

# Turbidity triggers larval release by the intertidal barnacle *Semibalanus balanoides*

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**ABSTRACT:** Gravid adults of the common intertidal barnacle *Semibalanus balanoides* (L.) brood fully developed larvae until individuals perceive some cue from the environment that triggers synchronous larval release. The prevailing hypothesis has been that phytoplankton blooms trigger release because they provide a food source for nauplius larvae. Through observations and field experiments, we tested the hypothesis that turbidity from any source, not just phytoplankton blooms, can trigger release. We documented 5 larval release events at 3 sites in the northeastern USA. Two events coincided with chlorophyll increases, and all 5 coincided with turbidity increases. In experiments, the larval release response was equivalent when adults were exposed to diatoms or inert synthetic beads, and it was significantly higher than under exposure to filtered seawater. We also tested the hypothesis that turbidity can decrease the risk of cannibalism for newly released nauplii. Under experimentally manipulated conditions, adults consumed significantly fewer nauplii in a high-turbidity environment. We suggest that reproduction in this species may have evolved to coincide roughly with the local onset of winter/spring phytoplankton blooms, but the timing of larval release may have been fine-tuned further by cannibalism and predation pressures. The potential for turbid conditions to serve as a refuge for planktonic larvae of other marine organisms merits further investigation.

**KEY WORDS:** Synchrony · Turbidity · Reproduction · Larvae · Cannibalism · Barnacles

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## INTRODUCTION

The plankton community in coastal waters of the temperate North Atlantic Ocean changes considerably with the seasons. In late winter or early spring, dense diatom blooms appear, and they are often followed shortly after by pelagic nauplius larvae of the common and widespread intertidal barnacle *Semibalanus balanoides* (Fish 1925). In some areas, *S. balanoides* larvae account for up to 15% of zooplankton individuals (Frolander 1955), but remain in the water column for only 3 to 6 wk (Barnes & Barnes 1958). Nauplii feed on phytoplankton and are themselves prey for carnivorous zooplankton and planktivorous fish (Lockhead 1936, Bousfield 1955). Therefore, the

timing of *S. balanoides* larval release relative to the seasonal population dynamics of other species could have an important effect on coastal marine food webs.

Gravid *Semibalanus balanoides* adults brood their larvae for days to months after the developmental sequence is complete until individuals encounter environmental conditions that prompt larval release in mass synchrony (Moore 1935, Barnes 1962). The synchronous release of nauplii often coincides with phytoplankton blooms (Barnes 1956, 1957, 1962), presumably to ensure a plentiful food supply for the larvae. However, in the field, larvae are sometimes released in the absence of diatom blooms (Barnes 1962), and adults in the laboratory often release

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when exposed to high concentrations of many kinds of plankton, including brine shrimp nauplii (Starr et al. 1991). Additionally, we (Gyory & Pineda 2011) found that the abundance of first-stage nauplii was strongly correlated with the passage of storms that increased water turbidity. We therefore suggested that larval release may be triggered by high turbidity (caused by phytoplankton blooms or other sources), because the weakly swimming, newly released larvae are better protected from cannibalism when the filter-feeding appendages of adults are temporally clogged by particles: the 'turbidity hypothesis.'

In the present study, we tested 3 predictions of the turbidity hypothesis. (1) Larval release in the field should coincide with periods of high phytoplankton abundance or high turbidity from other sources. (2) Adult barnacles should release larvae when exposed to high concentrations of phytoplankton or inert synthetic beads. (3) High turbidity should decrease the rate of cannibalism on newly released barnacle larvae.

## MATERIALS AND METHODS

### Field observations of larval release patterns

We tracked the larval release patterns of the barnacles *Semibalanus balanoides* at 3 sites along the northeastern coast of the USA to determine whether release was related to changes in turbidity, chlorophyll concentration, or various abiotic variables (water temperature, salinity, or depth). The 3 field sites were: (1) a dock in Little Harbor, Woods Hole, Massachusetts (41° 31.366' N, 70° 40.008' W), (2) the University of Rhode Island pier in Narragansett, Rhode Island (41° 29.524' N, 71° 25.145' W), and (3) the University of New Hampshire pier in New Castle, New Hampshire (43° 04.316' N, 70° 42.707' W) (Fig. 1). Larval release of *S. balanoides* is known to occur sequentially, in the respective order, in these 3 regions (Fish 1925, J. Pineda et al. unpubl. data). All sites had an abundance of *S. balanoides* adults distributed vertically in the intertidal zone from approximately high water to low water spring tide levels, which is the usual range for this species (Stubbings 1975).

From 21 November 2009 to 25 February 2010, we sampled barnacle adults to determine what proportion of the population was gravid and what proportion had empty mantle cavities. When a *Semibalanus balanoides* individual releases its larvae, all larvae leave the mantle cavity, usually within 24 h (Barnes 1955). Thus, a rapid increase in the proportion of

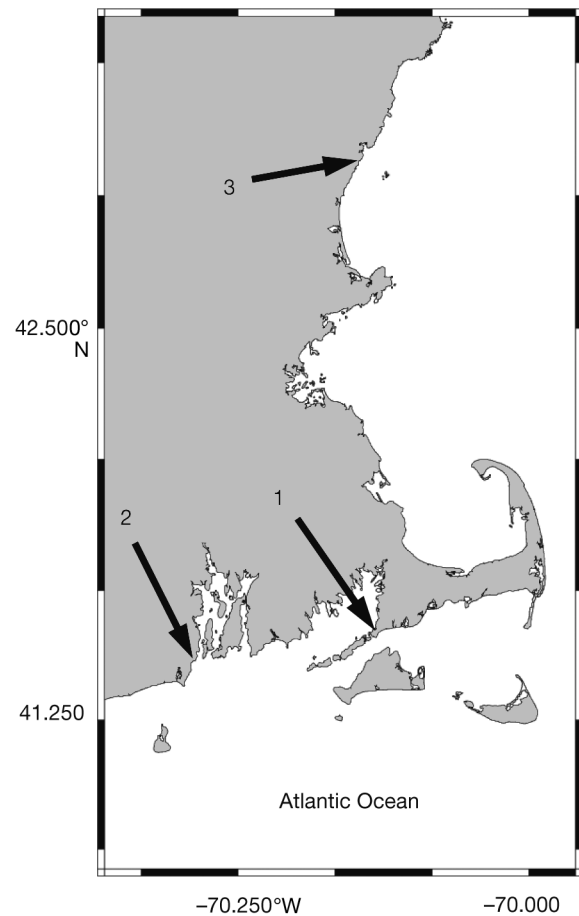


Fig. 1. Sampling sites along the northeastern coast of the USA: (1) Woods Hole, Massachusetts; (2) Narragansett, Rhode Island; and (3) New Castle, New Hampshire. *Semibalanus balanoides* release larvae sequentially, in this order, at these 3 sites

adults with empty mantle cavities signaled a larval release event. We randomly sampled at least 31 adult barnacles (mean = 60, SD = 19) daily whenever possible. On a few occasions, severe weather impeded sampling efforts.

At the 3 field sites, we measured water salinity, temperature, depth, turbidity, and chlorophyll fluorescence. A logger (Model XR-420, RBR) recorded temperature and salinity every 5 min. A fluorometer (dual-wavelength, single-angle sensor) measured turbidity and *in vivo* chlorophyll fluorescence simultaneously (Model ECO FLNTU, WET Labs). The instrument took a 'burst' of measurements ( $1 \text{ s}^{-1}$  for 5 s) every 5 min. In Massachusetts and Rhode Island, we strapped the instruments to pier pilings 0.5 m above bottom. The water depth was 1.5 to 2 m during the highest tides. In New Hampshire, it was not possible to strap the instruments to pier pilings, so the instruments were attached to a floating dock instead,

where they remained 0.5 m below the surface at all times. We obtained tide and water level data from the United States National Oceanic and Atmospheric Administration (Station ID numbers: 8447930, 8452660, and 8423898).

Instrumentation problems at the Massachusetts site caused loss of salinity data and required that we eliminate some bad values from the turbidity and chlorophyll data. A piece of macroalga wrapped itself around the *ECO* fluorometer, and every time the blades of the alga swept past the sensors, the readings were unrealistically high. We removed the bad values from the chlorophyll and turbidity data (in Massachusetts only) as follows. (1) Since the instrument sampled once per second for 5 s every 5 min, we computed the median for each 5 s sampling burst. This eliminated bad data in situations when only some of the values in the sampling burst were affected by the alga. (2) When all 5 values in a sampling burst were bad, we divided the sampling period into 2 h bins and calculated the mean and standard deviation of the values in the bins. If the standard deviation of the mean was equal to or greater than half of the mean, we eliminated the highest one-third of the values from the 2 h bin. (3) We calculated the median values for each 1 h bin, and those are the values used in the analyses (see Supplement 1 at [www.int-res.com/articles/suppl/m476p141\\_supp.pdf](http://www.int-res.com/articles/suppl/m476p141_supp.pdf) for figures of filtered and unfiltered data). After these corrections, the effective sampling rate for the instrument became 1 h<sup>-1</sup>.

### Larval release in response to phytoplankton or turbidity

We conducted experiments to test whether the larval release response was different when gravid adult barnacles were exposed to unfiltered seawater, seawater with diatoms added, or seawater with particles added. The diatom was *Skeletonema marinoi* Sarno et Zingone (Strain CCMP 1332 from the National Marine Phytoplankton Collection [NMPC] at Bigelow Laboratory for Ocean Sciences) added at 10<sup>7</sup> cells l<sup>-1</sup>. Although many previous studies on barnacle feeding reported using the diatom *Skeletonema costatum* (Greville) Cleve, a recent study discovered that *S. costatum* is actually a species complex made up of previously unrecognized species, including *S. marinoi* (Sarno et al. 2005). The strain we used from the NMPC had been identified initially as *S. costatum* when it was collected in 1956, but has been re-classified since then. It has a cell length of 6

to 14 µm, a cell width of 6 to 8 µm, and forms chains of 2 to 45 cells. The particles we used were neutrally buoyant Dynoseeds® 40 µm polystyrene beads (Microbeads AS) added at 10<sup>7</sup> beads l<sup>-1</sup>.

At each field site during low tide, we gathered barnacle-covered rocks that were small enough to fit inside a 1 l clear plastic jar. We placed 1 rock inside each jar and immediately filled it with 1 of the 3 treatments listed above. After sealing the jars with lids, we placed them inside plastic cages that floated just below the water surface and were tethered to the sampling dock. We assume that the floating cages maintained the jars at ambient water temperature and ambient light levels, and the slight to moderate wave action around the docks kept the phytoplankton and beads suspended inside the jars. After 24 h, we recovered the jars, filtered the water through 100 µm mesh, and counted the number of nauplii swimming in the water and the number of adults on each rock. We ran experiments twice in Rhode Island and twice in New Hampshire. Experiments contained multiple replicates of each treatment (Table 1).

The statistical analysis for these experiments tested the null hypothesis ( $H_0$ ) that there is no difference in the larval release response of adults when exposed to beads, *Skeletonema marinoi*, or unfiltered seawater, versus the alternative hypothesis ( $H_1$ ) that there is a difference among the 3 treatments. There were 2 complicating factors. First, not all the adults were gravid at the beginning of the experiments, and it was impossible to determine how many were gravid without sacrificing the animals. Second, the number of nauplii produced can be highly variable among individuals. To address these uncertainties, we developed a statistical model relating the observed number of nauplii in each jar to the unknown number of gravid adults and the distribution of the number of nauplii released by each of them. Based on this model, we performed a likelihood ratio test of the null hypothesis that the conditional mean number of nauplii released by an adult was the same for the 3

Table 1. Number of replicates for 3 treatments (*Skeletonema marinoi*, beads, and control) used in 4 experiments conducted in Rhode Island and New Hampshire

	Rhode Island		New Hampshire	
	11 Jan 2010	13 Jan 2010	31 Jan 2010	2 Feb 2010
<i>Skeletonema</i>	4	3	5	5
Beads	4	3	5	5
Control	2	1	5	5

experimental treatments (see Supplement 2 at [www.int-res.com/articles/suppl/m476p141\\_supp.pdf](http://www.int-res.com/articles/suppl/m476p141_supp.pdf) for details). We repeated the entire analysis while omitting the outlier from the *S. marinoi* treatment (see 'Results') because the outlier could have undue influence on the results.

We considered the possibility that the number of nauplii that we found in the jars at the end of each experiment could differ among treatments if the rates of cannibalism by adults were also different among treatments. Thus, in addition to comparing the number of nauplii in the jars, we also examined the percentage of treatment replicates in which adults were inferred to have participated in 'mass release' (defined as 95% or more of adults in a jar with empty mantle cavities). Mass release could only be inferred, not verified, because it was impossible to determine whether adults were gravid at the beginning of the experiment without sacrificing them.

#### **Predation rate of adults on newly released larvae under normal or turbid conditions**

We tested the null hypothesis that turbidity would not affect the rate of cannibalism on newly released barnacle larvae by exposing adults either to larvae and synthetic beads or to larvae alone. The experiment took place in New Hampshire on 19 February 2010. By this date, most (>75%) of the barnacles we sampled in the field had already released their larvae, so we assumed that the adults in the experiments also had released their larvae.

The experiment consisted of 5 jars with a control treatment (seawater filtered through 100  $\mu\text{m}$  mesh) and 5 jars with an experimental treatment (filtered seawater with 40  $\mu\text{m}$  Dynoseeds<sup>®</sup> added at  $10^7$  beads  $\text{l}^{-1}$ ). Each 1 l jar contained 1 rock covered with barnacle adults. The number of adults in a jar was random, and not significantly different among treatments. We added at least 250 live, actively swimming nauplii to each jar, noting the exact number used. To obtain the nauplii, we scraped adults off pier pilings along the uppermost limit of the barnacle colonies. A few (<25%) of these adults still had viable eggs inside their mantle cavities. We collected the eggs from 10 individuals and placed them in seawater (pre-filtered through 100  $\mu\text{m}$  mesh). The eggs hatched within minutes, and nauplii swam to the surface. Using a glass pipette, we suctioned actively swimming larvae and added them to the experimental jars. We sealed the jars with lids, placed them in the plastic cages described above, and hung the cages

off the pier so that the jars were submerged in seawater.

The experiment began at 14:00 h and ended at 20:00 h. At the end of the experiment, we filtered water from each jar through 100  $\mu\text{m}$  mesh and counted the number of nauplii that remained. We calculated the percentage of nauplii that survived in each jar without being consumed and performed a 1-way ANOVA to detect any differences in the means for the 2 treatments.

## **RESULTS**

### **Field observations of larval release**

There were 5 major larval release events at the 3 sites. Two of the events coincided with higher chlorophyll levels, but all 5 coincided with higher turbidity levels. Two release events occurred in Massachusetts, one between 12 and 14 December, and the other between 18 and 22 December (Fig. 2). On 8 December the increase in percent of empty adults might suggest that there was a release event, but that is unlikely because the next 3 samples had a lower percentage of empty adults. These barnacles reproduce once per year (Barnes 1963), so it is not possible for them to release larvae and become gravid again a few days later. Similarly, the decrease in percentage of empty adults on 17 and 24 December is likely due to sample variability. The percentage of adult barnacles that were brooding viable larvae generally increased until reaching a maximum on 17 December. The 2 decreases in this percentage coincided with the 2 larval release events.

Chlorophyll concentration fluctuated between approximately 0.6 and 3  $\mu\text{g l}^{-1}$  in Massachusetts (Fig. 2). A short-lived, modest increase in chlorophyll concentration occurred during the second larval release event, but not during the first. Turbidity ranged from approximately 0.8 to 6.5 nephelometric turbidity units (NTU). NTUs measure the amount of light scattered by particles. A high-turbidity event was ending when the instrument was placed in the water, and another event followed it the next day. These 2 events coincided with the first larval release event. A second high-turbidity event coincided with the second larval release event. Water level relative to mean lower low water fluctuated between  $-0.1$  and 1.4 m. Water temperature declined steadily from 11 to 1.5°C.

In Rhode Island, major larval release events occurred between 9 and 10 January and between 11 and 13 January (Fig. 3). During the first release, there

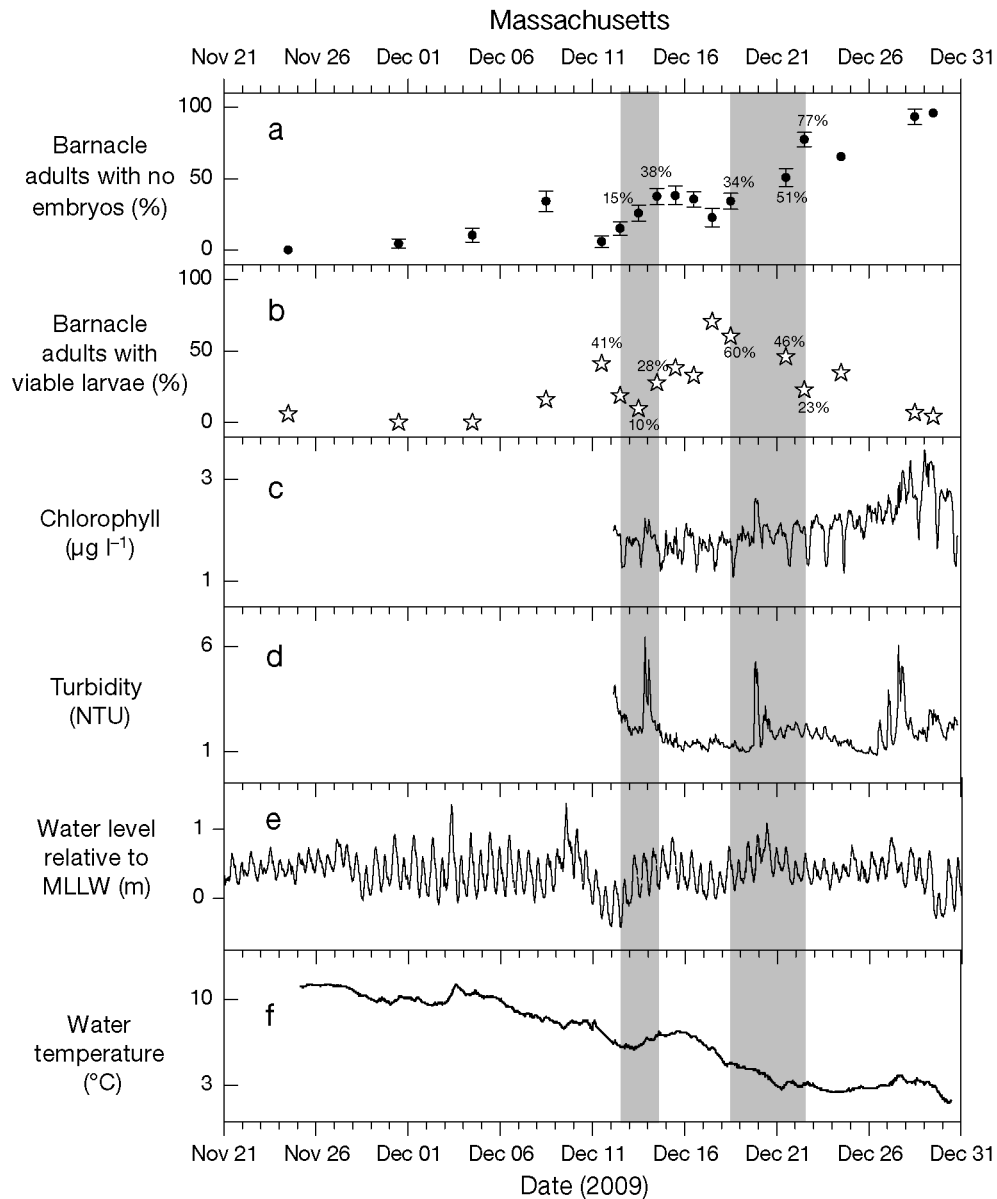


Fig. 2. *Semibalanus balanoides*. Field surveys of the reproductive condition of adult barnacles in Massachusetts in relation to environmental variables. (a) Percentage of adult barnacles with no embryos, shown with standard error bars, suggests that there were 2 major larval release events, indicated by grey vertical shading. (b) Percentage of adult barnacles that were brooding viable larvae. (c) Chlorophyll concentration. (d) Turbidity (NTU: nephelometer turbidity units). (e) Water level relative to mean lower low water (MLLW). (f) Water temperature

was an increase in turbidity, but no noticeable increase in chlorophyll. During the second release, there was 1 high-chlorophyll event and 2 high-turbidity events. The percentage of adult barnacles brooding viable larvae decreased during the larval release events. Water level fluctuated between  $-0.5$  and  $1.7$  m. Salinity and water temperature fluctuated with a semi-diurnal period, so they were probably tidally influenced. Salinity ranged from  $30.4$  to  $31.8$ . Water temperature ranged from  $1.4$  to  $3.9^{\circ}\text{C}$ . During

the evening of 12 January, an extreme low tide caused the instruments to be briefly exposed to air, so chlorophyll, turbidity, salinity, and water temperature data are missing for that period.

In New Hampshire, larval release occurred between 12 and 15 February (Fig. 4). The percentage of adult barnacles brooding viable larvae increased until it reached a maximum on 29 January. The percentage remained high until the larval release event began on 12 February. Chlorophyll values were gen-

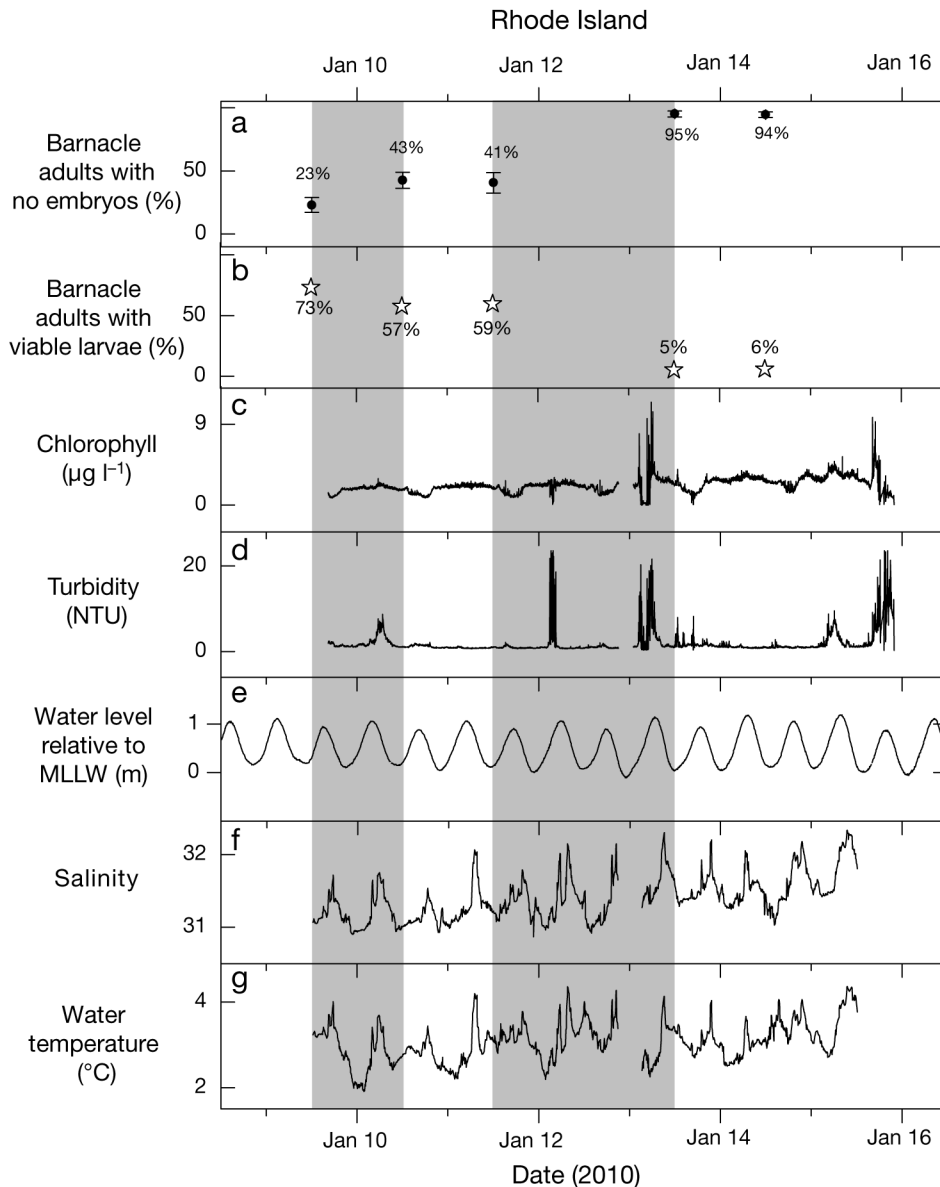


Fig. 3. *Semibalanus balanoides*. Field surveys of the reproductive condition of adult barnacles in Rhode Island in relation to environmental variables. (a) Percentage of adult barnacles with no embryos, shown with standard error bars, suggests that there were 2 major larval release events, indicated by grey vertical shading. (b) Percentage of adult barnacles that were brooding viable larvae. (c) Chlorophyll concentration. (d) Turbidity. (e) Water level relative to mean lower low water (MLLW). (f) Salinity. (g) Water temperature

erally low. Turbidity was generally higher near the beginning of the sampling period and then decreased, but there was an increase at high tide during the larval release period. Turbidity, salinity, and water temperature fluctuated semi-diurnally with the tides. Water level ranged from  $-0.7$  to  $3.5$  m. Salinity ranged from  $22.7$  to  $31.7$ . Water temperature ranged from  $0.7$  to  $4.2^{\circ}\text{C}$ . In general, salinity and temperature increased and decreased as the tide flowed and ebbed, respectively.

#### Larval release in response to phytoplankton or turbidity

Larval release response was significantly stronger (likelihood ratio [LR] test,  $p \ll 0.001$ ) in the phytoplankton and turbidity treatments than in the control treatments, even when the outlier in the *Skeletonema marinoi* treatment was removed (LR test,  $p \ll 0.001$ ). The difference in larval release response between the phytoplankton and turbidity



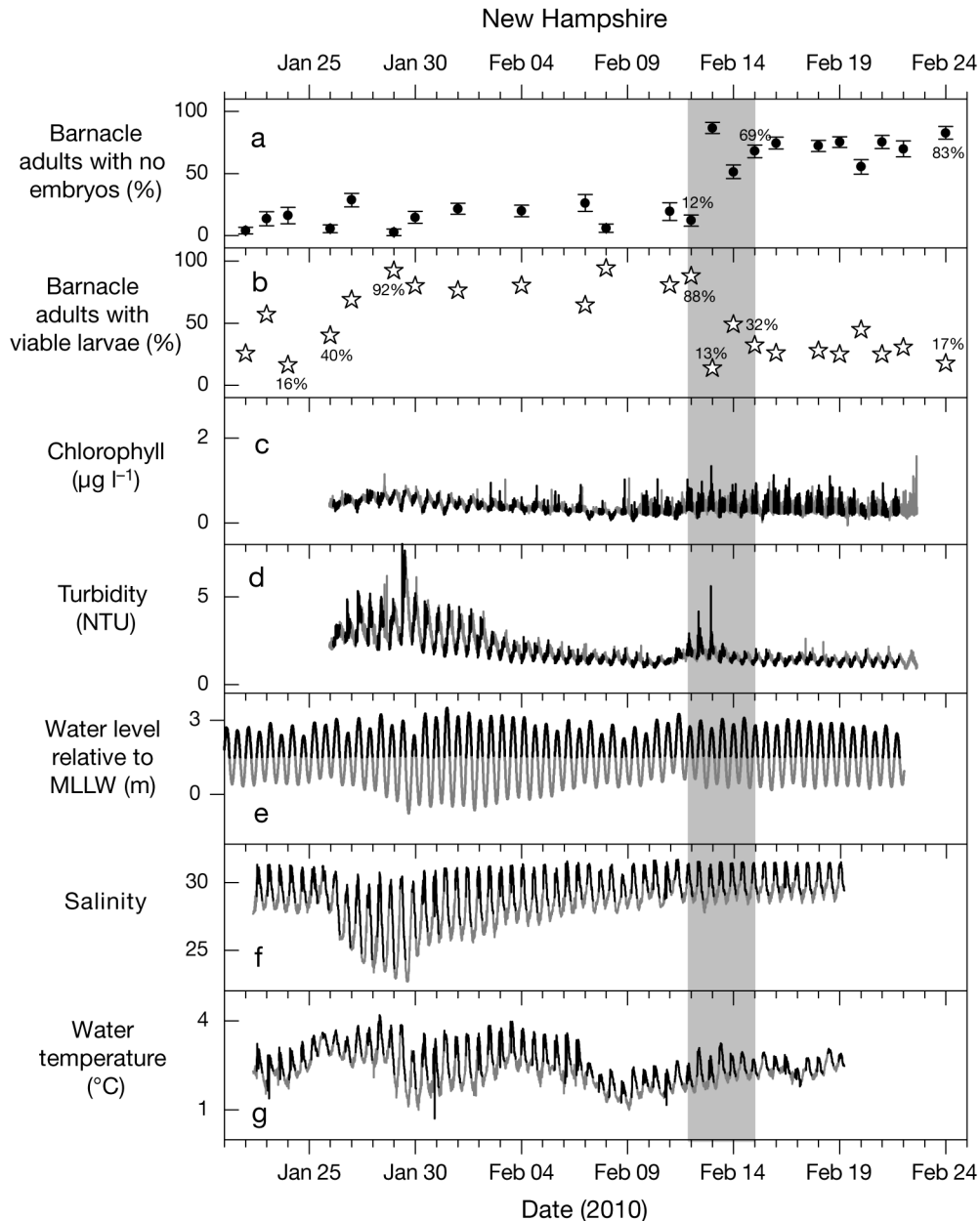


Fig. 4. *Semibalanus balanoides*. Field surveys of the reproductive condition of adult barnacles in New Hampshire in relation to environmental variables. (a) Percentage of adult barnacles with no embryos, shown with standard error bars, suggests that there was 1 major larval release event, indicated by grey vertical shading. (b) Percentage of adult barnacles that were brooding viable larvae. (c) Chlorophyll concentration. (d) Turbidity. (e) Water level relative to mean lower low water (MLLW). (f) Salinity. (g) Water temperature. In (c–g) the gray curves indicate values when water level was <1.5 m above MLLW, and the black curves indicate values when it was >1.5 m

treatments was not significantly different (LR test,  $p \approx 1$ ) (Fig. 5).

The statistical model estimates of  $\pi$  (the probability that an adult is gravid and receptive to a larval release cue) are shown as percentages in Table 2. The model estimates of  $\theta$  (the unknown shape parameter of the negative binomial distribu-

tion), along with the estimated mean number of nauplii released by each gravid adult, are shown in Table 3.

Twenty-seven percent of replicates for the control treatment had mass larval release. In contrast, 46 and 54 % of bead and diatom replicates, respectively, had mass release (Fig. 6).

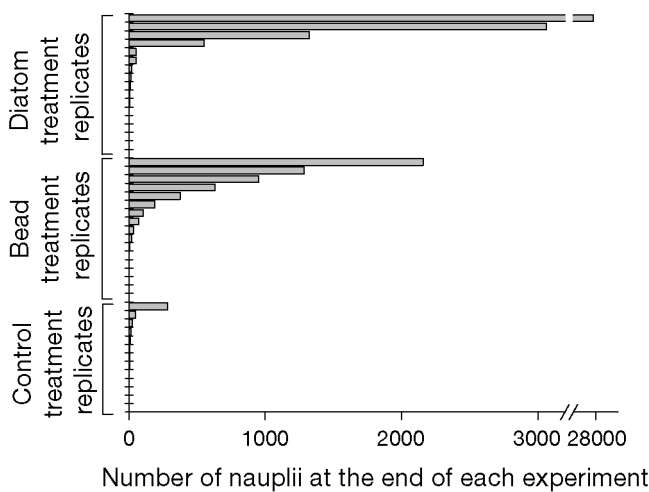


Fig. 5. *Semibalanus balanoides*. Pooled results of the Rhode Island and New Hampshire experiments in rank order. Each bar represents the number of nauplii released in each replicate jar at the end of experiments in which adult barnacles were exposed to *Skeletonema marinoi* diatoms, inert synthetic beads, or control treatment (plain filtered seawater). We rejected the null hypothesis that the larval release response was the same in all 3 treatments ( $p << 0.001$ ). We cannot reject the null hypothesis that the larval release response was the same for the *S. marinoi* and bead treatments ( $p \approx 1$ )

**Predation rate of adults on newly released larvae under normal or turbid conditions**

The mean percentage of nauplii that escaped predation in the turbidity treatment (85.4%) was significantly greater (ANOVA,  $p = 0.015$ ) than in the control treatment (64.7%) (Fig. 7).

**DISCUSSION**

Gravid *Semibalanus balanoides* barnacles brood their larvae until they perceive some cue from the environment that triggers naupliar release. The generally accepted hypothesis has been that barnacles release their larvae in response to phytoplankton blooms because high concentrations of phytoplankton provide abundant food for nauplii. In contrast, Gyory & Pineda (2011) proposed that high turbidity (which can be caused by phytoplankton blooms, sediments re-suspended by storms, or other sources) triggers the release of larvae, since a highly turbid environment may protect poorly swimming, newly released larvae from cannibalism and predation. Our field observations and experiments tested the predictions that: (1) high phytoplankton concentrations or (2) high turbid-

Table 2. *Semibalanus balanoides*. Probability, estimated by the statistical model, that an adult barnacle produced nauplii for each of the 4 experiments conducted in Rhode Island and New Hampshire

	Probability under $H_0$	Probability under $H_1$	Probability under $H_1$ with outlier removed
<b>Rhode Island</b>			
11 Jan 2010	31.0	24.0	18.0
13 Jan 2010	3.2	4.5	5.0
<b>New Hampshire</b>			
31 Jan 2010	3.0	3.0	3.0
2 Feb 2010	4.1	4.7	5.0

Table 3. *Semibalanus balanoides*. Estimates of  $\theta$  (the unknown shape parameter of the negative binomial distribution) under the null hypothesis and under the 3 experimental treatments (including and excluding an outlier), and the estimated mean number of nauplii that each gravid barnacle adult released

	Estimate of $\theta$	Estimate of $\theta$ with outlier removed	Estimated mean number of nauplii released per gravid adult
<b>Under <math>H_0</math></b>	0.0018	0.006	165.67
<b>Under <math>H_1</math></b>			
Control	0.038	0.042	22.81
Beads	0.005	0.0049	203.08
Diatoms	0.001	0.0051	195.08

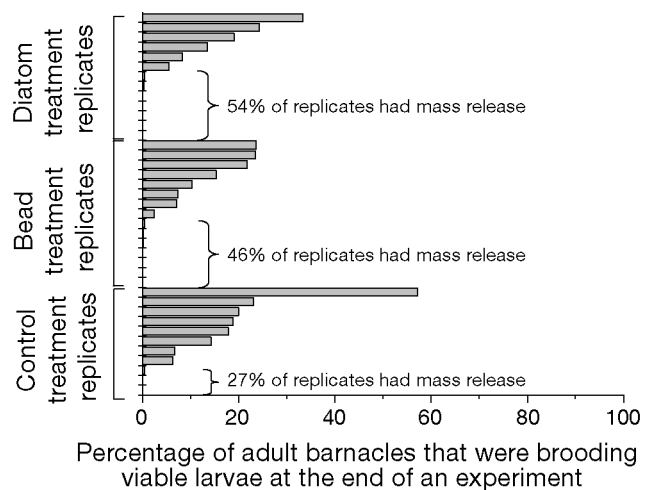


Fig. 6. *Semibalanus balanoides*. Pooled results of the Rhode Island and New Hampshire experiments in rank order. Each bar represents the percentage of adult barnacles that had not released larvae by the end of the experiment within a replicate jar. Replicate jars that had <5% of adults brooding larvae at the end of the experiment were considered to have undergone 'mass release'



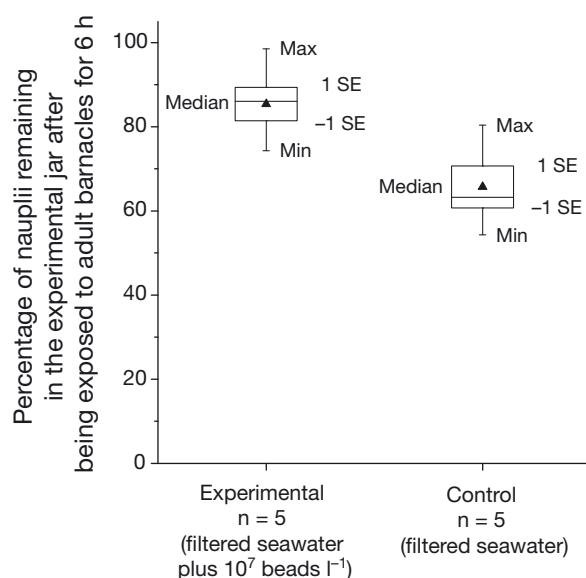


Fig. 7. *Semibalanus balanoides*. Results of experiments in which adult barnacles were exposed to newly released nauplii under high-turbidity (Experimental) or low-turbidity (Control) conditions. Predation rates by adult barnacles on nauplii were lower in high-turbidity than in low-turbidity conditions (ANOVA,  $p = 0.015$ ). Triangles represent the means, boxes represent the median and standard error of the mean, and whiskers represent the minimum and maximum values

ity levels trigger larval release in *S. balanoides*. We found that larval release in the field and in controlled experiments could be triggered by high-turbidity events in the absence of phytoplankton blooms.

We observed 5 major larval release events at 3 sites along the northeastern coast of the USA. Two events coincided with increased chlorophyll concentrations, 3 did not, but all 5 events coincided with increased turbidity. Other authors have also noted that *Semibalanus balanoides* sometimes releases larvae in the field in the absence of phytoplankton blooms. Barnes (1962) identified 2 yr (1950 and 1960) in which larval release in Millport, Scotland, occurred in the absence of blooms. Another barnacle species, *Chamaesipho brunnea*, has been observed to release larvae under conditions when turbidity would be expected to be high. In New Zealand, they brood mature larvae during neap tides and calm weather, and release them during spring tides and stormy weather (Foster 1965 as cited in Luckens 1970).

In Massachusetts, the 2 larval release events coincided with an increase in turbidity. There was a small increase in chlorophyll during the second event, but not during the first. Since macroalgal interference with our instrument sensors required eliminating bad

values from the data, it is possible that we failed to detect short-lived pulses in chlorophyll. This is unlikely, though, because we were able to detect short-lived pulses in turbidity after filtering the data, so we should have been able to do the same with chlorophyll. There was an increase in the percentage of adults with no embryos from 35% on 18 December to 51% on 19 December with seemingly no corresponding increase in chlorophyll or turbidity. The process of filtering data may have obscured an increase in one or both of these variables. In Rhode Island, there were increases in both turbidity and chlorophyll at the second larval release event, but not during the first.

In New Hampshire, there was an increase in turbidity at the time of larval release, but there was no major increase in chlorophyll. Ninety-two percent of adults were brooding viable larvae during the highest turbidity event of the time series, on 29 January. Why did the barnacles fail to release during the high-turbidity events at the end of January? We speculate that the extreme salinity fluctuations associated with the spring tide may have stressed the barnacles and caused them to close their opercular openings. Cawthorne & Davenport (1980) found that when gravid barnacles in the laboratory were exposed to large and rapid salinity fluctuations, they closed their opercular openings, halting larval release. Moreover, the peaks in turbidity in late January and early February occurred as the tide was ebbing, so a substantial portion of the adult population may have been out of the water and unable to release larvae. Finally, there is the possibility that another factor not taken into account here also affects larval release.

To examine the relationship between phytoplankton abundance and the timing of barnacle larval release, we used *in vivo* chlorophyll fluorescence to estimate chlorophyll *a* concentrations, though this is known to be an imperfect method. The ratio of fluorescence to chlorophyll *a* can vary depending on the species composition of the phytoplankton, the health of the cells, and the ambient light conditions (e.g. Loftus & Seliger 1975, Dandonneau & Neveux 1997). In our data, we see decreases in fluorescence almost daily during the middle of the day. This is likely due to non-photochemical quenching. Non-photochemical quenching processes protect phytoplankton from photooxidative damage when light energy exceeds the capability of the cell to utilize it (Müller et al. 2001). Quenching appears as a reduction in fluorescence during periods of high light intensity. Thus, care must be taken in interpreting the data from the brightest period of the day.

The results of laboratory and field experiments lend further support to the hypothesis that turbidity triggers larval release. Starr et al. (1991) found that, in the laboratory, the larval release response is strongest when adult barnacles are fed phytoplankton in concentrations 3- to 6-fold greater than those found in typical blooms. Barnacles in that study may not have been responding to the phytoplankton per se, but to the mechanical stimulus from turbidity caused by high concentrations of phytoplankton cells. This would explain why the barnacles did not respond to phytoplankton culture filtrates, only to the presence of the cells themselves (Starr et al. 1991). The barnacles also released when they were exposed to high concentrations of brine shrimp nauplii, which are not a normal food item for them or their larvae in the field (Starr et al. 1991).

In the present study, we conducted field experiments to examine the larval release response of gravid adults to *Skeletonema marinoi* diatoms and synthetic beads. The larval release response was stronger when barnacles were exposed to the diatoms and beads than when they were exposed to control conditions. The responses to diatoms and to beads did not differ, suggesting that the barnacles respond to mechanical stimulation from the particles, not to the identity of the particles.

Starr et al. (1991) suggested that particles in the water column might indicate that a phytoplankton bloom is underway. Gyory & Pineda (2011) proposed that cannibalism and predation may be an important source of mortality for newly released larvae, and that particles in the water column would signal turbid conditions that may provide a temporary refuge for barnacle nauplii. *Semibalanus balanoides* will consume its own nauplii in the laboratory (Crisp & Patel 1960), and the gut contents of other barnacle species sometimes contain substantial numbers of conspecific larvae (Navarrete & Wieters 2000). Because suspension-feeding barnacle adults tend to be found in high abundance and high densities in the intertidal zone, larvae released into this environment could be at risk of cannibalism. A highly turbid environment may reduce that risk by temporarily swamping the filter-feeding appendages of adults with other particles. The results of our predation experiments showed that *S. balanoides* adults consumed fewer nauplii in turbid conditions than in control conditions, suggesting that mortality of larvae is indeed lower when turbidity is high.

Our study provides a new explanation for the synchrony of larval release in the barnacle *Semibalanus balanoides*. We show that high turbidity triggers re-

lease, whether the source of turbidity is a phytoplankton bloom or not. However, it is possible that phytoplankton blooms also play an important role in the timing of release. The timing of reproduction in this species may have evolved so that larvae are developmentally ready to be released by the onset of winter/ spring phytoplankton blooms in order to maximize the likelihood of a plentiful food supply, and the actual timing of larval release may have been fine-tuned further by cannibalism and predation pressures. As seen in our data, increases in phytoplankton abundance were often very brief, so the food limitation hypothesis would imply that short-lived increases in food supply have a substantial benefit on the growth or survival of larvae. Turbidity increases were also very brief, but the potential benefit to larval survival (reduced risk of cannibalism) would only be needed for a short period until nauplii dispersed away from the adult population. Other crustaceans employ larval release strategies that reduce predation on newly released larvae (e.g. Morgan & Christy 1995). Releasing larvae during turbid conditions to protect them from cannibalism or predation may be a strategy shared by other marine organisms that release propagules into the water column.

*Acknowledgements.* We are grateful to John Ahern for his help in setting up instrumentation in the field and for help with field sampling logistics. We thank the University of Rhode Island and the University of New Hampshire for access to their research facilities. We thank Victoria Starczack, Carin Ashjian, Thomas Peacock, and Peter Wiebe for help with the design of these experiments and for helpful comments that improved this manuscript. Thanks also to the 3 anonymous reviewers who provided helpful feedback on an earlier version of this manuscript. David Ralston and Heidi Sosik generously lent their oceanographic instruments and trained J.G. in their use. Support for this work came from a National Science Foundation Graduate Research Fellowship and a student award from the Coastal Ocean Institute at Woods Hole Oceanographic Institution (both to J.G.). Our experiments and sample collections comply with the laws and regulations of the United States of America and the states of Massachusetts, Rhode Island, and New Hampshire.

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*Editorial responsibility: Steven Morgan, Bodega Bay, California, USA*

*Submitted: June 15, 2012; Accepted: November 19, 2012  
Proofs received from author(s): February 11, 2013*