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Larval and post-larval vertical distribution of the mussel *Mytilus edulis* in the White Sea

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ABSTRACT: The vertical distribution of veligers, pediveligers and post-larvae of the mussel *Mytilus edulis* L. was examined in Kandalakshsky Gulf (White Sea), Russia. Plankton samples showed that about 65% of all planktonic larvae were collected from a depth of 1.5 to 3 m. Maximum numbers of veligers were found at 3 m, immediately above the thermocline. The vertical distribution of veligers was stable throughout the study. The vertical distribution of pediveligers, however, varied over time. Pediveligers were mostly observed at 3 m before settlement peaked while they migrated closer to the water surface (1.5 m) during the settlement period. Pediveliger concentrations were correlated positively with small phytoplanktonic cell (<150 µm) and dissolved organic matter concentrations before settlement peaked. Both factors were correlated negatively with pediveliger concentrations during the settlement period. Newly settled post-larvae mainly colonized settlement panels situated at 1.5 m below the water surface (ca 70% of total post-larvae abundance). These results support the hypothesis that planktonic larvae of *M. edulis* change their vertical distribution in relation to larval stages, which in turn, increases settlement success.

KEY WORDS: Habitat selection · Larvae · Mussel · *Mytilus edulis* · Settlement · Vertical distribution · White Sea

INTRODUCTION

Most marine invertebrates produce plankton larvae. Once released, larvae are dispersed by currents over long distances from their spawning site. In the open sea and in estuaries, larvae act as passive organisms that are carried away from suitable settlement habitats. Thus, it is important for larvae to adapt specific behaviour patterns that could help them to stay near or to select suitable habitats. The main factors that affect the vertical distribution of larvae are light, gravity and water flow (Crisp 1974, Stancyk & Feller 1986). The effects of these factors vary during the larva's lifespan. Young larvae of many invertebrates stay near the water surface (Thorson 1950, Ryland 1974, Bayne 1976, Crisp 1984, Manuel et al. 1996). After a period of time, however, the overall behaviour of larvae is modified. Larvae, originally phototopositive and geonegative, typically display photonegative and geopositive responses as they become competent and tend to descend into deeper water where they will ultimately settle (Thorson 1950).

Temperature, salinity and food concentration affect the vertical distribution of many marine invertebrate larvae (e.g. Crisp 1984, Stancyk & Feller 1986, Pearce et al. 1996, Railkin 1998). These factors vary over various spatio-temporal scales (e.g. daytime versus nighttime, tidal cycle, seasons) and drive the vertical migration of larvae. The influence of these factors may also vary in relation to larval stage (Cragg 1980). For instance, pediveligers of the giant scallop *Placopecten magellanicus* have been shown to leave discontinuity layers (e.g. thermocline) after reaching competency in favour of the surface layer in mesocosm experiments (Gallager et al. 1996).

The bivalve *Mytilus edulis* is an important aquaculture species in the boreal-polar White Sea. The larvae of *M.*

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edulis are observed in plankton from late June to late August (Oshurkov & Oksov 1983, Shilin et al. 1987, Kulalovsky & Shamarin 1989) and are usually found near the water surface (Shilin et al. 1987, Maximovich et al. 1996). Settlement peaks are observed in early August (Oshurkov & Oksov 1983, Shilin & Oshurkov 1985, Maximovitch et al. 1996) and occur on the shore where the filamentous green alga *Cladophora rupestris* is common (Oshurkov & Oksov 1983, Dobretsov & Railkin 1996, Dobretsov 1999). Larvae of *M. edulis* respond to light, gravity and pressure gradient (Bayne 1964a,b). These behavioural responses, as for other marine invertebrate species, vary with larval age. For instance, early trochophores are not sensitive to the above factors, while veligers display photonegative reactions, eyed veligers and veliconchs photopositive reactions, and pediveligers photonegative and geonegative reactions (Bayne 1976). Variations in the vertical distribution of the various larval stages and final substratum selection in *M. edulis* could be related to changes in the above taxis.

Though the species has been the subject of many studies, habitat selection mechanisms are still poorly understood. Many physical (e.g. colour, surface wettability, roughness) and biological (e.g. biofilms, conspecifics) factors are known to influence small-scale habitat selection in most sessile marine invertebrate species (reviews: Hadfield 1984, 1998, Burke 1986, Pawlik 1992, Rodriguez et al. 1993, Pechenik 1999). To our knowledge, only a few investigators have considered, or partially examined, the relationship between larval supply, larval settlement, habitat selection and recruitment in mussel species (e.g. Seed & Suchanek 1992, Cáceres-Martínez et al. 1993, 1994, Hunt & Scheibling 1996, 1998). Cáceres-Martínez & Figueras (1998) investigated the distribution and abundance of larvae and post-larvae of *Mytilus galloprovincialis* off the coast of Vigo in Spain. The authors did not, however, study the vertical distribution of this mussel species in the water column. The aims of this study were to: (1) describe the vertical distribution of veliger and pediveliger larvae; (2) assess the influence of various common abiotic and biotic factors on their vertical distribution; (3) compare the vertical distribution of planktonic larvae and settled post-larvae of *M. edulis* in the White Sea; and (4) test the likelihood that veliger larvae dwell primarily in food-rich surface layers and that pediveliger larvae migrate to deeper zones in order to settle onto habitats especially suitable for juveniles (e.g. growth, survival).

METHODS

Study site. The study was conducted from 20 July to 20 August 1996, at a fixed location near Matryonin Island in the Kandalakshsky Gulf of the White Sea, Russia (66° 18′ N, 33° 40′ E). The study site was characterised by a mean tidal amplitude of 1.5 m where water height varied between 10 to 11.5 m during the tidal cycle. During the study, water temperature and salinity ranged from 8.1 to 12°C and 20.2 to 26.5 psu, respectively. Weather conditions were stable throughout the sampling season. Storms or windy days were not observed.

Distribution of planktonic larvae and settled post-larvae. The vertical distribution of *Mytilus edulis* planktonic larvae was assessed using 2 different sampling techniques carried out simultaneously. The first technique used a 50-µm mesh plankton net (0.3 m inner diameter) hauled at 6 different depths (1.5, 3, 4.5, 6, 7.5 and 9 m) from a boat. Fifteen replicate samples were taken at each depth. Depth of plankton hauls was determined by measuring the length and angle of the tow line while sampling. The second sampling technique used a set of 6 specially designed plankton traps moored at the study site. Traps were placed at the selected depths on a mooring line (Fig. 1). Traps, which used a solid wire frame, had the following characteristics: mesh size: 50 µm; length: 0.25 m; opening diameter: 0.08 m; mid-section diameter: 0.13 m. Swivels above and below each trap allowed its front side to

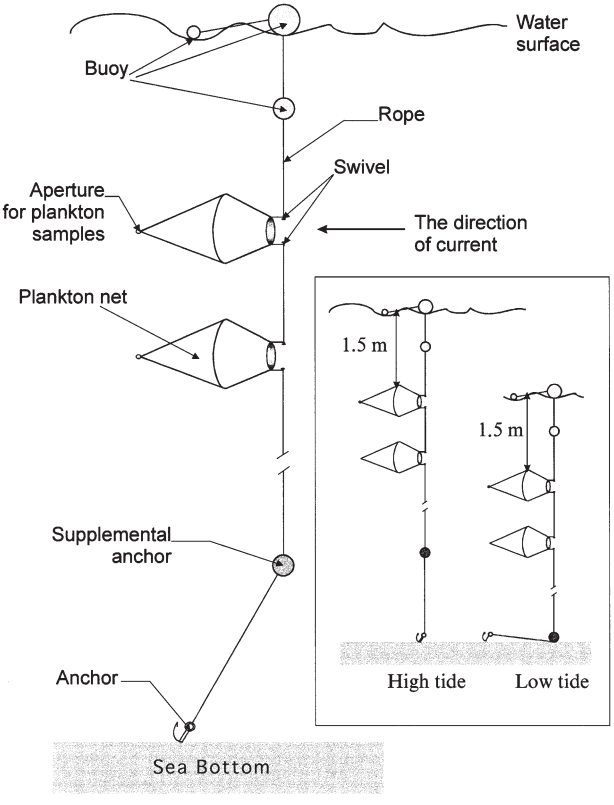

Fig. 1. Plankton trap and mooring line designs used in the planktonic larvae vertical distribution study

face the current at all times. The design of the trap and the use of swivels above and below each trap prevented clogging and the backwash of traps. Buoys and 2 sets of anchors allowed us to sample the same water depths throughout the tidal cycle (Fig. 1). Plankton samples were taken from the trap's small rear-end aperture when lines were hauled on the boat. Two similar mooring lines, 15 m apart, were used for a total of 2 replicates per depth. Current speeds were measured at each selected depth using an ZGO VMM-1 hydraulic whirl every 2 hours during 2 consecutive days (14 to 15 August). Samples from both sampling techniques were fixed in 4% buffered formalin and larvae later identified, measured (shell length) and counted in the laboratory at a magnification of 32× with a Lomo MBS-9 stereomicroscope. All sampling was carried out simultaneously every second day at noon. The effects of light, tide and migration for food on the vertical distribution of larvae were minimised while using the plankton trap technique since larval concentration was integrated over a period of 48 h (Currie et al. 1998). Table 1 provides a summary of details related to all methods used in the present study.

Sets of panels were placed at the study site in parallel to the planktonic larvae study to follow the settlement of post-larvae during the sampling period. Panels used in this experiment consisted of 5 × 7 cm plastic plates made from Petri dishes. A first set of 90 panels was placed on 3 mooring lines. Five panels were fixed at the 6 previously described depths, for a total of 30 panels per line, and left undisturbed for a mo to determine preferential settlement depths. A second set of 60 panels was placed at 1.5 m from the surface on 3 mooring lines to determine when settlement peaked, each line holding 20 panels. Three replicate panels were retrieved from the field every second d. All mooring lines consisted of buoys and anchors that allowed us to sample the same water depths throughout the tidal cycle (design similar to the one described in the planktonic larvae survey). All retrieved plates were taken to the laboratory where settled post-larvae were counted with a stereomicroscope at a magnification of 16×.

Water samples. Water samples (6 l) were collected simultaneously with larval sampling using Bathometer BM-48 sampling bottles at all described depths. Water samples were used for phytoplankton and organic matter analyses and salinity determination. Salinity was measured with a Lomo GM-65M electric salinometer. Temperature was measured on site at all depths using a mercury seawater thermometer. Water samples were divided into 2 aliquots by filtration through a 150 µm net which allowed us to collect 1 aliquot with large phytoplankton cells (>150 µm) and 1 with small phytoplankton cells (<150 µm). Each aliquot were then filtered through a nylon membrane (pore diameter of 0.2 µm) using a vacuum pump. Membranes were air-dried and later put into a test-tube. Four ml of acetone (90%) was added in tubes for chlorophyll extraction. Test-tubes were stored at 3°C for 24 h. Extracts were poured into another test-tube. Four ml of acetone (90%) was added to the original tube to finish the extraction. Tubes were stored for another 12 h. Both extracts were then combined. Chlorophyll concentration was determined at 663 and 750 nm with a Lomo SF-26 photometer using the method described by Rodier (1978). Only the small planktonic cell aliquots were used after the settlement peak (3 August) since concentrations of large planktonic cells were too low after settlement peaked. Phytoplankton concentrations were calculated using Vinberg's equation (1960). Concentrations of DOM were determined using the method described by Lowry et al. (1951). Bovine albumen was used as a control.

Data analysis. The number of planktonic larvae caught by traps was expressed in terms of volume of water that had passed through them (ind m^{-3}) according to the following equations:

$$N = A\,U^{-1};\;\; U = HRVT$$

where N: average larval concentration at a given depth (ind. m^{-3}); A: number of larvae in a given plankton trap; U: volume of water that passed through the trap at a given depth (m^3); H: height of water column that passed through the trap (m); R: radius of the

Table 1. Summary of methods used for the study of planktonic larvae and settled post-larvae

Method	Depth	Number of replicates	Purpose
Horizontal plankton net hauls	From 1.5 to 9 m, every 1.5 m	15	Correlation between vertical distribution of larvae and abiotic/biotic factors
Plankton traps	From 1.5 to 9 m, every 1.5 m	2	Vertical distribution of larvae integrated over 48 h
90 settlement panels	From 1.5 to 9 m, every 1.5 m	3	Preferential settlement depth
60 settlement panels	1.5 m	3	Time of settlement peak

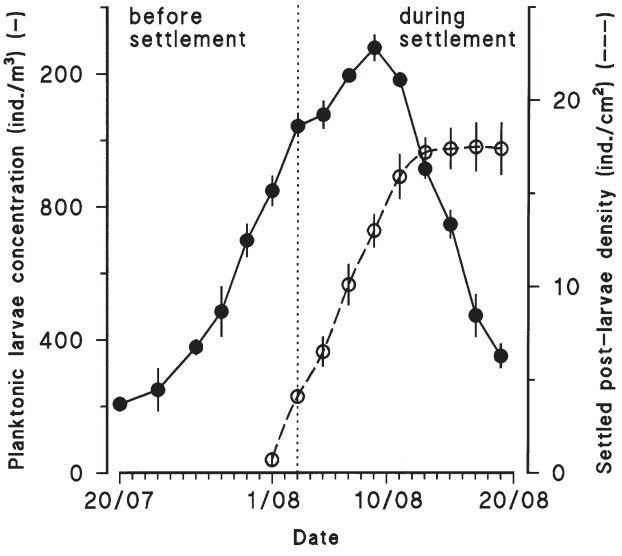

Fig. 2. *Mytilus edulis*. Vertical distribution of pediveliger larvae (250 to 350 µm) before and after the settlement peak (mean relative abundance ± SE; n = 2)

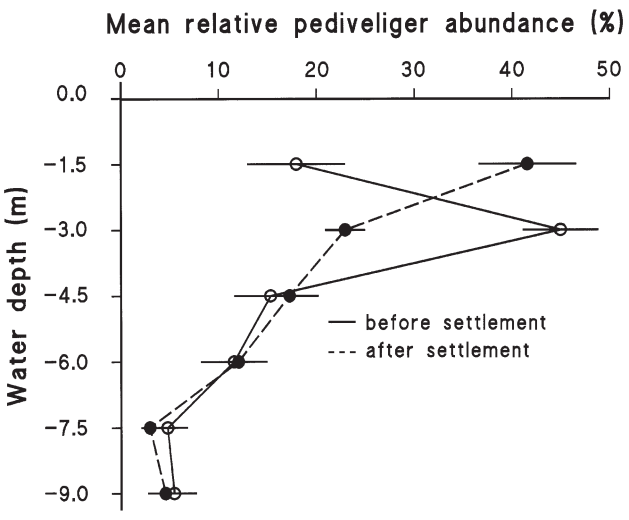

Fig. 3. *Mytilus edulis*. Vertical distribution of veliger larvae (100 to 200 µm) before and after the settlement peak (mean relative abundance ± SE; n = 2)

trap (m); *V*: current speed at a given depth (m sec^{-1}); *T*: time exposed (sec). The actual volume of water that pass through each net was probably over or underestimated because of minute variations of the current speed over time. However, this temporal current speed variation was integrated within a 48 h period for each depth, and larval concentrations standardised with the volume of water that was determined. Larval concentrations (ind m^{-3}) were then comparable. Comparison of larval concentrations at a given depth was carried out using average relative concentrations (number of larvae m^{-3} at a given depth divided by the number of larvae captured at all depths ×100) (see Figs 3 & 4). The influence of abiotic and biotic factors on vertical distribution was carried out using linear correlations. We also used a stepwise multiple regression and a principal component analysis (PCA) to complement the analyses of the vertical distribution of larvae before and during settlement. The PCA was based on both environmental (salinity, temperature and depth) and biological (DOM and phytoplankton cell concentrations, temperature) factors. Factors with eigenvalues > 1 were later used for the stepwise multiple regression. This statistical procedure allowed us to reduce the number of factors which explained the variability of our results. Absolute larval concentration numbers were used in all statistical analyses to avoid data distribution problems in the analysis. Densities of post-larvae (ind cm^{-2}) on panels at each depth were compared using ANOVAs followed by a post hoc least square difference (LSD) test. Data were log-transformed in cases were normality and homoscedasticity conditions were not met. Level of significance in all tests was 5%.

RESULTS

Distribution of planktonic larvae and settled post-larvae

The concentration of planktonic larvae peaked on 9 August (Fig. 2). About 65% of the total number of larvae were found between the surface and the 3 m depth line (Figs 3 & 4). The precise vertical distribution of planktonic larvae, however, varied in relation to larval size and time. For instance, average relative pediveliger concentrations (250 to 350 µm) peaked at 3 m

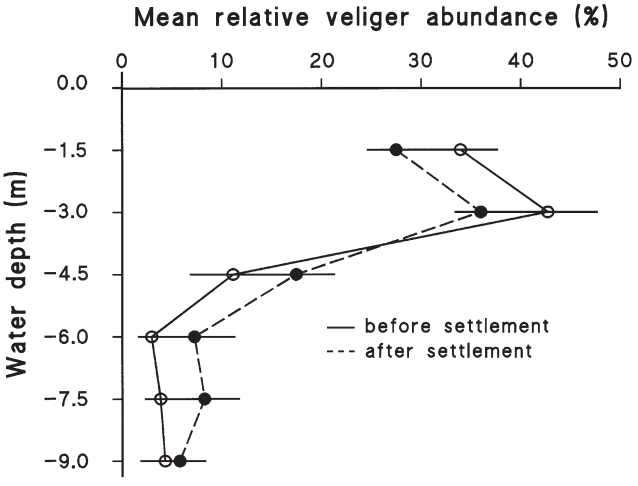

Fig. 4. *Mytilus edulis*. Temporal variation of planktonic larvae (mean number of ind m^{-3} ± SE; n = 15; left *y*-axis) and newly-settled post-larvae (mean number of ind cm^{-2} ± SE; n = 3; right *y*-axis) densities during the sampling period. Planktonic larvae densities are given before and after the settlement peak

Table 2. *Mytilus edulis*. Vertical profile of current speed (mean cm s^{-1} ± SE, n = 15), temperature (t°C ± SE, n = 15), salinity (psu ± SE, n = 15), dissolved organic matter (DOM) (mg m^{-3} ± SE, n = 15), phytoplankton biomass (mg m^{-3} ± SE, n = 15) and settled post-larvae (mean ind cm^{-2} ± SE; n = 3). Current speed was measured every 2 h during a period of 48 consecutive h. Temperature, salinity, DOM and phytoplankton were measured at 2 d intervals and averaged over the entire sampling period. Vertical distribution of larvae were observed during the sampling period on 60 experimental panels moored at the study site. Means having dissimilar letters differ significantly from each other (Tukey's multiple comparisons test)

Depth (m)	Current speed (cm s^{-1})	Temperature (°C)	Salinity (psu)	DOM (mg m^{-3})	Phytoplankton Concentration (mg m^{-3})	Density of post-larvae (ind cm^{-2})
1.5	$9.7 \pm 1.8^{a,b}$	11.6 ± 0.5^{a}	23.23 ± 0.13^{a}	254 ± 21^{a}	$0.71 \pm 0.22^{a,b}$	17.1 ± 2.2^{a}
3.0	$6.1 \pm 2.0^{b,c}$	11.5 ± 0.3^{a}	24.35 ± 0.04^{b}	257 ± 16^{a}	0.99 ± 0.36^{a}	10.4 ± 1.2^{b}
4.5	2.1 ± 0.6^{d}	$10.4 \pm 0.9^{a,b}$	24.91 ± 0.05^{c}	173 ± 32^{b}	$0.66 \pm 0.27^{a,b}$	6.1 ± 1.4^{c}
6.0	5.0 ± 1.2^{c}	$9.8 \pm 0.7^{b,c}$	25.18 ± 0.03^{d}	158 ± 32^{b}	$0.63 \pm 0.35^{a,b}$	3.9 ± 0.4^{d}
7.5	10.0 ± 2.1^{a}	$8.7 \pm 0.7^{b,c}$	25.30 ± 0.05^{e}	174 ± 16^{b}	$0.41 \pm 0.13^{b,c}$	0.7 ± 0.1^{e}
9.0	11.5 ± 2.9^{a}	8.3 ± 0.8^{c}	25.54 ± 0.06^{f}	175 ± 29^{b}	$0.43 \pm 0.14^{b,c}$	0.5 ± 0.2^{e}

before the settlement period (45% of total number of pediveligers) while it peaked at 1.5 m during the settlement period (42%) (Fig. 3). Settlement on panels started on 31 July and increased exponentially up to 12 August (Fig. 2) followed by sporadic settlement. Settlement peaked between 3 and 20 August 1996. Time when the peak of settlement occurred (3 August) was defined as the time when 75% of all settled larvae recruited on panels during the study period. Planktonic larvae concentrations at depths greater than 3 m did not vary over time (ca 35% all depths confounded). The vertical distribution profiles in the case of smaller planktonic larvae (100 to 200 µm) were very similar before and after the settlement peak. Overall, average relative concentrations of planktonic larvae at depths greater than 3 m increased at all selected depths after the settlement peak while concentrations decreased in the first 3 m. Both profiles, however, displayed concentration peaks at 3 m before (43% of total small larvae) and after (36%) post-larvae settlement peaked (Fig. 4). Relative densities of settled post-larvae observed on panels after 30 d decreased significantly with increasing depth ($F = 4.3$, $p = 0.01$) (Table 2). About 70% of post-larvae settled in the first 3 m with a settlement peak at 1.5 m. All densities differed significantly from each other except ones observed between 7.5 and 9 m.

Environmental factors

Environmental factors, averaged over the study period, are presented in Table 2. Overall, temperature decreased with increasing depth while salinity increased. Temperature and salinity profiles indicate that the first 3 m of the water column was more homogeneous than the greater depths and that a narrow halocline occurred between 3 and 4.5 m depths. This stratification (first 3 m versus depth greater than 3 m) appears to be consistent with DOM and phytoplankton concentration readings. Concentrations of DOM were significantly higher in the first 3 m while phytoplankton concentration peaked at 3 m depth. Finally, high current speeds were observed near the surface (9.7 ± 1.8 cm s^{-1}) and at the bottom (11.5 ± 2.9 cm $^{-1}$). The lowest current speeds were recorded at 4.5 m (2.1 ± 0.6 cm s^{-1}).

Relationships between biotic and abiotic factors

Significant correlations were found between concentrations of planktonic larvae and certain abiotic and biotic factors (Tables 3 & 4). The degree of significance of these correlations (probability level and direction of the association) varied in relation to the time the peak of settlement occurred. For instance, concentrations of pediveligers were positively correlated with small phytoplanktonic cell concentrations before settlement peaked (Table 3). The same factors were negatively correlated after the peak of settlement (Table 4). No correlation was observed between concentrations of planktonic larvae and concentrations of large phytoplanktonic cells before settlement peaked (Table 3). Water temperature and DOM concentrations were also positively correlated with concentrations of planktonic larvae (Table 3). DOM concentrations were negatively correlated with pediveliger concentrations after the peak of settlement. No significant correlation was observed between concentrations of planktonic larvae and water temperature after the peak of settlement. DOM concentrations were correlated with the distribution of small phytoplanktonic cells before and after the peak of settlement (Tables 3 & 4).

The relationships between pediveliger concentrations and the biological and environmental characteristics of the water column was examine through 2 PCA factors before (90.4% of variance) and after (95.2% of variance) the settlement peak (Table 5). Factor 1 (small phytoplancton cell and DOM concentrations and tem-

Table 3. *Mytilus edulis*. Summary of results from linear correlations (*r*) between various sets of biotic and biotic parameters before the settlement peak. DOM is dissolved organic matter. Probability levels appears between brackets

Factor	Large phytop. cells	Small phytop. cells	Pediveligers	DOM	Depth	t°	‰
Density of large phytop. cells	*	−0.16 (0.75)	−0.35 (0.50)	−0.46 (0.35)	0.68 (0.14)	−0.87 (0.02)	0.69 (0.13)
Density of small phytop. cells		*	0.86 (0.00)	0.68 (0.03)	−0.38 (0.28)	0.59 (0.07)	−0.04 (0.91)
Density of pediveligers			*	0.64 (0.04)	−0.41 (0.23)	0.63 (0.05)	−0.15 (0.68)
DOM				*	−0.66 (0.03)	0.68 (0.03)	−0.39 (0.27)
Depth					*	−0.83 (0.00)	0.77 (0.01)
t°						*	−0.51 (0.13)
‰							*

Table 4. *Mytilus edulis*. Summary of results from linear correlations (*r*) between various sets of biotic and biotic parameters after the settlement peak. DOM: dissolved organic matter. Probability levels given in parentheses

Factor	Small phytop. cells	Pediveligers	DOM	Depth	t°	‰
Density of small phytop. cells	*	−0.65 (0.04)	0.98 (0.00)	0.28 (0.75)	0.70 (0.01)	0.99 (0.00)
Density of pediveligers		*	−0.67 (0.03)	−0.26 (0.67)	−0.37 (0.35)	−0.67 (0.09)
DOM			*	0.26 (0.11)	0.72 (0.01)	1.00 (0.00)
Depth				*	0.19 (0.68)	0.25 (0.49)
t°					*	0.72 (0.01)
‰						*

perature) may be interpreted as a characteristic of the biotic component of the environment while Factor 2 (depth, salinity and, temperature) may be interpreted as the abiotic component of the environment. The influence of the biotic component varied through time (before versus after settlement peaked: Tables 5 & 6). Pediveliger concentrations varied significantly with Factor 1 before settlement peaked (63.4% of variance), indicating strong positive component loadings for small phytolankton cell and DOM concentrations as well as temperature. The distribution of larvae varied significantly with Factor 1 after the settlement peak (65.9% of variance) with negative component loadings for small phytoplancton cell and DOM concentrations. Factor 2 did not vary too much during the study (<30% of variance). Component loadings were positive for salinity and negative for depth throughout the study period. Component loadings for temperature varied from positive before settlement peaked to negative after the settlement peak.

Table 5. *Mytilus edulis*. Summary of principal component analysis carried out before and after settlement peaked. Only factors with eigenvalues >1 and components with loadings >0.5 or <−0.5 are shown. Components of each Factor are presented in order of descending loading. Components: D = depth; T = temperature; S = salinity; SP = small phytoplankton cell concentration; LP = large phytoplankton cell concentration; DOM = dissolved organic matter concentration. LP was not used in the analysis during the settlement period (see 'Methods')

Time	Eigenvalue	% Variance explained	Components
Before settlement			
Factor 1	3.2	63.4	SP, T, DOM
Factor 2	1.1	27.0	−D, T, S
After settlement			
Factor 1	4.0	65.9	−DOM, −SP
Factor 2	2.3	29.3	S, −D, −T

DISCUSSION

Our results show that planktonic larvae of *Mytilus edulis* were not homogenously distributed in the water column in the White Sea. Larvae were predominantly found between the water surface and the thermocline/halocline depth at approximately 4.5 m. Larval aggregation in marine invertebrate larvae above discontinuity layers has been documented by many authors (see reviews in Stancyk & Feller 1986, Young 1995). Haloclines, for instance, are known to be used by the scallop *Placopecten magellanicus* larvae as a depth marker (Gallager et al. 1996).

Small variations in vertical distribution were observed in this study in relation to the time when settlement peaked as well as to the size of the larvae. Larvae between 100 and 200 µm (veligers) were observed in greater number at 3 m throughout the study. This temporal distribution stability could be related to a positive phototaxis behaviour, characteristic of small-

Table 6. *Mytilus edulis*. Summary of stepwise multiple regression analysis between the vertical distribution of larvae and factor scores obtained by the principal component analysis. Only significant variables are shown. F1 and F2 = principal component analysis from Table 5

Time	Model	R^2	p
Before settlement	−2.61 + 1.7(F1)	0.74	0.001
After settlement	0.32 + 0.5(F1)	0.68	0.040

sized larvae (veliconch and veliger larvae) (Bayne 1976, Mileikovski 1974), as well as to an aggregation resulting from a high food concentration near the surface (phytoplankton and DOM concentrations) (Maslov 2000). Larvae of scallop species are also known to migrate to food-rich depths (Raby et al. 1994, Gallager et al. 1996). This, however, is believed to be a partial explanation when looking at forces driving the vertical migration behaviour of scallop larvae (Manuel et al. 1996). The vertical distribution of mussel pediveligers (250 to 350 µm) in this study, was slightly different before and after settlement peaked. Pediveligers migrated closer to the water surface leaving the discontinuity layer depth during settlement. Competent mussel larvae are known to show negative phototaxis and geotaxis responses (Bayne 1964b, Mileikovski 1974). These 2 behaviours may determine the direction of the migration. Apparently, the influence of negative phototaxis in this study was overridden by the other taxis during settlement, which in turn lead larvae closer to the water surface.

Our results demonstrated that behavioural variations might drive changes in the vertical distribution of larvae. Similar results have been shown for veligers of *Mercenaria mercenaria* (Carriker 1961). Thorson (1950) and Bayne (1976), however, showed that competent larvae of North Sea *Mytilus edulis* usually migrate to deeper levels. The presence of the filamentous green alga *Cladophora rupestris* in this study, probably accounts for the high settlement numbers observed near the water surface. Oshurkov & Oksov (1983), Dobretsov (1999) and Dobretsov & Wahl (in press) showed that this alga is often fouled by *M. edulis* in the White Sea and that it is usually found between depths of 0.5 and 1.5 m. Hunt & Scheibling (1996, 1998) also documented a relationship between *M. edulis* and various macrobenthic assemblages including a filamentous alga of the *Cladophora* gender on the east coast of Canada. *M. edulis* from the North Sea are known to settle near or on filamentous red algae such as *Ceramium rubrum* and *Cystoclonium purpureum*, which are found at greater depth (de Blok & Geelen 1958, Eyster & Pechenik 1987). Manuel et al. (1996) documented different veliger vertical migration behaviour for different populations of *Placopecten magellanicus*, suggesting that recruitment strategies may vary within the same species in order to increase recruitment success in relation to the specific habitat where the larvae are found. Variations in habitat selection process by *M. edulis* between the North Sea and White Sea populations appears to confirm the suggestion of Manuel et al. (1996).

The vertical distribution of mussel larvae is determined by various abiotic and biotic factors. In this study, correlation, PCA and multiple regression analyses demonstrated that small phytoplanktonic cell (<150 µm) and DOM concentrations were the main factors explaining the distribution of larvae before settlement peaked. Veligers (non-competent larvae) preferentially occupied depths where small-size phytoplanktonic cells and DOM occurred in high concentrations. Phytoplanktonic cells are known to be the main food source of mussel larvae (Chipperfield 1953, Bayne 1965, Eyster & Pechenik 1987). This study also showed, through multiple regression and PCA analyses, that concentrations of pediveligers (competent larvae) were negatively correlated with small phytoplanktonic cell and DOM concentrations after the settlement peak. The degradation of the velum and development of the foot of the pediveliger (Bayne 1965) may modify the larva's feeding behaviour. Competent pediveligers do not feed. They may then migrate to depths where food is more limited.

The settlement experiment showed that post-larvae of *Mytilus edulis* settled at 1.5 m. Very few individuals were found at depths ≥7.5 m (only 13% of settlement occurred at depths greater than 4.5 m). The distribution of pediveligers and settled post-larvae were very similar. The concentration of pediveligers and density of post-larvae decreased with increasing depth. These results are consistent with those reported by Oshurkov & Okshov (1983) who investigated mussel settlement in the White Sea. Our investigation showed that small larvae (100 to 200 µm) preferentially occupied the 3 m depth level before and after settlement peaked. During the same period, pediveligers migrated from 3 to 1.5 m depth where settlement of post-larvae peaked. Such behaviour may allow competent individuals to aggregate in the water column at a given level, increasing the probability of successfully settling on a suitable substratum at a corresponding level. Post-settlement migration behaviour likewise contributes to the overall vertical distribution of post-larvae (Chipperfield 1953). This, however, is probably limited to small-scale redistribution. Differential predation upon new recruits may also explain some of the variability in the overall vertical distribution of mussel juveniles. This has been suggested by Pechenik (1999) and later documented by Newell et al. (2000) on newly metamorphosed oysters in Cheasapeake Bay. Differential predation on new recruits was probably not very important in the

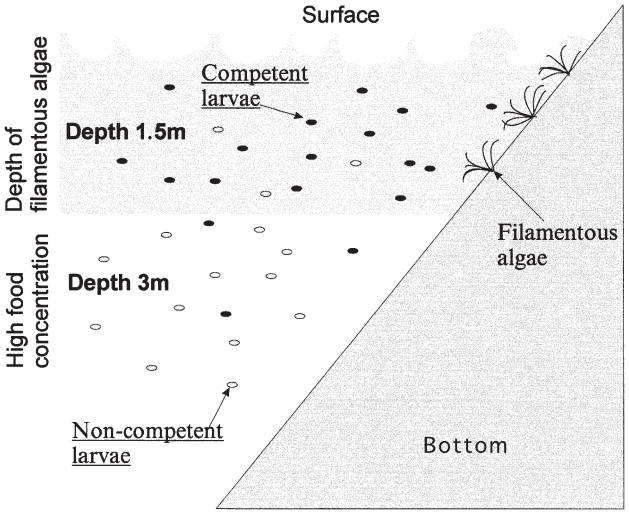

Fig. 5. Vertical distribution of planktonic competent and non-competent mussel larvae showing the selection of suitable water depth and the substrate for settlement

present study since predators in the boreal-polar White Sea are rare (Dobretsov pers. obs.) and that exposure to predators was low (duration of the settlement experiment).

The relationship between planktonic larvae, newly-settled larvae and juvenile/adults distributions has been documented for many marine sessile species (barnacles: de Wolf 1973, Grosberg 1982, Connell 1985, Minchinton & Scheibling 1991; colonial ascidians: Hurlbut 1991) including *Mytilus edulis* (Hunt & Scheibling 1996, 1998). The strength of the relationship between larval abundance at a particular level in the water column and the abundance of new recruits on the shore in *M. edulis*, however, still needs to be investigated. Results from this study show that habitat selection by larvae of *M. edulis* is a multistage process. As suggested by Bourget (1988) and Miron et al. (1995, 1999, 2000) in models using barnacle species, competent *M. edulis* larvae may select a height in the water column where they can settle onto the shore at a similar level (see Fig. 5). The selection of this particular depth may be initiated by a change in the behaviour of the larvae in relation to light and gravity. Larvae of *M. edulis* then select a habitat where the filamentous alga *Cladophora rupestris* occur (Dobretsov & Wahl in press). Once surface contact has been made, the larvae may then actively respond to exogenous factors such as biological, chemical and physical cues, singularly or in combination, to find a proper final attachment site. Metabolites of macroalgae and biofilms which repel or attract larvae could drive this process (Dobretsov 1999). For instance, Dobretsov & Railkin (1996) showed that hydrophobic rough substrata covered with a microbial film were fouled more intensively by larvae of *M. edulis* compared to other substrata tested.

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