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High-frequency observations of early-stage larval abundance: do storms trigger synchronous larval release in *Semibalanus balanoides*?

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Abstract The acorn barnacle, *Semibalanus balanoides*, is thought to release larvae in response to phytoplankton blooms, but there is evidence that another, unidentified cue for release may exist. We conducted high-frequency sampling in Little Harbor, Massachusetts, USA, to determine whether early-stage larval abundance was related to several environmental variables, and to characterize vertical distributions of the larvae. Larval concentrations peaked at 2.52 and 1.02 individuals l^{-1} during two storms. Larvae were more abundant near the surface than near the bottom. We suggest the hypothesis that turbid conditions and upward-swimming behavior may protect newly-released larvae from predation and cannibalism. Future studies should test this hypothesis with barnacles and other invertebrates.

Introduction

Synchronous reproduction is common among marine invertebrates. When individuals in a population release gametes or larvae synchronously, large pulses of biomass are introduced into the water column. The gametes and larvae are preyed upon by many organisms, and planktotrophic larvae prey on other organisms as well. Consequently, the timing of synchronous reproduction can have a large impact on the structure of marine food webs and the recruitment success of the organisms involved. *Semibalanus balanoides* (L.) is among the coastal marine invertebrates that reproduce synchronously. It is a highly abundant, boreo-arctic barnacle species found on rocky intertidal zones along the eastern and western coasts of North America and the northwestern coast of Europe. It reproduces once per year in the winter or spring. Within a population, planktonic larvae are released in one or more bursts, and the release period generally ends in less than 2 weeks (Barnes 1956; Crisp 1959; Lang and Ackenhusen–Johns 1981; Pineda et al. 2004). The larvae can constitute 15% of zooplankton in coastal waters of the northeastern United States (Frolander 1955), but their pervasiveness is limited, since the planktonic larval stage typically lasts only 3–6 weeks (Barnes and Barnes 1958). Since *S. balanoides* nauplii make up a substantial but temporary part of the zooplankton, identifying the factors that trigger larval release would help elucidate patterns of zooplankton community variability.

Field and laboratory studies have identified high food concentration as the environmental cue that triggers larval release in *Semibalanus balanoides*. Barnes (1956, 1957, 1962) reviewed multiple years of field data from several locations in the North Atlantic and showed that nauplius abundance generally increased when diatom blooms occurred. Laboratory studies (Crisp 1956; Barnes 1957; Crisp and Spencer 1958; Starr et al. 1991) found larval release in response to feeding, as long as the food was provided in high concentrations. As these authors noted, high food concentration may be a sign that a phytoplankton bloom is underway, and it would be beneficial for nauplii to be released into an environment of high food abundance.

However, some data suggest that there could be a different or additional cue for larval release. First, field studies have shown that release is often, but not always, synchronized with phytoplankton blooms. In his review of 9 years of data from Millport, Scotland, Barnes (1962)

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found 2 years (1950 and 1960) when nauplius release occurred in the absence of a diatom bloom. Second, barnacles in the laboratory release larvae in response to food, but the response is substantial only when the food is given in concentrations much higher than those in typical blooms (Starr et al. 1991). Third, barnacles do not seem to be able to recognize phytoplankton chemically: When exposed to phytoplankton culture filtrates in the laboratory, adults did not respond (Starr et al. 1991). Fourth, release can be triggered by exposure to high concentrations of brine shrimp larvae, which is not a typical food item for adult barnacles or their nauplii (Starr et al. 1991). In summary, there are indications that the timing of larval release is often correlated with phytoplankton blooms, but the blooms themselves may not be the trigger. Instead, *Semibalanus balanoides* may be using an unidentified cue for larval release.

A limitation of the field studies (e.g. Barnes 1956, 1957, 1962) performed so far is that the sampling resolution was on the order of days, and this may not be sufficiently high to determine the environmental characteristics at the exact moment of release. Environmental conditions can change on the scale of hours or minutes, and once they are liberated, the larvae could be transported away from the site of release within hours. Studies conducted at fine temporal scales are rare (but see Macho et al. 2005) because they are logistically difficult, but they can provide valuable insight into phenomena such as synchronous larval release.

In addition to the environmental conditions at the time of release, the behavior of newly-released larvae can provide clues about the factors that are most important in shaping synchronous release behavior. For example, larvae that swim to deep waters during the day may be avoiding visual predators, and this might explain why adults of some species release larvae synchronously at nighttime (Morgan and Christy 1996). The final (cyprid) stage of *Semibalanus balanoides* larvae tends to be found near the middle of the water column (Bertness et al. 1996). Distribution and behavior of the early naupliar stages has received less attention. Early-stage nauplii in the laboratory are attracted to light, presumably so that they will swim toward the surface to escape the benthic environment and its associated planktotrophic predators (Singarajah et al. 1967; Macho et al. 2005). Some studies (e.g. Bousfield 1955) have stated that newly-released nauplii occur near the surface, but we were unable to find published studies that quantified vertical distributions. If nauplii indeed swim toward the surface to escape planktotrophic predators, then synchronous larval release would be expected to occur under environmental conditions that would facilitate this escape.

The present study investigated whether larval release is related to environmental variables that have received less attention in the published literature. These variables include water temperature and salinity, tidal height, lunar phase, air temperature, wind speed, precipitation, and atmospheric pressure (a proxy for storminess). To obtain high-resolution measurements, we sampled larvae on the scale of hours and environmental variables on the scale of minutes. We also quantified the vertical distribution of early-stage nauplii to determine whether their concentrations are higher near the surface than near the bottom.

Materials and methods

Study site

This study was conducted in Little Harbor, located in the town of Woods Hole, Massachusetts, USA (41° 31.249′ N, 70° 39.952′ W). Little Harbor is an embayment that is oriented with its long axis in the North–South direction (Fig. 1). The mouth is located along the southern end. The bay is 0.63 km long. Its width is approximately 200 m along the northernmost half, and 300 m along the southernmost half. The shores of the bay are lined with rocks, boulders, a few concrete piers, and numerous smaller wooden docks. Adult *Semibalanus balanoides* are attached to these surfaces all around the bay. Other barnacle species are also present. *Chthamalus fragilis* Darwin can be found just above *S. balanoides* in the intertidal zone. *Balanus crenatus* Brug., *B. eburneus* Gould, and *C. stellatus* (Poli) have also been reported near Woods Hole (Fish 1925). The bottom of the bay is mainly sand. Most of the bay is shallow, with an average depth of approximately 2–3 m, but the center has a 60-m-wide dredged channel that is approximately 4 m deep. The mean tidal range is 0.43 m (NOAA 2010a).

Timing of larval release in relation to environmental variables

Previous research (Fish 1925; Lang and Ackenhusen–Johns 1981; Pineda et al. 2002, 2004) showed that *Semibalanus balanoides* in the Woods Hole area release their larvae in mid-December to early January. Therefore, we conducted our high-frequency larval samples from December 27, 2006 to January 10, 2007. Plankton samples were taken every 2 h from the northernmost pier in Little Harbor. Out of 167 possible samples during this time period, 141 were obtained. Sampling was impossible during 26 instances due to equipment failure, severe weather, or shortage of volunteer helpers.

Plankton samples were obtained with an Ebara submersible sewage semi-vortex impeller pump, which had strong suction and a flow rate of approximately 200 l min^{-1}.

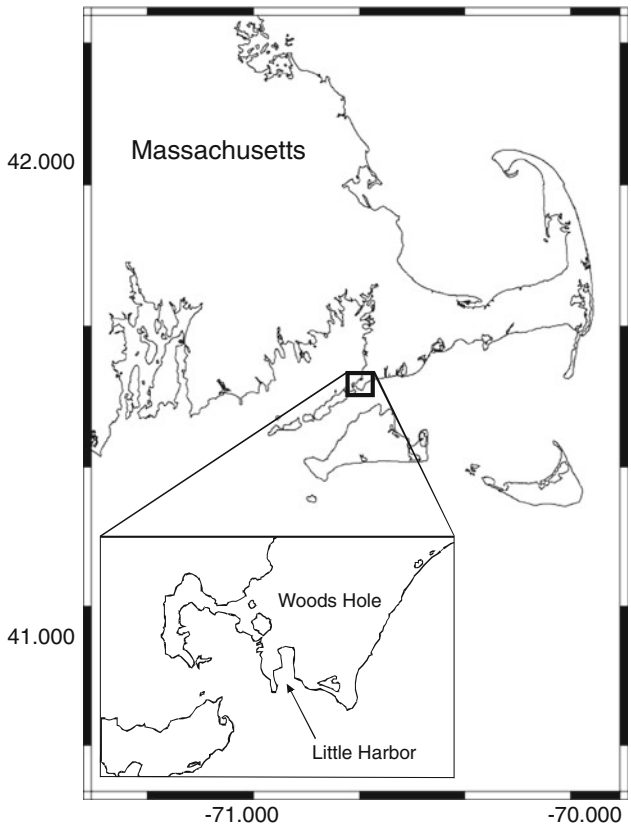

Fig. 1 The study site was Little Harbor, an embayment in the northeastern coast of the United States

The actual volume pumped for each sample was measured with a flow meter (Great Plains Industries, model TM200). Because water does not flow through the pump impeller, crustacean larvae are not damaged during sampling. The pump hung from a pier piling approximately 1 m above the bottom. At the sampling site, total water depth was approximately 2.5 m at high tide and 2.1 m at low tide. When possible, at least 1,000 l of water were pumped and filtered through a 100-μm mesh. On a few occasions, large quantities of suspended sediments after a storm made it difficult to filter such a large volume, so smaller samples were taken.

Most samples were preserved in 95% ethanol immediately after filtering. When immediate preservation was not possible, samples were stored in a cooler with ice packs for less than 12 h, and then preserved in ethanol. Stage I and II *Semibalanus balanoides* nauplii were identified according to Crisp (1962). It can be difficult to identify stage I and II nauplii to species, but the differences in the reproductive season of local barnacles provided certainty that the nauplii in the samples belonged to *S. balanoides*. The reproductive season of *Chthamalus fragilis* is July–August (Fish 1925; Lang and Ackenhusen–Johns 1981). *Balanus crenatus* nauplii are found from June until the middle of July (Fish 1925). *B. eburneus* and *C. stellatus* nauplii have been observed in August (Fish 1925).

The concentration of stage I and II nauplii in each sample was calculated. Only the first two naupliar stages were counted because *Semibalanus balanoides* transition from stage I to stage II within minutes to hours of being released (Barnes and Barnes 1958), and from stage II to stage III in approximately 3 days (Harms 1984). Focusing on the first two stages increased the probability that we were sampling larvae that had been released very recently at our site, and not larvae that had been advected from elsewhere.

While taking plankton samples, we used a YSI probe to measure water temperature and salinity. Additionally, weather data were downloaded from the weather underground website (www.wunderground.com) for the weather station KMAOAKBL1, which is located at 6 m elevation in Oak Bluffs, MA (41° 27′ 14″ N, 70° 34′ 43″ W). The weather station is 10.5 km away from the study site. Its record is the most complete out of all the weather stations in the area, and the data are nearly indistinguishable from the available records of other stations that are closer to the site (data not shown). Tidal height data were obtained from the dock at the Woods Hole Oceanographic Institution with a Paroscientific pressure gauge. The measurements are relative to mean sea level.

Statistical analysis of the relationship between larval abundance and atmospheric pressure

Initial assessment of the field sampling data suggested a strong relationship between larval abundance and winter storms, which can be identified by periods of low atmospheric pressure, high wind speeds, increased precipitation rate, and sometimes lower salinity. Since those three environmental variables are related, we focused on the relationship between nauplius abundance and atmospheric pressure. We conducted a superposed epoch analysis (SEA) to determine whether the relationship was significant. SEA is a tool for analyzing time-series data. It is analogous to a *t*-test in the sense that it can be used to compare two means, but it is a non-parametric test (Prager and Hoenig 1989). Superposed epoch analysis was developed by Chree (1912) for the analysis of geophysical data (Singh and Badruddin 2006). Since then, it has been applied to physical-biological relationships such as sea level and recruitment success of chub mackerel (Prager and Hoenig 1989); wind direction or water stratification and settlement of barnacle larvae (Ladah et al. 2005); and hydroclimatic variability and abundance of salps (Licandro et al. 2006).

Superposed epoch analysis compares the average nauplius concentration during "key events" to the average concentration during "background periods", and determines

whether the differences are statistically significant. A "key event" is defined here as a time period in which the atmospheric pressure was at least one standard deviation below the mean "winter" atmospheric pressure. "Winter" is defined here as the period between December 1, 2006 and February 6, 2007, since this is when the atmospheric pressure data were available. "Background periods" are the times in which a key event is not taking place.

Mean nauplius concentrations were calculated for the key events and for the background periods, and then they were compared by using the *W*-statistic as defined in Prager and Hoenig (1989). The null distribution of the *W*-statistic was determined with a Monte Carlo randomization. Then, a *P*-value was calculated to determine whether the null hypothesis could be rejected. The null hypothesis here is that *for this dataset*, there is no relationship between atmospheric pressure and larval abundance. Since the key events were defined *after* the data had been examined, and since only one year of data is available for one location, the results of the SEA analysis cannot be used to test the general hypothesis that larval abundance is related to atmospheric pressure. However, the results of the SEA analysis can be used to formulate the general hypothesis, which can then be tested with future datasets and experiments.

Three key events were identified: between 17:15 on January 1 and 07:16 on January 2, between 5:31 on January 6 and 21:16 on January 6, and between 06:30 on January 8 and 01:01 on January 10. The background periods were the time step before and the time step after each key event. Only the first two key events were used for this analysis because the third event was too close to the end of the time series, and one of its corresponding background periods would have fallen outside the time series. Moreover, during the third storm event, high turbidity clogged the plankton pump and prevented us from taking plankton samples for 8 h. It is possible that a larval release event occurred during this time period but went undetected.

Once the *W*-statistic had been calculated, it was necessary to determine whether its value was sufficiently large to reject the null hypothesis. To do this, the observed *W*-statistic was compared to the distribution of the *W*-statistic under the null hypothesis. The distribution under the null hypothesis was calculated by using a Monte Carlo simulation that randomly placed the key events (and their flanking background periods) along the time series. The *W*-statistic was then computed, and the simulation was repeated 100,000 times using a MATLAB program. For each iteration, if a key event or one of its background periods fell outside the range of the time series, then that iteration was discarded. The estimated *P*-value of the observed *W* was then calculated using the formula $(x + 1)/(v + 1)$, where x is the number of randomized values of *W* that were greater than the observed *W*, and v is the total number of randomly generated values of *W*.

Vertical distribution of barnacle larvae

From December 9, 2008 to January 23, 2009, larvae were sampled from the northernmost pier in Little Harbor with two pumps (Pondmaster). These pumps were different from the one used to investigate the timing of larval release—their suction was gentler, so they each sampled a narrower horizontal layer of the water column. One pump was placed 0.25 m above bottom. The other pump was placed 0.25 m below the surface. The total water depth was approximately 2.5 m at high tide. Twenty samples were taken over the 46-day sampling period. The time of sampling was chosen haphazardly, and included both daytime and nighttime hours. The pumps were designed to sample at a rate of approximately 16 l min^{-1}, but the exact volume of water pumped was measured with flow meters (Great Plains Industries). The mean volume of water per sample at the surface was 39.8 l (SD = 18.7, $N = 17$), and the mean volume per sample near the bottom was 43.5 L (SD = 19.4, $N = 17$). Samples were filtered through 100-μm mesh. Stage I and II nauplii were counted less than 12 h after sample collection. The difference in nauplii concentrations near the surface and near the bottom was analyzed by using a paired comparisons *t*-test (Sokal and Rohlf 1995). The analysis did not include samples in which surface and bottom larval concentrations were zero.

Results

Timing of larval release in relation to environmental variables

Two large peaks in nauplius abundance occurred during the two-week sampling period (Fig. 2a). The first peak was at 23:00 on January 1, and the second peak was at 11:00 on January 6. Smaller peaks occurred in between. The two main peaks coincided with two storm events, which were characterized by low atmospheric pressure (Fig. 2b), precipitation (Fig. 2e), and lower salinity (during the first event only, Fig. 2f). The highest wind speeds of the time series occurred less than 12 h before the peaks in larval abundance (Fig. 2c). During storm events, high turbidity was observed (but not measured) in the water. The two large peaks in larval abundance also occurred within 24 h of strong winds that were from the south or had a southerly component (Fig. 2c, d). Almost all average daily wind velocities had a westerly component, which is typical for this location at this time of year (NOAA 2010b).

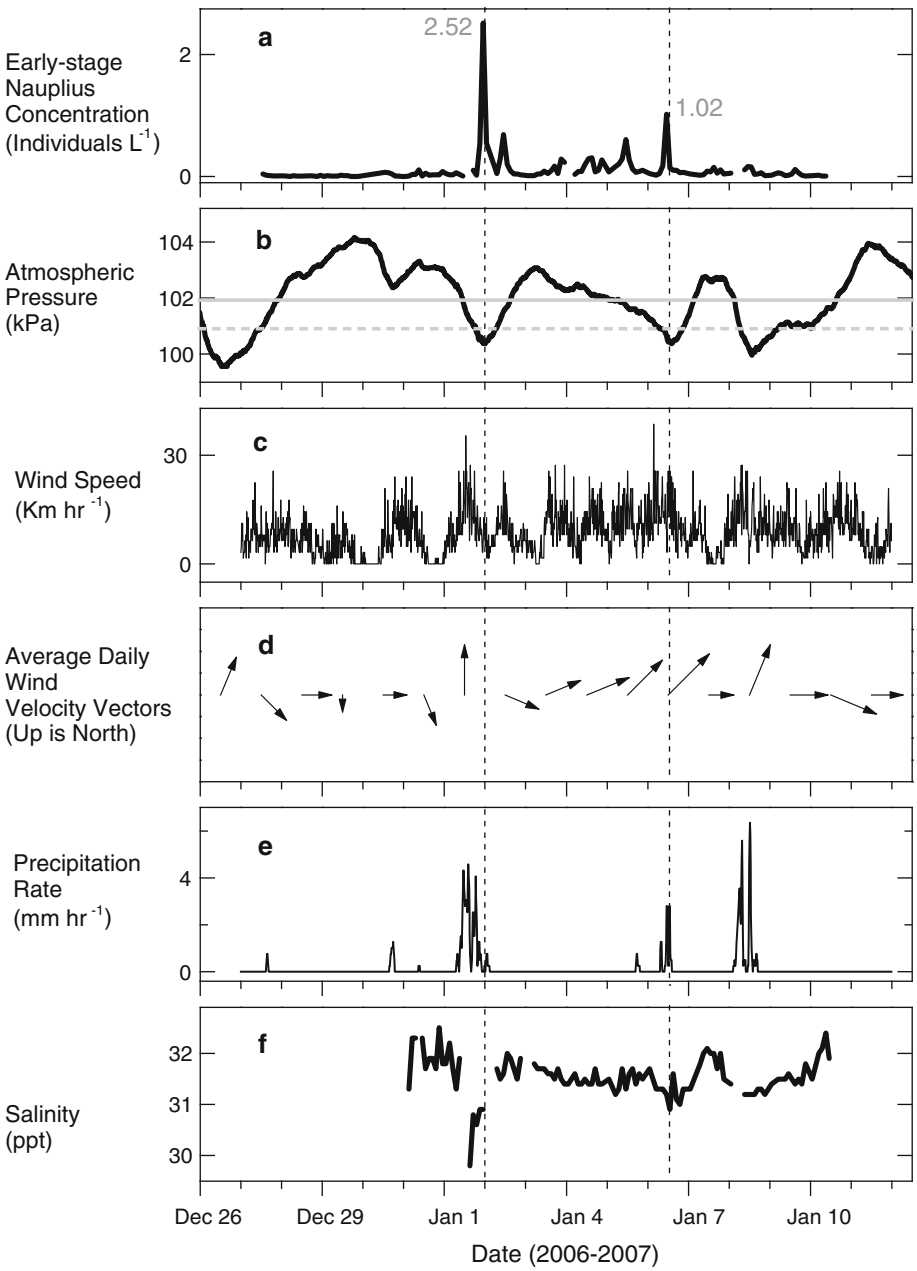

Fig. 2 **a** Early-stage nauplius abundance in Little Harbor shows *two large peaks* and a few smaller ones. *Vertical dashed lines* have been drawn for ease of comparison. **b** The mean atmospheric pressure between December 1, 2006 and February 6, 2007 is shown by the *horizontal grey line*. The *horizontal dashed line* represents one standard deviation below the mean. The *two largest peaks* in nauplius abundance coincide with two periods of low atmospheric pressure that occurred during stormy weather. The *two peaks* in larval abundance occurred within 24 h of high wind speeds (**c**) that were from the south or had a southerly component (**d**). **e** Precipitation rates increased with the arrival of the storms. **f** A sharp drop in salinity was associated with the first storm, but not the second

Larval release occurred around the time of the full moon (Fig. 3a). Although the peaks in larval abundance coincide with periods of high water level, they did not occur at the same phase of the tide (Fig. 3b). The first peak happened during an ebbing tide, and the second peak happened during a high tide. Larval concentrations did not appear to be related to air temperature (Fig. 3c) or water temperature (Fig. 3d).

The mean atmospheric pressure for the winter was 101.930 kPa (SD = 1.016, $N = 6{,}358$), so atmospheric pressures below 100.914 kPa were considered to be "key events" in the SEA analysis. The two largest nauplius abundance peaks coincided with two key events on January 1 and January 6 (Fig. 2b). According to the SEA analysis, this relationship was statistically significant. The observed value for the *W*-statistic was 2.824. Out of 100,000 iterations of the Monte Carlo simulation, 31,379 had to be discarded because a key event and/or one of its background periods fell outside the range of the time series. This left 68,621 usable calculations of the *W*-statistic. Out of these, 2,139 were greater than the observed *W* value of 2.824. Thus, the *P*-value of the observed *W* was 0.031, which is less than the chosen α level of 0.05.

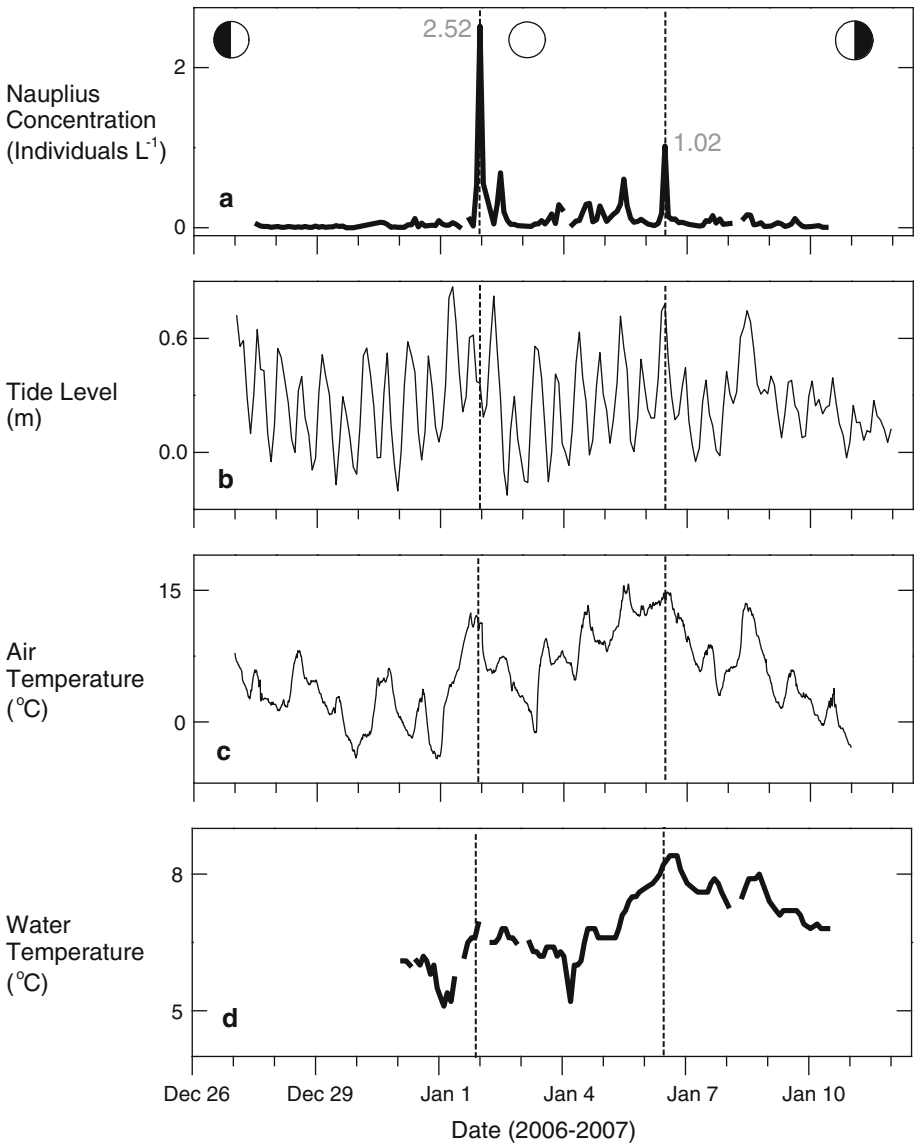

Fig. 3 **a** Early-stage nauplius concentration in Little Harbor presented again for comparison with other variables that we investigated. The *shaded* and *unshaded circles* represent the phases of the moon. Larval release occurred near the full moon. **b** The *two peaks* in larval abundance did not occur during similar tidal phases; the *first peak* happened during an ebbing tide, and the *second peak* occurred during a high tide. **c** Air temperatures were high during the peaks in larval abundance, but they were also high during times when peaks were not observed. **d** The peaks in larval abundance do not seem to be related to water temperature

Vertical distribution of barnacle larvae

Mean nauplius concentration near the surface was 2.20 nauplii l^{-1} (SD = 3.45, $N = 17$) (Fig. 4). Mean nauplius concentration near the bottom was 0.31 nauplii l^{-1} (SD = 0.67, $N = 17$). The difference between the two means was highly significant ($P < 0.001$).

Discussion

High food concentration has been identified repeatedly as the trigger for larval release in *Semibalanus balanoides* (e.g., Barnes 1956, 1957, 1962; Crisp 1956; Crisp and Spencer 1958; Starr et al. 1991). Through high-frequency sampling, we observed that early-stage larval abundance of *S. balanoides* in Woods Hole was significantly related to winter storms. These storms are not likely to cause winter-spring phytoplankton blooms in our study area. Research on sub-arctic and temperate shallow, coastal waters has shown that the onset of winter-spring blooms is determined partly by the amount of solar radiation available to phytoplankton cells. High turbidity from storm activity can reduce the amount of light available and delay the onset of blooms (Gran and Braarud 1935; Pingree et al. 1986; Townsend and Spinard 1986; Townsend et al. 1994).

Nevertheless, winter storms resuspend benthic diatoms and other organic matter (Fish 1925; Parmenter et al. 1983), perhaps triggering larval release even in the absence of a full-blown bloom. Water turbulence and feeding rate may have an impact on larval release in *Semibalanus balanoides*. Turbulence increases the feeding activity of barnacles (Barnes and Barnes 1982), presumably increasing the rate of food intake. As feeding rate increases, so

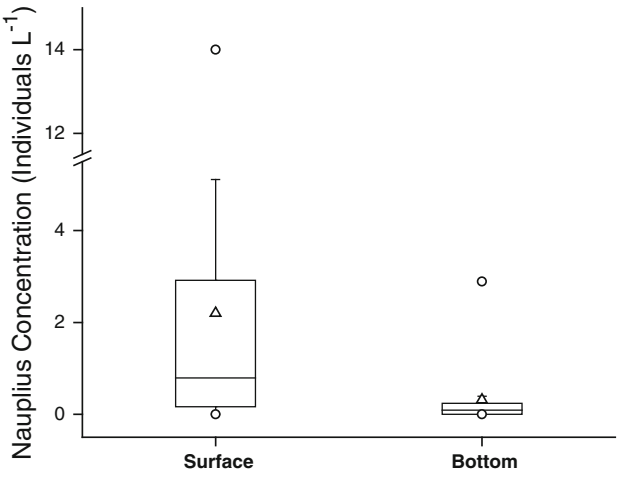

Fig. 4 Mean nauplius concentration (indicated by *triangles*) was significantly greater near the *surface* than near the *bottom* in December 2008–January 2009. The *horizontal lines* of the *boxes* depict the 25th percentile, the median, and the 75th percentile. The *whiskers* represent the 5th percentile and the 95th percentile. The *circles* identify the minimum and maximum values

does the rate of molting (Barnes and Barnes 1982). Starr et al. (1991) found that the rate of molting is positively correlated with larval release in the laboratory, so they suggested that larval release is positively related to feeding. Since storms increase the strength of water turbulence and the availability of food particles, they have the potential for stimulating larval release. Barnacle larvae may feed on the resuspended material, but if it sinks again when wind stress decreases, then this would not be a sustainable food source.

Semibalanus balanoides seems to time its reproductive season to coincide roughly with the onset of winter-spring phytoplankton blooms. This pattern has been observed along the eastern coast of North America and the northwestern coast of Europe (Barnes 1956, 1957, 1962). In northeastern North America, both diatom outbursts and *S. balanoides* larval release generally occur sometime between February and April, and the events tend to occur later with increasing latitude (Barnes 1957). Woods Hole is an anomaly in this pattern. Diatom outbursts and larval release occur earlier there than in locations north or south, for reasons that remain unclear (Fish 1925; Barnes and Barnes 1959; Lang and Ackenhusen–Johns 1981). Crisp (1964) proposed that barnacle populations may be genetically adapted to local bloom patterns and time their fertilization so that embryos are ready to be released by the time that blooms usually appear. We suggest an additional hypothesis regarding the timing of reproduction: on a finer temporal scale, adult barnacles release larvae in response to high turbidity to protect the larvae from predation.

Increased turbidity during storms could provide a predation refuge if it swamps predators with high concentrations of additional particles. Potential predators include neighboring barnacle adults of the same species. Since *Semibalanus balanoides* lives in high densities and the larvae are weak swimmers when they first emerge, there is risk of cannibalism at the time of release. In the laboratory, *S. balanoides* have been observed to consume their own nauplii (Crisp and Patel 1960). In the field, nauplii comprised 16% of the food items in the gut of the barnacle *Semibalanus cariosus* (Pallas) (Navarrete and Wieters 2000). Storms can also intensify currents and reduce the residence time of water in the surf zone, so larvae released in stormy conditions may have a survival advantage if they are transported away quickly from planktotrophic predators associated with the surf zone (Amend and Shanks 1999; Onitsuka et al. 2007).

Our finding that *Semibalanus balanoides* nauplii concentrate near the surface is consistent with the idea that predation is an important danger that larvae face during the early stages of development. It has been suggested previously that swimming upward toward light allows larvae to escape incidental ingestion by adults (Singarajah et al. 1967, Macho et al. 2005). We confirmed that early-stage nauplii in the field tend to be found near the surface. It is unclear whether larvae would be able to stay near the surface under very turbulent conditions. Nonetheless, we suggest that high turbidity could protect larvae during high turbulence events, and upward-swimming behavior could protect them during low turbulence periods.

In our observations, peaks in larval concentration were short-lived, lasting less than 8 h. Previous studies of *Semibalanus balanoides* larval release have sampled on a daily (or less frequent) time scale, but our results show that a higher sampling frequency is required to properly characterize the patterns of larval release in the field. The ephemeral nature of high larval concentrations also suggests that nauplii were transported away quickly, which is an advantage for larvae that face strong predation pressure near the site of release. It is possible that the peaks in larval abundance in our data were caused by larval patches advected from elsewhere. We think that this is unlikely, however, because by including only the first two naupliar stages, we maximized the likelihood that the larvae in our samples had been in the water column for a short time and thus had been released locally.

Early-stage nauplius abundance seemed related to wind velocity. The highest concentrations of larvae occurred less than 24 h after periods of strong winds with a southerly component. Little Harbor is oriented in the North–South direction, with the mouth of the harbor in the southern end. Thus, it is possible that winds from the South led to retention and accumulation of larvae in the harbor. However, if wind-driven transport was causing the patterns in larval abundance, then we would have expected the high larval concentration on January 6 to keep increasing until at

least the following day, since the wind had a strong southerly component on the 6th and then died down to a light westerly breeze on the 7th (Fig. 2c, d). This suggests that the peak in abundance occurred not as a result of the accumulation of individuals that were already in the area, but as a result of mass liberation of nauplii at that time.

An alternative explanation for our results is that more larvae were sampled during storms because the water column was well mixed. We showed that larval concentrations are highest near the surface, yet our semi-vortex impeller pump was 1–1.5 m below the surface. However, the pump had a very strong suction, and if it had not been sampling larvae adequately near the water surface, then we would have expected to see the highest concentrations of nauplii during low tides, when the pump was closer to the surface. We did not see such a pattern in our data. Instead, the two highest peaks in nauplius concentration occurred during some of the highest tides of the sampling period (Fig. 3b). Furthermore, even though high-wind conditions lasted approximately 24 h during each storm event, the peaks in larval concentrations did not last more than 8 h (Fig. 2a, c).

In summary, through our high-frequency sampling of *Semibalanus balanoides* early-stage larvae, we observed that peaks in larval abundance coincided with the passage of winter storms. We suggest that the adult barnacles responded to high turbidity levels, since releasing under those conditions could protect their larvae by swamping potential predators. Furthermore, strong storm-generated currents might sweep larvae away from the surf zone. Swimming upward toward the surface could also help larvae escape benthic predators, when turbidity decreases after a storm. Perhaps food availability for nauplii leads *S. balanoides* to release larvae near the average date of local winter-spring phytoplankton blooms, but predation on newly-released nauplii may fine-tune the timing of release to coincide with high-turbidity events. Other benthic invertebrates may also employ the same strategy to protect their larvae from planktotrophic predation. Future experimental and observational work should test this hypothesis.

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