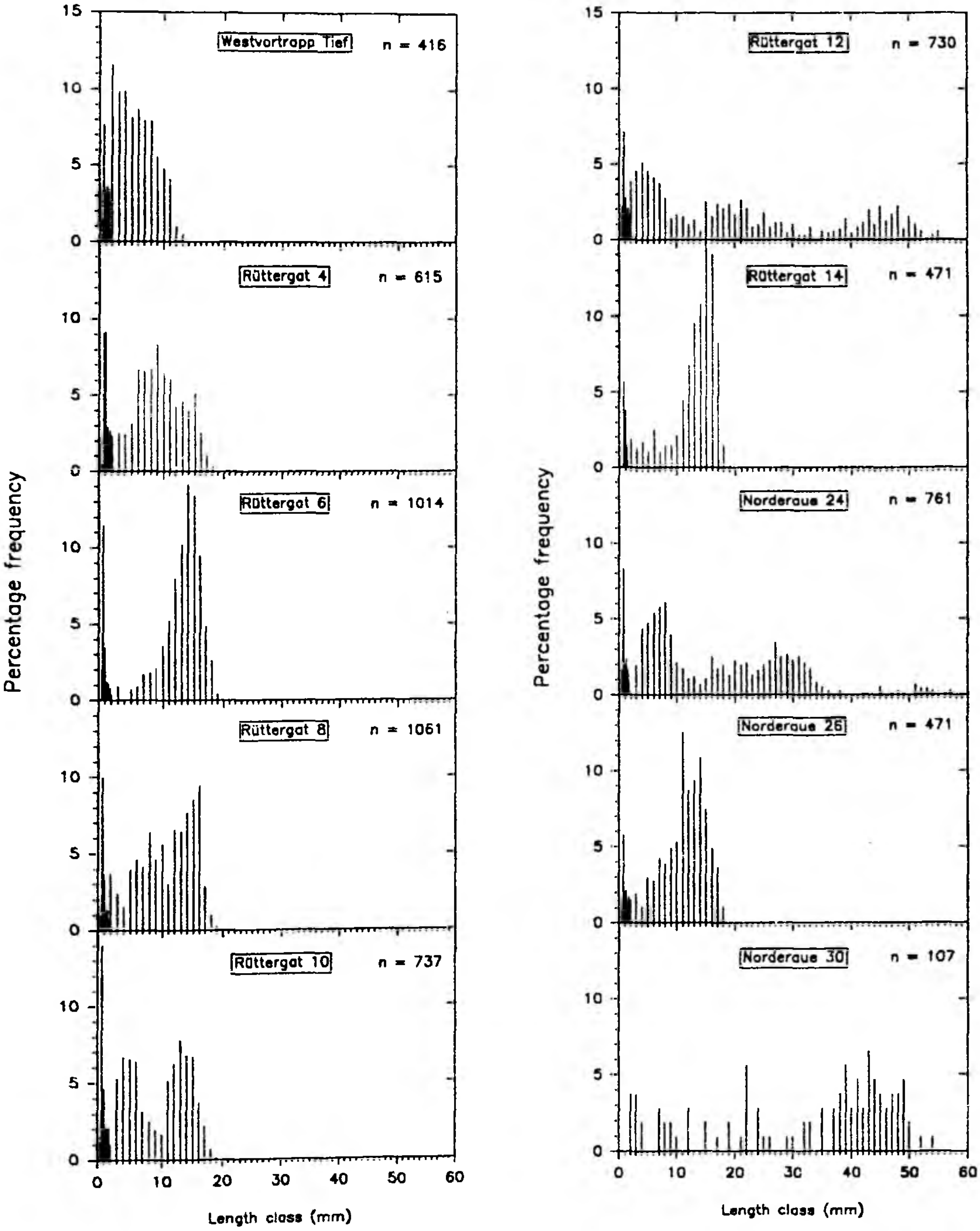

Figure 5.2 Length-frequency distributions of mussels fouling navigational buoys indicated in Fig. 1.1 (Herein Rüttergat = RG; Norderaue = NA; Westvortrapptief = WVTP). Individuals >2 mm measured to the nearest mm, those <2 mm measured to the nearest 0.25 mm. Sampling date: 25 June 1992. n = number of specimens measured.

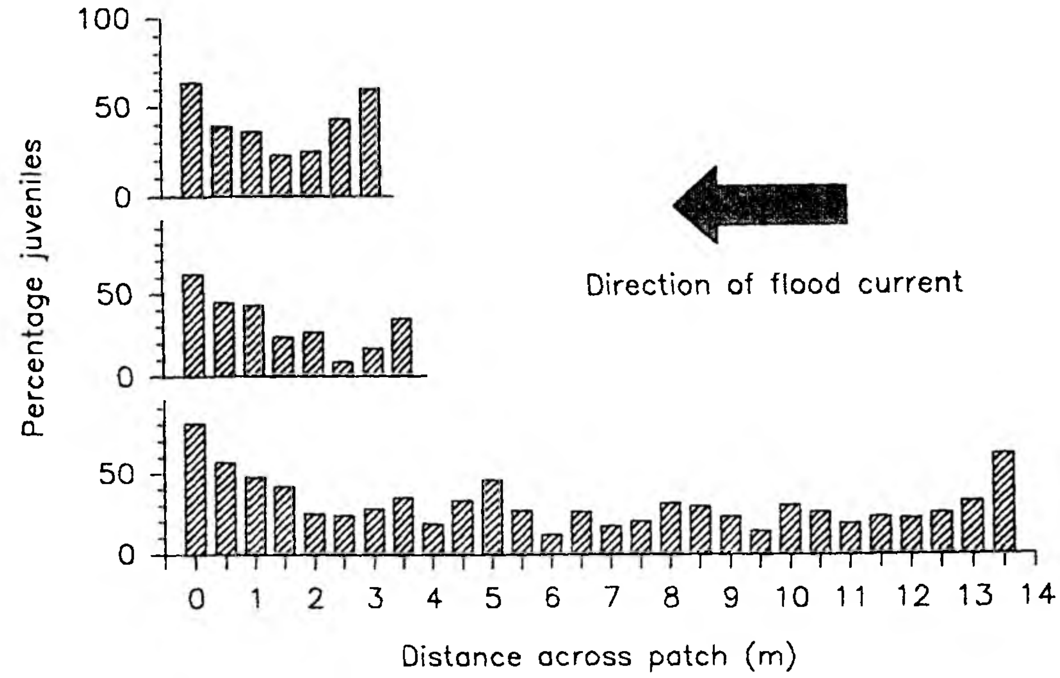

Figure 5.3 Percentage juvenile mussels (<21 mm) in samples taken in three transects across an intertidal mussel bed. Sample size ranged between 23 and 141 specimens per core. Date of sampling: 12 October 1990.

In 1992, recruitment on the intertidal and subtidal beds began in February with the appearance of over-wintered plantigrades derived from the autumn 1991 spawning, peaking in June. Although some rejuvenation of the intertidal bed occurred during summer, recruitment levels on both beds remained weak throughout the year. The expected settlement peak in autumn, which should have originated from the spring spawning, failed to appear.

During winter 1992/93 both intertidal and subtidal spat populations remained low. An early settlement between remaining subtidal adults in January and February marked the start of a series of strong subtidal recruitments in June (derived from delayed-larvae) and, more pronounced, in August. On the intertidal bed, however, only two settlement peaks were observed, the partial ice cover in February rendering conditions generally unfavourable for intertidal settlement.

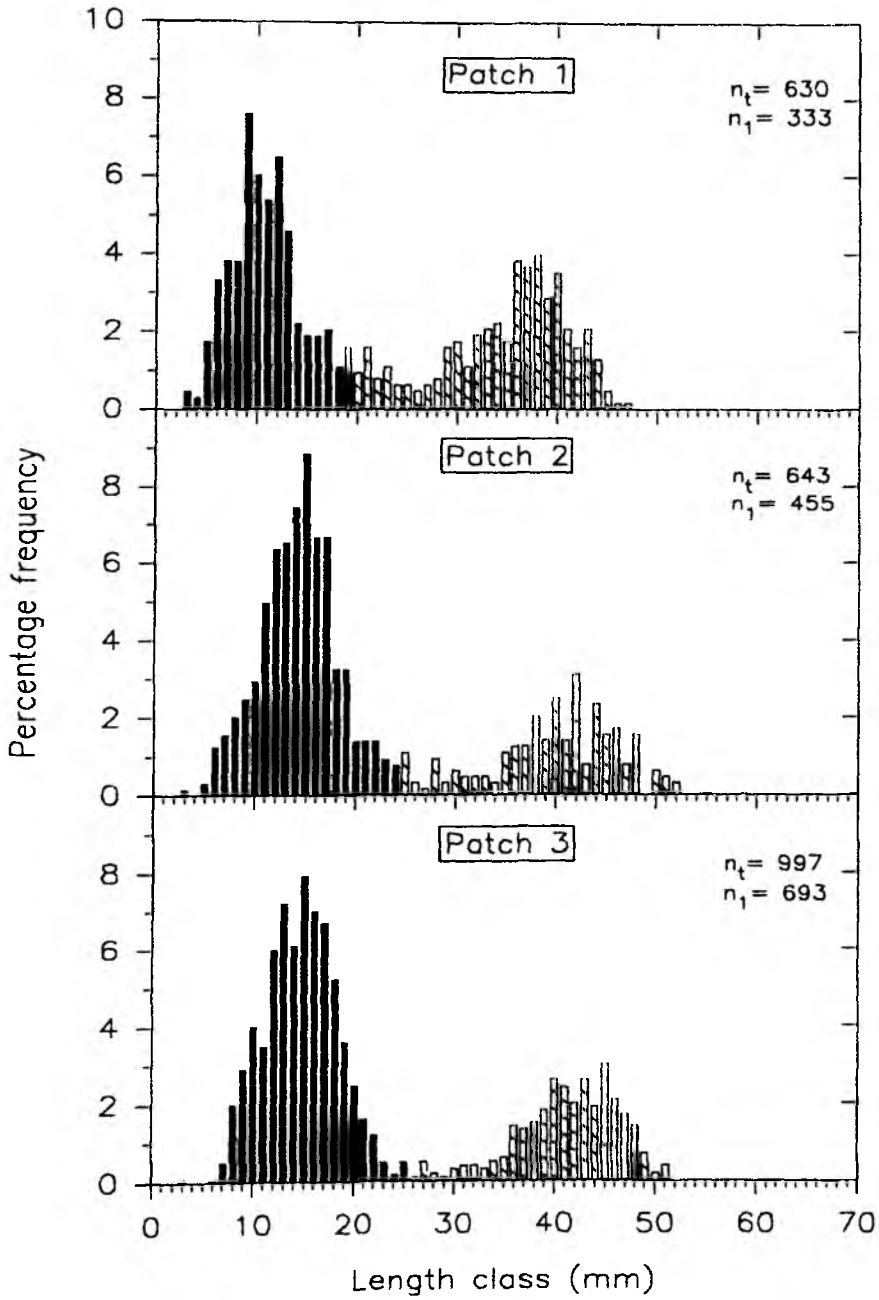

Figure 5.4 Length-frequency distributions of mussels in Patches 1, 2 and 3. For location of patches see Figs 1.1 and 1.2. Numbers in the total sample (n_t) and in the first cohort (n_1)(solid bars), are given. Patches sampled within a fortnightly period in October 1990.

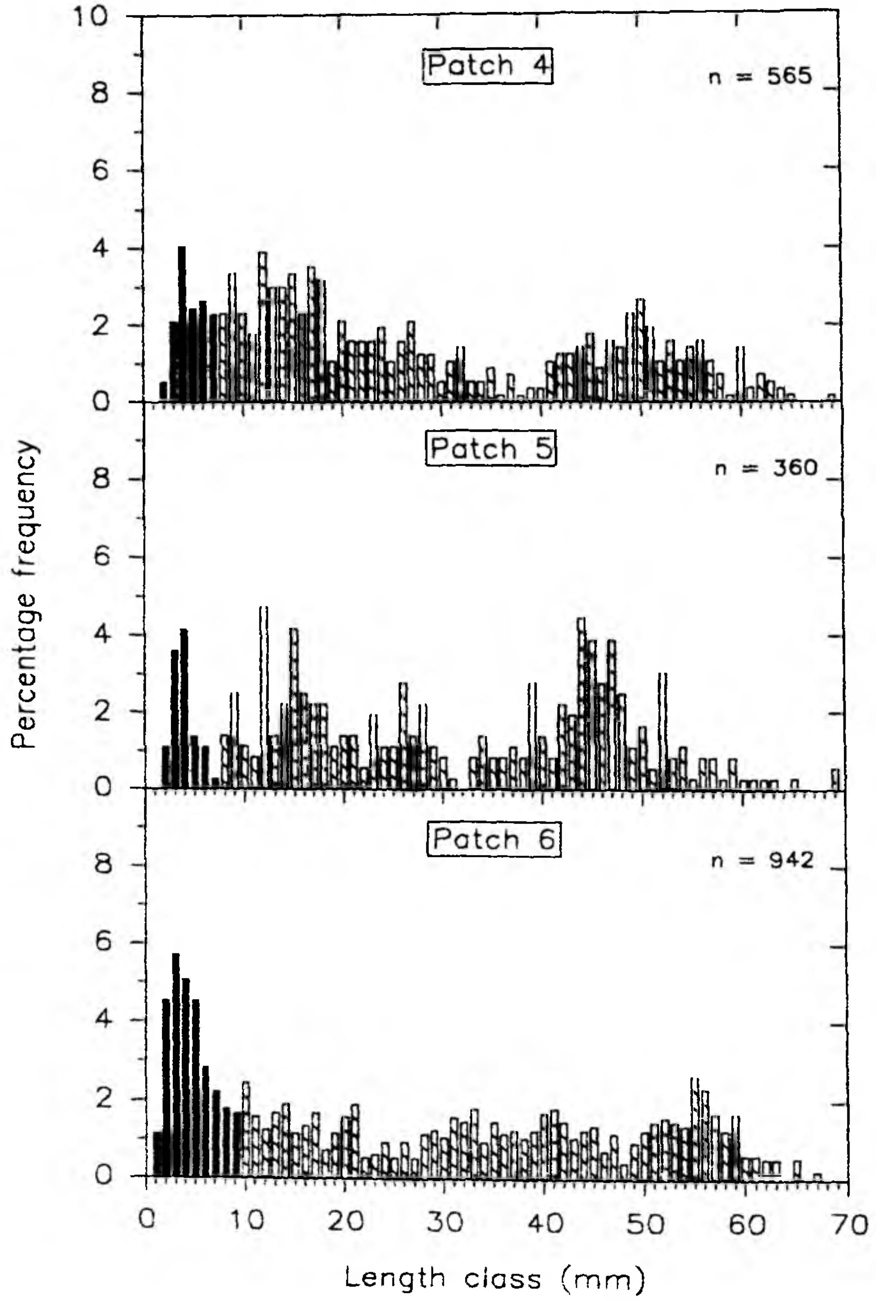

Figure 5.4 Length-frequency distributions of mussels in Patches 4, 5 and 6. For location of patches see Figs 1.1 and 1.2. The size range of the youngest cohort is indicated by the solid bars. Patches 4 and 5 sampled on 24 July 1992, Patch 6 sampled on 17 September 1992.

Recruitment on Navigational Buoys

From regular monitoring of the numbers of juveniles settling between conspecific adults on mussel beds, it was determined that average recruitment during 1992 was lower than observed in previous years. Isolated heavy settlements of mussels were, however, found on navigational buoys marking the shipping channels. Whereas buoys marking the Rüttergat/Norderaue channel received heavy settlement, those in the Hörnum/Vortrapp region remained virtually free of mussels. Below water mark, the buoys were initially covered by barnacles, which were overgrown by hydroids and filamentous algae. These were, in turn, overgrown by a dense layer of mussels. Consistent, clear distribution patterns of mussels were observed on the buoys, with mussels occurring only 1.5 - 2 m below the water surface, on the side of the buoy in the lee of the flood current. This non-random distribution of mussel settlement in an area where predation and fishing mortality are strongly reduced or lacking, suggests that these recruitment patterns were not random or coincidental.

Figure 5.2 illustrates the length-frequency distribution of mussels fouling buoys in the Rüttergat and Norderaue (see Fig. 1.1). These isolated populations show strong multimodality, with up to 4 cohorts being recognizeable. The mussels had high flesh weights and thin, pale shells characteristic of rapid growth. From Table 5.1 it can be seen that these fast-growing mussels can, in fact, reach market size (50 mm shell length in Schleswig-Holstein) within 15 months on these buoys.

Recruitment Patterns

All mussel patches investigated were found to be oriented with their long axes perpendicular to the direction of the main current flow, as occurs with most intertidal mussel beds (Fréchette & Bourget, 1985). An ANOVA (Scheffé range test, $p > 0.05$) of the proportion of juveniles in samples taken across these beds confirmed that the proportion of age-class 0 mussels (those < 21 mm) was significantly higher within 1 m of the edge of each patch, than nearer the centre (Figs 5.3 and 5.3a in Appendix IV). In addition, fewer juveniles inhabited patch edges facing the oncoming flood current, than the lee edges, although these differences were insignificant at the 95%-level.

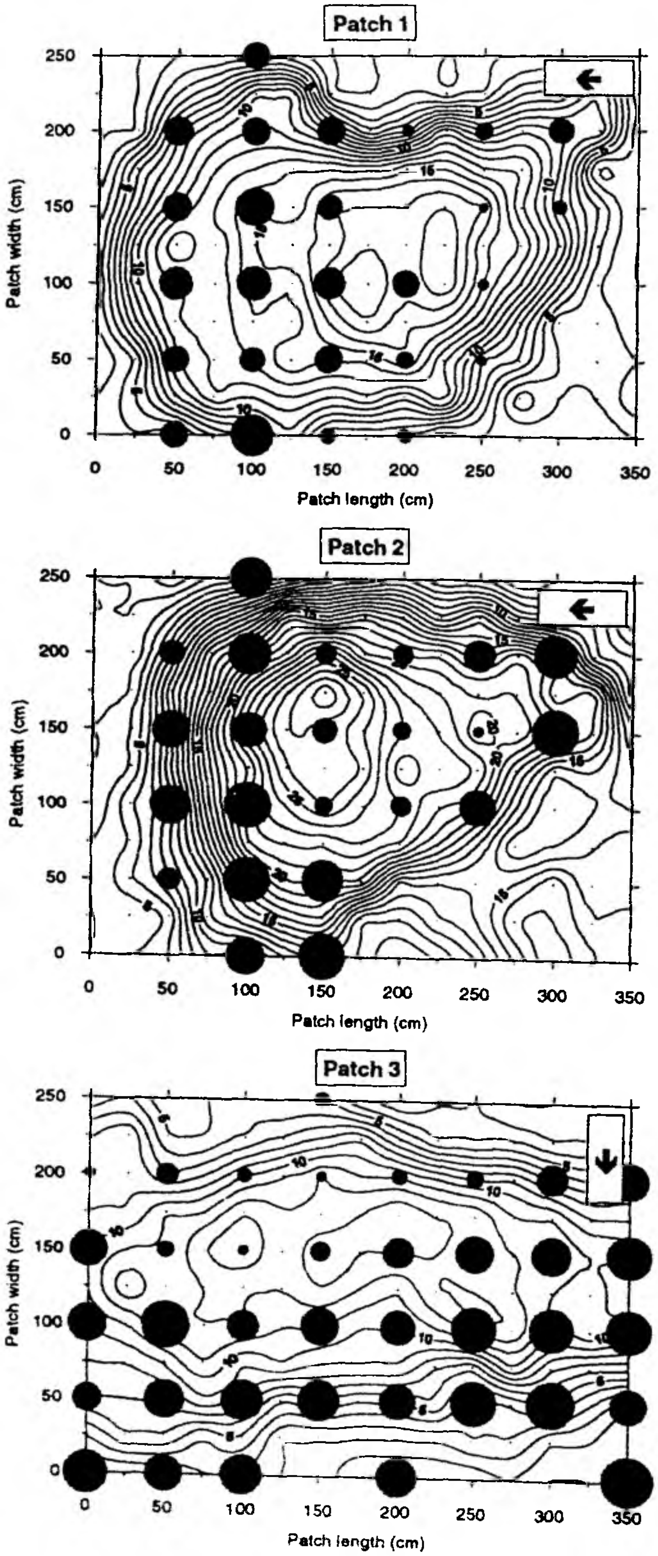

Figure 5.6 Proportion of age class-0 mussels in samples taken within a grid across mussel Patches 1, 2 and 3 at different tidal elevations (see Figs 1.1 and 1.2. for location of patches). Arrows indicate direction of flood current. Isolines represent topographical height (cm) of the mussel patches. Dot diameter represents the proportion of juveniles in the core sample.

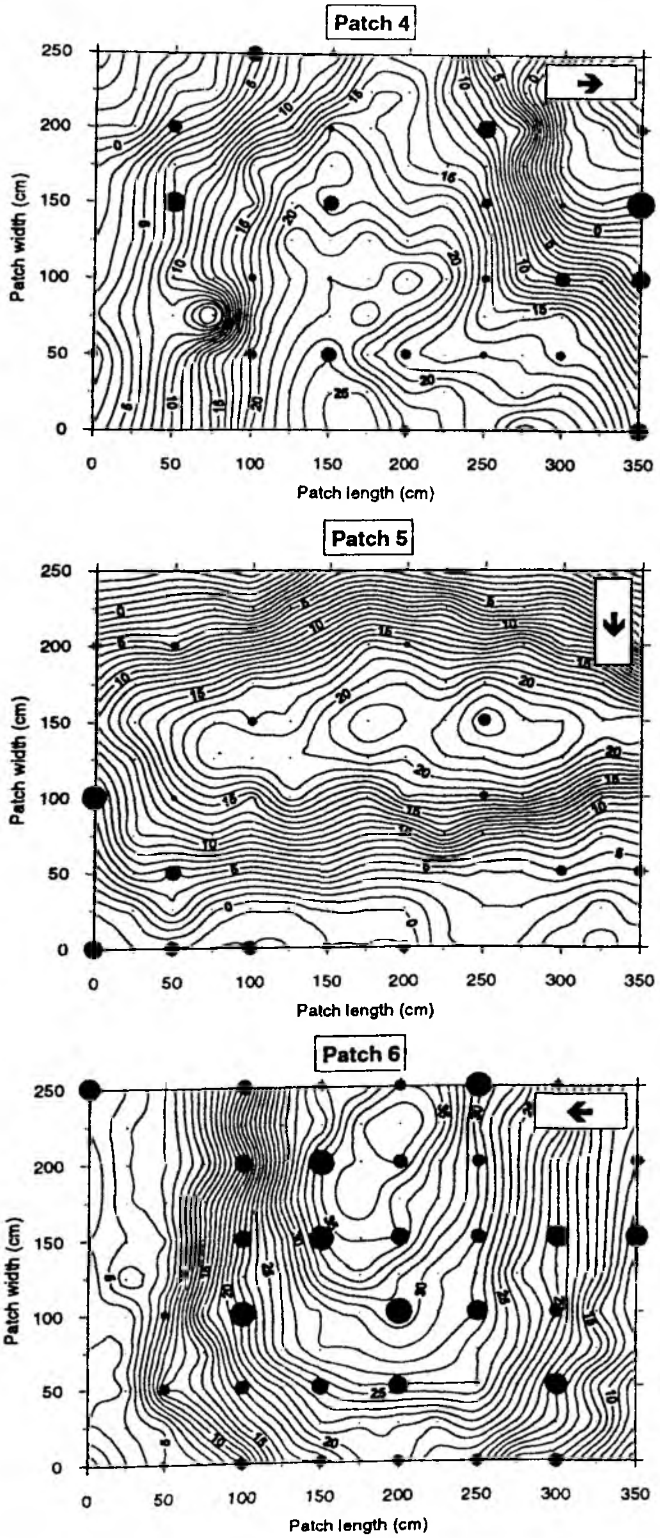

Figure 5.7 Proportion of age class-0 mussels in samples taken within a grid across mussel Patches 4, 5 and 6 (see Figs 1.1 and 1.2. for location of patches). Arrows indicate direction of flood current. Isolines represent topographical height (cm) of the mussel patches. Dot diameter represents the proportion of juveniles in the core sample.

Length-frequency samples of mussels in the patches sampled (Figs 5.4 and 5.5), showed similar multi-modal distributions as those previously noted in mussel populations in the Wadden Sea (Brinkman, 1993; Ruth, 1994). The topographic distributions of juveniles in Patches 1, 2 and 3 are shown in Figure 5.6. Juvenile distributions in the comparison Patches 4, 5 and 6 are shown in Figure 5.7. General linear model MANOVA results indicated that the frequency of mussels, and the summed length of all individuals in each patch, was significantly higher (at the 95%-level) in the low elevation Patch 1 than on Patches 2 and 3 further up the shore (Table 5.2 and 5.3 in Appendix IV). The proportion of juveniles was also lower in Patch 1 (53%) than in the upstream hummocks (71% in Patch 2 and 70% in Patch 3).

Samples taken near the edges of the sampled patches contained few mussels and, consequently, widely varying proportions of juveniles. It is also possible that juvenile distributions were affected by specific edge effects, such as faster growth rates, increased survival or differential predation (Tsuchiya & Nishihira, 1985, 1986). Initial inclusion of the edge samples in the GLM relating juvenile abundance to patch topography therefore resulted in high variances and a poor model fit. The model was not able to extract the underlying systematic process from noise caused by samples from the patch margins until data limits had been set to exclude these samples (see Table 5.4 in Appendix IV). After excluding edge samples, results indicated that age-class 0 mussels occurred at significantly higher proportions in the immediate flood lee of the patch apex than in the upstream slope of the patch in Patches 1, 2, 3 and 6, (see Table 5.5 in Appendix IV). Abundances of juveniles in Patches 4 and 5 were too low to indicate any significant recruitment patterns, with only one transect on each of these patches exhibiting the expected distribution of juveniles.

DISCUSSION

Sporadic settlements were found to be responsible for periodic peaks in mussel plantigrade abundance in adult beds, and for the establishment of totally new mussel beds. The appearance of large numbers of plantigrades on the intertidal and subtidal study sites during the summer of 1990 resulted from an exceptionally high spatfall, following

2 years of recruitment failure in the Schleswig-Holstein Wadden Sea (Ruth, 1994). The settlement noted in spring 1990 must have resulted from plantigrades originating from the autumn spawning in the previous year. It appears that the mild but stormy winter exposed relatively large expanses of suitable hard substrate for use by overwintering larvae. During the following spring, some of these over-wintered larvae migrated inshore to rejuvenate the intertidal beds. The majority, however, remained on the hydroid and barnacle covered pebble-ground to form an extensive subtidal bed in the spring. Larval development and migration were found to take approximately 6 - 8 weeks in this area, so the settlement peak observed in July 1990 must have resulted from the spring spawning and high planktonic larval abundances in May (see Figs 3.3 - 3.5). The recruitment patterns observed on the two sampled mussel beds therefore closely reflect the typical temporal changes in the population structure of mussel stocks in the Schleswig-Holstein Wadden Sea discussed by Ruth (1994).

Substantial declines noted in juvenile numbers following settlement peaks indicate that, even with continuous settlement, recruitment gains are rapidly countered by losses to natural mortality, predation and fishing. The juvenile abundance data collected from dredge samples (see Fig. 5.1) therefore result from the interaction of all the above factors, and indicate a balance between recruitment and loss during most of the year. Intertidally, decreases in juveniles result primarily from predation and growth out of the 3 mm - 5 mm size range. Starfish (*Asterias rubens*) and shore crabs (*Carcinus maenas*) are the most destructive predators of wild and cultivated mussel stocks in northern Europe (Seed, 1969b; Sloan & Aldridge, 1981; Dare, 1982). In these intertidal populations, population fluctuations therefore occur mainly in summer, and tend to stabilize in winter, when spat growth is reduced and predator activity diminishes (Scherer & Reise, 1981; Jensen & Jensen, 1985).

The intensive fishery for seed mussels, particularly during the winter, is the main cause of reduction of juvenile numbers on subtidal beds. Reynolds (1969) and Petersen (1984b) reported higher numbers of recruits in other parts of the northern Atlantic Ocean in the late summer, but the main crop-producing spatfall in Schleswig-Holstein appears to occur early in the year. This agrees with the findings of Dare

(1976) for mussel populations off England. These autumn-spawned plantigrades over-winter subtidally, resume rapid growth in the spring, and establish themselves before recruitment of invertebrate predators occurs. Doyle (1975) hypothesized that delayed metamorphosis and reduced substrate discrimination during periods of limited predation pressure would result in increased fitness and higher recruitment. This appears to be the case with these over-wintered larvae, which are able to outgrow the vulnerable size range before the predators arrive.

Intensive mussel settlements at the mean low water mark, and on floating or subsurface 'collectors', are not unusual (Chipperfield, 1953; Meredyth-Young & Jenkins, 1978; Gabaev, 1981; Dare *et al.*, 1983; Buyanovskii & Kulikova, 1984), as older, drifting post-larvae are known to occur in large numbers in surface plankton (Rees, 1954; Bayne, 1964). This is confirmed by the dense, multi-modal recruitment of mussels on navigational buoys in the Wadden Sea (also reported by Duge, 1914). Predation on juvenile mussels is greatly reduced on these buoys, and the distribution of mussels in such settlements provides insight into original settlement patterns, relatively unaffected by substantial simultaneous mortality. Mussels are successful, yet seasonal colonizers, capable of invading, and finally dominating, communities of all ages (Chalmer, 1982). As with the formation and establishment of a subtidal mussel population, the successful colonization of navigational buoys appears to depend on the presence of earlier colonists. Established communities of barnacles and hydroids on these buoys provide drifting plantigrades with surfaces for settlement, accelerating their succession to dominance (Duge, 1914; Dean, 1981; Okamura, 1986a).

Previous studies on the structure of mussel communities have noted that older mussels tend to be located nearer the centre of a patch, with progressively younger mussels arranged around them (Seed, 1969b). Tsuchiya & Nishihira (1985, 1986) concluded that the periphery of *Mytilus* patches has an environment different from the central part, and attributed this to different effects of water movement and reduced competition for food and space. The patch periphery will remain moist longer, as water drains out of the patch at ebb tide, and the edge often remains in contact with residual water bodies. Here adult mussels and dead shells offer settlement substrates for ephemeral epizooic algae and hydroids, which in turn provide suitable filamentous surfaces for larval attachment. Settled spat subsequently crawl in between the adult mussels. Juvenile crabs and starfish are often found associated with the edges of mussel beds adjoining residual water bodies, and it may be expected that predation at patch edges would be higher than within patches. However, previous studies have found these differences to be insignificant (Okamura, 1986a; Farrell, 1989). Predation pressure therefore does not appear to control the distribution of juvenile mussels in patches, and spatial variation in settlement patterns appear to result principally from interactions between local current flows and patch topography.

The ability of the larvae and spat of *M. edulis* to regulate their vertical position in the water column confers some ability to preferentially settle out on particular areas of the seabed. Having settled, however, unattached larvae are passively transported by bed-load transport processes. Eckman (1979, 1983, 1990) found that even small seabed irregularities can produce local deposition and entrainment of particles transported by water flow, by altering flow rates and creating turbulence. Increased accumulation will result from physical trapping of larvae or spat in hydrodynamic baffles created by filamentous algae or hydroids projecting into the water (Butman, 1986; Jackson, 1986; Peterson, 1986). Similar accumulation will occur around obstructions in open water, as the larvae and spat are passively advected into localised areas of turbulence in the lee of mussel beds or navigational buoys (Ertman & Jumars, 1988; Eckman, 1990).

The exhalent currents of adult mussels, and the roughness of mussel patches, cause increased turbulence in water flow, particularly in the area down-stream of a mussel patch. This increased turbulence results in the accumulation of larvae on and around mussel patches (Ertman & Jumars, 1988). Here the mean near-bottom water velocities are slower than in the less turbulent flows over the sandflats, enabling searching and active habitat selection in mussel patch micro-environments (Butman, 1987). Sufficiently high near-bottom water velocities (> 0.5 $m.s^{-1}$, as during ebb and flood tides) will tend to confine sinking larvae and spat to bed-load transport within a seabed boundary-layer. Re-suspension out of the benthic boundary layer to permit wider re-distribution will then only occur at slack tide (Jonsson *et al.*, 1991). Verwey (1966) found that the number of plantigrades near the surface does tend to increase at low water slack. These plantigrades appear to utilize the flood tide for transport within a bed, or further up the shore, and the ebb currents for large-scale dispersal.

Variability in current directions in the study area (see Fig. 1.3) should enable juvenile mussels to establish all around the periphery of patches. However, the higher velocity and longer duration of the flood tide result in an increased settlement of juveniles in the flood-tide lee of mussel patches. These settlement patterns are relatively consistent, indicating a fairly uniform and unidirectional flood current in the intertidal zone. At higher elevations and greater distances from tidal gulleys, current velocities and direction becomes more diffuse (see Fig. 1.3), probably explaining why spat settlement patterns in Patches 4 and 5 do not comply with the predictions of the patch-effect model. As expected, the navigational buoys are also only colonized in the current lee, which is confined to one side, as the buoys swivel away from the prevailing current.

Altered patterns of water flow around mussel patches should also enhance availability of food to mussels (Fréchette *et al.*, 1989). Mussels growing on the edge of groups grow faster than those within a bed (Wildish & Kristmanson, 1984; Okamura, 1986a; Newell, 1990), probably as a result of reduced competition. A combination of these factors may also result in increased recruitment in the flood lee of mussel patches, due to differential post-settlement survival. Hydrodynamic effects can thus help to explain positive correlations between settler densities and numbers of plantigrades already present found by Lukanin & Oshurkov (1981), Petersen (1984b) and Peterson (1986). Increased growth rate on the edge of a mussel patch will enable plantigrades to quickly grow beyond the size range vulnerable to predators, balancing the higher predation pressure on patch edges. In subtidal populations, Carlson *et al.* (1984) and Newell (1990) noted depletion of seston downstream of mussel patches, reducing the growth of individuals in the patch lee. This could explain the absence of plantigrades amongst culture mussels, where the high filtration capacities of fast growing adults may present excessive competition for the spat.

Whilst undergoing bysso-pelagic migration and re-distribution near the water surface, a combination of hydrographic and meteorological parameters can have the effect of concentrating drifting plantigrades. The Wadden Sea is characterized by strong and complex tidal currents. Localized manifestations of wind-generated surface currents over the tops of tidal currents can result in sharply de-limited zones of convergence and downwelling. Horizontal surface drift of flotsam into these convergence zones form surface slicks (Shanks, 1986; Shanks & Wright, 1987), recognizable as glassy water masses and striations with an enhanced abundance of flotsam. These slicks can remain stable for longer periods, and are carried inshore by tidal movement or prevailing westerly winds. Shoreward transport of invertebrate larvae in surface slicks has been suggested by Shanks (1986), and would serve to explain the "bands" of *M. edulis* spat reported by Rees (1954) in the North Sea, and the localized recruitment on navigational buoys (Duge, 1914; and this study). The onshore drift of such concentrations of migrating larvae, particularly in combination with filamentous flotsam, such as twisted strands of *Enteromorpha*, could thus account for the variability of spat settlement, the banded nature of dense recruitments, and the subsequent banded structure of mussel beds.

6.

DISCUSSION AND CONCLUSIONS

Regular and intensive monitoring is usually necessary to follow seasonal variations in marine benthic populations. This seems to be particularly true in the case of mussel populations in a dynamic water body such as the Wadden Sea, where sporadic bursts of spat settlement are super-imposed on a continual, year-round rejuvenation of wild mussel beds. The spawning seasons of adult mussel populations must be determined if periods of maximum recruitment are to be anticipated, and this is best done by frequent sampling of adults to provide data on gonad development and condition. Actual reproductive success can be followed by periodic short-term studies on planktonic larval abundances, and subsequent observation of settlement of larvae and recruitment of juveniles should provide reliable information on the timing and potential intensity of recruitment to the parent stock. It is important, however, to distinguish between settlement and post-settlement processes, and to determine their respective effects on subsequent population structure.

Figure 6.1 presents a summary of the cycles of reproduction, larval abundance, settlement and recruitment observed in the Schleswig-Holstein mussel stock over a period of 4 years, commencing in 1990. Spawning is extended, continuing throughout the year with maxima in early summer and autumn. It is unlikely that spawning intensity is directly affected by food scarcity in the eutrophic Wadden Sea, where phytoplankton and benthic diatoms are available in sufficient quantities throughout the year (Ruth, 1991). Phytoplankton species composition may, however, have some influence on nutritive condition and gamete production. The most likely factor affecting egg quality and fertilization success is temperature. Mild winters are reported to cause reduced egg quality, as mussels then have higher basal metabolic rates, thus decreasing the energy available for gamete production in the spring (Mann, 1988; Dijkema, 1992). Furthermore, Seaman (in prep.) found that the quantity of suspended sediment in the Wadden Sea may have a negative influence on fertilization success. Nonetheless, the main spawning peak in spring coincides with phytoplankton blooms, thereby maximizing food availability and larval survival.

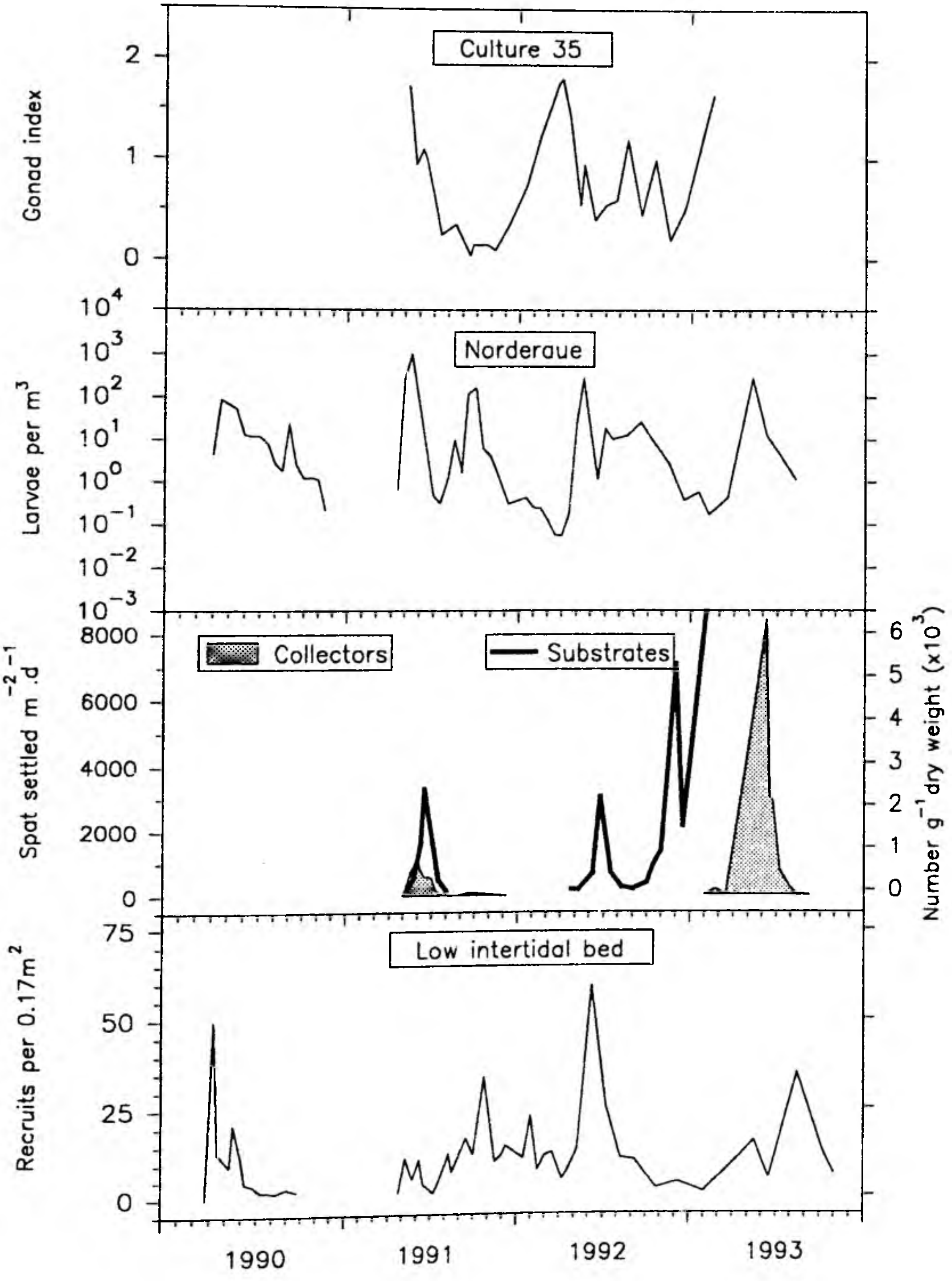

Figure 6.1 Summary of reproduction and recruitment investigations of *Mytilus edulis* populations of the Schleswig-Holstein Wadden Sea.

Improved condition and increased growth rates of low elevation and subtidal mussel populations confirm the benefits of re-laying intertidally fished mussels onto subtidal culture plots for growth and fattening. However, marked differences in flesh weight between equally sized individuals from different locations should be considered when choosing source mussels. Mussels fished from subtidal or low intertidal beds will reach market size sooner than those from stunted high shore populations. Recruitment on these beds is often slow or lacking (Ruth, 1991), indicating that fishing pressure on high-shore mussel beds should be minimized.

Due to the danger of diarrhetic and paralytic shellfish poisoning (DSP and PSP) during the warm summer months, landing restrictions have been imposed on commercial mussel fishermen in Schleswig-Holstein from 15 April to 31 July. As a result, the fishing season is not timed to optimally exploit the natural resource, as it fails to exploit the period of peak meat condition in summer. Although mussels are in a sufficiently good condition for commercial harvesting in autumn and spring, some problems are experienced with the landing and transport of mussels in the spring. If mussels are fished just prior to a spawning event, rough handling and agitation during transport can result in a substantial loss of total meat weight due to induced gamete release (Field 1922; Leuschel, mussel fisherman, Schlüttsiel, pers. comm.).

Interactions between environmental factors, such as temperature, food availability and tidal elevation, and the growth, condition and reproductive processes of *M. edulis* appear to be complex. Although intertidal mussel populations contribute regularly to seasonal gamete production, their relatively poor condition compared to subtidal mussels results in reduced fecundity and larval survival. Subtidal populations living under more advantagous conditions of temperature and food supply are therefore a more fecund and consistent source of robust gametes. Transfer of mussels from poorly situated or ephemeral settlements to optimally situated subtidal culture plots should therefore result in increased total reproductive output from the Wadden Sea mussel stocks, as cultured mussels usually spawn at least once before being harvested.

An understanding of the spawning and settlement cycles of *M. edulis* in the Wadden Sea can benefit the commercial mussel fishery by facilitating the development of optimal strategies for collection of source mussels, and schedules for harvesting of mussels in prime condition. Combined monitoring of seasonal changes in gonad maturity stages and population condition indices can provide accurate indication of spawning events. The CI-5 condition index (Davenport & Chen, 1987), non-linear condition index standardisation method (Brinkman, 1993) and simplified gonad maturity staging used in this study provide efficient tools for routine monitoring of mussel condition and spawning events. However, as a result of the numerous factors influencing survival, distribution and settlement of mussel larvae, recruitment success cannot be directly predicted from the duration or intensity of spawning by adult populations.

Plankton larval densities are affected by selection pressures exerted by a wide variety of bio-physical factors. Larval survival and development is dependent upon species-specific temperature and turbidity ranges, and markedly affected by fluctuations in food abundance, food quality and predator abundance. These biotic and abiotic parameters affect various larval species differently, and resultant inter-annual variations in the composition of larval stocks surviving to metamorphosis can markedly influence benthic community composition and structure (Thorson, 1966; Osman, 1977; Okamura, 1986b). For example, intense filtration by large stocks of resident bivalve species, or a series of unusually strong recruitments of planktivorous predators, could explain the low larval densities in Schleswig-Holstein in comparison to other areas.

Planktonic larval abundances 2 - 4 weeks after peak spawning by local mussel populations suggests that the majority of larvae originate from parent stocks in the immediate vicinity. However, certain larval peaks, such as those observed in July 1991 and August 1992 (see Fig. 3.3), cannot be related to local spawning, indicating immigration of larvae from the adjacent North Sea. These imported larvae either delay metamorphosis during transport in offshore waters, where phytoplankton biomass and temperatures are lower, or are post-larvae which have previously undergone primary attachment on suitable substrates in deeper waters.

The occasional appearance in the plankton of bivalve species foreign to the area (eg. the saddle mussel *Anomia ephippium*) confirms the incursion of pelagic larvae transported from distant locations. Sprung (1983) found the spawning season of *M. edulis* on Helgoland to extend from April to June. Although dependent on prevailing wind regimes, the mean duration for a particle drifting in surface currents from Helgoland to Amrum is estimated at 4 - 8 weeks (Schrumm, University Hamburg, pers. comm.). The arrival of such larvae would therefore correspond to the unexplained larval abundance peaks observed in this study during July and August. Another possible source of imported larvae could be the mussel stocks off the coast of Lower Saxony.

The Schleswig-Holstein mussel stocks are concentrated in the north Frisian region of the Wadden Sea. The extended spawning season of these adult mussel populations, combined with the sporadic importation of larvae from the North Sea, result in a continual presence of planktonic mussel larvae in the area. High tidal ranges and resultant strong currents cause rapid and fairly homogeneous distribution of larvae, resulting in the similarity of larval densities at different sites around the island of Amrum. It is likely that plankton samples from the vicinity of the Eiderstedt peninsula, or from waddens to the north of Sylt island, will show noticeable differences to those from Schleswig-Holstein, as the bivalve species diversity and *M. edulis* biomass are very different in these regions.

Identification of planktonic bivalve larvae has been plagued by difficulty and controversy for almost a century (Stafford, 1912; Kändler, 1926; Nelson, 1928; Miyazaki, 1962; Werner, 1940; Jørgensen, 1946; Thorson, 1946; Sullivan, 1948; Rees, 1950; Loosanoff *et al.*, 1966). In particular, there are no comprehensive identification guides available for North Sea species, like the photo-series of shell shapes and sizes of North American bivalve larvae published by Sullivan (1948) and Loosanoff *et al.* (1966). Identification methods based on valve hinge morphology or larval culture are too impractical and time consuming for long-term plankton monitoring studies, so the larval shell form descriptions of Sullivan (1948) and Loosanoff *et al.* (1966) were used for identification of bivalve genera in this study. Although somewhat subjective, regular use of this method provided reliable identification of bivalve genera. Size and shape of larval bivalve veliconchal shells varies considerably (Jørgensen, 1946; Loosanoff & Davis, 1963; Bayne, 1965), but the detailed descriptions of the shell morphology of *M. edulis* (Sullivan, 1948; Loosanoff *et al.*, 1966; de Schweinitz & Lutz, 1976; Fuller & Lutz, 1989) made identification of this species relatively easy. However, the use of plankton samples for long term monitoring of bivalve reproduction and recruitment is inappropriate, as their analysis is too slow and labour intensive.

In contrast to the adults, the larvae of *M. edulis* undergo an extended, highly dispersive phase. Planktonic mussel larvae (as well as those of other bivalve groups) show sharp peaks in abundance, which are usually closely related to spawning events and phytoplankton blooms. Moreover, their continuous presence throughout the winter shows that larvae can delay metamorphosis during unfavourable conditions. This dispersive planktonic phase is, however, subject to high mortality due to extreme environmental conditions, ingestion by filter-feeders, predation, starvation or shortage of suitable settlement substrates (Thorson, 1966; Jørgensen, 1981). Sporadic importation of larvae from the North Sea could also contribute to fluctuations in larval abundance, despite relatively stable local mussel populations. These factors all combine to make prediction of recruitment to adult mussel stocks from larval densities unreliable.

After a variable period of residence in the plankton, mussel larvae appear to respond to specific cues which prompt settlement and attachment to filamentous substrates. This settlement can be successfully monitored using natural substrates or artificial collectors. Spat collectors have the advantage of being standardized, and so of being directly comparable between sites. The gauze collectors used in this study proved to be successful in emulating natural filamentous settlement substrates, and provided quantitative settlement data which reflected the same settlement trends observed on adjacent hydroids and algae. However, as a result of the often localised, patchy and site-selective settlement patterns of mussel spat, collector data may be strongly biased if collectors are badly situated. Collector deployment therefore needs to be planned to optimally collect the required data. Natural substrates, particularly those with a wide geographic and seasonal coverage, are often the best indicators of suitable mussel settlement areas. Preliminary evaluation of settlement densities on such natural substrates may therefore provide an efficient way of selecting suitable mussel settlement areas for subsequent deployment of collectors.

The peak intertidal and subtidal settlement period in summer occurs 3 - 4 weeks after maximum planktonic larval abundance (see Fig. 6.1). In autumn, intertidal availability of annual algae and hydroids decreases sharply, and the autumn settlement peak occurs primarily on perennial, subtidal hydroids. Although the ability of the larvae to delay metamorphosis and undergo bysso-pelagic migration can extend the interval between spawning and settlement to several months, the availability of suitable substrates may control subsequent settlement intensity. Extreme winter storms or freshwater run-off, which strongly influence the development and survival of localized macroalgae and hydroid populations, may therefore ultimately determine plantigrade settlement success. The existence of large expanses of hydroids and algae without attached mussel spat indicate that the recruitment success of mussels in the Wadden Sea is not limited by the availability of settlement surfaces in the summer. In contrast, it is possible that suitable settlement areas become limiting to autumn settlers, when hydroid and algal densities decrease. However, the extended spawning and settlement seasons of *M. edulis* facilitate the year-round opportunistic exploitation of any suitable settlement substrates which become available.

Mussel spawning and planktonic larval abundances in the Schleswig-Holstein Wadden Sea are more pronounced in spring and early summer than in autumn. However, higher predator densities in the summer result in high mortalities of larvae, plantigrades and juveniles. Recruitment to mussel beds from the summer spawning is therefore usually limited. The summer spatfall therefore only appears to contribute significantly to recruitment when settlement is so intense that it outweighs predation. These plantigrades then recruit to the adult beds in autumn (eg. 1991; see Fig. 6.1).

Availability of sufficient metabolic reserves to delay metamorphosis over winter enables autumn-spawned spat to avoid predation by benthic invertebrates. The crab and starfish populations decrease, or become quiescent, during winter, resulting in reduced predation on over-wintering plantigrades. These spat resume growth in the spring, rapidly outgrowing the size range most vulnerable to predation before predator activity resumes. The establishment of these new cohorts is recognizeable on adult mussel beds prior to the early summer attachment peaks on filamentous substrates (Fig. 6.1), and has frequently been reported from other areas (Reynolds, 1969; Seed, 1969b; Dayton, 1971; Möller & Rosenberg, 1983; Ceccherelli & Rossi, 1984). Despite the relative stability of annual abundances of planktonic mussel larvae during the study period, variations in predator biomass and availability of suitable substrates for attachment may have influenced the observed timing and intensity of settlements, and subsequent recruitment. Strong competition or predation should favour the evolution of extended reproductive seasons (Young & Chia, 1981), and the observed adaptations in larval settlement strategies do appear to increase the competitive success of *M. edulis* larvae and spat in the Wadden Sea (Suchanek, 1978).

In marked contrast to the observed spatial homogeneity in planktonic larval abundances in the study area, settlement and recruitment concentrations were highly localised. Intertidal settlements were usually confined to established mussel beds near low water. In these areas, plantigrades either settle directly between adult mussels, or migrate into the beds after primary attachment on filamentous substrates in residual water bodies between mussel hummocks. In years of extremely heavy recruitment, settlement may also occur higher up the shore on bare sand or mud, or in *Zostera* beds. Residual water bodies are absent in high elevation beds, but the seagrass growing between the hummocks traps a thin film of water. Rejuvenation of high shore beds therefore only occurs when suitable bio-physical conditions coincide with years of heavy settlement.

In contrast, the development of subtidal beds depends largely on processes which affect the substratum. In calm conditions, areas of hard, consolidated subtidal substrate tend to become covered by soft, unconsolidated sediments, particularly where mussel beds produce a cover of pseudofaeces. Removal of mussel beds or turnover of softer sediments by storms or fishing activities, with subsequent removal of overlying sediment by current action, can re-expose suitable hard settlement areas. The abundance and diversity of invertebrate larvae in the plankton will determine the sequence of colonization, and thus ultimately the community structure, of such exposed areas (Osman, 1977 Okamura, 1986b). Initial succession communities develop rapidly following an exposure event, although the sequence and rate of development depends on the order and extent of species invasions. The composition of resultant benthic communities is therefore largely unpredictable (Sutherland & Karlson, 1977). In the Wadden Sea, developing communities usually culminate in a climax community dominated by mussels, which are extremely successful invaders and colonizers. Although these mussel communities would probably remain stable if left undisturbed, the frequent disturbances typical of the Wadden Sea result in continual change in the structure of established mussel beds. Various bio-physical processes can even cause the large-scale destruction of mussel beds (Dare, 1976). As a result, subtidal populations are highly dynamic, and it is only in relatively few, particularly suitable settlement areas that substantial mussel recruitments occur regularly.

The major subtidal crop-producing spatfall in the Vortrapptief in spring 1990 occurred as described above. Strong winter storms and tidal scour re-exposed a large area of stony seabed and provided a new settlement area for the establishment of a succession community. Subsequent intense mussel spat settlement was extremely localized, being confined to an area of about 0.8 km². This mussel population rapidly attained high densities and production rates, smothering the primary colonizing species. However, during the summer, the biomass declined rapidly due to intense predator pressure, instability as a result of loose embyssment on the accumulating mussel-mud, and the commercial seed fishery. The commercial transfer of harvested seed mussels to culture plots was, however, probably beneficial to the stock. Re-distribution made space available for new settlers, and the fishery tended to enlarge the area, because mussel clumps fall through the nets during hauling, disperse with the current, and provide dispersed settlement niches for gregarious plantigrades.

It has been proposed that the intensity of mussel spatfall is related to previous winter temperatures, optimum recruitment following abnormally cold winters (Reynolds, 1969; Beukema *et al.*, 1978; Möller & Rosenberg, 1983; Meixner, 1985, amongst others). However, heavy spatfall in Schleswig-Holstein in 1990 following a mild, although stormy winter, and the parallel recruitment failure in adjacent Wadden Sea areas (Ruth, 1994), suggests that recruitment intensity is not governed by temperature alone. Although egg quality and fertilization success improve at lower temperatures, it appears that the intensity and success of subsequent recruitment is strongly influenced by factors which maintain the diversity of the habitat available for settlement.

Intertidal and subtidal spat collectors confirmed the mussel spawning cycles determined during gonad histology and condition index investigations. They also provided information on the vertical preferences of primary and secondary settling spat, and on the predicted timing and potential intensity of recruitment to the parent stocks. The cylindrical Type 3 collectors, using polyester gauze as an artificial substrate, are easy to construct, deploy and change. They also appear to be effective spat collectors, and should therefore be adequate for future monitoring of mussel settlement. However, collector settlement data should be supplemented by monitoring of natural filamentous and creviced substrates from intertidal and subtidal regions, to detect possible changes in the migratory behaviour or substrate preferences of the growing plantigrades. This should ensure that attachment and settlement can be followed throughout the year. Sampling intervals should also be kept short to detect rapid changes resulting from disturbance, predation or fishing, to determine the duration and intensity of settlement peaks, and to follow the growth and survival of the juvenile mussels.

Hydrodynamic processes also play an important role in determining mussel recruitment patterns. Although they are able to regulate their position in the water column, the large-scale dispersal of *M. edulis* larvae appears to be determined largely by physical processes. Tidal currents and local hydrodynamic processes are important in transporting larvae and plantigrades to suitable settlement areas, where they may subsequently choose to settle or remain unattached, depending on settlement preferences. The observed spatial variation in density of settled spat may result from differential survival (Butman, 1987), but the comparitively low larval abundances and associated high mortalities suggest that redistribution and accumulation of settlers is more likely to be responsible for observed recruitment patterns.

Mussel larvae are reported to attach primarily in areas offering some shelter from water currents (Verwey, 1952; Chipperfield, 1953; Vakily, 1989). In the Wadden Sea, where current velocities >0.5 $m.s^{-1}$ are common even on the tidal flats, this has important implications for the establishment and distribution of mussel communities. Typical swimming speeds of marine invertebrate larvae range from 0.001 - 0.01 $m.s^{-1}$ (Chia *et al.*, 1984), and water velocities as low as 0.01 $m.s^{-1}$ are sufficient to dislodge potential settlers (Lane *et al.*, 1985). Active substrate selection in natural environments characterized by much higher flow rates therefore seems to be particularly difficult. The colonization of only the the lee side of navigational buoys exposed to high current speeds confirms this. However, the presence of even minor obstructions can result in turbulence patterns which create sheltered areas in which larvae can accumulate and settle. Hydrographic processes are therefore probably capable of accounting for much of the observed patterning in *Mytilus* settlements, without having to evoke excessively active larval behaviour (Eckman, 1983, 1990).

Recent research on invertebrate attachment behaviour has found that larvae not only respond to chemical and tactile settlement cues, but also to reduced current velocities and small-scale turbulence (Hannan, 1984; Keough & Downes, 1986; Wethey, 1986; Savidge & Taghon, 1988; Butman, 1989). Furthermore, larval size and sinking speed will alter the effect of physical factors on settlement rates (Sigurdsson *et al.*, 1976; Lane *et al.*, 1985; Butman, 1987). Once larvae enter the near-bottom flow, small-scale hydrographic processes predominate, as the larvae or spat are passively transported over the sea bed. Subsequent larval distribution and accumulation should therefore respond to the same factors which control sediment transport and deposition (Verwey, 1952; Baggerman, 1953; Butman, 1987, 1989). The bottom topography of an area can thus play a major role in determining the locality of larval accumulations. For example, the onshore current is slowed and deviated by large subtidal sandbars in the Vortrapptief, permitting the development of succession communities in the area. Similarly, the Hornsriff bank north-west of Esbjerg is the first major obstruction to the northerly flowing long-shore current in the German Bight, with the effect that it accumulates passively transported plantigrades and results in the establishment of a large subtidal seed population (Leuschel, mussel fisherman, Schlüttsiel, pers. comm.).

On a smaller scale, the sediment-type patchiness and micro-relief of intertidal waddens is also largely determined by local current patterns. Larvae and spat, behaving like passive particles, will therefore also be deposited on these waddens in areas of reduced current velocity. Whether as free larvae, or attached to drifting weed in late summer and autumn when algae degenerate and detach, plantigrades therefore accumulate in localized areas, either rejuvenating an established population or forming a new mussel bed. Further variation in settlement density will result from reduced settlement or survival of spat in higher shore areas with longer aerial exposure. Within such localised areas, further patterns in the density of recruits occur. Variations in the water flow around a mussel hummock can concentrate the drifting spat, as turbulence and reduced water velocity in the patch lee release the larvae from the current, to allow for active habitat selection. If suitable niches are encountered between the adult mussels, the spat will attach and settle. If not, they may continue to drift until a suitable microhabitat is encountered.

The rapid growth of mussels in the Wadden Sea has been attributed to eutrophication of the area over the last few decades (Postma, 1985; Beukema & Cadée, 1986; Kleinsteuber *et al.*, 1988). However, the exceptional growth rates of mussel populations fouling navigational buoys in the area are comparable with those reported from suspended cultures in Ireland (Aldrich & Crowley, 1986) and New Zealand (Hickman & Illingworth, 1980). In fact, Duge (1914), reported that mussels on navigational buoys in the Wadden Sea could reach a length of 50 mm in 8 months, indicating that the effects of recent eutrophication may be insignificant. Fouling populations on buoys are able to feed continually in strong surface currents, where phytoplankton production is high. As a result of daily aerial exposure, decreasing phytoplankton concentrations towards the seabed, and rapid phytoplankton depletion by filter-feeders in slow-flowing currents, growth rates of intertidal mussels are reduced (Fréchette & Bourget, 1985; Wildish & Kristmanson, 1985). Decreasing phytoplankton concentrations downstream of established banks probably result in decreased settlement, reduced growth rates and decreased survival, resulting in smaller hummock size with increased tidal elevation. This is indicated by the reduced proportion of juveniles, and the smaller mean size of the youngest cohort, on the high elevation study patch (Fig. 5.4, top).

Certain recruitment patterns, such as those observed on navigational buoys and other surface structures, cannot be explained by accumulation and transport of spat in the seabed boundary-layer. These settlements may result from some active behavioural component in the otherwise passive dispersal and accumulation of mussel larvae and spat, such as active vertical migration and bysso-pelagic drifting at the surface. Certain combinations of hydrographic and weather conditions can concentrate such surface-drifting plantigrades into slicks, which are moved inshore by the prevailing winds and flood tides. Passive accumulation in the reduced flow rates in the current lee of obstacles such as navigational buoys will subsequently result in settlement, in much the same way as occurs in the lee of seabed mussel patches.

On a smaller scale, the biota serving as preferred initial attachment substrates may also alter the settlement microhabitat. By modifying the relief of the initial substrate and changing the quality and quantity of settling surfaces, even small structures can increase turbulence and induce settlement. Such structures may signal habitats of higher species survival (Dean, 1981), acting as cues to induce active settlement of larvae, although resultant behavioural responses (eg. sinking speeds, substrate contact, perception of cues and re-suspension) will still be constrained by local, small-scale hydrodynamic processes.

Large-scale processes controlling coastal morphology and geology produce a characteristic set of local physical conditions, which can create, alter or maintain potential mussel settlement sites. Knowledge of the local hydrography and sediment transport patterns can therefore be useful in predicting potential settlement sites, or possible subtidal seed sources. In turn, different sites will have characteristic levels of settlement density and recruitment, depending on local substrate and hydrodynamic characteristics. Consistently higher recruitment has been observed to occur in certain areas, indicating that the mechanisms affecting recruitment at those sites can act consistently over long time periods (Connell, 1985). Disturbance of these areas can have far reaching effects on the distribution and intensity of recruitments, and on the subsequent establishment of mussel populations. Man-made influences, such as the building of dams and dykes which alter water flow patterns, can therefore have a marked effect on mussel populations. Similarly, natural forces such as storms, winds, extreme tides and high river run-off may also markedly affect mussel settlement patterns through temporary alteration of advective and depositional regimes.

During the period of this study, the total biomass of fishable intertidal adult mussel populations in the Schleswig-Holstein Wadden Sea fluctuated between an approximate minimum of 16 000 t and a maximum of 60 000 t (Ruth, 1994). Estimation of the biomass of the highly variable subtidal stocks is more difficult, but these have been estimated to support a combined natural and cultured biomass of at least 100 000 t (Ruth, 1994). Peaks in intertidal biomass appear to alternate with peaks in subtidal biomass, resulting in a relatively stable total mussel biomass of up to 200 000 t, after including the small, non-fishable, scattered mussel patches. Although this biomass estimate is ten times the current annual commercial catch of approximately 20 000 t, ice damage can destroy up to 90% of the existing mussel biomass in a single severe winter (Ruth, Institut für Meereskunde, Kiel, pers. comm.).

Mussels in the Schleswig-Holstein Wadden Sea do not exhibit any clear stock-recruit relationship. Annual settlement densities bear little relationship to adult spawning stock sizes, and recruitment success appears to be determined principally by post-settlement survival. Regardless of initial values, spat numbers decline rapidly as a result of predation, natural mortality or migration (Muus, 1973; Möller & Rosenberg, 1983). The combined effects of biotic and abiotic factors on spawning, larval abundance and plantigrade settlement result in frequent rejuvenation of the natural beds, and juvenile recruitment is possible at any time of year. It is usually possible to forecast major spatfall periods from gonad condition indices or planktonic larval abundances, but recruitment of over-wintered or imported larvae is inherently unpredictable. Furthermore, the marked effect of hydrodynamic and biotic factors on settlement makes the reliable prediction of effective mussel recruitment from planktonic larval densities, or from the intensity and distribution of primary spat settlement, impossible.

Reduced fecundity and recruitment failures were considered by Hancock (1973) to be density-regulating mechanism in over-populated marine benthic populations. Although the establishment of commercial bottom cultures has resulted in an increase in subtidal mussel biomass, the continuous fishing of cultured and wild beds appears to prevent the mussel populations in the Wadden Sea from reaching the carrying capacity of the area (Ruth, 1991). However, the impact of repeated exploitation on residual spawner biomass and stock sustainability is difficult to assess due to the highly variable and unpredictable environmental conditions. Continued harvesting could have detrimental long term effects on resident mussel populations, if settlement and recruitment rates become reduced below sustainable levels. However, the poor stock-recruit relationship and dramatic inter-annual variation in recruitment indicate that the resource is robust to exploitation at current rates, provided that adequate harvest refugia remain available to adult mussels.

In conclusion, periodic peaks in mussel plantigrade numbers are common in the Schleswig-Holstein Wadden Sea. However, re-colonization of established beds, or the formation of localized subtidal beds are episodic events superimposed on a background of continuous settlement and loss. The intensity of episodic recruitment varies both spatially and temporally, and strongly influences the distribution patterns of mussel populations in the Wadden Sea. The distribution and abundance of plantigrades appears to be controlled by near-bottom water flow, and local hydrographic processes significantly affect spat settlement and subsequent recruitment patterns. Settlement of larvae and drifting plantigrades may be induced by biological assemblages, or by passive accumulation in eddies around topographic structures. Any factor creating localized alterations in the hydrodynamic regime can therefore directly influence the structure of benthic assemblage in an area (Savidge & Taghon, 1988). Finally, initial mussel settlement patterns can be markedly altered by disturbances such as storms, ice scour or fishing, and by post-larval immigration into mussel beds.

The recruitment of *Mytilus edulis* in the Wadden Sea is therefore characterized by extreme variability, unpredictable episodic events and strong modification of settlement patterns by physical and biological factors. The planktonic and benthic distribution and settlement strategies displayed by mussel larvae and spat constitute a successful recruitment strategy, designed to opportunistically exploit a wide variety of settlement opportunities, with mechanisms for extending larval survival during unfavourable conditions. Local mussel beds can also be re-colonized by larvae from outside sources, facilitating the rapid recovery of denuded areas. The combination of these factors has resulted in the development of large, enduring and highly productive mussel stocks in the Wadden Sea. However, the highly variable nature of planktonic larval survival and spat settlement success means that effective recruitment cannot be predicted directly from the monitoring of spawning cycles in local mussel beds. Effective management procedures for the wild and cultured mussel fishery in the Schleswig-Holstein Wadden Sea will therefore have to rely on the detection and quantitative assessment of post-settlement (1 mm - 5 mm) mussel spat, and the implementation of fishery methods to optimize the subsequent cultivation and harvest of successful settlements.

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APPENDIX I

Table 2.3a Average indices of condition for the high intertidal site (see Fig. 1.2) with the coefficients of variation (cv) (%). Grand means and coefficients of variation (cv*) for the individual cv's are given.

a)	CI 1		CI 2		CI 3		CI 4		CI 5	
Date	mean	cv	mean	cv	mean	cv	mean	cv	mean	cv
910427							0,385	23,63	0,275	17,48
910509					0,079	21,09	0,435	28,81	0,299	18,56
910522			0,214	55,45	0,093	39,33	0,460	39,76	0,306	25,99
910605			0,208	28,02	0,103	52,79	0,487	33,68	0,323	22,16
910619			0,201	8,06	0,102	23,04	0,509	25,17	0,333	16,90
910705			0,205	19,19	0,087	27,73	0,429	23,51	0,297	16,75
910717			0,204	8,94	0,074	23,30	0,365	24,28	0,264	18,27
910805					0,069	20,00	0,346	22,14	0,255	16,38
910820			0,200	10,88	0,075	23,50	0,424	21,81	0,295	15,89
910901			0,177	13,75	0,070	21,11	0,386	21,38	0,276	15,83
910919			0,183	9,63	0,062	19,91	0,336	19,69	0,250	15,04
910930			0,184	10,93	0,056	24,08	0,296	24,26	0,226	19,74
911025			0,195	40,50	0,055	31,31	0,292	31,76	0,222	25,31
911112			0,189	10,07	0,045	31,50	0,234	28,98	0,187	24,12
911212			0,192	16,48	0,055	21,97	0,340	21,98	0,252	16,42
920115			0,163	15,74	0,045	30,05	0,241	29,41	0,192	23,57
920214			0,188	14,02	0,051	20,72	0,287	20,16	0,221	15,68
920317			0,180	15,91	0,046	25,35	0,273	48,15	0,212	19,56
920328			0,168	11,10	0,044	28,74	0,233	28,87	0,186	24,31
920409			0,191	11,06	0,048	29,23	0,255	26,33	0,201	23,26
920422			0,189	19,29	0,064	27,56	0,419	17,39	0,289	22,42
920509			0,156	13,90	0,073	35,54	0,419	31,19	0,288	23,82
920521			0,176	9,93	0,075	39,39	0,384	37,07	0,268	29,73
920610			0,198	10,68	0,076	30,36	0,369	45,05	0,264	23,10
920702			0,207	7,49			0,410	27,81	0,285	23,34
920722			0,194	21,86	0,075	30,31	0,396	30,73	0,278	22,39
920817			0,186	14,17	0,068	27,57	0,326	28,20	0,242	21,86
920914			0,211	10,03	0,055	37,50	0,295	36,81	0,224	29,81
MEAN			0,190	16,23	0,067	28,58	0,358	28,50	0,257	20,99
cv*			7,522	64,37	24,84	26,18	21,16	25,94	15,66	19,66

Table 2.3b Average indices of condition for the low intertidal site (see Fig. 1.2) with the coefficients of variation (cv) (%). Grand means and coefficients of variation (cv*) for the individual cv's are given.

b)	CI 1		CI 2		CI 3		CI 4		CI 5	
Date	mean	cv	mean	cv	mean	cv	mean	cv	mean	cv
910427			0,242	4,63	0,123	23,57	0,509	22,00	0,334	14,63
910509			0,218	13,07	0,113	33,63	0,525	33,73	0,336	22,71
910523			0,203	11,48	0,113	37,70	0,558	37,01	0,347	24,22
910605			0,210	12,27	0,112	30,75	0,536	33,45	0,344	23,91
910618			0,217	8,86	0,112	27,74	0,520	28,33	0,336	19,14
910703			0,220	8,74	0,100	24,28	0,460	25,08	0,311	17,66
910717			0,218	18,75	0,094	21,06	0,440	19,98	0,303	14,00
910805			0,203	9,57	0,078	20,82	0,383	18,35	0,275	13,17
910818			0,207	10,24	0,080	24,79	0,392	25,49	0,278	18,85
910901			0,200	15,71	0,085	20,32	0,404	17,01	0,286	11,99
910918			0,206	11,03	0,086	24,29	0,431	19,77	0,298	14,18
910928			0,182	18,41	0,076	23,67	0,369	21,34	0,267	16,36
911025			0,210	12,73	0,075	24,19	0,417	20,78	0,292	14,49
911112			0,195	15,00	0,073	24,43	0,378	21,05	0,270	17,32
911211			0,170	14,89	0,070	23,33	0,335	22,43	0,249	16,18
920115			0,184	64,57	0,063	19,68	0,375	19,50	0,271	14,28
920215			0,188	15,26	0,073	27,49	0,421	35,94	0,299	30,92
920317			0,173	13,30	0,063	20,27	0,337	18,92	0,250	14,45
920328			0,182	19,26	0,063	20,15	0,372	22,22	0,268	16,22
920409			0,178	11,46	0,065	22,49	0,362	20,82	0,264	15,47
920422			0,204	10,60	0,077	27,94	0,437	27,43	0,298	19,56
920508					0,103	42,22	0,500	39,46	0,322	26,59
920521			0,201	8,10	0,101	37,64	0,502	37,24	0,324	24,66
920610			0,228	14,42	0,116	34,73	0,516	36,35	0,330	24,76
920702			0,249	8,77	0,152	25,03	0,617	25,63	0,376	16,35
920722			0,246	9,93	0,136	25,47	0,552	22,06	0,352	14,25
920817			0,230	12,63	0,114	31,85	0,489	25,51	0,324	17,67
920914			0,242	50,68	0,097	49,93	0,411	23,51	0,288	16,75
MEAN			0,208	15,78	0,093	27,48	0,448	25,73	0,303	18,24
cv*			10,38	79,48	24,92	26,48	16,53	25,75	10,88	25,47

Table 2.3c Average indices of condition for the subtidal culture population (see Fig. 1.2) with the coefficients of variation (cv) (%). Grand means and coefficients of variation (cv*) for the individual cv's are given.

c)	CI 1		CI 2		CI 3		CI 4		CI 5	
Date	mean	cv	mean	cv	mean	cv	mean	cv	mean	cv
910523			0,219	23,12	0,124	31,50	0,584	33,25	0,359	19,97
910606	89,4	3,14	0,226	34,28	0,127	44,92	0,561	26,85	0,354	16,87
910620	90,0	3,37	0,236	10,06	0,116	27,72	0,494	25,80	0,326	16,84
910704	89,4	4,58	0,236	11,04	0,127	26,77	0,539	21,41	0,344	15,13
910719	91,9	2,43	0,235	12,61	0,133	22,94	0,566	19,64	0,358	12,69
910807	92,4	5,84	0,232	10,55	0,136	22,44	0,584	18,77	0,366	12,02
910818	93,4	2,10	0,236	12,38	0,145	22,25	0,613	17,63	0,377	11,01
910902	94,3	1,45	0,238	26,33	0,144	31,85	0,604	17,46	0,374	10,72
910918	92,5	2,97	0,232	24,33	0,130	32,37	0,555	26,65	0,356	19,68
910928	91,6	5,44	0,229	9,87	0,123	27,02	0,533	21,61	0,344	14,13
911025	90,8	4,04	0,242	8,86	0,117	23,75	0,482	18,41	0,323	12,66
911113	88,9	7,53	0,201	15,10	0,107	27,22	0,435	25,24	0,299	19,16
911211	89,4	5,88	0,257	46,15	0,096	29,94	0,477	23,77	0,319	16,33
920116	88,2	7,38	0,221	10,92	0,090	27,18	0,403	20,97	0,285	14,90
920215			0,210	13,11	0,083	28,39	0,398	27,35	0,280	18,90
920317			0,191	10,86	0,079	28,64	0,409	24,50	0,287	17,36
920328	84,0	9,48	0,211	40,29	0,089	33,17	0,499	20,24	0,330	13,60
920411	83,1	13,8	0,172	25,28	0,085	26,67	0,446	30,86	0,303	21,13
920424			0,209	33,24	0,116	23,75	0,507	24,08	0,332	15,87
920507	86,1	4,52	0,230	6,42	0,139	36,25	0,693	32,33	0,396	20,90
920522	85,0	4,65	0,214	8,37	0,098	27,63	0,461	28,43	0,311	17,57
920611	89,1	3,37	0,233	8,47	0,138	30,02	0,595	28,12	0,364	19,53
920704	93,3	1,71	0,237	45,57	0,190	36,38	0,818	23,34	0,444	13,32
920724	91,3	4,48					0,756	20,32	0,426	11,63
920817	91,1	7,00	0,245	12,70	0,154	31,13	0,624	24,92	0,378	16,35
920914	92,0	4,45	0,267	9,72	0,153	36,99	0,564	30,75	0,353	19,73
MEAN	89,9	4,98	0,226	18,79	0,122	29,48	0,546	24,34	0,346	16,08
cv*	3,33	55,5	8,747	64,26	21,47	17,61	18,52	18,45	11,55	19,59

Table 2.4a. Parameters and statistics of linear regressions of length-cooked weight data.

Date	Slope	Intercept	s.e.	corr.coef.
High intertidal				
910427	2,792	-4,389	0,075	0,960
910507	2,082	-3,199	0,079	0,879
910523	1,978	-3,020	0,066	0,947
910606	2,198	-3,374	0,061	0,969
910620	2,338	-3,565	0,058	0,972
910704	2,709	-4,221	0,065	0,983
910719	2,641	-4,165	0,074	0,967
910807	2,825	-4,513	0,073	0,980
910819	2,872	-4,473	0,065	0,983
910902	2,871	-4,523	0,068	0,979
910918	2,808	-4,461	0,069	0,984
910928	2,657	-4,273	0,079	0,972
911025	2,549	-4,090	0,099	0,943
911112	2,715	-4,426	0,099	0,963
911211	2,748	-4,372	0,095	0,960
920116	2,384	-3,861	0,099	0,930
920215	3,114	-5,023	0,079	0,979
920317	3,098	-5,014	0,080	0,980
920328	2,457	-4,013	0,101	0,937
920411	2,418	-3,917	0,103	0,932
920424	2,541	-3,921	0,095	0,951
920507	2,368	-3,654	0,078	0,954
920522	2,056	-3,154	0,068	0,960
920611	2,457	-3,863	0,070	0,964
920704	2,683	-4,209	0,094	0,965
920724	2,719	-4,241	0,107	0,958
920817	2,607	-4,161	0,086	0,954
920914	2,468	-3,937	0,118	0,948
Low intertidal				
910427	2,642	-4,012	0,050	0,990
910507	2,120	-3,190	0,060	0,978
910523	2,093	-3,093	0,084	0,959
910606	2,108	-3,129	0,060	0,980
910620	2,374	-3,577	0,072	0,975
910704	2,591	-3,968	0,091	0,966
910719	2,835	-4,377	0,071	0,985
910807	3,065	-4,824	0,075	0,981
910819	2,685	-4,170	0,096	0,965
910902	2,941	-4,575	0,071	0,963
910918	3,069	-4,758	0,082	0,961
910928	2,969	-4,661	0,083	0,971
911025	3,236	-5,068	0,090	0,980
911112	3,008	-4,702	0,080	0,983
911211	3,353	-5,353	0,079	0,986
920116	3,117	-4,898	0,087	0,976
920215	3,547	-5,585	0,101	0,981
920317	3,228	-5,120	0,066	0,984
920328	3,275	-5,150	0,068	0,980
920411	3,023	-4,749	0,078	0,980
920424	2,576	-3,933	0,063	0,980
920507	2,132	-3,207	0,068	0,958
920522	2,163	-3,200	0,068	0,973
920611	2,169	-3,194	0,078	0,957
920704	2,544	-3,745	0,063	0,983
920724	2,891	-4,364	0,079	0,981
920817	3,231	-4,959	0,111	0,969
920914	3,308	-5,137	0,106	0,976
Subtidal culture				
910523	2,029	-2,975	0,076	0,951
910606	2,209	-3,294	0,078	0,937
910620	2,532	-3,913	0,083	0,967
910704	2,648	-4,064	0,087	0,972
910719	2,778	-4,303	0,084	0,979
910807	3,100	-4,830	0,075	0,985
910819	3,242	-5,044	0,059	0,992
910902	3,259	-5,084	0,065	0,985
910918	3,479	-5,501	0,082	0,983
910928	3,436	-5,444	0,085	0,976
911025	3,524	-5,627	0,078	0,975
911112	3,422	-5,501	0,083	0,972
911211	3,389	-5,356	0,091	0,976
920116	3,523	-5,665	0,088	0,978
920215	3,448	-5,531	0,100	0,975
920317	3,390	-5,480	0,086	0,982
920328	3,173	-4,521	0,059	0,989
920411	2,275	-3,527	0,068	0,981
920424	2,757	-4,307	0,086	0,977
920507	2,165	-3,151	0,089	0,961
920522	2,124	-3,177	0,084	0,951
920611	2,198	-3,282	0,089	0,957
920704	2,654	-3,864	0,078	0,984
920724	2,931	-4,387	0,078	0,983
920817	3,195	-4,916	0,092	0,979
920914	3,333	-5,238	0,122	0,947

Table 2.4b Parameters and statistics of linear regressions of length-dry weight data.

Date	Slope	Intercept	s.e.	corr.coeff.
High intertidal				
910509	2,342	-4,342	0,073	0,910
910523	2,101	-3,918	0,062	0,959
910606	2,413	-4,405	0,075	0,963
910620	2,411	-4,381	0,063	0,969
910704	2,915	-5,231	0,078	0,978
910719	2,804	-5,121	0,077	0,969
910807	3,136	-5,709	0,088	0,976
910819	3,043	-5,493	0,081	0,977
910902	3,026	-5,506	0,080	0,974
910918	2,931	-5,395	0,083	0,978
910928	2,948	-5,454	0,086	0,972
911025	2,623	-4,935	0,115	0,927
911112	2,694	-5,113	0,118	0,949
911211	2,986	-5,504	0,096	0,965
920116	2,367	-4,560	0,098	0,930
920215	3,086	-5,728	0,086	0,975
920317	3,076	-5,748	0,091	0,974
920328	2,414	-4,658	0,101	0,934
920411	2,399	-4,617	0,111	0,922
920424	2,588	-4,914	0,089	0,959
920507	2,281	-4,272	0,083	0,946
920522	2,145	-4,000	0,065	0,966
920611	2,590	-4,752	0,065	0,971
920722	2,884	-5,233	0,127	0,950
920817	2,908	-5,321	0,102	0,949
920914	2,598	-4,881	0,130	0,943
Low intertidal				
910427	2,570	-4,512	0,061	0,989
910509	2,233	-4,038	0,062	0,979
910523	2,086	-3,779	0,094	0,949
910606	2,226	-3,998	0,072	0,974
910620	2,505	-4,455	0,082	0,971
910704	2,693	-4,797	0,091	0,969
910719	3,048	-5,393	0,088	0,981
910807	3,349	-5,983	0,085	0,979
910819	2,899	-5,209	0,107	0,963
910902	3,144	-5,590	0,081	0,980
910918	3,370	-5,953	0,097	0,978
910928	3,307	-5,909	0,089	0,973
911025	3,331	-5,938	0,080	0,986
911112	3,479	-6,214	0,108	0,974
911211	3,518	-6,301	0,083	0,986
920116	3,336	-6,030	0,086	0,980
920215	3,354	-6,034	0,083	0,985
920317	3,309	-5,982	0,072	0,982
920328	3,279	-5,918	0,067	0,988
920411	3,096	-5,613	0,087	0,977
920424	2,552	-4,644	0,058	0,983
920507	2,014	-3,702	0,076	0,965
920522	2,178	-3,921	0,074	0,968
920611	2,302	-4,068	0,085	0,958
920704	2,728	-4,655	0,085	0,974
920722	3,089	-5,301	0,099	0,974
920817	3,497	-6,038	0,130	0,964
920914	3,490	-6,093	0,155	0,954
Subtidal culture				
910523	2,174	-3,898	0,089	0,942
910606	2,203	-3,940	0,095	0,910
910620	2,590	-4,637	0,093	0,960
910704	2,709	-4,795	0,087	0,955
910719	2,939	-5,205	0,080	0,972
910807	3,329	-5,850	0,089	0,982
910819	3,544	-6,183	0,068	0,991
910902	3,572	-6,254	0,080	0,982
910918	3,855	-6,770	0,091	0,983
910928	3,821	-6,733	0,088	0,978
911025	3,819	-6,757	0,089	0,973
911112	3,633	-6,479	0,089	0,974
911211	3,713	-6,604	0,099	0,976
920116	3,809	-6,910	0,098	0,977
920215	3,633	-6,524	0,099	0,978
920317	3,556	-6,482	0,096	0,980
920328	3,532	-6,368	0,119	0,965
920411	2,736	-5,045	0,102	0,965
920424	2,268	-4,154	0,062	0,984
920507	2,199	-3,912	0,082	0,968
920522	2,167	-3,928	0,062	0,955
920611	2,241	-3,988	0,095	0,953
920704	2,876	-4,900	0,105	0,975
920817	3,436	-5,949	0,109	0,974
920914	3,607	-6,287	0,140	0,942

Table 2.5 Parameters and statistics of the non-linear length-whole cooked weight data.

Date	a	r^2	Weight (g)
High intertidal			
910427	0,000225	0,93	6,545
910509	0,000226	0,89	6,559
910522	0,000231	0,95	6,706
910605	0,000228	0,92	6,638
910619	0,000229	0,96	6,657
910705	0,000241	0,96	7,017
910717	0,000229	0,94	6,668
910805	0,000214	0,97	6,235
910820	0,000241	0,94	7,023
910901	0,000234	0,96	6,816
910919	0,000234	0,98	6,795
910930	0,000234	0,93	6,818
911025	0,000231	0,95	6,704
911112	0,000217	0,96	6,306
911212	0,000235	0,94	6,835
920115	0,000233	0,95	6,766
920214	0,000222	0,96	6,455
920317	0,000231	0,97	6,706
920327	0,000223	0,93	6,480
920409	0,000229	0,95	6,660
920422	0,000247	0,96	7,170
920509	0,000241	0,95	7,017
920521	0,000250	0,94	7,260
920610	0,000229	0,95	6,669
920702	0,000236	0,93	6,871
920722	0,000251	0,94	7,302
920817	0,000244	0,96	7,097
920914	0,000222	0,94	6,451
Low intertidal			
910427	0,000252	0,98	12,610
910509	0,000240	0,97	11,999
910523	0,000254	0,98	12,723
910605	0,000246	0,98	12,318
910618	0,000246	0,97	12,294
910703	0,000246	0,97	12,301
910717	0,000255	0,97	12,767
910805	0,000240	0,98	12,016
910819	0,000259	0,96	12,939
910901	0,000252	0,97	12,601
910918	0,000271	0,95	13,566
910928	0,000256	0,94	12,814
911025	0,000256	0,96	12,806
911112	0,000264	0,96	13,219
911211	0,000250	0,96	12,480
920115	0,000257	0,96	12,859
920215	0,000252	0,97	12,609
920317	0,000248	0,97	12,406
920327	0,000270	0,96	13,517
920409	0,000263	0,96	13,136
920422	0,000271	0,95	13,526
920508	0,000249	0,95	12,459
920521	0,000267	0,96	13,336
920610	0,000269	0,93	13,436
920702	0,000277	0,95	13,836
920722	0,000281	0,96	14,025
920817	0,000290	0,96	14,480
920914	0,000280	0,95	14,019
Subtidal culture			
910523	0,000209	0,93	10,462
910606	0,000200	0,91	10,010
910620	0,000199	0,95	9,926
910704	0,000202	0,93	10,091
910719	0,000198	0,96	9,878
910807	0,000203	0,94	10,128
910819	0,000216	0,96	10,795
910902	0,000217	0,95	10,870
910918	0,000213	0,94	10,668
910928	0,000210	0,95	10,482
911025	0,000206	0,93	10,314
911113	0,000202	0,95	10,118
911211	0,000223	0,96	11,130
920116	0,000212	0,95	10,622
920216	0,000211	0,9	10,544
920317	0,000189	0,93	9,474
920328	0,000214	0,94	10,722
920411	0,000182	0,93	9,082
920424	0,000197	0,93	9,836
920507	0,000214	0,96	10,710
920522	0,000197	0,95	9,833
920611	0,000199	0,88	9,965
920704	0,000263	0,97	13,157
920724	0,000250	0,95	12,490
920817	0,000249	0,97	12,454
920914	0,000222	0,92	11,100

APPENDIX II

Table 3.1 Coefficients of variation (%) of the total numbers of bivalve larvae sampled in three major tidal streams around the island of Amrum (see Fig. 1.1 for location of sampling stations).

Date	Norderaue	Süderaue	Hörnum Tief
900414	32,26	19,48	32,30
900424	15,63		
900513	45,21		
900606	53,28		
900619	33,39		
900707	12,84		
900717	22,58		
900731	19,51		
900814	23,81	15,99	24,02
900828	6,49		
900913	21,47		
900925	24,92	26,31	21,82
901010	15,58		
901101	13,10		
901127	29,81		
910425	12,60	34,78	32,27
910509	11,11		
910524	25,86	25,80	25,43
910607	22,70		
910621	58,49	21,23	10,02
910705	58,78		
910719	40,36	11,68	28,49
910809	16,70		
910821	12,77	30,95	6,73
910903	14,42		
910920	18,83	14,71	13,74
911004	9,60		
911024	23,78	10,08	10,98
911114	29,38		
911215	4,45	19,64	15,74
920117	31,92	22,35	24,69
920216	41,06	30,98	30,98
920303	36,51		
920317	22,27		
920329	14,05	27,25	15,47
920411	10,60		
920424	19,85		
920509	8,38		
920522	12,52		
920612	27,97	13,89	58,44
920705	9,73		
920723	16,72	9,67	39,42
920820	13,00	4,93	24,51
920916	29,35	11,71	26,59
921017	29,26	33,19	20,70
921115	28,84	12,43	18,88
921218	18,07	38,52	24,11
930116	37,57		
930213	31,62	36,51	35,36
930320	31,62		
930416	25,33		
930513	12,97		
930610	33,14		
930710	27,41		
930814	21,12		

Table 3.2 The bivalve mollusc larvae identified in the Wadden Sea plankton during this study. Taxonomy according to Høisaeter (1986).

Mytilus edulis	Linné,1758
Modiolus modiolus	Linné,1758
ANOMIIDAE	
Anomia ephippium	Linné,1758
LASAEIDAE	
Montacuta ferruginosa	Montagu,1808
Mysella bidentata	Montagu,1803
CARDIIDAE	
Cerastoderma edule	Linné,1758
MACTRIDAE	
Mactra corallina	Linné,1758
Spisula solida	Linné,1758
Spisula subtruncata	da Costa,1778
SOLENIDAE	
Ensis americanus (=directus)	Conrad, 1866
Ensis siliqua	Linné,1758
Phaxas pellucidus	Pennant,1777
TELLINIDAE	
Macoma balthica	Linné,1758
Tellina tenuis	da Costa,1778
Tellina fabulina fabula	Gmelin,1791
DONACIDAE	
Donax vittatus	da Costa,1778
SCROBICULARIIDAE	
Abra alba	W. Wood,1802
Scrobicularia plana	da Costa,1778
PETRICOLIDAE	
Petricolaria pholadiformis	Lamarck,1818
MYIDAE	
Mya arenaria	Linné,1758
Mya truncata	Linné,1758
CORBULIDAE	
Corbula gibba	Olivi,1792
HIATELLIDAE	
Hiatella arctica	Linné,1758
PHOLADIDAE	
Barnea candida	Linné,1758
Pholas dactylus	Linné,1758
Zirfaea crispata	Linné,1758
TEREDINIDAE	
Teredo navalis	Linné,1758
VENERIDAE	
Dosinia sp.	Scopoli,1777
Chamelea stratula	da Costa,1778

Table 3.3 Mean size (mm) of the first and second cohorts of *Mytilus edulis* larvae in the Norderaue plankton. Cohorts determined by the Bhattacharya method (see text for details); n = number of specimens measured.

DATE	COHORT I	COHORT II	n
910509	0.207	0.238	80
910524	0.247	-	623
910607	0.209	0.294	781
910621	0.211	0.284	563
911004	0.226	0.264	382
911024	0.220	0.235	139
920509	0.209	-	51
920522	0.229	0.262	412
920612	0.220	0.283	70
920723	0.214	0.239	154
920820	0.208	0.239	59

APPENDIX III

Table 4.2 Algae, hydroid and polychaete species on which plantigrades of *Mytilus edulis* were found attached.

- CHLOROPHYTA
  - *Acrosiphonia sp.*
  - *Cladophora sp.*
  - *Enteromorpha compressa*
  - *Enteromorpha torta*
  - *Enteromorpha sp.*
  - *Ulva lactata*
  - *Zostera marina*
- RHODOPHYTA
  - *Ceramium rubrum*
  - *Dumontia incrassata*
  - *Polysiphonia nigrescens*
- PHAEOPHYTA
  - *Fucus vesiculosus*
- HYDROZOA
  - *Electra pilosa*
  - *Laomedea gelatinosa*
  - *Laomedea flexuosa*
  - *Laomedea sp*
  - *Nigellastrum sp.*
  - *Sertularia cupressina*
  - *Sertularia tenera*
- POLYCHAETA
  - *Lanice conchilega*

Table 4.3 Mean size (mm) of distinguishable cohorts in the length-frequency distributions of plantigrades attached to the Type 1 collectors (see Fig. 4.1A) during 1990. Cohorts determined by the Bhattacharya method (see text for details).

DATE	COHORT I	COHORT II	COHORT III
900510	0.432	-	-
900525	0.594	-	-
900607	0.614	0.925	1.226
900620	0.350	0.740	1.116
900714	0.329	0.940	1.393
900731	0.550	0.900	-

Table 4.4 Mean size (mm) of distinguishable cohorts in the length-frequency distributions of plantigrades attached to the Type 2 collectors (see Fig. 4.1B) during 1991. Cohorts determined by the Bhattacharya method (see text for details).

DATE	COHORT I	COHORT II	COHORT III
910530	0.502	-	-
910605	0.447	-	-
910615	0.300	0.623	-
910620	0.463	0.648	-
910623	0.582	0.795	1.000
910703	0.500	0.826	-
910710	0.500	0.818	-
910714	0.720	1.078	-
910725	0.733	1.129	-
910720	0.880	1.220	-
910925	0.182	-	-
911025	0.200	0.376	-
911211	0.227	-	-

Table 4.5 Mean size (mm) of distinguishable cohorts in the length-frequency distributions of plantigrades attached to the Type 2 horizontal collector during 1992 and 1993. Cohorts determined by the Bhattacharya method (see text for details).

DATE	COHORT I	COHORT II	COHORT III
920722	0.497	0.861	-
920808	0.677	0.807	-
921016	0.240	0.863	-
930214	0.596	1.104	-
930415	0.476	0.600	0.929
930610	0.490	0.749	-
930623	0.621	0.839	1.000
930708	0.876	1.524	-

Table 4.6 Mean size (mm) of distinguishable cohorts in the length-frequency distributions of plantigrades attached to the Type 3 collectors (see Fig. 4.1C) during 1993. Cohorts determined by the Bhattacharya method (see text for details).

DATE	COHORT I	COHORT II	COHORT III
930228	0.631	0.963	-
930530	0.474	-	-
930608	0.561	0.808	-
930610	0.515	0.757	-
930621	0.518	0.882	1.343
930627	0.494	0.797	1.464
930708	0.535	0.874	1.190
930720	0.628	1.069	-
930804	0.794	1.132	-

Table 4.7 Mean size (mm) of distinguishable cohorts in the length-frequency distributions of plantigrades attached to hydroids and filamentous algae during 1991. Cohorts determined by the Bhattacharya method (see text for details).

DATE	COHORT I	COHORT II	COHORT III
910526	0.429	-	-
910608	0.543	0.990	-
910622	0.780	1.218	-
910704	0.472	0.870	1.727
910714	0.708	1.050	1.585
910918	0.460	-	-

Table 4.8 Mean size (mm) of distinguishable cohorts in the length-frequency distributions of plantigrades attached to the subtidal hydroids and filamentous algae during 1992. Cohorts determined by the Bhattacharya method (see text for details).

DATE	COHORT I	COHORT II	COHORT III
920523	0.332	1.128	1.494
920620	0.503	0.793	0.987
920708	-	0.856	1.212
920722	0.549	0.851	1.399
920807	0.535	0.926	-
920915	0.555	0.906	1.228
920930	0.694	0.881	-
921016	0.461	0.898	-
921029	0.540	0.812	-
921115	0.607	0.898	1.374
921204	0.656	0.948	1.200
921219	0.762	1.136	1.379

Table 4.9 Mean size (mm) of distinguishable cohorts in the length-frequency distributions of plantigrades attached to hydroids and filamentous algae during 1993. Cohorts determined by the Bhattacharya method (see text for details).

DATE	COHORT I	COHORT II	COHORT III
930207	0.729	1.027	1.650
930213	0.730	0.942	1.466
930513	0.550	0.834	1.102
930608	0.650	1.642	-
930708	0.852	1.160	-

Table 4.10 Mean size (mm) of distinguishable cohorts in the length frequency-distributions of plantigrades attached to subtidal barnacles during 1993. Cohorts determined by the Bhattacharya method (see text for details).

DATE	COHORT I	COHORT II	COHORT III
930207	0.941	1.862	-
930213	0.971	1.445	-
930321	1.089	1.967	-
930416	0.980	1.845	-
930527	0.637	2.158	-
930608	0.724	2.511	4.096
930622	0.941	1.228	-
930708	1.274	2.159	-
930720	0.921	1.310	2.240

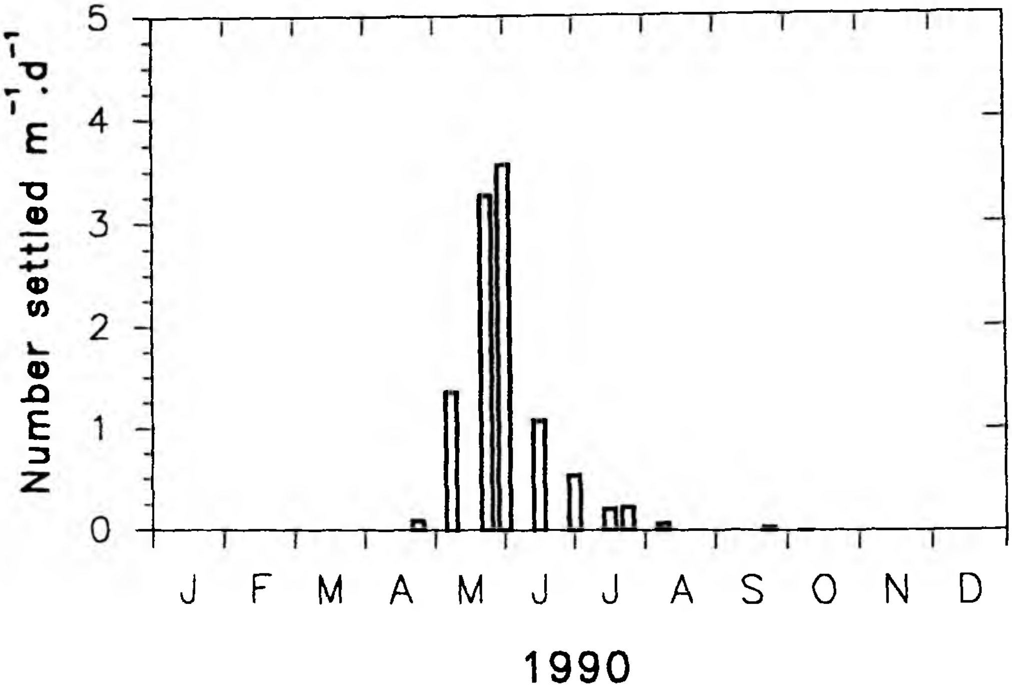

Figure 4.4a Temporal variations in plantigrade attachment to the Type 1 rope collectors (see Fig. 4.1A) during 1990. Sampling commenced mid-April and continued until October.

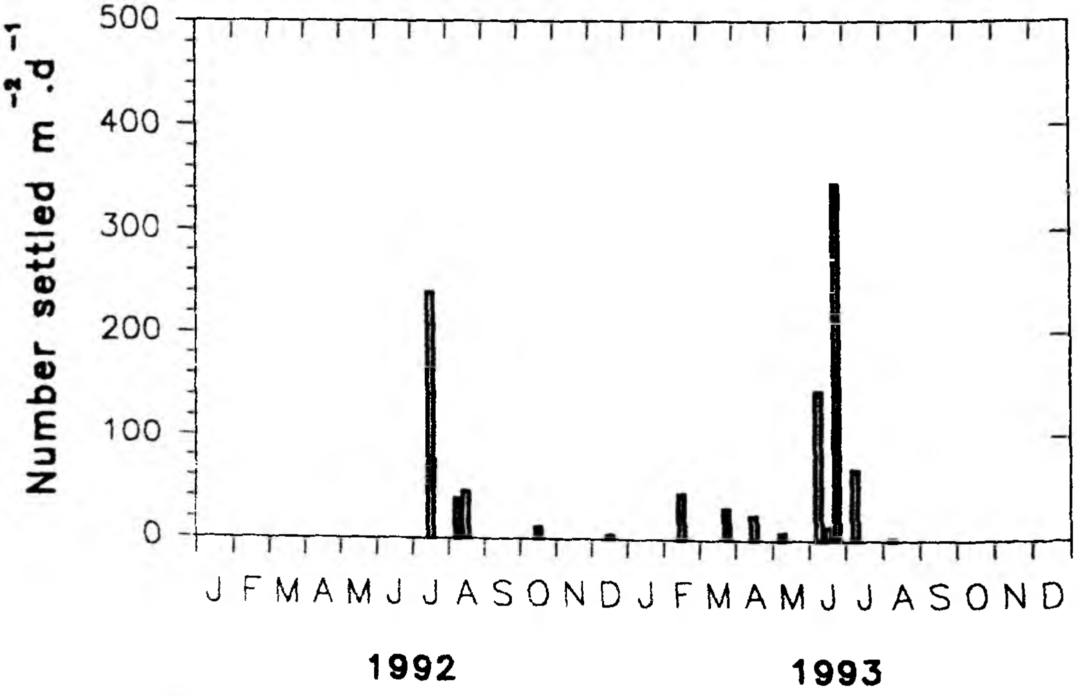

Figure 4.4b Temporal variations of plantigrades attached to the horizontal collector set in a residual water body. Sampling commenced in late June 1992 and continued until August 1993.

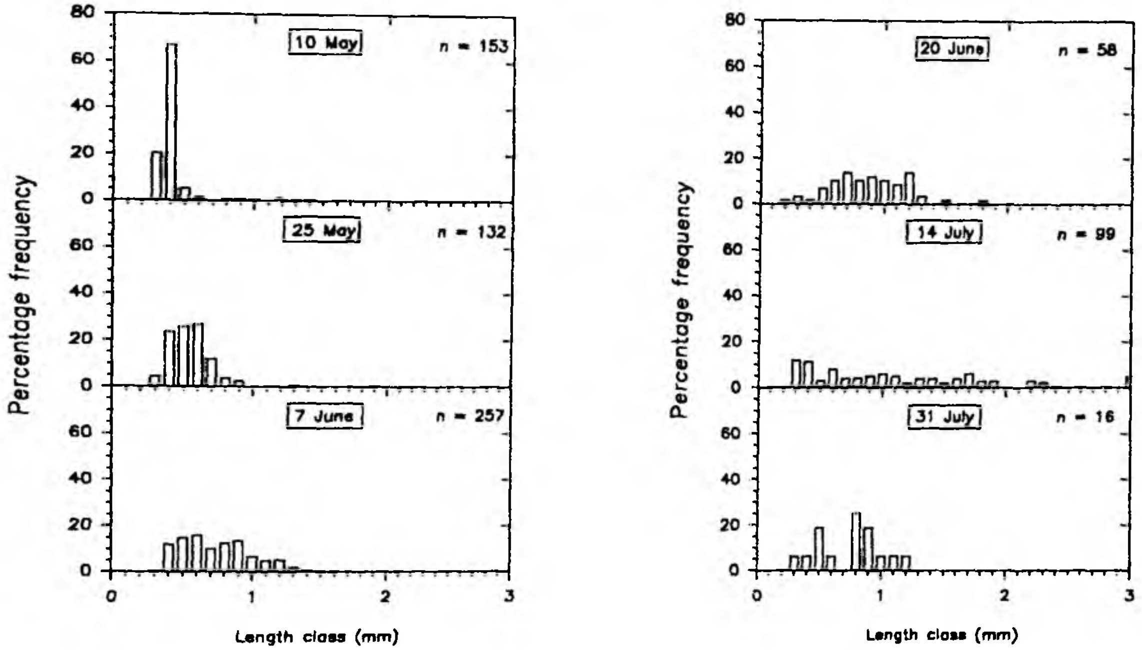

Figure 4.8a Size frequency distribution of plantigrades attached to the Type 1 rope collectors (see Fig. 4.1A) during 1990; (n = number of specimens measured).

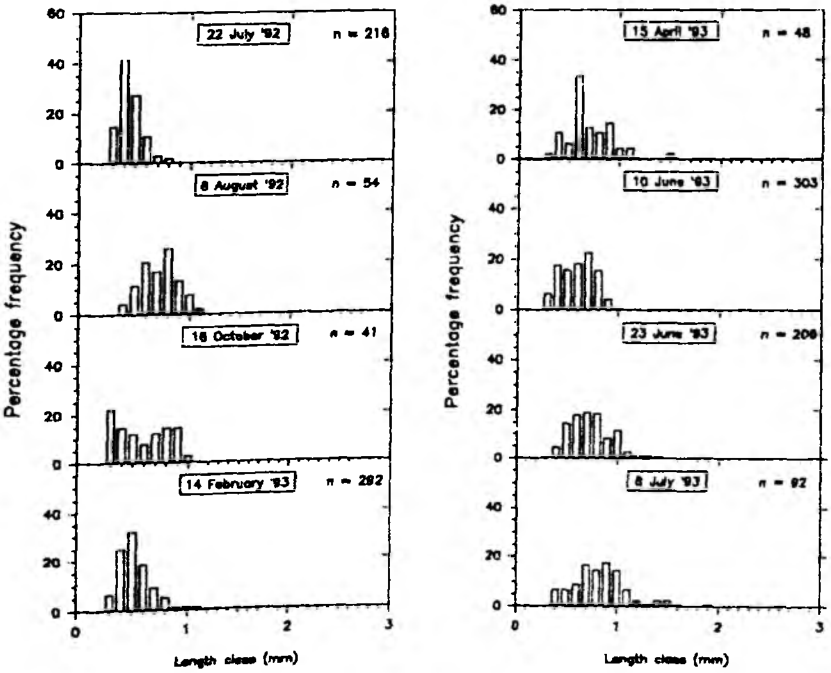

Figure 4.8b Size-frequency distributions of plantigrades attached to the Type 2 horizontal collectors set in a residual water body; (n = number of specimens measured).

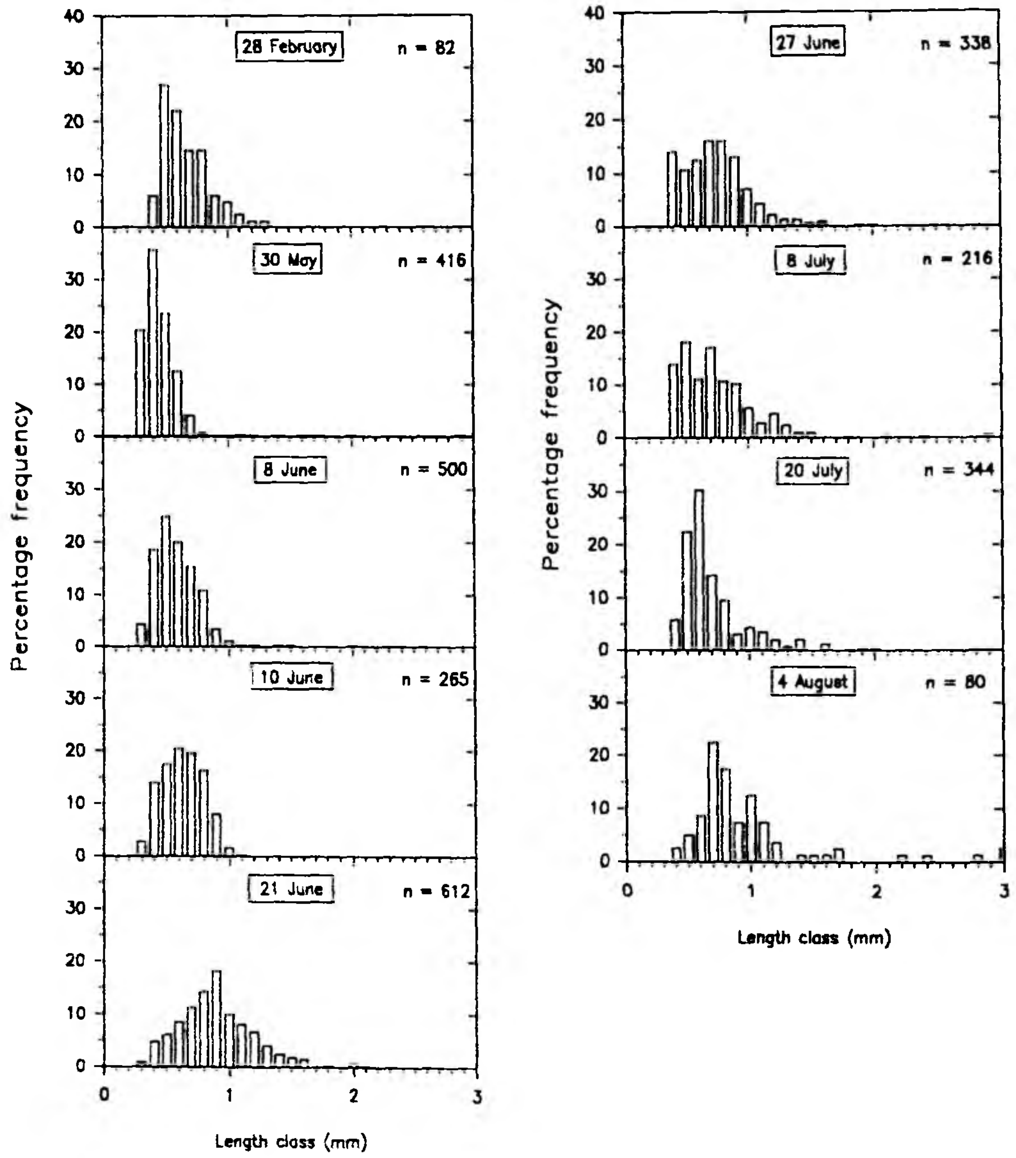

Figure 4.8c Size-frequency distributions of plantigrades attached to the Type 3 vertical profile collector units (see Fig. 4.1C) during 1993; (n = number of specimens measured).

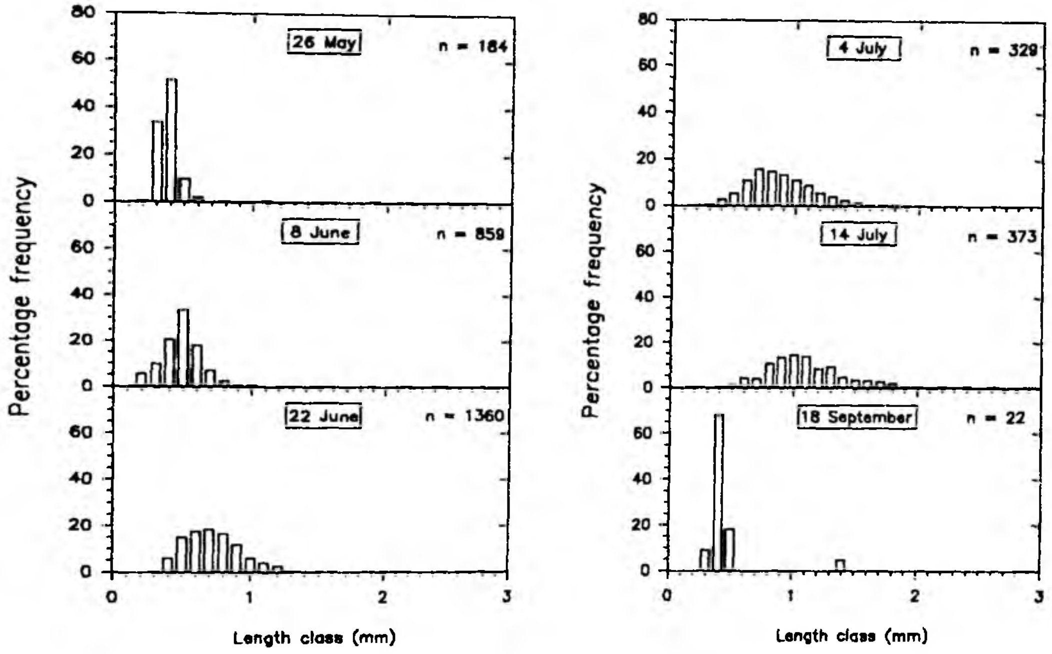

Figure 4.9a Size-frequency distribution of plantigrades attached to intertidal hydroids and filamentous algae during 1991; (n = number of specimens measured).

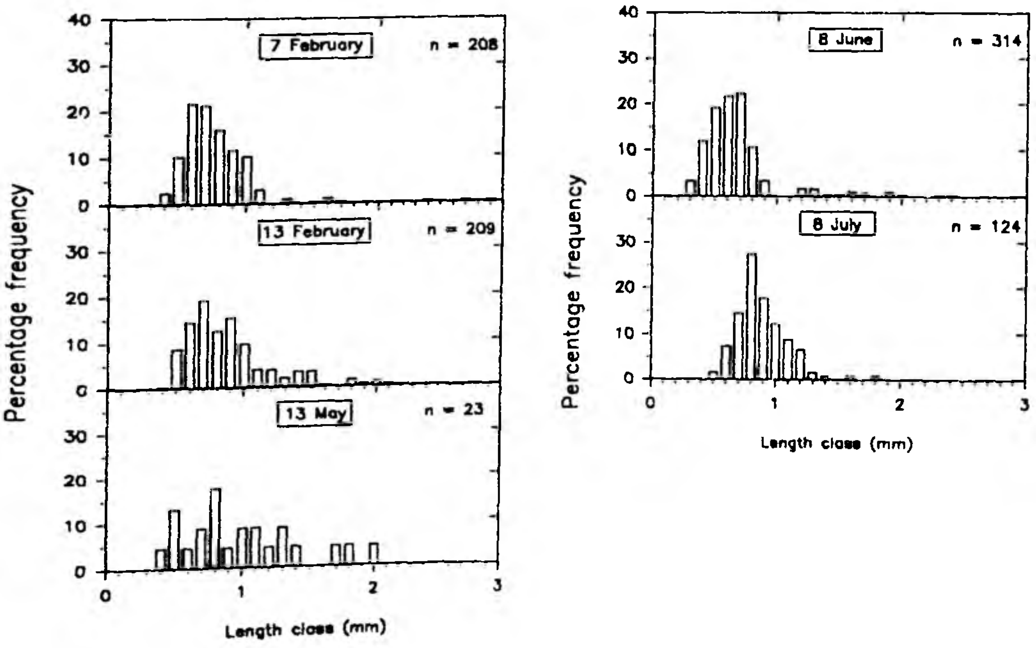

Figure 4.9b Size-frequency distribution of plantigrades attached to subtidal hydroids and filamentous algae during 1993; (n = number of specimens measured).

APPENDIX IV

Model 5.1 General linear model to test the distribution of juveniles in relation to the patch apex.

```
%macro glm(infile,outfile,y_LL,y_UL,x_LL,x_UL,z_div,x_div,classvar,model);

   data time;
      Start = time();

   proc printto print=&outfile new;
   options pageno=1;

  /*** Printout header for statistic output file ***/

  data _null_;
     file print notitle;
     put 79*'_';
     put " ";
     put @10"G E N E R A L   L I N E A R   M O D E L ";
     put 79*'_';
     put " ";
     put @10"Data-input    : &infile";
     put @10"Data-output    : &outfile";
     put " ";
     put @10"Sortcriteria : &classvar (= classes)";
     put " ";
     put @10"Lowerlim. for y   : &y_LL";
     put @10"Upperlim.  for y   : &y_UL";
     put @10"Lowerlim. for x   : &x_LL";
     put @10"Upperlim.  for x   : &x_UL";
     put " ";
     put @10"Divisor for x    : &x_div";
     put @10"Divisor for z    : &z_div";
     put " ";
     put @10"Model            : Proportion = &model";
     put 79*'_';

   data rawdata;
      missing A M U _;
      infile &infile;
      input x y z mussels total small;
      if ((x >= &x_LL) and (x <= &x_UL));
      if ((y >= &y_LL) and (y <= &y_UL));
      x_split = int(x / &x_div);
      z_split = int(z / &z_div);
      if total > 0 then proportion = small / total;
               else proportion = 0;
      keep x x_split y z z_split small total proportion;


   proc sort data=rawdata out=sortdata;
      by &classvar;

   proc print data=sortdata;
      title1 "______________________________________________";
      title2 " ";
      title3 "Data sorted by [&classvar]";
      title4 "______________________________________________";
```

```
  proc glm data=sortdata;
      class &classvar;
      model proportion = &model / solution noint;
      output out=plotout r=r_pro choose p=pro_hat;
      title1 "______________________________________________";
      title2 " ";
      title3 "GLM (Class variable is: [&classvar])";
      title4 "______________________________________________";

  proc plot data=plotout;
      plot r_pro*proportion='1';
      plot ant_hat*proportion='2';

  data time;
      file print notitle;
      set time;
      End      = time();
      Sec_Diff = (End - Start);
      Min_Diff = Sec_Diff/60;
      Hr_Diff = Sec_Diff/3600;
      put 80*'_';
      put " ";
      put @10 "Run begin : " Start time.;
      put @10 "Run termination   : " End time.;
      if (Sec_Diff < 60) then put @10 "Run duration  : " Sec_Diff "Sec.";

        else if (Sec_Diff < 3600) then
                  put @10 "Run duration  : " Min_Diff "Min.";
              else put @10 "Run duration  : " Hr_Diff "Hr.";
      put 80*'_';

  data time;
  run;
%mend;

%glm('a:patch1.dat','a:patch1_!.txt',75,175,100,360,5,1,y z_split,y y*z_split);
%glm('a:patch2.dat','a:patch2_!.txt',50,200,100,250,5,1,y z_split,y y*z_split);
%glm('a:patch3.dat','a:patch3_!.txt',50,250,50,360,5,1,x,x);
```

Model 5.2 General linear model in combination with a MANOVA to test the influence of tidal elevation.

```
%macro glm(infile,outfile);

   data time;
      Start = time();

   proc printto print=&outfile new;
   options pageno=1;

  /***Printout header for statistic output file ***/

  data _null_;
     file print notitle;
     put 79*'_';
     put " ";
     put @10"G E N E R A L   L I N E A R   M O D E L";
     put 79*'_';
     put " ";
     put @10"Data-Input     : &infile";
     put @10"Data-output    : &outfile";
     put 79*'_';

   data rawdata;
      missing A M U _;
      infile &infile;
      input length frequency patch;
      tot_len = length * frequency;

   proc sort data=rawdata out=sortdata;
      by patch;

   proc means data=sortdata fw=8 maxdec=2 sum mean var std cv;
      var tot_len frequency;
      class patch;
      title1 "______________________________________________";
      title2 " ";
      title3 "STATISTICS";
      title4 "______________________________________________";

   proc glm data=sortdata;
      class patch;
      model tot_len frequency = patch / solution noint;
      contrast 'Patch 1 vs. Patch 2' patch 1 -1 0;
      contrast 'Patch 1 vs. Patch 3' patch 1 0 -1;
      contrast 'Patch 2 vs. Patch 3' patch 0 1 -1;
      title1 "______________________________________________";
      title2 " ";
      title3 "MANOVA (Model : Length  frequency = Patch";
      title4 "______________________________________________";

   data time;
      file print notitle;
      set time;
      End      = time();
      Sec_Diff = (End - Start);
```

```
        Min_Diff = Sec_Diff/60;
        Hr_Diff = Sec_Diff/3600;
        put 80*'_';
        put " ";
        put @10 "Run begin : " Start time.;
        put @10 "Run termination   : " End time.;
        if (Sec_Diff < 60) then put @10 "Run duration  : " Sec_Diff "Sec.";

          else if (Sec_Diff < 3600) then
                    put @10 "Run duration  : " Min_Diff "Min.";
                else put @10 "Run duration  : " Hr_Diff "Hr.";
        put 80*'_';

    data time;
    run;
%mend;

%glm('a:lengfreq.new','a:lengfreq.txt');
```

Table 5.2 Statistics resulting from Model 5.2 for the summed lengths of all individuals and the frequency of mussels on three patches of different tidal elevation (see Fig. 1.2 for location of patches); (n = number of observations; C.V. = coefficient of variation).

PATCH	n	Variable	Mean	Variance	Std Dev.	C.V.
1	71	Tot. length	192.83	59 528.17	243.98	126.53
		Frequency	8.87	122.97	11.09	124.97
2	71	Tot. length	197.03	55 396.00	235.36	119.46
		Frequency	9.06	170.97	13.08	144.38
3	71	Tot. length	320.96	159 207.00	399.01	124.32
		Frequency	14.04	413.53	20.34	144.82

Table 5.3 Statistics resulting from contrasts of three mussel patches of different tidal elevation (see Fig. 1.2 for location of patches), for summed lengths of all individuals and frequency of mussels; (Pr = probability).

CONTRAST		Patch 1 vs. 2	Patch 1 vs. 3	Patch 2 vs. 3
Mean tot. length	F value	0.01	6.38	5.97
	Pr > F	0.93	0.01	0.02
Mean frequency	F value	0.01	4.02	3.74
	Pr > F	0.94	0.05	0.05

Table 5.4 Lower and upper limits imposed on the x-axis and y-axis components for Model 5.1.

PATCH	Lower X	Upper X	Lower Y	Upper Y
1	100	360	75	175
2	100	250	50	200
3	50	360	50	250
4	75	225	0	150
5	100	360	100	250
6	150	360	100	200

Table 5.5 Statistics resulting from Model 5.1 having imposed the data limits in Table 5.4 above. Only those values for transects along which samples were taken are given. A probability value <0.05 indicates that on that transect age class-0 mussels occur at significantly higher proportions in the immediate flood lee of the patch apex.

PATCH	PARAMETER	T - VALUE	PROBABILITY
1	y = 100	4.59	0.0001
	150	2.60	0.0123
2	y = 50	2.46	0.0180
	100	3.31	0.0019
	150	2.39	0.0216
	200	3.15	0.0030
3	x = 50	2.92	0.0043
	100	2.24	0.0272
	150	2.94	0.0040
	200	2.77	0.0066
	250	3.49	0.0007
	300	3.91	0.0002
	350	3.87	0.0002
4	y = 0	0.96	0.3434
	50	3.56	0.0009
	100	1.02	0.3118
	150	1.57	0.1244
5	x = 100	1.76	0.0828
	150	0.00	1.0000
	200	1.17	0.2446
	250	3.82	0.0003
	300	0.00	1.0000
	350	0.00	1.0000
6	y = 100	2.45	0.0187
	150	4.23	0.0001
	200	2.65	0.0142

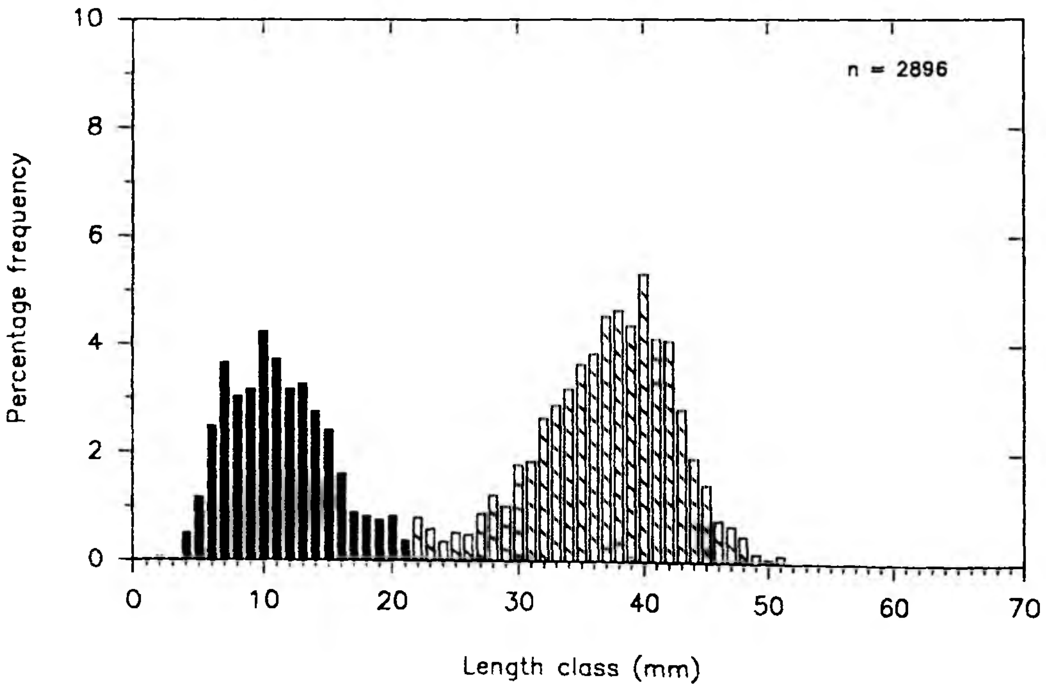

Fig. 5.3a Length-frequency distribution of mussels in the 'transect' patch. Size range of youngest cohort is depicted by solid bars; n = number of specimens measured.