Marine Biology (2002) 140: 789–800
DOI 10.1007/s00227-001-0751-z

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Semibalanus balanoides in winter and spring: larval concentration, settlement, and substrate occupancy

Received: 26 March 2001 / Accepted: 2 November 2001 / Published online: 11 January 2002

Abstract This study measured the progression from pelagic larvae to juvenile barnacles, and examined whether recruitment of barnacles, *Semibalanus balanoides* Linnaeus, at two intertidal sites in contrasting hydrodynamic regimes was determined by pre-settlement or post-settlement processes. The two sites were 1.5 km apart in the vicinity of Woods Hole, Mass., USA. Quantitative plankton samples were taken twice weekly from December 1997 to May 1998 at a nearby site as an estimate of nearshore larval abundance. The presence of *S. balanoides* nauplii was noted, and cyprids were enumerated and measured. Larval settlement at the two sites [Gansett Point, Buzzards Bay (GP) and Little Harbor, Vineyard Sound (LH)] was estimated from examination of replicate settlement plates exposed for 2 or 3 days throughout the settlement season, and from replicate plots on marked rock quadrats at each site. On both plates and rocks settled cyprids and metamorphs were enumerated. Space occupancy on unmanipulated rock quadrats by all stages from cyprids to adult barnacles was also examined. Settlement occurred from 2 January to 20 May, and major settlement peaks coincided with peaks in pelagic cyprid concentration at LH, but not at GP. Space occupied by juvenile barnacles was close to zero up until late February despite substantial settlement prior to that. At LH, juvenile barnacle cover was zero at the end of the observations; all settlement failed. Almost 100% of settled cyprids failed to metamorphose within 2 days from late January to late March. Then the proportion metamorphosing increased sharply coinciding with a sudden increase of 3°C in water temperature. Observed site differences in space occupancy by juvenile barnacles suggest that while cyprid supply is a necessary condition for barnacle settlement, other factors affecting metamorphosis of settled cyprids and early juvenile mortality determine recruitment.

Introduction

The question whether spatial distribution of *Semibalanus balanoides* is established by settlement or post-settlement processes was posed in the 1930s (Hatton and Fischer-Piette 1932; Hatton 1938). The resolution of this question for spatial distributions of benthic organisms and their temporal counterpart, population fluctuations, has been the focus of much experimental research since then. Understanding how settlement determines adult distribution and abundance requires understanding the dependencies of settlement rate, for hard substrate organisms, the rate at which pelagic larvae take up permanent contact with the substrate. Several processes influence settlement rate, including larval pool dynamics (e.g. Johnson 1939; Efford 1970), larval transport from pelagic to adult habitats (Bousfield 1955; Ebert 1983; Epifanio 1988), and local settlement processes. Factors affecting local settlement include nearshore larval concentration ("larval supply", e.g. Yoshioka 1982; Gaines et al. 1985; Minchinton and Scheibling 1991), amount of suitable substrate for settlement (Bertness et al. 1992; Pineda 1994; Osman and Whitlatch 1995a), behavior (Wethey 1984; Raimondi 1990; Hills and Thomason 1996; Olivier et al. 2000), and small-scale (within a few centimeters) hydrodynamics (Eckman 1990; Mullineaux and Butman 1991). After settlement, larvae suffer high mortality (e.g. Thorson 1966; Gosselin and Qian 1996, 1997; Hunt and Scheibling 1997) due to factors ranging from pelagic larval experience (e.g. Jarrett and Pechenik 1997), to metamorphosis failure (Jarrett 2000, and

Communicated by J.P. Grassle, New Brunswick

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personal observations), predation, stress, and disturbance (e.g. Denley and Underwood 1979; Elmgren et al. 1986; Osman and Whitlatch 1995b; Sousa 2000).

S. balanoides is an intertidal, boreal circumpolar species, and in the western Atlantic it occurs from Cape Hatteras (about 35°N) to Cumberland Sound, Puffin Island (about 65°N), and in western Greenland, to about 72°N (reviewed by Stubbings 1975). *S. balanoides* is the most abundant intertidal metazoan species in the New England upper rocky intertidal (e.g. Menge 1976), including non-estuarine intertidal environments in Vineyard Sound and Buzzards Bay, our study area. *S. balanoides* is an obligate cross-fertilizing hermaphrodite and releases nauplius I larvae, which subsequently molt six times in the water column to produce nauplii II–VI, and a final non-feeding cyprid stage. In laboratory and field studies, larval development times range from 30 days at 3°C to 10 days at 18°C (Barnes and Barnes 1958; Harms 1984). *S. balanoides* appears to produce only one brood per year at Bangor, UK (Barnes 1989). Competent cyprids settle, and, after some time, they may metamorphose into "young barnacles" (for a distinction between settlement and metamorphosis, see Scheltema 1974).

The objective of the present study was to measure the progression from pelagic larvae to juvenile barnacles ("recruitment"). We monitored settlement and nearshore larval concentration, an operational measure of larval supply, for about 6 months, from late fall 1997 to late spring 1998 in Woods Hole, Mass., USA. This time period was chosen because of the reported high abundance of *S. balanoides* larvae in daily samples during the winter (mid-December to mid-May) in Woods Hole (Fish 1925). In Narragansett Bay, 50–60 km east of Woods Hole, Lang and Ackenhusen-Johns (1981) found *S. balanoides* larvae from December to April. We also measured macrobiota cover area, which is dependent on free substrate and young and old *S. balanoides* in our study sites (e.g. Menge 1976; Bertness 1999). We monitored recruitment at two sites with contrasting hydrodynamic regimes (coarse-scale, 1–10 km). The mean and maximum tidal current velocities and the water flux at Little Harbor are much greater than at Gansett Point. Furthermore, it is expected that residence times of nearshore waters would be longer at Gansett Point than at Little Harbor, as Gansett Point is within Buzzards Bay, a semi-enclosed bay, while Little Harbor is in Vineyard Sound, an open coast (see Fig. 1). Plankton samples were obtained at the Woods Hole pier, a few hundred meters from Little Harbor.

We addressed the following questions. What are the winter and spring patterns in nearshore cyprid concentration and larval settlement? Do barnacle larvae settle in winter? Are there temporal patterns in the proportion of settled cyprids that metamorphose into "young barnacles" within a given time period? Is juvenile barnacle cover correlated with settlement cover? Are there temporal patterns in the transition from settlers to juvenile barnacles?

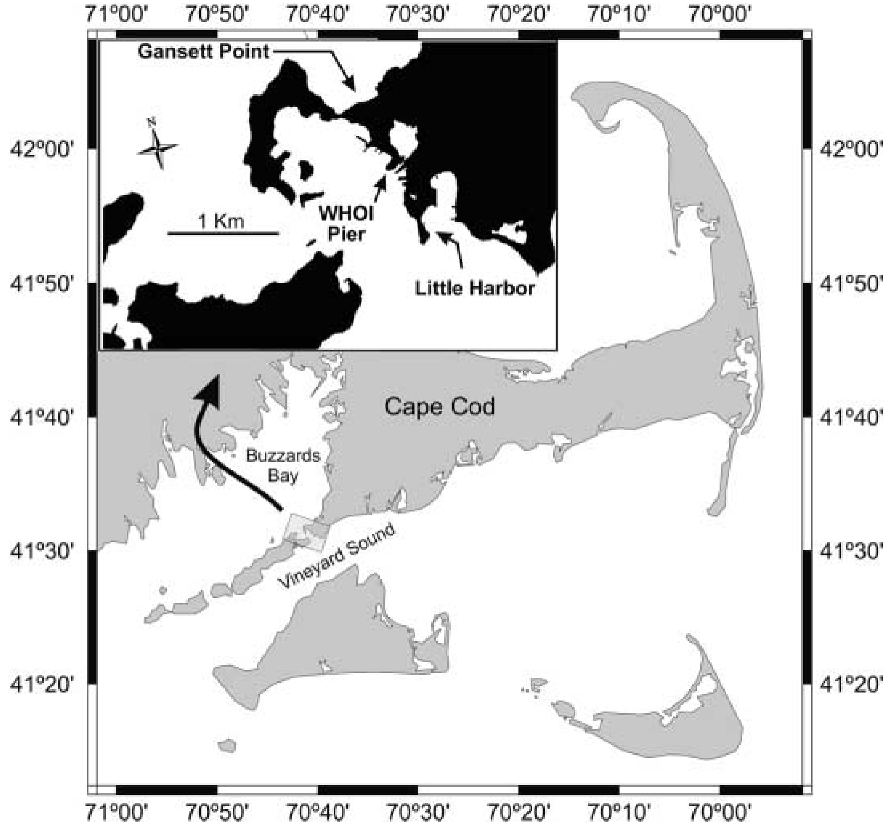


Fig. 1 Map of study sites (*upper left map* modified from Fish 1925)

Materials and methods

Observational and experimental periods are given in Table 1. Larval samples were collected at the Woods Hole Oceanographic Institution (WHOI) pier, Woods Hole, Mass., USA (water depth ~17 m; Fig. 1). The settlement measurements were conducted at Little Harbor (LH) and Gansett Point (GP) in Woods Hole. The Little Harbor sites are characterized by cobble and large boulders (ca. 0.3–0.7 m diam.), 0–50 m from the harbor entrance. Gansett Point is characterized by coarse sand, cobble, and pebbles (ca. 0.1–0.2 m diam.) and a few large boulders (ca. 1–1.5 m diam.).

Little Harbor and the WHOI pier are separated by a few hundred meters (Fig. 1) and are characterized by strong tidal currents, regularly attaining speeds of ca. 200 cm s^{-1} (Anonymous 1997). The Gansett Point site is less energetic than LH with currents ca. <50 cm s^{-1} (Anonymous 1997). During spring tides, currents off LH can be six times faster than those at GP. Surface gravity-wave energy is generally very low in both systems, as the sites are well protected from the open-ocean swell.

Surface water temperature has been measured in front of the Woods Hole Northeast Fisheries Science Center, near (<300 m) the WHOI pier, from 1986 to date. Average water temperature during the sampling period (December 1997–May 1998) was slightly warmer (0.7°C) than the 1986–1997 average. Temperatures measured during the sampling period were well within the range of observed minima and maxima.

Larval concentration and cyprid size

We distinguished between attached cyprids and "young barnacles", and, as Pineda (1994), used the term "metamorphs" for recently metamorphosed cyprids that had lost their shell and were <3 days old. The concentration of larvae in the water column was measured by conducting surface plankton tows from the WHOI pier (net diam. = 29 cm, mesh size = 335 µm). Volume filtered, determined with a mechanical flow meter (General Oceanics), ranged from 2.3 to 14.4 m^3 ($\bar{x} = 7.4\,\mathrm{m}^3$). Plankton samples were collected twice a week, every 3 and 4 days, but on a few dates the interval was >4 days (sampling dates and intervals shown in Fig. 2). The presence of barnacle nauplii was noted and cyprids were counted and measured using a dissecting microscope. Nauplii were not enumerated because some are small enough to possibly pass through the 335 µm mesh plankton net we used (Crisp 1962). All nauplii and cyprids were identified as *Semibalanus balanoides*, which were the only larvae found by Fish (1925) in Woods Hole waters near the WHOI pier from mid-December to mid-May. There are four other common species of acorn barnacles in the Woods Hole region: *Balanus crenatus*, *B*, *eburneus*, *B. improvisus*, and *Chthamalus stellatus*. *B. crenatus*, *B. eburneus*, and *C. stellatus* breed in late spring (June) and early summer (Fish 1925), so it was unlikely that their cyprids would be present in our plankton samples. *B. improvisus* cyprids are present in the region from December to March, but in lower salinity waters (not >27‰) (Lang and Ackenhusen-Johns 1981). Moreover, *B. improvisus* cyprids had a mean length (±SD) of 523±12 µm in a study in the Irish Sea (Jones and Crisp 1954), which is considerably less than the lengths of *S. balanoides* cyprids reported from high-latitude field studies (Bassindale 1936; Crisp 1962), and less than the cyprids in our samples (range = 720–1,300 µm).

Carapace lengths of cyprids were measured using an ocular micrometer (to within 30 µm). Because of the great variation in cyprid concentrations, some samples were split with a plankton splitter (McEwen et al. 1954). The number of cyprids measured per sample averaged 113 (range = 8–297) (Fig. 2). Trends in mean cyprid length were analyzed using linear regression. The critical values for all statistical tests were drawn from two-tailed distributions with $\alpha = 0.05$.

Table 1 *Semibalanus balanoides*. Observational and experimental periods for larval sampling, cyprid size, plate settlement, rock settlement and space occupancy

	Start	End
Larval sampling	3 Dec 1997	20 May 1998
Cyprid size	27 Jan 1998	4 Apr 1998
Plate settlement	28 Nov 1997	28 May 1998
Rock settlement	4 Feb 1998	8 May 1998
Space occupancy	1 Feb 1998	4 May 1998

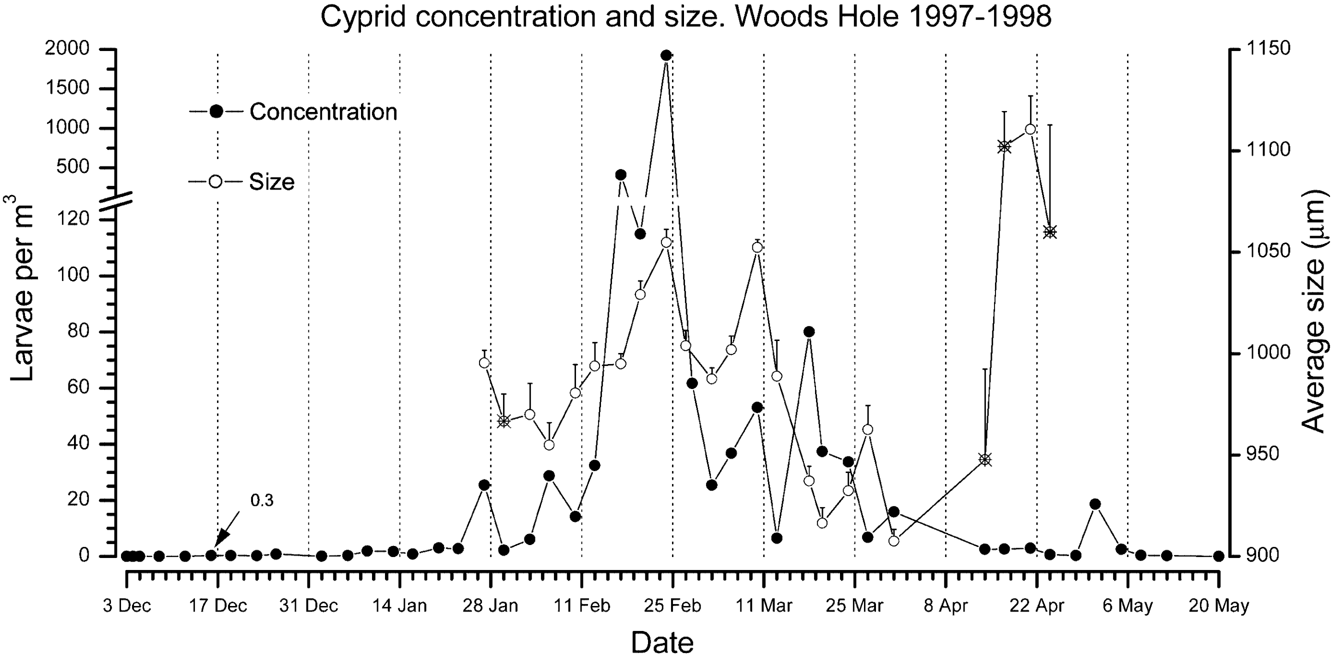


Fig. 2 *Semibalanus balanoides*. Cyprid concentration and mean cyprid carapace length (+SE) at WHOI pier from 3 December 1997 to 20 May 1998 and from 27 January to 24 April 1998, respectively. *Asterisks* on larval size symbols are dates when $n < 30$

Settlement and proportion of unmetamorphosed settlers

Plates and rock settlement

At Little Harbor and Gansett Point, seven settlement plates were located between 0.3 and 0.5 m above mean lower low water (MLLW), and separated by 7 to 80 m. Plates were immersed 79–39% of the time, the mean tidal range being about 0.6 m. Plates were made of white polyvinyl chloride pipes (2.5 cm inner diam., 11 cm long) cut in half along their longitudinal axis. Three grooves, 9.5 cm long and 0.6 cm wide, were machined into the inner surface, and a hole with a diameter of 1.2 cm in the middle of each plate accommodated a nylon screw that was cemented with epoxy onto the rocks. The total summed perimeter of the grooves per plate was 58 cm (Pineda 1994). The available suitable substrate per plate was 9.8 cm^2. Settlement plates were recovered and replaced during low tide three times a week, yielding sampling periods of 3, 2, and 2 days each week. At the end of the settlement season only two samples were recovered at 7-day intervals. Attached live and dead cyprids and metamorphs were identified in the field and examined in the laboratory under a dissecting microscope. All cyprids and metamorphs were found at the junction of the wall and bottom of the machined grooves; maximum width of a metamorph was 0.084 cm. After counting, the plates were thoroughly brushed and washed with freshwater. All 3- and 7-day settlement data were linearly converted to 2-day numbers.

Settlement on natural substrate was monitored on five rocks at each site. Natural substrates at the two sites appeared similar in texture and surface roughness. All rocks were 0.1–0.5 m above MLLW. A transparent plastic template with a printed 40×40 mm quadrat was used to count newly settled barnacles. Holes drilled on the rocks, to which marks on the plastic could be aligned, permitted repeated sampling of the same area. Rocks were sampled on the same days as the plates. A soft brush was used to remove all settlers after counting on both substrate types.

Proportion of unmetamorphosed settlers on settlement plates

Time series of the average ratio of unmetamorphosed settlers to total settlement were obtained for LH and GP after discarding all values obtained with a sampling interval different than 2 days, and by discarding data where total settlement was <5 individuals. Elimination of sampling intervals other than 2 days was necessary to remove the confounding effect of time dependency on metamorphosis (a 3-day interval would be expected to have a larger proportion of metamorphs than a 2-day interval). Water temperatures with comparable time steps were obtained by averaging 3 days of temperature with the third day corresponding to a sample day (e.g. for April 30, temperatures for April 30, 29, and 28 were averaged).

The non-parametric Wilcoxon z signed-rank test was used to test for differences between average settlement, and the average proportion of unmetamorphosed settlers at LH and GP; date was used for blocking. A non-parametric Spearman test (r_s) was used to test for correlation between plate and rock settlements at LH and GP, and between the unmetamorphosed proportion at LH and GP. Only data collected from 2 January to 20 May (when the first and last settlers were recorded) were used in the plate settlement correlation analysis. We did not test for statistical correlation between nearshore cyprid concentration and plate settlement because of the mismatch in sampling dates, and because of the uncertainty of correlating a point measurement of larval concentration with a time-integrated variable such as settlement (Pineda 2000).

Space occupancy in unmanipulated substrates

The proportions of area covered by: (1) attached cyprids, (2) metamorphs, (3) juvenile barnacles, (4) adult barnacles, (5) free substrate, and (6) dead juvenile barnacles were measured on five rocks haphazardly selected at each study site. Total settler cover was the sum of (1) and (2). As for the rock settlement, a 40×40 mm quadrat with a 1 mm grid (i.e. 1,600 points on the grid) printed on a transparent sheet was used as a template to repeatedly sample the same areas on the rocks. The observed quadrat was never manipulated. To quantify the magnitude of the above six variables, 40 pairs of x–y grid coordinates were drawn randomly from a uniform distribution on each sampling date. Metamorphs were identified by their shape and color and were individuals with <1.0 mm diameter. Juvenile barnacles were defined as individuals with 1.0–4.0 mm diameter. Adult barnacles were larger individuals that apparently recruited before the winter of 1997/1998. Empty shells of juvenile barnacles were counted as dead juvenile barnacles. For each sample date, the sum of the proportions of cyprids, metamorphs, juvenile barnacles, adult barnacles, free substrate, and dead juvenile barnacles summed to 1.0. Sampling interval was from 2 to 7 days, with two exceptions with longer intervals.

A single-factor ANOVA was used to test for significant changes over time. All proportions were arcsine–square root transformed prior to analysis (Zar 1984). A correlation test between free substrate cover and juvenile barnacle cover was not attempted because the temporal series of the two variables are auto-correlated (i.e. values at a given date are partially dependent on values on previous dates). Instead, we used a non-parametric Spearman test to examine the correlation between differences in free substrate on two consecutive dates, and the corresponding differences in juvenile barnacle cover (Chatfield 1989). Average adult barnacle cover at LH and GP was compared using the Wilcoxon signed rank test. Because substrate occupancy at LH and GP were often not taken on the same day, but on two contiguous days, a 2-day period was used for blocking. This is justified because the little change in space occupancy by adult barnacles from one day to the next is expected. Non-paired data were discarded from the statistical analysis.

Results

Larval concentration and size

Nauplii were present in the water column from early December through early May. The first cyprids appeared in mid-December and were present throughout the study period (Fig. 2). Cyprid larvae were present in low concentrations throughout December and most of January, rarely exceeding 5 larvae m^{-3} (Fig. 2). Cyprid concentration increased in late January and February, reaching a seasonal peak of about 2,000 larvae m^{-3} on 24 February. Cyprid concentration declined during March and April, and was typically <5 larvae m^{-3} during April and May. Carapace lengths of cyprids in net samples ranged from 720 to 1,300 μm. There was no consistent trend over time for average cyprid size ($R^2=0.048$, $P=0.316$; Fig. 2), but cyprids in the 24 February sample were on average larger than cyprids sampled before. Peaks in cyprid size on 24 February and 10 March coincided with peaks in concentration. A sudden increase in size was apparent at the end of the season when concentrations were low.

Settlement

Settlement occurred from 16 January to 20 May at LH and from 2 January to 4 May at GP (Fig. 3). Settlement was low until the middle of January, when it increased at

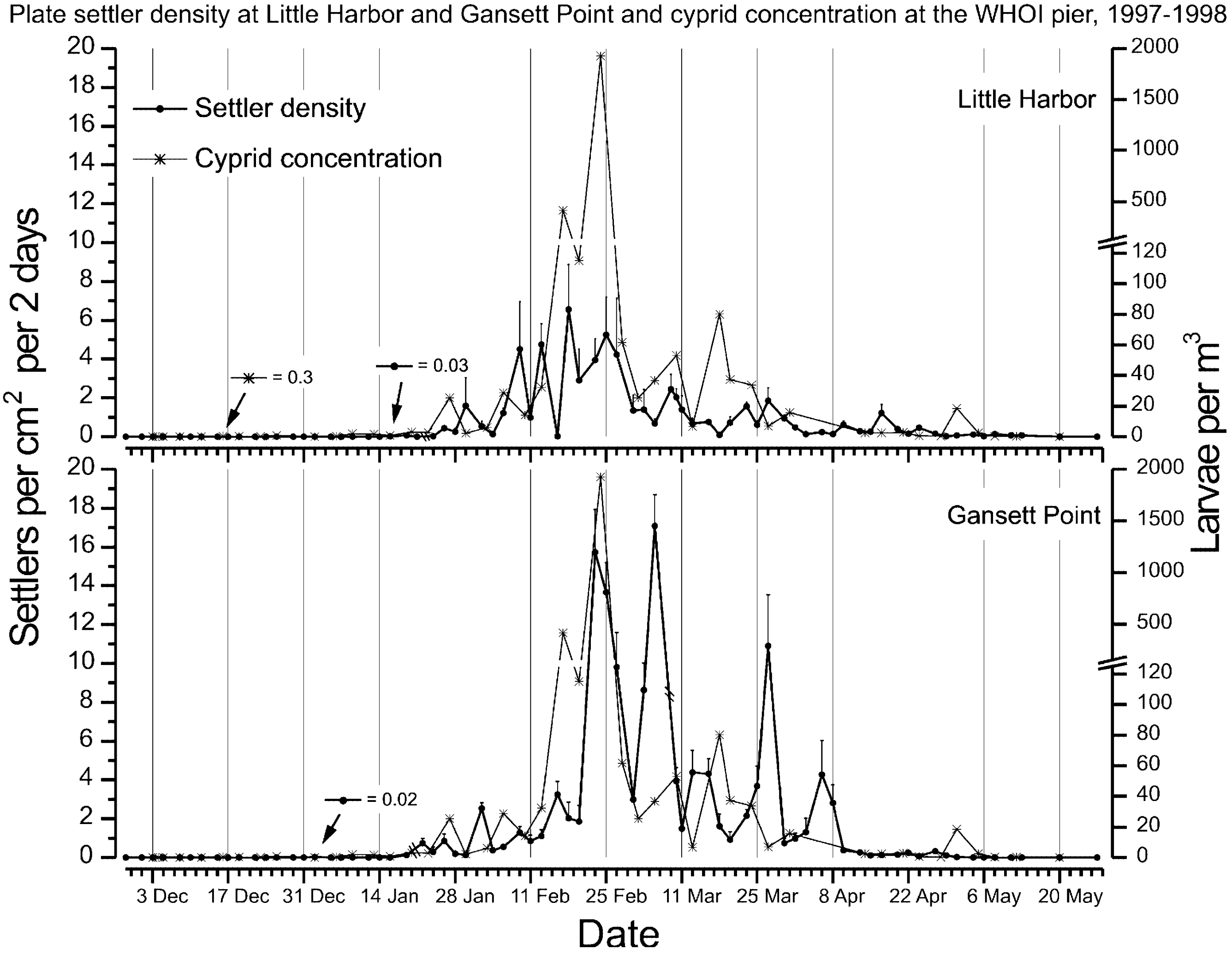


Fig. 3 *Semibalanus balanoides*. Mean settlement rate (+SE) per square centimeter per 2 days in settlement plates from 28 November 1997 to 20 May 1998 and larval concentration for the corresponding period. The same larval concentration curve is plotted in both panels to facilitate comparison. *Arrows* pointing to *x*-axes give date and density of the first settlers (*upper and lower panels*) and first cyprids (*upper panel*). *Breaks in the curves* represent missed sample days

both sites. At LH, settlement was higher on plates than on rocks ($P < 0.001$, $n = 27$), while at GP settlement was comparable on the two substrates (Table 2). Plate and rock settlement at LH were correlated with settlement at GP (plates: $r_s = 0.702$, $P < 0.001$, $n = 58$; rocks: $r_s = 0.878$, $P < 0.001$, $n = 27$).

Gansett Point had significantly higher settlement than LH on plates and rocks (Fig. 3; Table 2; $P < 0.05$ and $P < 0.001$, $n = 74$ and $n = 27$). However, the differences between both sites were much larger for rocks than for plates. The ratio of total average settlement on GP rocks to LH rocks was 20.6, and 2.9, for plates (Table 2). Differences in settlement between GP and LH for plates versus the differences for rocks were tested with a Wilcoxon signed-ranked test. The test for matched sampling dates indicated that differences were statistically significant ($P < 0.01$, $n = 27$), with larger positive differences for rocks than for plates in 20 of 27 cases.

Proportion of unmetamorphosed settlers on settlement plates

The proportion of unmetamorphosed settlers was close to 1 at LH and GP during the winter, indicating that relatively few attached cyprids metamorphosed within the 2-day sampling period (Fig. 4). From late March to early May, there were large fluctuations in this proportion, with values ranging from 0.125 to 0.950. There was an apparent inverse relationship between a sudden increase in water temperature and increased variability in the proportion of unmetamorphosed settlers. A sharp increase in the proportion of settlers that transitioned into metamorphs (from ca. 0 to 0.6) coincided with an increase in temperature. Correlation analysis was not attempted because it was expected that the temperature data are auto-correlated. There was no significant difference between the unmetamorphosed proportion at GP and LH, but there was evidence of a correlation between the two sites ($r_s = 0.859$, $P < 0.01$, $n = 26$).

Table 2 *Semibalanus balanoides*. Time-averaged settlement per unit area (cm^2) on plates and natural substrates. *Plates – matched* represent the plate's averages for a period of time matching the rock observations (2 February to 8 May). For each substrate category, only matching dates were included. This resulted in the exclusion of one datum from the plates (all data) and three data from the natural substrates

Little Harbor			Gansett Point		
Plates – all data	Plates – matched	Rock	Plates – all data	Plates – matched	Rock
0.76 *n* = 74	1.32 *n* = 27	0.29 *n* = 27	1.75 *n* = 74	3.86 *n* = 27	5.96 *n* = 27

Space occupancy in unmanipulated substrates

The proportion of area covered by cyprids, metamorphs, and juvenile barnacles tended to be greater at GP than at LH (Table 3), consistent with higher settlement rates at GP than at LH (Fig. 3; Table 2). The time-averaged adult barnacle cover, on the other hand, was larger at LH than at GP ($P < 0.001$, $n = 13$; Table 3). Adult percentage cover changed little over time (results not presented).

At Little Harbor, cyprid and metamorph cover peaked at 6% early in the season, with metamorphs lagging behind cyprids. Both cyprid and metamorph cover significantly declined to 0% later in the season ($P < 0.001$) (Fig. 5). Juvenile barnacles at LH occupied up to 10% of the available space in mid-March; they were absent early in the season, increased in late February, and disappeared by mid-April. All barnacles observed at LH failed to transition from juvenile to older stages. Changes in the proportion of area covered by juvenile barnacles were significant ($P < 0.001$), and appeared to be inversely related to the pattern of free substrate, but this was not significant ($r_s = -0.194$, $n = 18$). The mean percentage of free substrate did not vary significantly over the season, with a seasonal average of 70% (Fig. 5; Table 3). The fraction of dead juvenile barnacles was nearly constant at 0% throughout the season (data not shown).

At Gansett Point, space occupied by cyprids and metamorphs peaked early in the season and then declined ($P < 0.001$), reaching its minimum as juvenile cover peaked. Juvenile barnacle cover was nil during early February, peaked in mid-March at about 25%, and decreased afterwards ($P < 0.001$). Maximum juvenile barnacle cover coincided with a minimum in free substrate, and changes in juvenile barnacle cover were significantly correlated with changes in free substrate ($r_s = -0.512$, $P < 0.05$, $n = 18$). Free substrate at GP

Fig. 4 *Semibalanus balanoides*. Proportion of unmetamorphosed settlers in total settlement, and surface water temperature. Settlement data from settlement plates. Only 2-day settlement data were plotted. Temperature is average of data corresponding to settlement date and two prior days

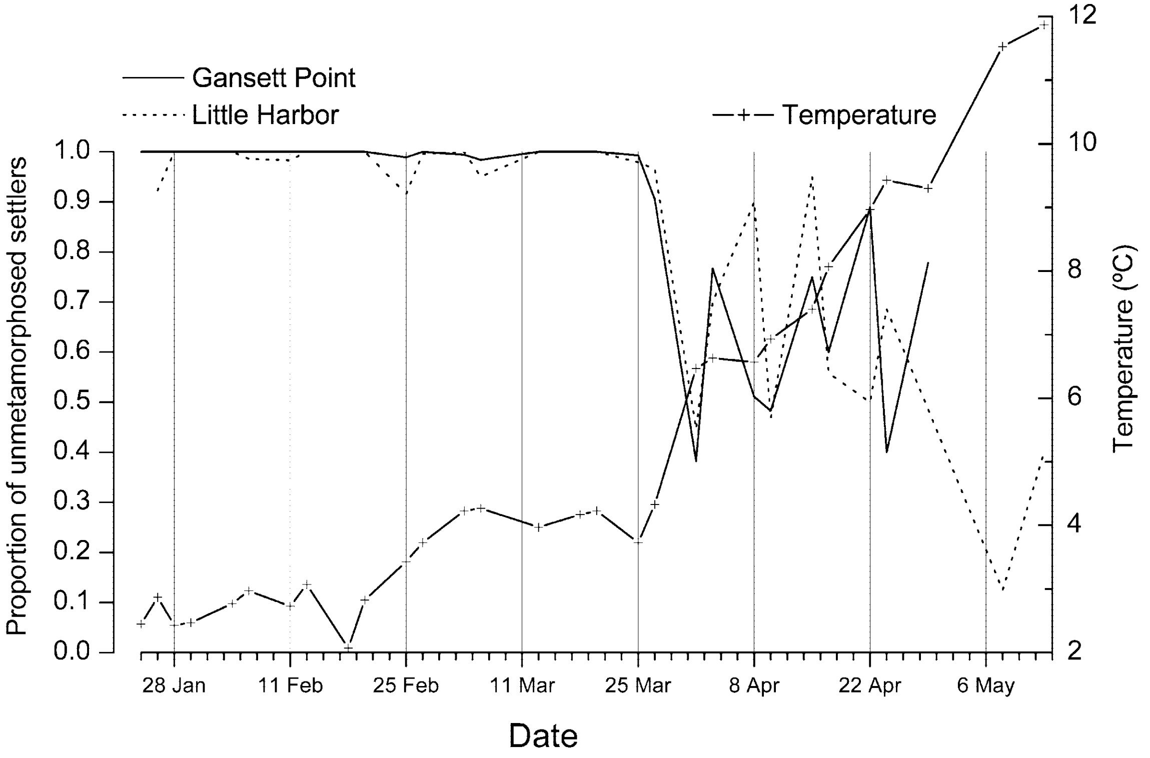


Table 3 *Semibalanus balanoides*. Time-averaged $\bar{x} \pm$ SE percentages for space occupancy observations (natural substrates), $N = 19$. Total settlers are cyprids plus metamorphs

	Little Harbor	Gansett Point
Free substrate	70.26 ± 0.92	69.39 ± 1.94
Adult barnacles	24.54 ± 0.71	13.85 ± 0.51
Cyprids	0.58 ± 0.32	2.08 ± 0.51
Metamorphs	1.15 ± 0.44	2.23 ± 0.59
Total settlers	1.73 ± 0.56	4.31 ± 0.94
Juvenile barnacles	3.45 ± 0.78	12.00 ± 2.16
Dead juvenile barnacles	0.03 ± 0.03	0.45 ± 0.16

began to decrease from mid-February, reached its minimum in mid-March, and then increased until the end of the season ($P < 0.01$) (Fig. 6). Dead juvenile barnacles were present only toward the end of the season, and the percentage cover was always very low (maximum = 2%).

At Gansett Point, and to a lesser extent at LH, the major increases in juvenile barnacle cover on consecutive dates tended to coincide with sharp decreases in settler cover. This is to be expected as settlers grow into juveniles (and with settlement decreasing sharply from one date to the next).

Overall, time-averaged space occupancy was greater at GP than at LH for cyprids, metamorphs, and juvenile barnacles, contrasting with adult barnacle cover which was less at GP than at LH (Table 3).

Cumulative pelagic larva concentration, settlement density, settlement cover, and juvenile barnacle cover

The cumulative curves for plate-settler density (no. cm^{-2}), and settler and juvenile barnacle cover on natural sub-

Fig. 5 *Semibalanus balanoides*. Little Harbor, natural substrate. Mean proportion cover (± 1 SE) of total settlers, cyprids, metamorphs, juvenile barnacles, and free substrate from 2 February to 4 May 1998. Probability from single-factor ANOVAs testing changes over time

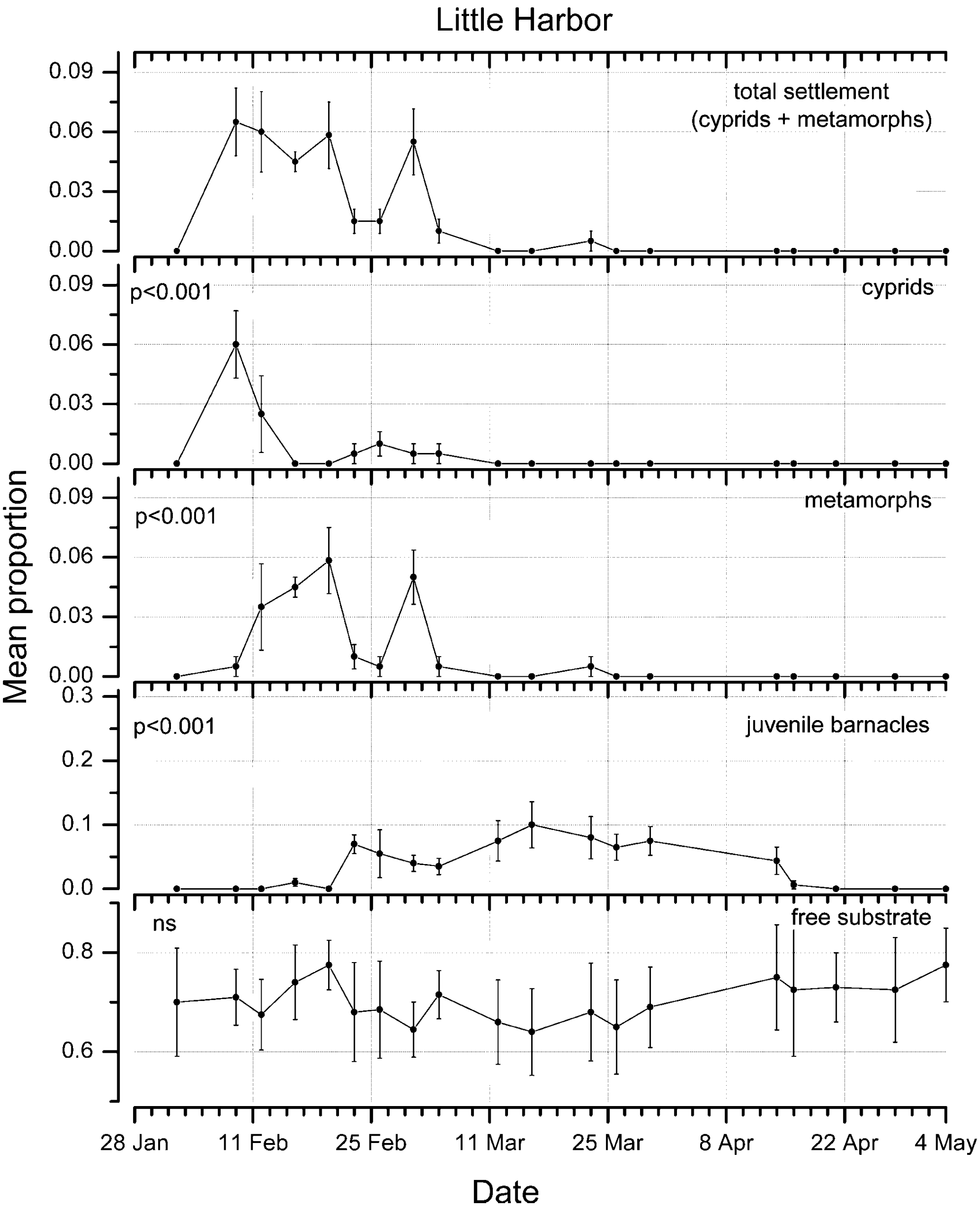
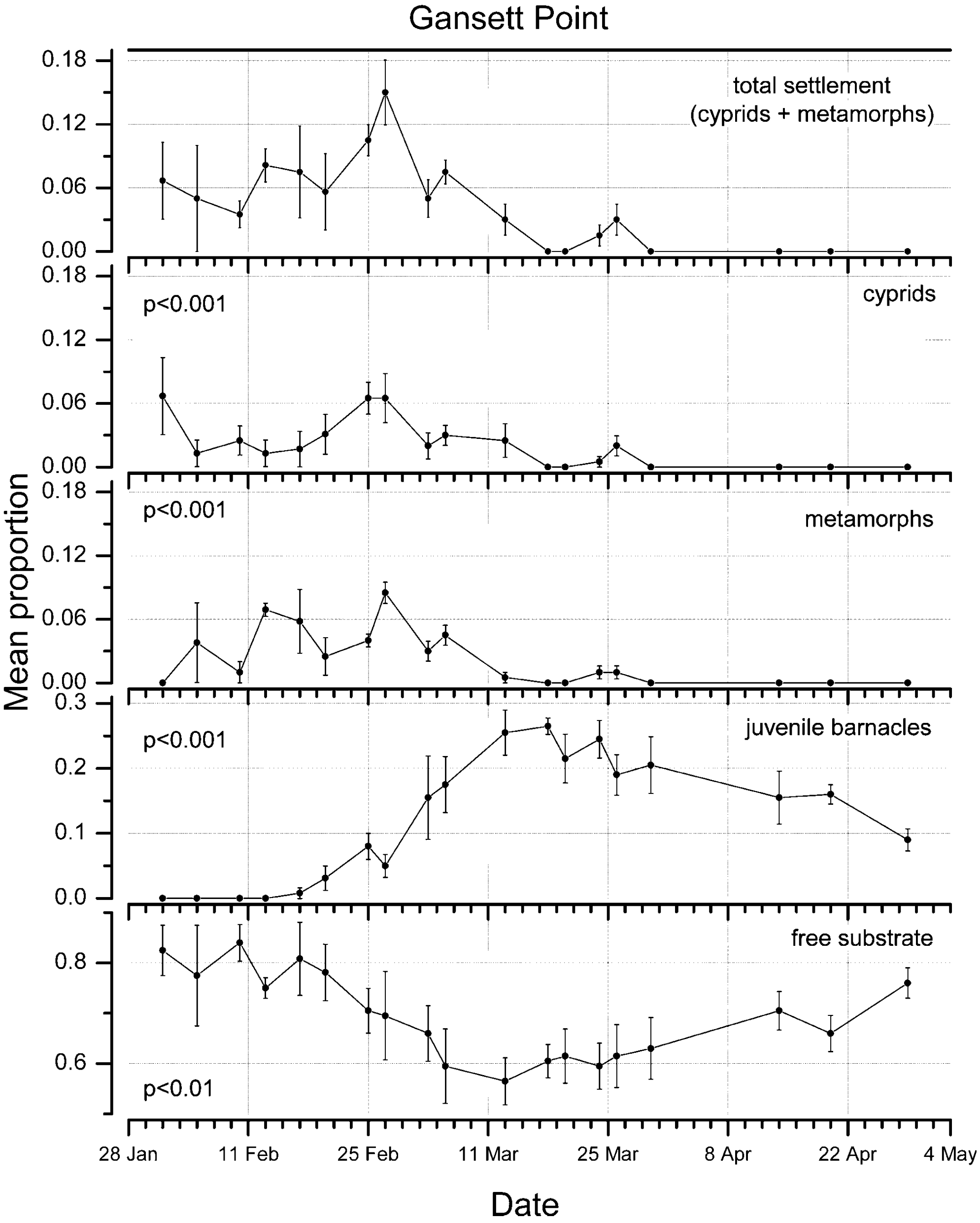


Fig. 6 *Semibalanus balanoides*. Gansett Point, natural substrate. Mean proportion cover (± 1 SE) of total settlers, cyprids, metamorphs, juvenile barnacles, and free substrate from 1 February to 29 April 1998. Probability from single-factor ANOVAs testing changes over time



strates (%) were plotted as functions of sampling date; all time series were standardized to sum to 100% (Fig. 7). The values used in the density of settlers (plate) were taken from the original sampling intervals (not those standardized to 2 days). The interpretation of these curves for settler density and settler cover differs. In settler density observations larvae settle on fresh substrates, while in settler cover measurements larvae experience the accumulation of individuals settling on previous sampling dates.

Half of the plate settlement density was sampled before 25 February at LH and before 4 March at GP (Fig. 7); thus, 50% of total settlement occurred about 1 week earlier at LH than at GP. The results were identical for settlement density on natural rock. The settler cover time series also shows earlier settlement at LH than at GP (half of the settler cover was reached on 16 February at LH and on 25 February at GP; Fig. 7). Half of the settlement cover, however, occurred earlier than half of the settlement density. The juvenile barnacle cover reached 50% about 4 weeks later than settler density cover (Fig. 7). This lag is in part due to the failure of metamorphs to transition to juvenile barnacles. Settler cover from 1 to 16 and 17 February at LH and GP accounted for 51.8% and 37.6% of the total, respectively. Settler cover during that period would be expected to account for practically all juvenile barnacle cover from 1 to 20 February. Juvenile cover during that period was very low (1.5% at LH and 1.7% GP), and it increased sharply at both sites after 20 February. Thus, from 1 to 20 February very few settlers transitioned from metamorphs to juvenile barnacles (Fig. 7). Note that average pelagic cyprid size increased on 20 February (Fig. 2).

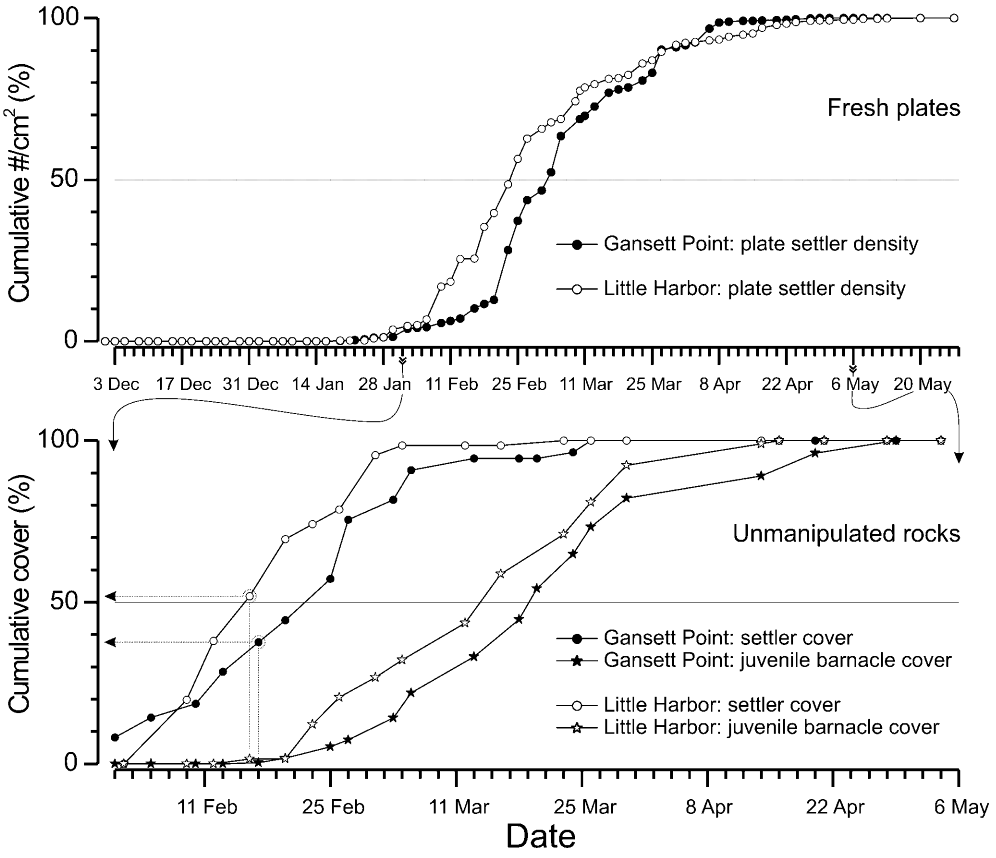


Fig. 7 *Semibalanus balanoides*. Cumulative density of plate settlers (*upper panel*) and cumulative percent cover of settlers and young barnacles on unmanipulated rocks (*lower panel*); *x–y arrows* in lower panel highlight period of low transition from settler to juvenile barnacle at both sites coinciding with differences in cumulative settler cover between the two sites

Discussion

Pelagic larvae: patterns in larval concentration and cyprid size

Semibalanus balanoides nauplii were collected from the WHOI pier from early December, and the first cyprids were sampled in mid-December. Cyprids were most abundant from February through mid-March. Fish (1925) found *S. balanoides* nauplii in the plankton during fall and cyprids in mid-winter. Barnes and Barnes (1958) reported *S. balanoides* nauplii in Woods Hole waters in late fall and cyprids in early winter. That larvae are present in the plankton for >5 months (Fish 1925; present study) suggests either a very long reproductive season or larval advection from other regions where barnacles have different reproductive schedules.

The cyprid length data showed no consistent trends over the season. Yet, two striking coincidences were that two peaks in larval concentration coincided with peaks in cyprid length and that the last three observations on mean larval size were the maxima for the entire season. This raises the question of the origin of these larger cyprids, which could have come from colder waters, either deep or north, or from within a large bay (such as Buzzards Bay). Crisp (1962) reported larger *S. balanoides* cyprids in arctic than in British waters (1,332 µm vs. 1,025 µm), and Gaines and Bertness (1992) found larger *S. balanoides* cyprids in Narragansett Bay than along the open coast.

Settlement and pelagic cyprid temporal patterns

Settlement and nearshore larval concentration series of invertebrates have rarely been collected at similar sampling frequencies during an entire settlement season and at a high frequency (e.g. 3–4 day^{-1}). Our data provide an opportunity to investigate nearshore larval concentration and settlement temporal patterns. Concentration of *S. balanoides* cyprids and settlement were low at the beginning and at the end of the observations, with maxima in February and early March. Half of all cyprids were sampled by 24 February, while half of all settlement at LH had occurred by 25 February. Other studies have found more vernal *S. balanoides* settlement north and southeast of Woods Hole. Settlement started in April at St. Andrews (450 km north of Woods Hole: Bousfield 1954), and peaked in late March and late April/early May at Nahant (~100 km north of Woods Hole: Wethey 1984; Jarrett 1997). (Settlement observations by Wethey and Jarrett did not begin until late March.) Settlement peaked in late February and March in Narragansett Bay (Bertness et al. 1992); this is consistent with Fish (1925), who pointed out that the *S. balanoides* breeding season appeared later at this bay than that at Woods Hole. The apparent paradox of a later *S. balanoides* settlement season for sites both north and southeast of Woods Hole has been noted (see Fish 1925; Barnes and Barnes 1959), but hypotheses explaining this phenomenon have not been tested. There is also the possibility that the earliness of the 1997/1998 settlement may represent an extreme. It appears clear, however, that the early winter occurrence of *S. balanoides* larvae in this region is a common phenomenon (Fish 1925; Lang and Ackenhusen-Johns 1981; present study).

Temporal patterns in settlement at LH corresponded roughly with the temporal patterns in cyprid concentration at the WHOI pier; the two largest peaks in settlement were near the two largest peaks in cyprid concentration. These results and the coincidence between half cyprid concentration and half settler density suggest that the coarse temporal patterns in Little Harbor settlement were determined by the availability of cyprids, a result also found in other systems (e.g. Yoshioka 1982; Minchinton and Scheibling 1991; Bertness et al. 1992). What is unknown is the functional relationship between nearshore larval concentration and settlement; two critical elements in this relationship are plankton patchiness and sampling interval (Pineda 2000). Temporal patterns of settlement at GP were less synchronous with cyprid concentration at the WHOI pier, with two of the three largest peaks in settlement (6 and 27 March) coinciding with relatively low cyprid concentration. Nearshore cyprid concentration at the WHOI pier appears to give a better estimate of potential larval supply at LH than at GP. The peaks in settlement at GP, in Buzzards Bay, on 23 February and 6 March were followed by corresponding peaks in settlement at LH, and cyprid concentration and size at the WHOI pier on 24–25 February and 9–10 March. This suggests that on those dates settlement at GP was by large Buzzards Bay cyprids, and that these large cyprids were later recorded at LH and the WHOI pier.

Disproportionate differences in settlement and gregarious behavior

Settlement rates were consistently higher at GP than at LH for both plates and rocks. Consistent spatial differences in settlement within a species are most likely related to local variability in nearshore larval concentration close to the settlement sites (Minchinton and Scheibling 1991), the amount of suitable substrate (Pineda 1994; Pineda and Caswell 1997), and small-scale hydrodynamics (Eckman 1990). Presumably, settlement differences between GP and LH were related to differences in nearshore larval concentration and not to the amount of suitable substrate or small-scale (within a few centimeters) hydrodynamics. This is because free substrate was about the same at GP and LH and because, while our natural and artificial settlement substrates were situated in a variety of hydrodynamic microenvironments, the differences in settlement between the two sites were consistent.

Settlement differences between the two sites were much larger for rocks than for plates. The disproportional differences may be related to gregarious larval behavior. Juvenile and adult barnacles often surrounded the quadrats on natural substrate, and this may have produced increased settlement due to gregariousness (e.g. Barnett and Crisp 1979) on rocks relative to the PVC plates. In sites with differences in nearshore larval concentration, this would produce disproportionate differences in settlement. Spatial differences in settlement reflecting spatial differences in nearshore larval concentration could therefore be enhanced by gregarious settlement behavior.

Proportion of unmetamorphosed cyprids

Relatively few settled cyprids metamorphosed within the 2-day sampling periods in the winter, but the proportion increased abruptly between 27 March and 1 April, coinciding with a 3°C increase in water temperature. It is clear that in winter some cyprids eventually metamorphosed after 2 days, as metamorphs were found on the natural substrates sampled at 3- to 7-day intervals from early February to late March. Connell (1961) reported that cyprids of *S. balanoides* transition to metamorphs in about 1.5 days, but the timing and environmental conditions of these observations were not reported. Jarrett (2000) found that most *S. balanoides* cyprids metamorphosed within 1 day, and that "no cyprid was observed to remain attached more than 3 days and still successfully metamorphose"; these observations at Nahant were from early April to late May, with water temperature ranging from 4.5°C to 12°C (J. Jarrett, personal communication). In the present study, the abrupt change in the proportion of unmetamorphosed cyprids in late March may be related to the sudden increase in water temperature, as higher temperatures shorten the larval period in other crustacean taxa (e.g. Uye 1988), and may speed up metamorphosis. Preliminary laboratory experiments suggest that successful metamorphosis is higher at 8°C than at 4°C for settled cyprids collected in middle and late March.

In southern California, from late April to early September, the proportion of unmetamorphosed *Chthamalus* spp. settlers to total settlers in daily samples was typically low (median $< 5\%$), but intermittently the proportion increased to $> 40\%$ (Pineda 1994). This phenomenon had an approximate fortnight periodicity (about 14.75 days), and it was suggested that metamorphosis was dependent on immersion times, with no metamorphosis in cyprids left dry by the receding tide (Pineda 1994). Data in the present study show that other factors with low-frequency variability, such as the seasonal change in water temperature, may determine the duration of metamorphosis in settling cyprids. The population consequences of trends in metamorphosis time in barnacle cyprids are unknown. Pyefinch (1948) asserted that "roughly 50%" of *S. balanoides* settlers die during metamorphosis, while

Connell (1961) reported that 70–95% of the attached cyprids metamorphosed. Power et al. (1999) suggested that differences in settlement/recruitment ratios in two chthamalid barnacles in Ireland might be explained by differences in metamorphosis success. Jarrett (2000) found generally higher mortality in attached *S. balanoides* cyprids than in metamorphs, and the cyprid mortality varied among five cohorts, from 15% to 43%. Metamorphosis success from cyprid to metamorph may thus be species-specific (Power et al. 1999), depend on immersion time (Pineda 1994), water temperature (present study) or larval pelagic feeding experience, as is the case for juvenile growth (e.g. Jarrett and Pechenik 1997).

Space occupancy

Free substrate can be a limiting resource for barnacles (Hatton 1938), but since free substrate accounted for ca. 70% of the total space, it was probably not limiting in the present study. Space occupied by settlers peaked in February and March and decreased to zero afterwards. Juvenile cover lagged settler cover by about 4 weeks at GP and LH. At LH, juvenile barnacle cover decreased from a maximum of 10% to nil at the end of the observation period. Thus, all settlement failed. These observations of zero survival contrast with previous studies on *S. balanoides*, in which there was some survival in all cases (Connell 1961; Wethey 1986; Jarrett 2000). At GP, juvenile barnacle cover peaked at 25%, and decreased to 10% by the end of the observation period. The changes in free-substrate cover at GP, the site with highest settlement, appeared to be determined by juvenile barnacle cover, since metamorphs and cyprids occupied very little space and percent cover in adults did not change.

Our results suggest that small differences in the timing of settlement and non-lagged, coherent (spatially correlated) mortality of the settlers may produce large differences in juvenile cover. Very low transition from settler to juvenile barnacle at the two sites in early February, together with earlier settlement at LH than at GP, had the potential to enhance juvenile cover at GP relative to LH. The importance of this phenomenon cannot be assessed, because GP also had higher settlement rates, which may contribute to higher juvenile barnacle cover. While juvenile barnacle cover at GP was higher than at LH, adult cover was consistently lower. Adult cover is dependent on juvenile barnacle survival and post-settlement mortality, including the effects of predation prior to our observations, and therefore we cannot evaluate the relative contributions of these two variables to the observed adult cover. However, there is some evidence that very high settlement in *S. balanoides* may result in negative density dependence, with no survival to reproduction (Connell 1985). This may help explain the result of lower adult cover at Gansett Point, the site with highest settlement.

Timing in settlement and space occupancy

Half of the total settlement cover in the unmanipulated quadrats occurred earlier than half of the total settlement density on the fresh plates and brushed rocks. Connell (1985) reported higher settlement of *S. balanoides* on fresh substrates than in unmanipulated ones, with larger differences late in the season than early on. Our results and Connell's are explained by higher settlement on fresh substrates than on unmanipulated plots later in the season. It is not clear, however, what mechanisms would explain this phenomenon (see also Wethey 1984; Raimondi 1990).

In summary, temporal variability in settlement was determined to some extent by nearshore cyprid concentration, while seasonal changes in juvenile cover were influenced by successful metamorphosis and juvenile mortality. We observed very different patterns of settlement and juvenile barnacle cover at two sites separated by about 1 km. Clearly, studies on settlement variability at ca. 100 km or larger scales should not neglect the 1–10 km scale. Finally, our results suggest that metamorphosis of attached cyprids was influenced by temperature.

Acknowledgements R. Scheltema first mentioned that C.J. Fish observed nauplii and cyprid larvae in late fall and winter. The NOAA Northeast Fisheries Science Center provided the temperature data. The NOAA Center for Operational Oceanographic Products and Services (CO-OPS) provided the Woods Hole "verified/historic" water level data for calculating immersion times and tidal range at Woods Hole (station number 8447930). We appreciate the comments and criticisms of C. DiBacco, H. Fuchs, J. Jarrett, E. Parnell, V. Starczak, F. Tapia, and two anonymous reviewers. This work was supported by the US National Science Foundation and by WHOI's Reinhart Center for Coastal Research. This is WHOI contribution 10,553.

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