

Neustonic niche for cirripede larvae as a possible adaptation to long-range dispersal*

J. Le Fèvre¹, E. Bourget²

¹Laboratoire d'Océanographie Biologique, Université de Bretagne Occidentale, F-29287 Brest Cedex, France

²GIROQ, Département de Biologie, Université Laval, Québec, Canada G1K 7P4

ABSTRACT: Fine-scale distribution of cirripede larvae was studied in the second half of July 1979 off the west coast of Brittany, France. The first ten 10 cm layers of water near the surface were sampled, as well as the whole water column. A significant proportion of the cyprid larvae of *Verruca stroemia* was observed to occupy a neustonic niche, while the vertical distribution of the nauplii was more uniform. This is taken as evidence that, prior to settlement, the late larval stages of this species actively select a near-surface habitat that ensures their dispersal over large areas. The nauplii and cypris were observed at stations near 100 km offshore, much farther than previously reported. The implication of these findings is that the long-distance dispersal of coastal species by meroplanktonic larvae may have been largely underestimated by neglecting to adequately sample the neustonic fauna.

INTRODUCTION

Recent studies on the recruitment of intertidal invertebrate populations emphasize the role of settlement intensity and larval abundance (Connell 1985). On open coasts, Gaines et al. (1985) showed that settlement of the barnacle *Balanus glandula* Darwin was more important in areas where cyprid larvae were more abundant in the nearby plankton, while, in a small harbour, Grosberg (1982) related the zonation of *B. glandula* to the vertical distribution of cyprid larvae. More recently, Shanks (1986) observed unidentified barnacle cyprid larvae in surface slicks at a station located about 1 km from the shore. To account for their upper shore settlement, he hypothesized, from various circumstantial evidence, that the larvae could be transported inshore by some circulation pattern associated with internal waves.

The evidence concerning the vertical distribution of barnacle larvae in estuarine environments is more detailed. The classic study of Bousfield (1955), in a shallow estuary (4 m average depth), reports changes in the vertical distribution of the larvae associated with their ontogeny. While early naupliar stages of *Balanus improvisus* Darwin and *B. crenatus* Bruguière were

more abundant in the upper half of the water column, above the level of no net motion, the later stages, particularly the cypris, were mostly located near the bottom. In *Semibalanus balanoides* (L.), there are only very indirect indications, from the relative distribution of recruitment of a few barnacle species on mooring chains in open waters (see below), that the larvae would remain closer to the surface than in the former species. De Wolf (1973), however, did not find a clear-cut pattern in the vertical distribution of barnacle larvae in an inshore environment.

The relative abundance of the adults of typically intertidal species (e.g. *Semibalanus balanoides*) at different depths on offshore moorings (Bousfield 1954) suggests that the offshore and inshore vertical distributions of settling larvae could be different. Indeed, Bousfield (1954) showed that species characteristic of the intertidal levels could be very abundant on moorings, even at relatively large depths.

All available evidence suggests that barnacle larvae of littoral species do not disperse very far offshore. Southward (1962) observed that larvae of *Verruca stroemia* (Müller) were largely restricted to within 17 km of the coast. In the North Sea, oil rigs at a distance greater than 20 km are reportedly not colonized by the shore barnacle *Semibalanus balanoides* (Flowerdew 1983, Southgate & Myers 1985). A similar observation was made by Ardisson et al. (1990) on collectors moored at different distances from the coast in the Gulf of St. Lawrence.

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This paper presents fine-scale vertical distributions of barnacle larvae in the upper water column at different distances from the coast. We show that: (1) cyprid and naupliar larvae of a species such as *Verruca stroemia* disperse to distances greater than 70 km from the coast; (2) cypris of *V. stroemia* can adopt a neustonic distribution, which may account for this long-distance dissemination. The implication of these findings is that the long-distance dispersal of littoral species by meroplanktonic larvae may have been largely underestimated by neglecting to adequately sample the neustonic fauna.

MATERIAL AND METHODS

Neuston collection took place during daytime on cruise SATIR 1, which was carried out from 16 to 26 July 1979 as part of a larger programme devoted to the study of the relationships between plankton and frontal structures off the west coast of Brittany (see Le Fèvre 1986). The sampling gear used was a modified version of that used by Champalbert (1969) in a study of the neuston of the Gulf of Marseilles, France. Ten rectangular, 1 m wide, nets (mesh width of 200 μm vs 250 μm for the original system) were superimposed in a common frame; the upper net was 20 cm high and the others 10 cm high. The weight and buoyancy of the apparatus were adjusted, through preliminary trials, in such a way that the middle of the top net could be maintained at sea-surface level during operation by controlling the towing speed, thus enabling the simultaneous sampling of ten 10 cm thick layers between the surface and a depth of 1 m. Deployment of the sampler from the side of the ship, on a circular pathway around station nominal positions, ensured that the hydrodynamic disturbance in the vicinity of the surface was kept at a minimum.

Subsampling was performed using a 5 ml Stempel pipette after the volume of the samples had been adjusted to 250 ml. Most organisms were enumerated by examining 5 successive elementary fractions (1/10 of the sample); some very abundant forms were, however, enumerated in smaller volumes (down to a single fraction) and some rare ones in the whole sample. Numbers of animals were standardized to a unit volume of 10 m^3 (to avoid small numbers with several decimal places). Because flow-meters are impractical with the sampler, the volume filtered by each net was estimated roughly by multiplying the mouth area (0.1 m^2) by distance towed (assuming a 4 knot speed), usually over a 5 min duration. The large number of neuston samples collected proved impractical to analyse exhaustively. In order to set up a working compromise, a preliminary examination was undertaken of

the vertical distribution of the conspicuous, typically neustonic, calanoid copepod *Anomalocera patersoni* Templeton. Given the levels between which clear-cut changes took place in the abundance of this test species, it was determined that the distribution of neustonic animals could, in practice, be satisfactorily described by systematically counting the samples from levels 1 (0–10 cm), 2 (10–20 cm), 4 (30–40 cm) and 8 (70–80 cm) only. Cirripede larvae were at first counted globally as nauplii and cypris, without any taxonomical identification. Once the apparently neustonic distribution of some of these was discovered, however, taxonomic accuracy was felt necessary, and 30 to 40 nauplii and as many cypris were randomly taken out of each sample. These were subsequently identified to precise development stage and species by Dr M. T. Burrows at the Port Erin Marine Laboratory (Port Erin, Isle of Man, UK).

At all stations, with one exception (see below), vertical hauls were also carried out from near-bottom to the surface with a WP2 net which has a 200 μm mesh width and a mouth area of 0.25 m^2 . This net was originally designed in such a way that its filtration coefficient F should be close to unity (cf. Unesco 1968). This sampling gear collects plankton very efficiently, as field trials (e.g. Bhaud et al. 1974, Evans 1977, Razouls & Thiriot 1972–73) have shown F to be consistently in the range 0.95 to 0.98 in normal working conditions. Assuming a value of 1 therefore leads to negligible errors with respect to other biases involved in the estimation of plankton abundance. The volume filtered

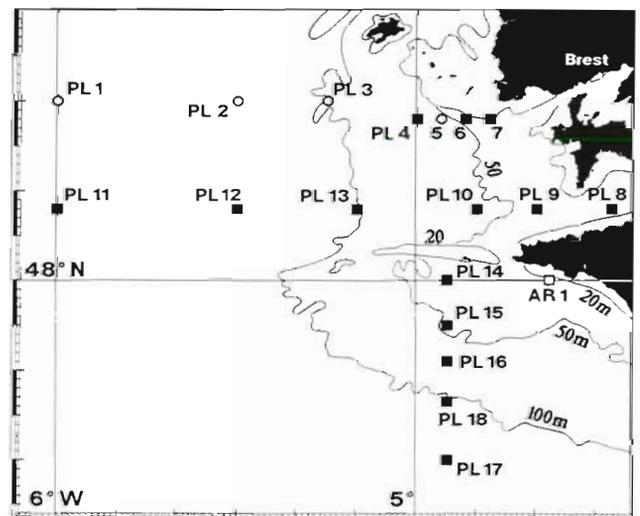


Fig. 1. Sampling network and station numbers to the west of Brittany, France; the cruise took place from 16 to 26 July 1979. Plankton and neuston sampling carried out at a given station is indicated as follows: (○) neuston data only; (○) total water column data only (vertical haul); (■) both neuston and total water column data. The 50 m isobath is not drawn where nearly coincident with the 20 m isobath

by the WP2 net was accordingly estimated in the present study by multiplying the mouth area by the height of the haul. Subsampling was carried out with a Stempel pipette as above. However, for each taxon, the number of 5 ml fractions used for counting the organisms was adjusted to reach a count of at least 30 individuals, except for the rarer species, which were enumerated in the whole sample. For cirripede larvae, only overall nauplii and cypris counts were performed on the samples from the vertical hauls. Numbers of animals were standardized both to a unit volume of 10 m^3 and to a unit area of 1 m^2 .

Fig. 1 shows the sampling station network and indicates those stations where neuston sampling and/or vertical plankton collection were carried out. No vertical net haul took place at AR 1 because the work at this station was preliminary (16 July 1979) and mainly devoted to the technical adjustment of some procedures, including the deployment of the neuston sampler. A typical station consisted of a hydrographic cast to collect data on temperature, salinity, nutrients and chlorophyll concentration at several levels in the water column, a vertical plankton haul and a neuston sampler tow. No neuston samples, however, were taken from Stns PL 1 to PL 3, occupied on 19 July, because the weather on that day, while fine enough for the other operations to be carried out, was not calm enough to allow the adequate deployment of the sampler. Working conditions became quite satisfactory in this respect for the rest of the cruise, and apparently undisturbed fine-scale neustonic vertical distribution patterns were found for several organisms, such as the copepods *Anomalocera patersoni* Templeton and *Labidocera wollastoni* (Lubbock) as well as some cirripede larvae. Neuston samples are also missing from Stn PL 5, however, because the steaming time from the previously occupied station was too short for the sampler to be ready again for use after processing the samples.

The stations were visited only once during the cruise, and the data obtained are considered to represent a snapshot view of the area. The region is characterized in summer by a very strong hydrographic structure (see below), which is well known not to exhibit significant changes over durations of several days or even a few weeks (see Le Fèvre 1986). The stability of the surface temperature field over the study area during cruise SATIR 1 was confirmed by infrared images from NOAA satellites provided by the Centre de Météorologie Spatiale, Lannion, France, in exchange for sea-truth data (see Grall et al. 1980). The overall hydrographic structure can then be regarded as also having remained stable; for all practical purposes, plankton abundance and distribution patterns can accordingly be assumed to have been reasonably constant over the cruise duration.

RESULTS

Hydrographic setting

Fig. 2 shows the overall hydrographic structure, in the form of 3 temperature transects. Areas deeper than 90 to 100 m on Transects A and B and deeper than about 50 m on Transect C appear to be strongly stratified, with a bottom-to-surface temperature difference of more than 6°C at the 2 westernmost stations. Some stratification also prevailed near the coast, especially in the vicinity of Stn PL 8, located in a shallow embayment (Baie de Douarnenez), while the water column was more homogeneous in between. The off-shore seasonal thermocline was rather sharp, outcropping at the surface in the form of a well-marked thermal front. This front, which is a regular feature of the area in summer, is known as the Ushant Front (Pingree

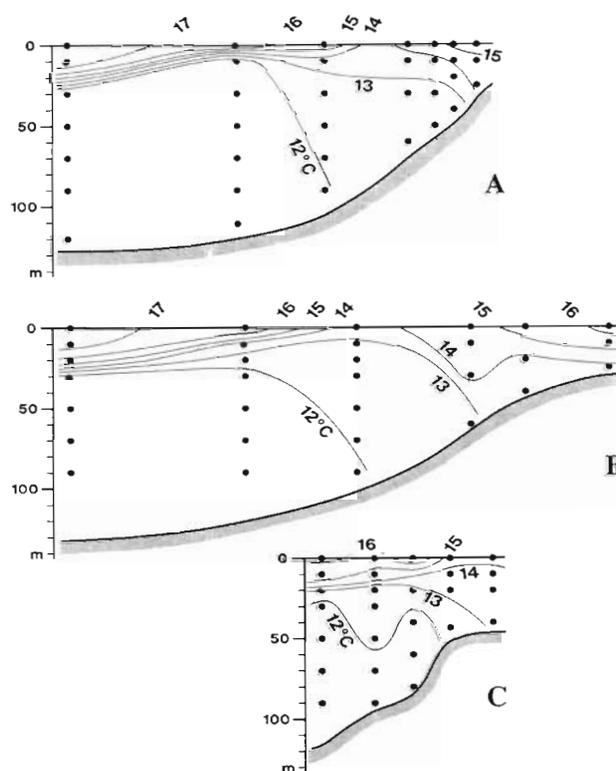


Fig. 2. Hydrographic structure on cruise SATIR 1. temperature transects at (A) about $48^\circ 20' \text{ N}$ (Stns PL 1 to PL 7 from W to E); (B) $48^\circ 08' \text{ N}$ (PL 11 to PL 8 from W to E); and (C) $4^\circ 55' \text{ W}$ (PL 17 to PL 14 from S to N). Each vertical series of dots corresponds to a station and individual dots correspond to measurements obtained with reversing thermometers. These measurements were complemented with less precise ($\pm 0.1^\circ\text{C}$) continuous surface records along the ship track, mechanical bathythermograph records at a number of positions between the stations, and satellite imagery of the surface temperature field. This information yielded details such as the outcropping of the isotherm 14°C at the surface between 2 stations on Transect A

et al. 1975) and usually runs across the whole western entrance to the English Channel. During cruise SATIR 1, this front followed a roughly north-south course at about $5^{\circ} 15'$ or $5^{\circ} 20'$ W across Transects A and B, then turned east to cross Transect C near Stn PL 15 and finally reached the coast in the vicinity of Stn AR 1. Gradients in both temperature and salinity contribute to the weaker frontal structure between the coastal shallows and the relatively well-mixed area; this structure is known as the Iroise Inner Front, described by Le Fèvre & Grall (1970). The whole hydrographic structure is dependent on spatial variations in the relationship between the height of the water column and the intensity of tidal currents. Once established, together with the seasonal stratification, such tidal frontal systems have been shown (Simpson & Bowers 1981) to develop a feedback mechanism through which the structure resists the fortnightly adjustment to the spring-neap cycle. A hydrographic situation such as the one at SATIR 1 is accordingly both stable and predictable, and the pattern found agrees well with the mathematical model of frontal positions on the northwest European shelf developed by Pingree & Griffiths (1978). Complex circulation patterns are associated with shelf-sea tidal fronts; as summed up by Simpson (1981), they include convergence and downwelling at the front, divergence where vertical mixing prevails, and cross-frontal exchange through large (about 20 km) cyclonic eddies. The residual circulation over an extent the size of the study area is still poorly known, due to the scarcity of direct Lagrangian measurements. Such measurements were, however, carried out in September 1982 in the area (unpubl. report by Mariette et al. 1983, quoted by Le Fèvre 1986 p. 187–189). They showed large differences in residual current speed and direction between stratified and vertically mixed zones; large differences were also found in the stratified zone between the surface and deep waters, and in the well-mixed zone, between trajectories of drifting buoys released at nearby locations. This, unfortunately, precludes any precise attempt at hypothesizing drift patterns of plankton organisms in relation to their dispersal.

Distribution of cirripede larvae: large-scale spatial pattern

The overall abundance of cirripede larvae (nauplii and cypris) in the whole water column is presented in Fig. 3. Three major points are apparent: (1) nauplii were roughly 5 to 10 times more abundant than cypris at nearly all stations; (2) from the coast to a distance of about 75 km offshore, larval densities decreased by a maximum factor of 900 for nauplii (from 8733 to 9.7

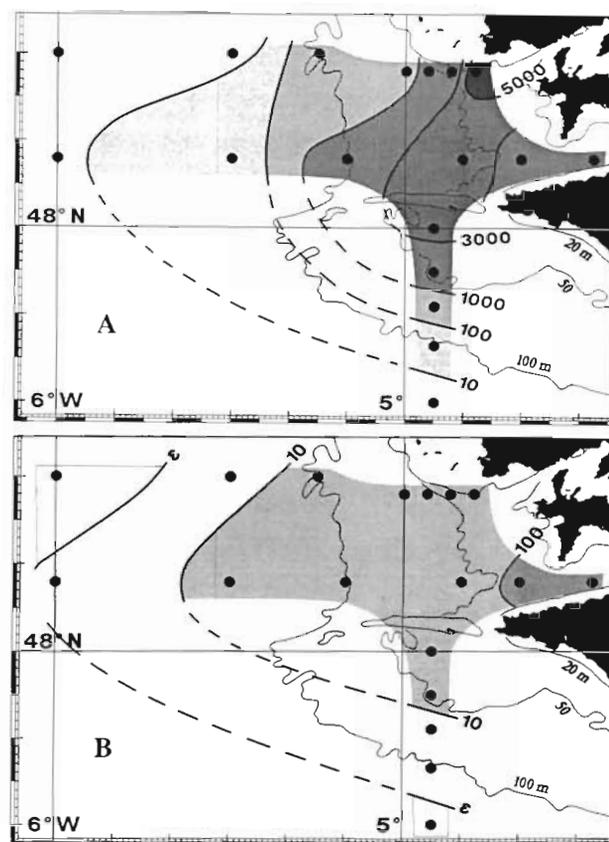


Fig. 3. Abundance of cirripede larvae in the whole water column (average density in numbers of individuals per 10 m^3). (A) Nauplii; (B) cypris. ϵ : limit between presence and absence

ind. 10 m^{-3} between Stns PL 7 and PL 11), and by a maximum factor of 300 for cypris (from 292 to 0.9 ind. 10 m^{-3} between Stns PL 9 and PL 11); (2) there was a definitely higher proportion of cypris larvae in the Bay of Douarnenez (Stns PL 8 and PL 9) than elsewhere. An effect of dilution with depth is unavoidably involved in the offshore decrease in larval density. This effect is eliminated by considering the values per unit area, which still show a decrease by a factor 230 for nauplii between Stns PL 7 and PL 11, and a decrease by a factor 100 for cypris between PL 9 and PL 11. The distribution patterns observed were roughly the same when only the top 1 m of the water column was considered, using the data from the neuston sampler (Fig. 4).

Fig 5 gives the percentage of cypris in the total population of cirripede larvae. In the whole water column (Fig. 5A), values above 10 % were observed in the Bay of Douarnenez, and in a ring of offshore stations; elsewhere, total numbers were low and proportions less reliable. Within the top metre (Fig. 5B), the proportion of cypris was generally greater and often reached values close to half the larval population, highest figures being found at offshore stations.

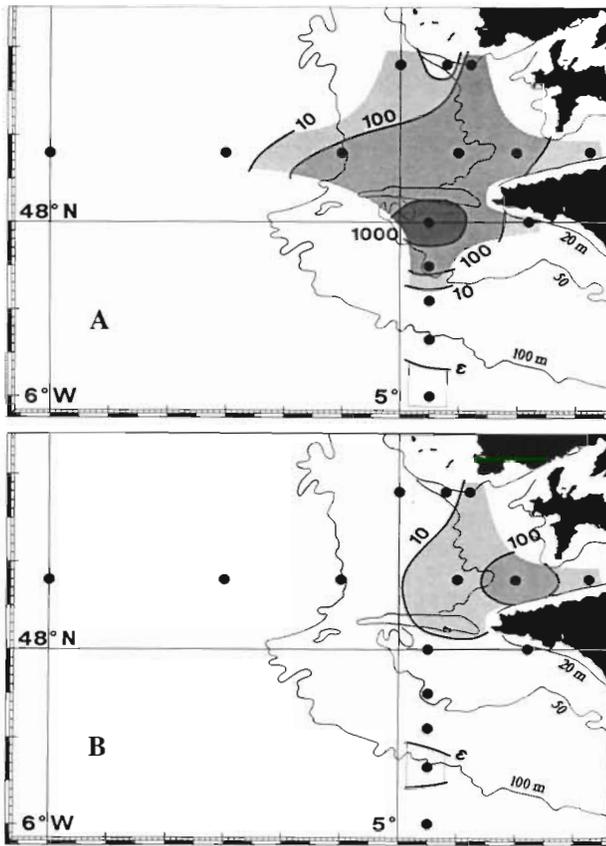


Fig. 4. Estimated abundance of cirripede larvae in the top 1 m of the water column (in numbers of individuals per 10 m^3). (A) Nauplii; (B) cypris. ϵ : limit between presence and absence. Numbers are derived from the 0–1 m integrated values (N m^{-2}), calculated as indicated in the text

Distribution of cirripede larvae: fine-scale vertical pattern

A significant proportion of the larvae was concentrated in the upper metre of the water column. When considering the detailed vertical distribution within this layer (Fig. 6), the most striking result was a pronounced increasing gradient in cypris abundance from about 30 cm to the surface 10 cm, where cypris even outnumbered nauplii at about one third of the stations. This neustonic distribution pattern was independent of the absolute density of the larvae, being observed at stations where cypris were abundant (PL 9, maximum $518 \text{ ind. } 10 \text{ m}^{-3}$ at the 0–10 cm level), at stations where they were scarce (PL 11, $7 \text{ ind. } 10 \text{ m}^{-3}$, and even PL 4, ca $2 \text{ ind. } 10 \text{ m}^{-3}$), and over the whole abundance range in between (e.g. PL 14, $20 \text{ ind. } 10 \text{ m}^{-3}$, or PL 10, $146 \text{ ind. } 10 \text{ m}^{-3}$). The pattern was also maintained irrespective of the hydrographic structure (see Fig. 2), at both relatively well-mixed stations (PL 10, $\Delta T = 1.4^\circ \text{C}$ from surface to bottom; PL 13, $\Delta T = 1.7^\circ \text{C}$) and strongly stratified stations (PL 11, $\Delta T = 6.2^\circ \text{C}$). Nauplii tended

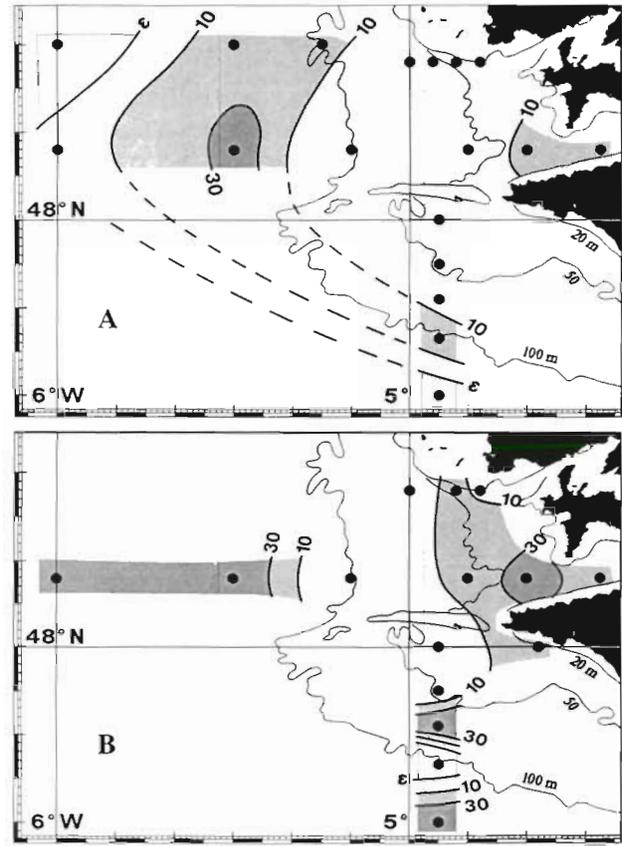


Fig. 5. Percentage of cyprid stages in the total population of cirripede larvae. (A) In the whole water column; (B) in the top 1 m. Values in (B) are calculated from integrated abundance figures (see text); total numbers are very low at the southernmost station and percentages there may be non-significant

to be more uniformly distributed within the top metre. Their vertical distribution profile, however, was opposite to a neustonic pattern at some stations relatively close to the coast (PL 4, PL 7, PL 15) and neustonic at other stations located farther offshore (PL 13, PL 16). The only clear-cut exception to the neustonic distribution of cypris was at a station very close to the shore (AR 1), where the dominant species was *Chthamalus montagui* Southward. Elsewhere, the samples mainly contained larvae of *Verruca stroemia*, with occasional specimens of *C. montagui* and other species. Nauplii of *V. stroemia* were particularly scarce at the most offshore stations (PL 11, PL 12, PL 17, PL 18), but otherwise the population tended to be dominated by later stages at greater distances from the coast.

Not all the cypris of *Verruca stroemia*, however, were neustonic, as exemplified by the distribution data at Stns PL 9 and PL 10, where they were most abundant at the surface. At Stn PL 9, the estimated number of cypris per unit volume in the 0–10 cm layer ($518 \text{ ind. } 10 \text{ m}^{-3}$) was almost twice the average value (292) for the entire water column. The integrated abundance (ind. m^{-2}) in

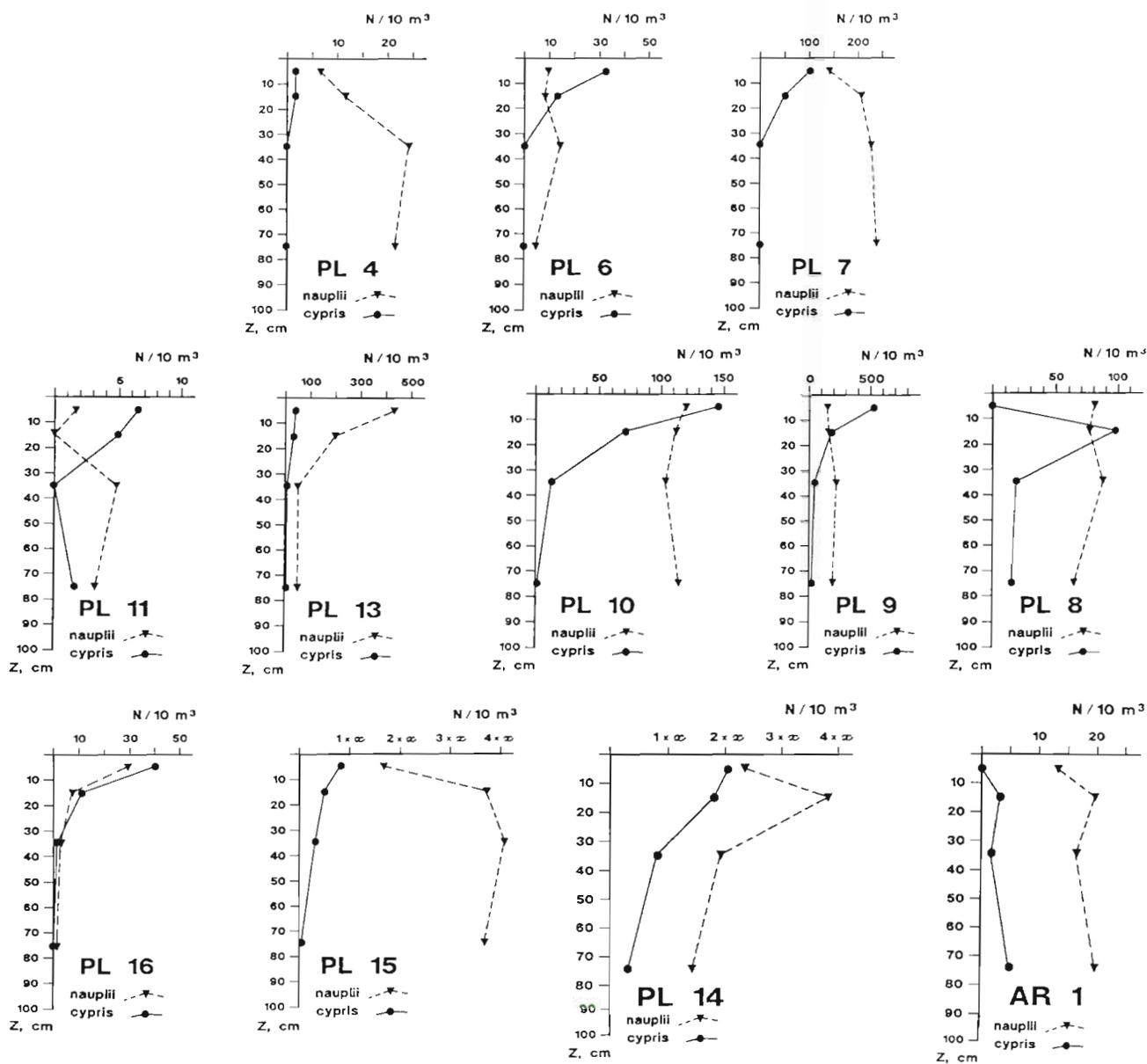


Fig. 6. Vertical distribution of cirripede larvae within the top 1 m of the water column. No graphs are provided for those stations (PL 12, PL 17, PL 18) where most numbers were so low that no significant profile can be obtained. At Stn PL 14, $x = 1000$ for nauplii and $x = 10$ for cypris; at Stn PL 15, $x = 100$ for nauplii and $x = 10$ for cypris

the 0–1 m layer can be roughly estimated as $0.1x_1 + 0.15x_2 + 0.3x_4 + 0.45x_8$, where x_1 is the larval density (ind. m^{-3}) in the 0–10 cm layer, x_2 the density in the 10–20 cm layer, x_4 the density in the 30–40 cm layer and x_8 the density in the 70–80 cm layer. This yielded, at Stn PL 9, a cypris content of about 10 ind. m^{-2} , i.e. less than 1 % of the content (1287 ind. m^{-2}) of the 44 m water column. Similarly, at Stn PL 10, the estimated cypris content of the 0–1 m layer (about 3 ind. m^{-2}) was only about 4 % of the content of the 64 m water column. The filtration coefficient of the neuston sampler is unknown and likely to be significantly less than unity. The volume filtered is therefore probably overesti-

ated, and the abundance values in the neuston samples underestimated, while total water column values, obtained with the WP 2 net, are more realistic (Unesco 1968). It is most unlikely, however, that the values in the neuston samples were underestimated by as high a factor as 24, which should be assumed if the cypris at Stn PL 10 were all restricted to the 0–1 m layer. The cirripede larvae in the samples from the vertical hauls were not subjected to detailed taxonomic identification, but the same species are likely to be observed throughout the water column, all the more so because: (1) *Chthamalus cypris*, even though non-neustonic in their fine-scale distribution pattern, were found within

the top 1 m where abundant (AR 1), so that the possibility of their being abundant at depth and entirely absent from the surface is slight; (2) the same dominant species was found in the neuston samples from all stations (cypris and nauplii), even though the latter were most often non-neustonic. The best way to reconcile the unmistakably neustonic pattern for *Verruca stroemia* cypris (e.g. a 100-fold decrease in abundance from the 0–10 cm layer to the 70–80 cm layer at Stn PL 10) with the whole water column values is accordingly to assume that an increase in abundance took place at a deeper level, probably near the bottom, i.e. that the vertical distribution of cypris was bipolar.

DISCUSSION

Horizontal distribution

One significant surprising result of this study is that larvae from barnacle coastal species are transported to relatively large distances offshore. Previous reports on the distribution of such larvae and on their recruitment on fixed collectors suggested a maximum dispersal range of the order of 10 to 20 km (Southward 1962, Crisp 1978, Southgate & Myers 1985, Ardisson et al. 1990, Bourget 1990). The horizontal pattern of larval distribution observed in the present study clearly shows that the overall abundance of barnacle larvae decreases with increasing distance from the coast. A 800-fold decrease in the total abundance of larvae per unit volume was observed over a 75 km distance from the shore, while dilution due to depth could account at most for a factor 4.4, i.e. the ratio of the water column height at the deepest and the shallowest stations. The results also clearly indicate that the densities of both nauplii and cypris decreased with distance, though much more rapidly for the nauplii than for the cyprid larvae. This is the normal pattern to be expected, given that: (1) larvae farthest offshore are likely to have stayed longer in the plankton than those at the inshore stations, and therefore to have been subjected to mortality factors for longer periods of time (Vance 1973); (2) with time nauplii eventually metamorphose into cypris. It should also be noted that, in this region, cirripede larvae can be found even farther away from the coast: in September 1985, cyprids and nauplii were collected in vertical hauls (top 200 m) over the continental slope at about 100 km off the coast of Brittany (Le Fèvre unpubl.).

The most important finding, however, relates to the small-scale distribution of the larvae of *Verruca stroemia* in the water column. A clear-cut neustonic pattern in the vertical distribution of cypris was observed at most stations, with a decrease in abun-

dance by a factor 5 to 100 from the 0–10 cm to the 70–80 cm level. In some cases, the presence of cypris within the upper metre of the water column was even restricted to the top 20 cm, with a significant decrease in abundance from 0–10 cm to 10–20 cm. Early nauplii, on the other hand, were more evenly distributed, while later stages also showed a tendency to become neustonic. To our knowledge, the only previous report of a neustonic distribution of cirripede larvae was that of unidentified *Balanus* nauplii in the Caspian Sea (Polishchuk 1966, quoted by Zaitsev 1970 p. 149–150).

The clear-cut neustonic distribution of a significant proportion of cypris larvae raises the question of passive versus active mechanisms of distribution for the settling stage of benthic animals. As pointed out by Hannan (1984), large-scale dispersal of larvae (greater than tens of km) has been assumed to be primarily a passive process under hydrodynamic control. Crisp (1976) referred to the possibility that cyprid cirripede larvae, which have a hydrophobic carapace, may be trapped by the surface film, while Shanks (1986) suggested that the larvae could become concentrated in slicks, e.g. at the downwelling junctions of convection cells (see Le Fèvre 1986). In contrast, Bousfield (1955) has shown that larvae of *Balanus improvisus* and *B. crenatus* progressively shifted their preferred distribution during ontogeny, the late naupliar and cyprid stages gradually selecting the deeper water layers. Bousfield's (1955) study was carried out in a shallow, protected, estuary. In such habitats, the barnacles apparently have evolved a behaviour which ensures retention. These results clearly indicate that the larvae of some barnacle species, those whose planktonic distribution in the field is best documented, are capable of actively regulating their depths, even at the cyprid stage. Passive mechanisms could play some role in the small-scale distribution in some regions, but, in the present case, the trapping of cyprid larvae by the surface film can be ruled out because: (1) at most stations, the decrease in their abundance from the 0–10 cm level to the 30–40 cm level was relatively progressive, the values being clearly intermediate at the 10–20 cm level; (2) the neustonic pattern was apparently species-specific, being found in *Verruca stroemia* and not in *Chthamalus montagui*, whose cypris are nevertheless very similar from a structural and physical point of view; (3) the nauplii of *V. stroemia* themselves, which are not known to have a hydrophobic carapace, showed a neustonic distribution at some stations. Indeed, the fact that there was a gradual shift in the distribution of nauplii (within the first metre) from being more abundant in the lower surface layers at nearshore stations to being slightly more abundant in the upper layers as one gradually moved offshore supports the hypothesis that the larvae (generally older at

stations furthest offshore) change their preference during ontogeny. The contrast found between the nauplii and cypris near-surface distributions in the present study, therefore, is best accounted for by assuming that the cypris larvae actively select the surface layer by migration. The neustonic distribution of cypris was observed at virtually all stations dominated by *V. stroemia*, those well-mixed as well as those stratified.

While there was definitely a neustonic component to the *Verruca stroemia* larval population sampled, densities in the vertical hauls suggest that there was also a significant proportion of the population which remained in the water column, or more likely near the bottom (see Bousfield 1955). If this bipolar distribution is correct for *V. stroemia*, then it would mean that some barnacles would behave in a similar way as observed for the bryozoans *Celleporella hyalina* (L.) and *Alcyonidium hirsutum* Flemming, 2 species showing bipolar distribution in a water column in the laboratory, i.e. large abundance near the surface and near the bottom (see Crisp 1976). This distribution pattern was interpreted by Crisp as resulting from a 'variable and indifferent' swimming behaviour. Other interpretations are possible, however. Some species occupy intertidal as well as subtidal niches, and this behaviour leading to a bipolar distribution of the larvae in the water column could optimize habitat selection in both zones. The distribution could also be interpreted as a strategy whereby the species maximizes its chances of remaining inshore (cypris near the bottom), the typical habitat of *V. stroemia*, while at the same time ensuring maximum dispersion and the likelihood of invading new habitats. Both interpretations, however, raise the question of genetic homogeneity of the population, and the long-term persistence of such strategies. Clearly more work needs to be carried out on the small-scale distribution of cirripede larvae on open coasts, the mechanisms responsible for these distributions, and small-scale genetic variations within populations, particularly between intertidal and subtidal components.

Ecological significance of the spatial patterns observed

The decrease in abundance of nauplii and cypris larvae as one moves offshore is not surprising since, presumably, these larvae have stayed longer in the water column than those found near the shore, and therefore, were exposed to mortality for a greater period of time (Vance 1973). However, the fact that nauplii were observed at distances as large as 75 km offshore suggests: (1) that dispersal of some inshore species is rapid (barnacle larvae are presumed to remain in the plankton for about 3 to 4 wk at summer

temperatures; cypris larvae have been kept for a maximum duration of about 8 wk in the laboratory at 8 °C; Crisp 1974) and much more significant than anticipated (see Crisp 1978); (2) that calculations of the dispersal of some nearshore species with meroplanktonic larvae, based on residual subsurface currents, may have underestimated dispersal of coastal species over one generation; and (3) that studies on larval dispersal (short or long distance) should consider that possibility of neustonic dispersal.

The relative importance of the dispersal process may tentatively be calculated from the data in the present study. The initial abundance N_0 , in nearshore waters, of the larval subpopulation of *Verruca stroemia* subject to long-range dispersal can be estimated from the observed abundance N_t at offshore stations by using the following equation, derived from the formula for mortality found in Strathmann's (1985) Table 1:

$$\ln(N_0/d) = \ln N_t + tm$$

where N_0 and N_t are both expressed per unit volume in the water column; d = the dilution factor due to the change in water column height from nearshore to offshore stations; t = time elapsed (d); m = mortality rate (d^{-1}).

In the present case, N_t may be taken as 1 ind. 10 m^{-3} and d as 4.5 (see above). The mortality rate for the larvae of *Verruca stroemia* is unknown, but may be tentatively considered equal to 0.06 d^{-1} , the value found by Pyefinch (1948) for nauplii of *Semibalanus balanoides* on the coast of Scotland. Assuming a duration of larval life of 30 to 50 d at summer temperatures, N_0 is found to be in the range 27 to 90 ind. 10 m^{-3} , i.e. between about 0.5 and 2 % of the total population observed at the coastal stations (ca 5000 ind. 10 m^{-3}). This percentage of migrants is small indeed, but may be sufficient to result in recruitment of larvae at distant sites.

We can, however, only speculate on the advantages of the neustonic distribution of a coastal species such as *Verruca stroemia*. The advantages of warm surface temperature for development, as well as possible feeding advantages, must be discarded on the basis that temperature can only increase metabolic costs in a fully developed and non-feeding larva such as the cypris (Crisp 1974). As pointed out above, the most likely reason why it would be advantageous for the cypris larvae of a species such as *V. stroemia* to use the 30 cm surface layer of the water column is that dispersal must be much more efficient in the near-surface layer than anywhere else in the water column. The surface layer is strongly influenced by winds and therefore the neustonic larvae are likely to be dispersed rapidly. Obviously this strategy involves a large cost in terms of losses, which must be compensated for by other,

unknown, advantages. In this respect, it is worth noting that the larvae of *Chthamalus montagui*, the barnacle living at the highest level on the shore in the region of study, did not show a neustonic behaviour, being more evenly distributed in at least the top of the water column than those of *V. stroemia*, a predominantly subtidal species. If repositioning of the larvae in the water column is apparently the strategy adopted by *Balanus glandula* on the west coast of North America (Grosberg 1982) to colonize the appropriate level on the shore, this does not appear to be the case in *V. stroemia* and *C. montagui*. The relative vertical distributions of their larvae indicate that both species eventually must actively select their permanent microhabitat on the shore independently of their position in the water column, presumably by detecting suitable characteristics to settle during the various exploration phases (Bourget 1988, Chabot & Bourget 1988, Letourneux & Bourget 1988).

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LITERATURE CITED

- Ardisson, P. L., Bourget, E., Legendre, P. (1990). Multivariate approach to study species assemblages at large spatiotemporal scales: the community structure of the epibenthic fauna of the estuary and gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.* 47: 1364-1377
- Bhaud, M., Bourdillon, A., Castelbon, C., Bastiani, F. (1974). Étude de la répartition verticale du zooplancton de deux secteurs de la Méditerranée: la campagne 'Médiplanc 1972' II. Analyse des méthodes d'échantillonnage. *Ann. Inst. océanogr. Paris* 59: 41-50
- Bourget, E. (1988). Barnacle larval settlement: the perception of cues at different spatial scales. In: Chelazzi, G., Vannini, M. (eds.) Behavioral adaptation to intertidal life. Plenum Publ. Corp., New York, p. 153-172
- Bourget, E. (1990). Behavioural, morphological and genetic changes in some North Atlantic populations of the barnacle *Semibalanus balanoides*. In: Garbary, D., South, G. R. (eds.) Evolutionary biogeography of the marine algae of the North Atlantic. NATO Advanced Research Workshop, Springer-Verlag, Heidelberg, p. 87-106
- Bousfield, E. L. (1954). The distribution and spawning seasons of barnacles on the Atlantic coast of Canada. *Bull. nat. Mus. Can.* 132: 112-154
- Bousfield, E. L. (1955). Ecological control of the occurrence of barnacles in the Miramichi estuary. *Bull. nat. Mus. Can.* 137: 1-69
- Chabot, R., Bourget, E. (1988). Influence of substratum heterogeneity and settled barnacle density on the settlement of cypris larvae. *Mar. Biol.* 97: 45-56
- Champalbert, G. (1969). L'hyponeuston dans le Golfe de Marseille. *Tethys* 1: 585-666
- Connell, J. H. (1985). The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. *J. exp. mar. Biol. Ecol.* 93: 11-45
- Crisp, D. J. (1974). Energy relationships of marine invertebrate larvae. *Thalassia jugosl.* 10: 103-120
- Crisp, D. J. (1976). Settlement responses in marine organisms. In: Newell, R. C. (ed.) Adaptation to environment: essays on the physiology of marine animals. Butterworths, London, p. 83-124
- Crisp, D. J. (1978). Genetic consequences of different reproductive strategies in marine invertebrates. In: Battaglia, B., Beardmore, J. A. (eds.) Marine organisms: genetics, ecology and evolution. Plenum Publ. Corp., New York, p. 257-273
- De Wolf, P. (1973). Distribution and dispersal of barnacle larvae. *Neth. J. Sea Res.* 6: 1-112
- Evans, F. (1977). Seasonal density and production estimates of the common planktonic copepods in Northumberland coastal waters. *Estuar. coast. mar. Sci.* 5: 223-241
- Flowerdew, M. W. (1983). The circumboreal *Balanus balanoides* (L.) and its subpopulations. In: Oxford, G. S., Rollinson, d. (eds.) Protein polymorphism: adaptive and taxonomic significance. Systematics Association Spec. Vol. 24, Academic Press, London, p. 75-83
- Gaines, S., Brown, S., Roughgarden, J. (1985). Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia (Berl.)* 67: 267-272
- Grall, J. R., Le Corre, P., Le Fèvre, J., Marty, Y., Tournier, B. (1980). Caractéristiques estivales de la couche d'eau superficielle dans la zone de fronts thermiques Ouest-Bretagne. *Oceanis* 6: 226-249
- Grosberg, R. K. (1982). Intertidal zonation of barnacle: the influence of planktonic zonation of larvae of vertical distribution of adults. *Ecology* 63: 894-899
- Hannan, C. A. (1984). Planktonic larvae may act like passive particles in near-bottom flows. *Limnol. Oceanogr.* 29: 1108-1116
- Le Fèvre, J. (1986). Aspects of the biology of frontal systems. *Adv. mar. Biol.* 23: 163-229
- Le Fèvre, J., Grall, J. R. (1970). On the relationship of *Noctiluca* swarming off the western coast of Brittany with hydrological features and plankton characteristics of the environment. *J. exp. mar. Biol. Ecol.* 4: 287-306
- Letourneux, F., Bourget, E. (1988). Importance of physical and biological settlement cues used at different spatial scales by the larvae of *Semibalanus balanoides*. *Mar. Biol.* 97: 57-66
- Pingree, R. D., Griffiths, D. K. (1978). Tidal fronts on the shelf seas around the British Isles. *J. geophys. Res.* 83: 4615-4622
- Pingree, R. D., Pugh, P. R., Holligan, P. M., Forster, G. R. (1975). Summer plankton blooms and red tides along tidal fronts in the approaches to the English Channel. *Nature, Lond.* 258: 672-677
- Pyefinch, K. A. (1948). Notes on the biology of cirripedes. *J. mar. biol. Ass. U.K.* 27: 464-503
- Razouls, C., Thiriou, A. (1972-73). Données quantitatives de mésoplancton en Méditerranée occidentale (saisons hivernales, 1969-70). *Vie Milieu Sér. B* 23: 209-241
- Shanks, A. L. (1986). Tidal periodicity in the daily settlement of intertidal barnacle larvae and an hypothesized mechanism for the cross-shelf transport of cyprids. *Biol. Bull. mar. biol. Lab., Woods Hole* 170: 429-440
- Simpson, J. H. (1981). The shelf-sea fronts: implications of

- their existence and behaviour. *Phil. Trans. R. Soc. A* 302: 531–546
- Simpson, J. H., Bowers, D. (1981). Models of stratification and frontal movement in shelf seas. *Deep Sea Res.* 28: 727–738
- Southgate, T., Myers, A. A. (1985). Mussel fouling on the Celtic Sea Kinsale field gas platforms. *Estuar. coast. Shelf Sci.* 20: 651–659
- Southward, A. J. (1962). The distribution of some plankton animals in the English Channel and approaches. II. Surveys with the Gulf III high-speed sampler. *J. mar. biol. Ass. U.K.* 42: 275–375
- Strathmann, R. R. (1985). Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. *Ann. Rev. Ecol. Syst.* 16: 339–361
- Unesco (1968). Zooplankton sampling. *Unesco Monographs on Oceanographic Methodology* 2: 1–174
- Vance, R. (1973). On reproductive strategies in marine benthic invertebrates. *Am. Nat.* 107: 337–352
- Zaitsev, Yu. P. (1970). *Marine neustonology*. Naukova Dumka, Kiev, Translated by Mercado, A. (1971). Israel Program for Scientific Translation

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