esa ECOSPHERE

Recruitment, abundance, and predation on the blue mussel (*Mytilus edulis*) on northeastern estuarine rocky shores

MARCY L. COCKRELL,[1,3] JOANNA R. BERNHARDT,[1,4] AND HEATHER M. LESLIE [1,2,]†

[1]*Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island 02912 USA*
[2]*Institute at Brown for Environment and Society, Brown University, Providence, Rhode Island 02912 USA*

Citation: Cockrell, M. L., J. R. Bernhardt, and H. M. Leslie. 2015. Recruitment, abundance, and predation on the blue mussel (*Mytilus edulis*) on northeastern estuarine rocky shores. Ecosphere 6(1):18. http://dx.doi.org/10.1890/ES14-00176.1

Abstract. We report on patterns of abundance, recruitment, and predation on the blue mussel (*Mytilus edulis*) in three human-dominated estuaries in the northeastern United States. Through replicate field experiments and observational studies at multiple sites nested within each of the three estuaries, we investigated the relative influences of local and regional scale variation in select bottom-up and top-down factors on blue mussel populations on wave-protected rocky shores. The most striking result was the decoupling between adult abundance and recruitment: mussel recruitment rates were highest in the most northern estuary, Casco Bay, while adult abundances were highest in the most southern estuary, Long Island Sound. We detected evidence of top-down forcing on adult abundance by consumers in the two more southern estuaries, Narragansett Bay and Long Island Sound, but not in Casco Bay. Finally, we observed some indications of bottom-up forcing on mussel abundance and recruitment at the within-estuary scale, but these signals were not consistent among estuaries or across the responses measured (e.g., adult abundances and recruitment rates). Our results support previous work demonstrating the importance of both top-down and bottom-up influences on rocky shore populations, and also highlight how future research—particularly integrating studies of the different ontogenetic stages of mussels—could further advance understanding of biological population dynamics in this and other systems.

Key words: abundance; estuary; marine; mussel; *Mytilus edulis*; northeastern United States; predation; recruitment; wave-protected rocky shore.

Received 10 June 2014; revised 16 October 2014; accepted 17 November 2014; final version received 16 December 2014; **published** 29 January 2015. Corresponding Editor: T. van Kooten.

[3] Present address: University of South Florida, College of Marine Science, St. Petersburg, Florida 33701 USA.

[4] Present address: University of British Columbia, Department of Zoology and Biodiversity Research Centre, Vancouver, British Columbia V6T 1Z4 Canada.

† **E-mail:** heather.m.leslie@gmail.com

INTRODUCTION

Rocky shore communities—shaped by strong environmental gradients and dominated by easily manipulated and often slow moving organisms—have served as important development and testing grounds for ecological theory (Paine 1994, Menge and Branch 2001). Mussels are one of several organisms that have given significant insights into rocky shore community dynamics worldwide. As filter feeding primary consumers, mussels link benthic and pelagic ecosystems and create habitat for many other species (Suchanek 1981, Witman et al. 2003). Investigations into how key life history traits in mussels (such as physiology, growth, survival, and/or reproduction) vary with exogenous factors including temperature (Helmuth and Hofmann 2001, Petes et al. 2007, Lesser et al. 2010), hypoxia (Altieri and Witman 2006), food availability (Menge et al. 1997, Leonard et al. 1998), and disturbance regimes (Paine and Levin 1981, Hunt and Scheibling 2001) have contributed substantially to understanding how environmental factors influence organismal and population performance, and community dynamics more broadly. Observations and experiments of predator-prey dynamics involving mussels have also yielded important insights, including understanding of how spatial and temporal variation in predation strength and predator identity can shape benthic community structure and functioning (Paine 1966, Robles et al. 1995, Navarrete and Menge 1996, Menge et al. 2004, Navarrete and Manzur 2008, Boudreau and Hamilton 2012).

Ecological processes may also be shaped by latitudinal clines in environmental conditions and concomitant biogeographic and oceanographic variation. The spatial scale of this heterogeneity need not be extreme. For example, previous studies have shown significant differences in marine communities within the Channel Islands, which span an oceanographic transition zone over the relatively short distance of 100 km (Airamé et al. 2003, and references therein). Ecological roles and species guilds may be similar between distant communities; however, differences in species composition and relative abundances of key interacting species could lead to differences in the dominant processes that shape community function. That is, the relative importance of predation, recruitment, and inter- and intraspecific competition may vary across a relatively small spatial scale with changes in species composition. Understanding if and how ecological processes may vary across biogeographic and oceanographic clines is critical for our broader understanding of community functioning in rocky shores, as well as other marine systems. Understanding processes in wave-protected estuarine settings is particularly critical, given the ecosystem's vulnerability to human impacts, rising temperatures, and other environmental stressors due to climate change (Helmuth et al. 2006, Gedan et al. 2011, Bernhardt and Leslie 2013).

This study examined abundance, recruitment, and responses to consumer exclusion across the biogeographic and oceanographic transition zone created by Cape Cod, on the northwestern Atlantic shore, using the blue mussel (*Mytilus edulis*) as a model organism. We quantified abundance, recruitment, and responses to consumer exclusion at four wave-protected sites nested within each of three estuaries: Casco Bay (Maine), Narragansett Bay (Rhode Island), and Long Island Sound (Connecticut and New York). We also synthesized data from diverse sources on key environmental variables (e.g., water temperature, salinity, chlorophyll-*a*, and human population density) to explore possible associations between mussel population processes and environmental conditions. This hierarchical experimental design allowed us to study the potential effects of local and regional-scale variation in environmental conditions on mussel population dynamics.

We hypothesized that mussel abundance and recruitment would be greater at the more southerly sites due to warmer temperatures (and thus increased metabolic rates), that mussels would be more abundant at sites with fewer predators, and that bottom-up factors would play a larger role at inner vs. outer bay sites due to increased nutrient loading (and thus greater primary production and food resources for filter feeding invertebrates). Here we report on the results of these investigations, and discuss outstanding research questions related to mussel population dynamics and their role in these wave-protected ecosystems. A complementary investigation of rocky shore community structure and successional dynamics at these sites will be reported separately.

METHODS

Study sites

We selected four sites within each of the three estuaries—Casco Bay (CB), Narragansett Bay (NB), and Long Island Sound (LI)—to quantitatively examine differences in *M. edulis* recruitment and susceptibility to predation (N = 12 experimental sites), with an additional two sites per estuary to quantify abundance of *M. edulis* and other rocky shore organisms during intertidal surveys (N = 18 total sites; Fig. 1, Appendix: Tables A1, A2). The sites spanned a total coastal distance of ~640 km, from Maine to New York state. We classified all sites a priori as one of two

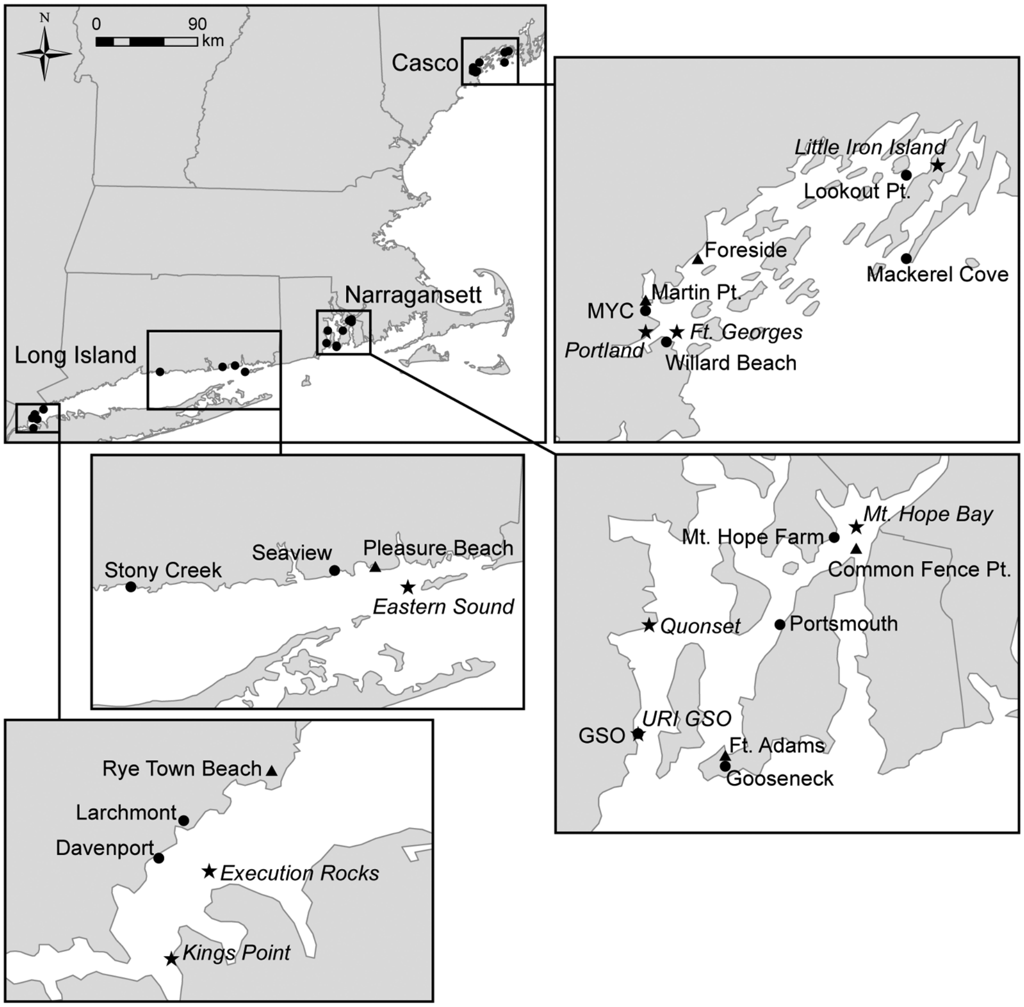

Fig. 1. Map of all experimental sites (circles), sites that were used only for surveys (triangles), and environmental monitoring stations (stars and italics). The three regions (north to south) are Casco Bay (CB), Narragansett Bay (NB), and Long Island Sound (LI). Insets for each region show specific site and station locations. Inner bay sites were: in CB: Maine Yacht Club (MYC), Martin Pt., Willard Beach; in NB: Common Fence Pt., Mt. Hope Farm, Portsmouth; in LI: Davenport, Larchmont, Rye Town Beach. Appendix A lists the geographic coordinates of all study sites and environmental monitoring stations.

location types: inner bay or outer bay. Half of the sites in each estuary were within each of the location categories (i.e., $n = 2$ inner bay and $n = 2$ outer bay sites per estuary for the recruitment monitoring and consumer exclusion experiment; $n = 3$ inner bay and $n = 3$ outer bay sites per estuary for intertidal surveys). Inner bay sites tend to be exposed to higher inputs of land-based nutrient pollution and more variable salinity (Valiela et al. 1992, National Research Council 2000, Boesch et al. 2001, Nixon et al. 2008), whereas outer bay sites tend to have greater oceanic influence, and consequently lower primary productivity and more stable salinity (e.g., as reported in Bertness et al. 1991). All sites were characterized by minimal tidal currents and wave action (i.e., they were wave-protected), and dominated by continuous rocky benches. However, Portsmouth in Narragansett Bay experiences relatively strong alongshore tidal currents (in comparison to the other sites we studied) and is comprised of a series of large (>2 m) boulders

Table 1. Summer air and water temperatures (mean + SE) by estuary.

		Air		Water	
Estuary	Station name	Min (°C)	Max (°C)	Min (°C)	Max (°C)
CB	Portland (8418150)	16.55 + 0.13	23.96 + 0.31	15.43 + 0.59	17.13 + 0.69
NB	Quonset (8454049)	19.06 + 0.13	25.20 + 0.22	20.87 + 0.17	23.16 + 0.10
LI	Kings Point (8516945)	20.61 + 0.16	27.35 + 0.15	20.51 + 0.47	22.49 + 0.37

Notes: CB = Casco Bay, NB = Narragansett Bay, LI = Long Island Sound. Data are from National Oceanic and Atmospheric Administration (NOAA) stations as listed. Values were calculated by (1) taking the min or max value for each day within the summer (i.e., June, July, August), (2) averaging for each year, for 2010–2012, and (3) calculating the grand mean of the three years. NOAA station data can be found at http://tidesandcurrents.noaa.gov/stations.html. Station names are followed by their numbers in parentheses.

separated by two to five meters (see Bertness et al. 1991 for more detail).

Primary sessile species at all sites included the acorn barnacle (*Semibalanus balanoides*), blue mussel (*Mytilus edulis*), and the long-lived algal species *Ascophyllum nodosum* and *Fucus* spp. Algal canopies were particularly prominent at the Casco Bay sites, but occurred throughout the study region. In terms of mobile species, the herbivorous snail *Littorina littorea* was very common and predatory whelks (*Urosalpinx cinerea* south of Cape Cod and *Nucella lapillus* north of Cape Cod) were found in abundance. Gulls (*Larus* spp.) were observed on occasion. Neither crabs (*Carcinus maenus, Hemigrapsus sanguineus, Cancer* spp.) nor seastars (*Asterias forbesi, A. vulgaris*) were often observed, although this could be due to the fact that we sampled the intertidal zone only at low tide, and not subtidally.

Environmental data

Environmental data including air and water temperature, salinity, dissolved oxygen, chlorophyll-*a*, and nutrients were synthesized from government and non-governmental organizations throughout the study region (Tables 1–4). Hourly air and water temperature data were downloaded for 2010–2012 from the US National Oceanic and Atmospheric Administration (NOAA; http://tidesandcurrents.noaa.gov/stations.html), and summer mean minimum and maximum values were calculated for each of the three years. The other environmental variables were synthesized from diverse sources for each estuary at the inner vs. outer bay scale (see Table 2 for references and Appendix: Table A2 for coordinates). Consequently, the environ-

Table 2. Water temperature data synthesized for the study region.

						Water temperature (°C)	
Estuary	Location	Station name	Data source	Sampling frequency	N	Mean + SE	Range
CB	Inner	Fort Gorges	FoCB	Monthly (2005–12)	76	11.04 + 0.66	0.59–19.00
CB	Outer	Little Iron Island	FoCB	Monthly (2005–12)	40	13.93 + 1.00	0.30–22.40
NB	Inner	Mt. Hope Bay	RI DEM FSMN/URI GSO	Every 15 min (2009–2011; approx. May–Oct)	34,000–40,000, depending on the parameter	21.50 + 0.02†	10.20–28.50†
NB	Outer	URI GSO Dock	RI DEM FSMN/URI GSO	Every 15 min (2009–2011); nutrients collected weekly	>22,000, depending on the parameter, except for nutrients (n = 63–155)	12.01 + 0.04	−0.16–24.45
LI	Inner	Execution Rocks	MYSound	Monthly (2009–2012)	22–47, depending on the parameter	8.77 + 1.77	0.60–23.72
LI	Outer	Eastern Sound	MYSound	Monthly (2009–2012)	7–32, depending on the parameter	13.16 + 1.12	2.74–19.85

Notes: FoCB = Friends of Casco Bay, RI DEM FSMN/URI GSO = Rhode Island Department of Environmental Management Fixed Station Monitoring Network/University of Rhode Island Graduate School of Oceanography, MYSound = Collaboration between the University of Connecticut, CT Department of Environment Protection, US Environmental Protection Agency, and NOAA. N = Number of observations taken. Location refers to inner or outer bay as defined in *Methods: Study sites*. Estuary is as listed in Table 1.

† Water temperature value is much higher than at the other stations as the winter months were not sampled. See Table 1 for more representative NB water temperatures.

Table 3. Salinity and dissolved oxygen data synthesized for the study region.

			Salinity (ppt)		DO (μm/L)	
Estuary	Location	Station name	Mean + SE	Range	Mean + SE	Range
CB	Inner	Fort Gorges	27.11 + 0.48	5.00–32.10	10.44 + 0.19	8.05–14.20
CB	Outer	Little Iron Island	30.34 + 0.17	27.80–32.10	10.11 + 0.30	7.70–14.40
NB	Inner	Mt. Hope Bay	27.33 + 0.01	15.70–30.99	7.54 + 0.01	4.10–15.45
NB	Outer	URI GSO Dock	29.97 + 0.01	19.62–32.52	8.61 + 0.01	4.23–14.67
LI	Inner	Execution Rocks	25.35 + 0.14	22.91–27.07	10.61 + 0.60	5.49–15.19
LI	Outer	Eastern Sound	30.13 + 0.20	27.60–31.30	8.37 + 0.26	7.03–11.27

Notes: Data sources, sampling frequency, and number of observations for each station are as in Table 2. Estuary is as in Table 1 and location is as in Table 2. ppt = parts per thousand (‰), DO = dissolved oxygen.

mental data vary in temporal resolution, spatial coverage, and sampling intensity (Tables 1–4). In all cases, data from surface samples ($\leq$1.5 m in depth) were extracted from larger datasets, to enable comparisons within and among the estuaries. Human population density was calculated from the 2010 US Census data (Minnesota Population Center 2011) using ArcGIS 10.1 (Environmental Systems Research Institute, Redlands, California, USA). We identified the closest hydrological unit code (HUC) 12-digit watershed to each study site, and clipped the census block data to that watershed in order to quantify the number of people living within the relevant watershed.

Intertidal surveys

Surveys of rocky shore community structure were conducted in Fall 2010 at 18 sites (n = 6 sites per estuary; see Fig. 1). At each site we used a point-intercept method along a 15–20 m transect to quantify sessile species abundance and a belt transect method to quantify mobile species abundance. Transect length varied slightly depending on relief and available space. Each of the two survey methods was performed in both the mid and high intertidal zones. The zones were identified based on biological distributions, i.e., the mid zone spanned the vertical distribution of mussels at the site, and the high zone spanned the middle of the vertical distribution of barnacles.

Along each transect we randomly selected five points, and then recorded the percent cover of all sessile species (e.g., algae, crustose coralline algae, barnacles, and mussels) using a 100-cm^2 quadrat. Percent cover estimates were not significantly different when estimated with a 100-cm^2 vs. 625-cm^2 quadrat (H. M. Leslie et al., *unpublished data*); the former was chosen for logistical reasons, given the small size of many of the barnacles and littorines at these sites. At each point we also conducted a belt transect (1 m long by 50 cm wide) to quantify all mobile organisms (e.g., crabs, littorine snails, and whelks) using a 625-cm^2 quadrat. The mobile organism counts were converted to densities (number per square meter) based on the belt transect area.

Recruitment monitoring

To quantify mussel recruitment rates at the 12 experimental sites, we used standardized plastic

Table 4. Nutrient and chlorophyll *a* data synthesized for the study region.

			$NO_2^- + NO_3^-$ (μmol/L)		DIN (μmol/L)		Chl a (μg/L)	
Estuary	Location	Station name	Mean + SE	Range	Mean + SE	Range	Mean + SE	Range
CB	Inner	Fort Gorges	3.23 + 0.37	0.00–20.39	8.06 + 0.88	0.01–54.61	. . .	. . .
CB	Outer	Little Iron Island	1.77 + 0.53	0.05–16.20	6.06 + 1.09	0.27–27.09	. . .	. . .
NB	Inner	Mt. Hope Bay	. . .	. . .	. . .	. . .	9.32 + 0.03	0.00–77.20
NB	Outer	URI GSO Dock	1.31 + 0.25	0.00–7.92	4.45 + 0.30	0.00–16.74	4.25 + 0.29	0.68–24.63
LI	Inner	Execution Rocks	10.38 + 1.29	0.29–27.79	. . .	. . .	11.68 + 1.79	1.64–24.88
LI	Outer	Eastern Sound	2.82 + 0.47	0.36–9.71	. . .	. . .	2.46 + 0.40	1.31–3.99

Notes: Data sources, sampling frequency, and number of observations for each station are as in Table 2. Estuary is as in Table 1 and location is as in Table 2. NO_2^- = nitrite, NO_3^- = nitrate, DIN = dissolved inorganic nitrogen, chl a = chlorophyll *a*, ellipses = data not available.

mesh collectors, or Tuffys (SOS Tuffy pads; Clorox, Oakland, California, USA) (sensu Menge 1992, Leonard et al. 1998). Each collector ($n = 8$ per site) was secured with a lag bolt and washer in the mid intertidal zone. The Tuffys were collected and replaced every one to two months from May through August 2010 and again from February through August 2011, so as to bracket the known recruitment window (Petraitis 1991, Leonard et al. 1998). Upon collection, each was placed in a sealed plastic bag and then stored at −20°C upon return to the lab. To quantify the number of recruits, each collector was thawed, and all organisms were rinsed off completely into a 425-μm sieve, then off the sieve into a clear dish. Mussel recruits were counted visually under a dissecting microscope, after the methods of B. Hayden and B. Menge (Menge et al. 2004). The total number of recruits was standardized to the number of days the collector was in the field, and we then calculated an average number of recruits per day for each site.

Consumer exclusion experiment

At each of the 12 experimental sites, we installed eight replicate consumer exclusion experiments (with the exception of Mt. Hope Farm [NB] and Stony Creek [LI], which only had seven due to space limitations). Each replicate was considered a "block" and consisted of three treatments: a control, a cage, and a cage-control (see Appendix: Fig. B1 for a photograph of the set-up). All three treatments were created initially by scraping all sessile species from the substrate and manually removing all mobile species. The plots were 225 cm^2 in size and marked on the corners with lag bolts and one number tag. Cages were 15 cm × 15 cm square, 5 cm tall, and constructed of one-quarter inch (6.35 cm) stainless steel hardware cloth, which was adequate to exclude the dominant consumers found at these and other northwest Atlantic rocky shore sites, including gulls, ducks, crabs, whelks, and seastars (Menge 1976, Petraitis 1990, Ellis et al. 2005, 2007, Boudreau and Hamilton 2012). This mesh size is slightly larger than that employed by Boudreau and Hamilton (2012) to exclude mussel consumers in New Brunswick; those authors did not observe caging artifacts. Nonetheless, we explicitly tested for such artifacts, as recommended by Miller and Gaylord (2007). Our cage-controls were identical to the cages, but were open on two sides to allow ambient levels of herbivory and predation. Observation of the cages and cage-controls with the rising and falling tides did not reveal any inhibition of flow.

Both the cages and cage-controls were secured as flush to the substrate as possible using lag bolts and washers. Treatments within a block were located within one-half meter from each other (Appendix: Fig. B1), and replicate blocks were located at least one meter apart. This spacing of blocks and treatments reflected the small size of many of our intertidal sites, most of which occupied well less than 0.5 km of shoreline. Blocks were assigned randomly, and placed in such a way so as to account for environmental heterogeneity present at each site.

Treatments at all sites were installed by April 2010, and monitored monthly from May to August 2010 and again in March, May, and August 2011. At each monitoring date the percent cover of all sessile species was estimated for each treatment plot. Very small individuals, such as littorines or whelks that had entered the cages, were manually removed. Cages and cage-controls were also cleared monthly of debris, diatom growth, or extraneous algal growth that had accumulated in and/or on the cage structures, to avoid possible shading and hydrodynamic effects.

Data analyses

ANOVA and all other tests were conducted in JMP 11.0 (SAS Institute, Cary, North Carolina, USA). We used post-hoc Tukey HSD tests and/or linear contrasts when appropriate to test for differences among estuaries, sites, or groups of sites. Test results were generally considered significant at an alpha level of 0.05, but significance levels were adjusted as appropriate when multiple comparisons were made. When site was included as an independent variable for any test, it was considered a fixed effect because all sites were chosen for specific criteria (i.e., proximity to urban centers, available access, a priori hypotheses about the effect of location type on mussel dynamics). Thus, all potential sites in an estuary were not equally likely to be chosen for the experiment. All other independent variables were considered fixed, except in the analysis for

Table 5. Results from the RM-ANOVA to test differences in mussel cover among caging treatments over time.

Effect	df	df-Den	F	p
Treatment	2	213	18.50	<**0.0001**
Time	6	208	7.21	<**0.0001**
Time × treatment	12	416	3.92	<**0.0001**

Notes: The p-values in boldface indicate a significant model effect. df-Den = denominator degrees-of-freedom used to test the significance of the F-ratio.

the consumer exclusion experiment, which included a random block effect nested within site and estuary.

To examine differences in *M. edulis* abundance among the estuaries as quantified in the intertidal surveys, we ran a nested ANOVA on percent cover data with estuary (n = 3) and site nested within estuary (n = 6 per estuary; N = 18 total) as fixed model effects. We used mid-zone data only because this is where *M. edulis* were primarily found at our sites and visual inspection of the data revealed that mid-zone abundance was driving overall trends. A Tukey HSD test was used to examine specific differences among estuaries and sites, and planned linear contrasts were used to examine differences between inner and outer bay locations.

To examine differences in mussel recruitment, we ran a nested ANOVA comparing peak recruitment rates at each site (total recruits per day), with estuary (n = 3) and site nested within estuary (n = 4 per estuary; N = 12 total) as fixed model effects. A Tukey HSD test was used to examine specific differences among estuaries and sites, and planned linear contrasts were used to examine differences between inner and outer bay locations. June through July is the peak recruitment season for this species (H. M. Leslie et al., *unpublished data*) and so June to July data were used in the analysis, except for the Seaview and Larchmont sites, where data ranged from June to August due to complications in the field. For this time period, the number of replicates available for Lookout Pt. (CB), MYC (CB), Willard Beach (CB), and Seaview (LI) were seven, five, six, and four, respectively. All other sites used eight replicates for analysis.

To examine differences in predation pressure based on the consumer exclusion experiment, we ran two ANOVAs with mussel percent cover as the response variable. Percent cover data were arcsine-square root transformed in order to better meet test assumptions before we performed the ANOVAs. Most sites had 8 replicate blocks, but we included data from only five replicates for Willard Beach (CB), six replicates for Stony Creek (LI), and seven replicates for Larchmont (LI) due to loss or repeated trouble maintaining particular cages in the field.

We first ran a repeated measures ANOVA (RM-ANOVA) with abundance data from all sampling time points to elucidate any interaction between time and caging treatment (i.e., cage, control, and cage-control treatments). Sites were pooled together (N = 12) with time, treatment, and time × treatment as model effects. Once we determined that there was a significant time × treatment interaction (see Table 5), we used only the terminal time point (August 2011) for the second ANOVA.

The second ANOVA examined among-estuary differences in mussel cover when predation pressure was reduced, as well as differences

Table 6. Results from the ANOVA to test differences in mussel cover among estuaries, sites, and treatments in August 2011.

Effect	df	SS	MS	MS-Den	df-Den	F	p
Estuary	2	2.83	1.413	0.107	77	13.21	<**0.0001**
Site [Estuary]	9	2.91	0.323	0.107	77	3.02	**0.004**
Treatment	2	7.60	3.799	0.063	154	60.62	<**0.0001**
Estuary × treatment	4	3.79	0.947	0.063	154	15.10	<**0.0001**
Site × treatment [Estuary]	18	5.39	0.299	0.063	154	4.77	<**0.0001**
Block [Site, Estuary] and random	77	8.23	0.107	0.063	154	1.71	**0.003**
Residual	154	9.65	0.063				

Notes: The nested terms are read from left to right (e.g., "site nested within estuary"). The p-values in boldface indicate a significant model effect. MS = mean square value for a given variable in the ANOVA model. MS-Den = mean square value used in the denominator to calculate the F-ratio (corresponds to either the block or residual mean square). df-Den is as in Table 5. See *Methods: Data analyses* for more details on F-ratio calculations.

among sites within each estuary and with the caging treatment (Table 6). This ANOVA was a nested mixed effects model run with the expected mean squares (EMS) method. The fixed effects in the model were estuary, site (nested within estuary), treatment, estuary × treatment, and site × treatment (nested within estuary). Block was included as a random effect (nested within site and estuary) to account for heterogeneity between the treatment blocks. The F-ratios for each independent variable in this model were calculated as either MS_{EFFECT} (the mean square for the model effect) divided by MS_{BLOCK} (the mean square for the block effect) or MS_{EFFECT} divided by $MS_{RESIDUAL}$ (the mean square for the residual error). The MS_{BLOCK} term was used in the denominator for estuary and site effect calculations. The F-ratios for the other variables, including the random block effect, were calculated using the $MS_{RESIDUAL}$. The denominator mean square value used for each F-ratio calculation is given by the "MS-Den" term in Table 6. The denominator degrees-of-freedom used to test the significance of each F-ratio is given by "df-Den" in Table 6; each df-Den corresponds to the degrees-of-freedom for either the block effect or the residual error.

To more fully examine significant model effects from the second ANOVA, Tukey HSD post-hoc tests were applied to compare treatment effects among the estuaries and sites, and also to investigate differences between the controls and cage-controls at each site. The latter test revealed that there was no significant difference between controls and cage-controls for any site (Appendix: Table C1) and so these two treatments were grouped together for successive post-hoc tests. Linear contrasts were also used to examine (1) which sites had significantly more mussel cover in the cage treatment in August 2011, and (2) whether the treatment effect was present in both location types (i.e., inner and outer bay) within an estuary. For question (1), mussel abundance was compared in cages vs. controls for each site (with control and cage-control treatments pooled; $N = 12$ individual contrasts). For question (2), the presence of an overall caging treatment effect in either location was examined by calculating linear contrasts for inner and outer bay sites separately. That is, all cages for inner bay sites were compared to all controls for inner bay sites; the test was then repeated for outer bay sites. Each location contrast was conducted separately for each estuary ($n = 2$ contrasts per estuary, $N = 6$ total contrasts), and control and cage-control treatments were pooled.

RESULTS

Environmental data

As expected, summer air and water temperatures were higher in the southerly estuaries, Narragansett Bay (NB) and Long Island Sound (LI), in comparison to Casco Bay (Table 1). Mean annual water temperatures were lower in the inner bay than the outer bay stations in Casco Bay and Long Island Sound (Table 2). In Narragansett Bay, data were not collected throughout the year, which precluded a three-way comparison of annual water temperatures. The three estuaries had comparable ranges and average salinities; however, inner bay stations tended to have lower means and exhibit a wider range of values, as expected (Table 3). Dissolved oxygen (DO) mean concentrations also were quite similar across the inner and outer bay stations; note however, the lower values in Narragansett Bay relative to the other two estuaries and recall that these data were only from the summer months (Table 3).

Based on the available chlorophyll-*a* and nutrient data, the inner bay stations in all three estuaries showed signs of higher nutrient inputs and primary productivity (Table 4). In Casco Bay and Long Island Sound the mean concentrations of nitrate + nitrite ($NO_3^- + NO_2^-$) were higher at the inner bay stations than the outer bay stations. The mean concentration of dissolved inorganic nitrogen (DIN) exhibited a similar trend in Casco Bay. In Narragansett Bay and Long Island, concentrations of chlorophyll *a*, a standard proxy for primary productivity, were also higher at the inner vs. the outer bay stations (Table 4).

Intertidal surveys

There was a significant difference in ambient mussel abundance both among estuaries ($F_{2,72} = 18.41$, $p < 0.001$) and among sites ($F_{15,72} = 4.41$, $p < 0.001$). Mussel abundances were greater in Long Island Sound than the two estuaries further north (Tukey HSD; Fig. 2A) and the three inner

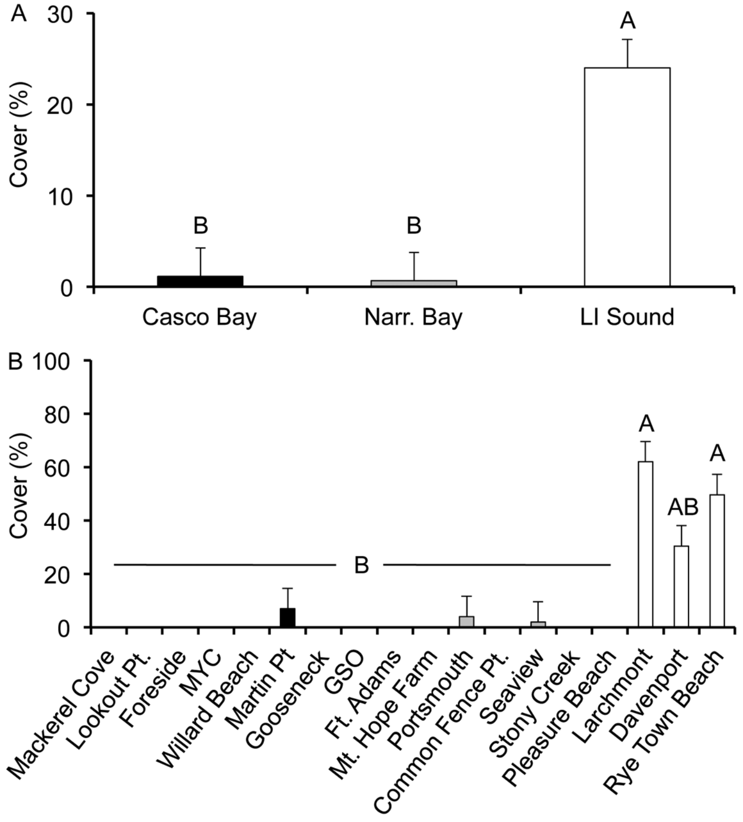

Fig. 2. Abundance (percent cover; LS mean + SE) of *Mytilus edulis* in the mid tidal zone from Fall 2010 surveys for (A) Casco Bay (black), Narragansett Bay (gray), and Long Island Sound (white), and (B) their respective sites. Letters represent a significant difference among estuaries in (A) and among sites in (B). Note the different scale bars between graphs.

bay (and most southerly) Long Island sites—Larchmont, Davenport, and Rye Town Beach—had the highest recorded mussel abundances of the 18 sites we surveyed (Tukey HSD; Fig. 2B). Within Long Island Sound, mussel abundances varied consistently with location within the bay. That is, the three inner bay sites (where we observed higher levels of nutrients and chlorophyll *a*) had higher abundances of mussels than the three outer bay sites (linear contrast, $p < 0.001$).

Crab densities were consistently low across the study region. *Carcinus maenus* (green crab) densities ranged from 0.0–2.67/m^2 across all sites, and the species was only observed at seven of the 18 sites surveyed (H. M. Leslie et al., *unpublished data*). *Hemigrapsus sanguineus* (Asian shore crab) was only found at Martin Point, in Casco Bay (average density of 0.67/m^2). Whelks were generally the most abundant predator, especially at the Long Island sites, and were found at 11 of the 18 sites.

Recruitment monitoring

There was a significant difference in the number of mussel recruits both among estuaries ($F_{2,74} = 81.15$, $p < 0.001$) and among sites ($F_{9,74} = 16.52$, $p < 0.001$). Mussel recruitment in Casco Bay was markedly higher than either Narragansett Bay or Long Island Sound (Tukey HSD; Fig. 3A). This trend appears to be driven by Maine Yacht Club (MYC) in Casco Bay, which had greater recruitment than the 11 other sites (Tukey HSD; Fig. 3B). However, when MYC was excluded from the ANOVA analysis, the difference among the estuaries remained ($F_{2,70} = 26.07$, $p < 0.0001$).

Within Casco Bay, recruitment rates varied

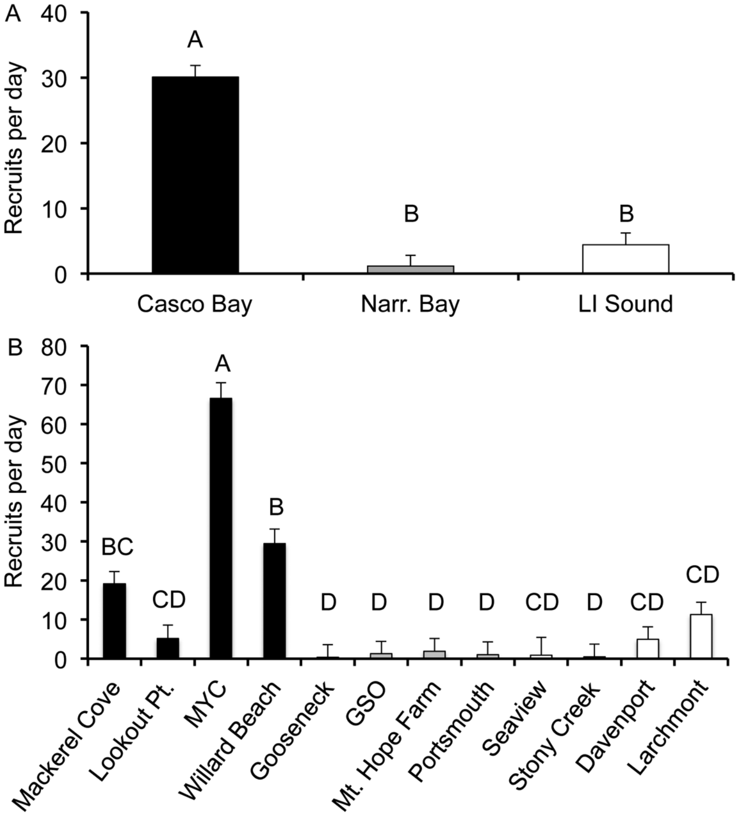

Fig. 3. Peak recruitment (recruits per day; LS mean + SE) in June–July 2010 (or June–August 2010 for Seaview and Larchmont) for mussel recruits larger than 425 μm in (A) Casco Bay (black), Narragansett Bay (gray), and Long Island Sound (white), and (B) their respective sites. Letters are as in Fig. 2. Note the different scale bars between graphs.

with location within the bay. That is, the two inner bay sites exhibited higher recruitment than the two outer bay sites (linear contrast, $p < 0.001$). Within Long Island Sound, there was a marginally significant difference in recruitment rates between locations (linear contrast, $p = 0.04$), with higher recruitment rates at the two inner bay sites.

Consumer exclusion experiment

There was a significant time × treatment interaction on mussel abundance ($F_{12, 416} = 3.92$, $p < 0.0001$; Table 5). That is, mussel cover in cages was significantly different overall in comparison to the controls and cage-controls (linear contrast, $p < 0.001$), and increased steadily over time. There was no difference among the three treatments from May through July 2010, but in August 2010 the cages began to accumulate more mussel cover. By March and August 2011, the cages had considerably more mussels than either of the other two treatments (Fig. 4). There was no significant difference overall between controls and cage-controls throughout the experiment (linear contrast, $p = 0.89$; Fig. 4).

At the end of the consumer exclusion experiment in August 2011, there was a significant difference in mussel abundance among the treatments ($F_{2, 154} = 60.62$, $p < 0.001$; Table 6) and a significant estuary × treatment interaction ($F_{4, 154} = 15.10$, $p < 0.001$; Table 6). That is, mussel abundance was greatest in the cage treatment for Narragansett Bay and Long Island Sound (Fig. 5A). Casco Bay had significantly lower mussel abundance overall than either of the other two estuaries (Tukey HSD; Fig. 5A).

There was also a significant interaction be-

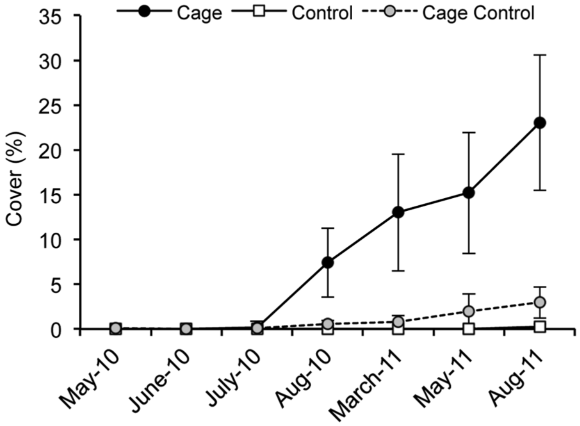

Fig. 4. Abundance (percent cover; mean ± SE) of *Mytilus edulis* as measured in the consumer exclusion experiment for all three treatments over time (all sites are pooled).

tween site and treatment ($F_{18,154} = 4.77$, $p < 0.001$; Table 6). We observed increased abundances of mussels for the experimentally caged plots, relative to the pooled controls, at all Narragansett Bay and Long Island sites (grand mean of the difference between treatments = 32.9% and 35.6%, respectively) and at one of the four Casco Bay sites (MYC). However, the increase in mussels as of August 2011 was only significant for seven of the 12 sites based on linear contrasts (Fig. 5B). In Narragansett Bay these sites were Portsmouth ($p < 0.001$), GSO ($p < 0.001$), and Gooseneck ($p = 0.03$), and in Long Island were Stony Creek ($p = 0.002$), Seaview ($p < 0.001$), Larchmont ($p = 0.03$), and Davenport ($p < 0.001$). The absolute difference in mussel cover (cages − controls) was greatest for Portsmouth (76%) and Seaview (65%). In Narragansett Bay, the absolute difference in mussel cover for GSO and Gooseneck was 38% and 14%, respectively, while in Long Island, Stony Creek, Larchmont, and Davenport had 18%, 27%, and 32% more mussels in cages, respectively. There was no significant difference between controls and cage-controls for any individual site in August 2011 (Tukey HSD; Fig. 5B; Appendix: Table C1).

Comparisons among inner and outer bay sites suggested that location within the estuary also affected the intensity of consumer pressure on mussels, albeit inconsistently. Mussel abundances increased in the caged treatment of the consumer exclusion experiment at both the inner and outer bay sites in Narragansett Bay ($p < 0.001$) and Long Island ($p < 0.001$) (see linear contrast 2 in *Methods: Data analyses*). Yet, the magnitude of the mussel response differed by location type between the two estuaries. In Narragansett Bay, the increase in mussel abundance with caging was greater for the inner bay sites: we observed an absolute difference of 40% more mussels in cages as compared to controls at the inner bay sites, in contrast with 26% more mussels in cages at the outer bay sites. In Long Island Sound, we observed a stronger response at the outer bay sites: there was an absolute difference of 30% more mussels in cages at inner bay sites and 42% more mussels in cages at outer bay sites. These results were likely driven by large increases at Portsmouth (NB, inner bay) and Seaview (LI, outer bay), as these sites had significantly more mussels in cages than all other sites in their respective estuaries (Fig. 5B; Appendix: Table C2). Abundance in controls was not significantly different between locations for Narragansett Bay or Long Island Sound, and all comparisons for Casco Bay were non-significant.

DISCUSSION

With a combination of experimental and observational studies, we have uncovered some intriguing patterns related to the population dynamics of the blue mussel, *Mytilus edulis*, on estuarine wave-protected rocky shores of the northeastern US. Here we focus on three patterns in particular: the spatial decoupling of adult and recruit abundances among the estuaries; estuary-scale differences in consumer pressure; and finally, within-estuary variation in these variables.

Spatial decoupling of adult and recruit abundances

Based on intertidal surveys, we observed greater ambient abundances of adult blue mussels in Long Island Sound as compared to Narragansett Bay and Casco Bay. This difference was most pronounced for the three inner bay sites in Long Island Sound, which were also the three most southerly sites of all 18 surveyed.

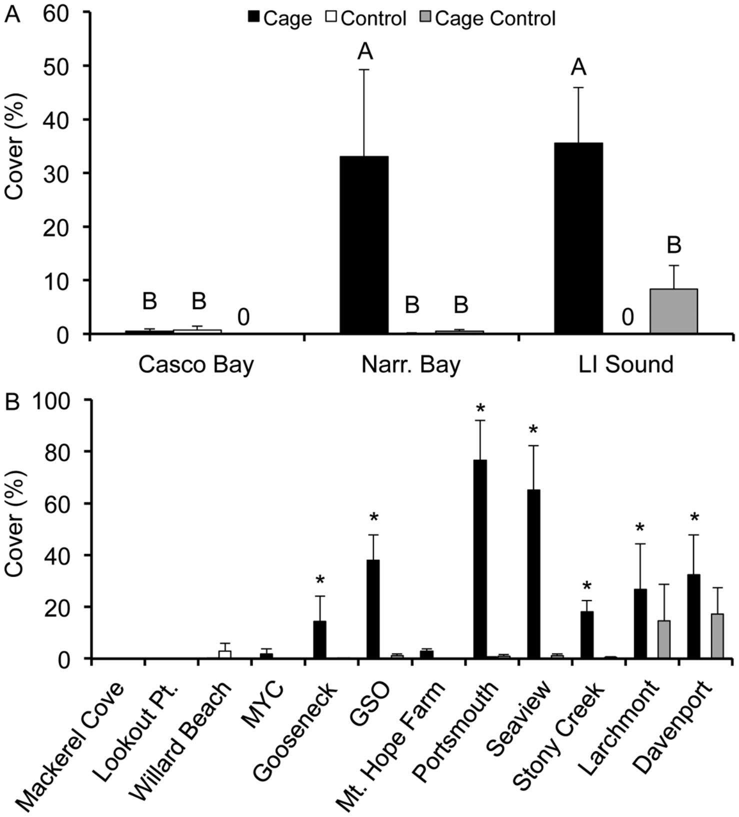

Fig. 5. Abundance (percent cover; mean + SE) of *Mytilus edulis* as measured in cages (black), controls (white), and cage-controls (gray) in August 2011 for (A) Casco Bay, Narragansett Bay, and Long Island Sound, and (B) their respective sites. Letters in (A) denote significant differences between treatments within an estuary (from Tukey HSD test) and asterisks in (B) denote a significant difference in abundance within cages as compared to the other two treatments (from linear contrasts). In (A), a zero denotes absence from the treatment. In (B), zeroes were omitted for visual clarity; lack of a bar denotes absence from the treatment, not missing data.

However, mussel recruitment rates exhibited the opposite pattern. That is, Casco Bay had the highest recruitment of *M. edulis* and low ambient adult percent cover, while Narragansett Bay and Long Island Sound had much lower recruitment rates and much higher ambient mussel cover. We predicted that recruit and adult abundances would vary across the three estuaries, given that the study region encompasses multiple biogeographic and oceanographic regions (with concurrent shifts in temperature, species assemblages, etc.). However, we expected to observe qualitatively consistent responses from the recruits and adults, based on the admittedly simple assumption that these different ontogenetic stages would respond similarly (i.e., in a species-specific manner) to environmental heterogeneity. Instead, we documented an intriguing disconnect between recruitment rates of new mussels and adult abundances (linear regression, $p = 0.81$). While mussel recruitment varies among years, our data do not seem unduly anomalous; analysis of multiple years of *M. edulis* recruitment at these sites reveals that the overall pattern among the estuaries has remained the same for the past two to three years (H. M. Leslie et al., *unpublished data*).

The decoupling of recruit and adult abundances within a given estuary is not completely unsurprising. Mussels, like many marine species with planktonic larvae, have the potential for long-distance dispersal and correspondingly, fairly open populations (Thorson 1950, Morgan 2001). Thus it is likely that many if not most of the new recruits we sampled in Casco Bay, for example, originated from spawning adults living at geographically distant sites, as has been observed with mussels and a number of other marine invertebrates (Palumbi 2004). However, at some broader geographic scale (within or beyond Casco Bay), mussel recruit and adult abundances must be connected, as Hughes et al. (2000) showed for corals on the Great Barrier Reef; this indeed is the basis of metapopulation theory and standard stock-recruitment models.

The concept of ontogenetic asymmetry (after Persson and De Roos 2013) provides a framework for these puzzling findings. Persson and De Roos (2013), building on stage structured ecological theory, show that differences in the energetics of juvenile and adult organisms ultimately can create asymmetry in the population dynamics of juvenile vs. adult individuals of a given species. That is, if rates of biomass accumulation (either as somatic growth or reproduction), mortality, or resource acquisition vary between juveniles and adults, then ontogenetic asymmetry occurs. This asymmetry can result in counterintuitive increases in juvenile biomass, adult biomass, or even total population biomass in response to variation in mortality or other exogenous factors, in contrast to the predictions of unstructured population models. In other words, the apparent variation in predation pressure among estuaries and sites nested within them (Fig. 5) and in nearshore ocean conditions (and presumably food for filter-feeding mussels, as suggested by Table 4) could perhaps create a strong bottleneck on juvenile individuals and thus reduce numbers of adult mussels, even in the face of high recruitment rates, such as we observed in Casco Bay. Two alternative explanations for the decoupling of adult and recruit numbers—particularly in Casco Bay—are (1) intense predation pressure removed the adult mussels, or (2) adult mussels were the result of a recruitment pulse during a previous year, not captured by our sampling. The first explanation is not consistent with the results of the consumer exclusion experiment, which showed essentially no consumer pressure on mussels at the Casco Bay sites, in contrast with the substantial effects in the more southerly estuaries (Fig. 5). The second explanation is certainly possible, and is consistent with the high variability in mussel recruitment documented by others (e.g., Le Corre et al. 2013). However, preliminary analysis of multiple years of mussel recruitment from these sites suggests that the data we presented were typical. Unfortunately we do not have the mussel size frequency and growth rate data needed to properly test this second hypothesis; those would be valuable to collect in the future, along with information on the proportion of primary vs. secondary settlers (Hunt and Scheibling 1998, Le Corre et al. 2013).

While we know far too little about mussel population dynamics at these sites to directly test these specific hypotheses, ontogenetic asymmetry provides a conceptual framework to organize what we do know, and highlights gaps that could be productive to address in the future. First, we know that rates of biomass accumulation in mussels decrease with size: smaller mussels gain more mass per unit time than larger individuals (e.g., Sukhotin et al. 2002, Negishi and Kayaba 2010). Second, differently sized mussels rely on overlapping (if not completely equivalent) resource pools: according to Widdows et al. (1979), adult mussels are non-selective filter feeders whose gills retain all particles larger than 5 μm. Field collected larval mussels from the western Gulf of St. Lawrence consumed plankton of 15–25 μm in size, with larger larvae preferring larger algal cells (Raby et al. 1997). Biomass accumulation and diet (along with particle selection, resource acquisition and assimilation) are well studied in blue mussels and other bivalves, given that these species are the target of substantial aquaculture activities globally.

In contrast, the modes and rates of mussel mortality is a much less investigated and arguably more complex topic, as it involves not only different ontogenetic stages of the organism, but also a varied set of predators and other mechanisms of mortality (e.g., disease, heat stress, direct disturbance via trampling and other physical impacts). Mussel mortality rates decrease with increasing body size (Petraitis 1995), and the causes of mortality differ among larval, juvenile (i.e., recruits), and adult blue mussels. Thus, a three-stage model (differentiating among larval, juvenile, and adult individuals) may be more appropriate to investigate ontogenetic asymmetry in this species, rather than the two-stage model, which includes only juveniles and adults.

Larval mortality rates of marine invertebrates are difficult to quantify, but a review by Rumrill (1990) indicated that they can be as high as 100% of the population per day and may be largely due to predation. Juvenile mussel mortality may be caused by direct predation or via indirect species interactions; for example, by algal whiplash or the herbivorous snail *Littorina littorea*. Whiplash can brush newly settled recruits off the substrate, thereby reducing barnacle recruitment (Menge 1976, Leonard 1999), and reducing the surface rugosity required for mussel recruitment. *L. littorea* can reduce mussel recruitment, even in the absence of whelk predation, by either grazing algae known to enhance mussel recruitment or by 'bulldozing' barnacles, which in turn alters the surface rugosity critical for mussels (Petraitis 1987, Petraitis 1990).

The population and community level consequences of ontogenetic asymmetry are potentially profound, and may include emergent alternate stable states, Allee effects, and facilitation (Persson and De Roos 2013). Placing our empirical results in this broader context highlights what is known about stage specific rates of biomass accumulation, mortality, and resource acquisition in *Mytilus edulis* and related species, and what gaps could be productively filled in order to generate site-specific estimates of these parameters and perhaps explain both the spatial decoupling of recruit and adult numbers that we documented (Figs. 2–3), as well as the surprising lack of consumer effects in Casco Bay (Fig. 5). Quantifying size-specific mortality, and its causes, seems particularly important given the information synthesized above. Moreover, depending on whether development or reproduction is the energetically limiting step, different types of population dynamics—referred to as either development control or reproductive control—can emerge. Development control refers to a class of asymmetric dynamics where the rate of development (e.g., from a juvenile to adult mussel) is the energetically limiting process for the population, rather than the rate of reproduction. This is analogous to what marine ecologists refer to as 'supply side ecology' (e.g., Hughes et al. 2000), and thus is a reasonable null model for mussel populations given their planktonic and highly dispersive larval phase and tremendous fecundity (Bayne 1976). Interestingly, empirical evidence suggests that such situations are rare (Persson and De Roos 2013), and thus marine systems may well be productive testing grounds for ontogenetic asymmetry, particularly for the case of development controlled dynamics.

Estuary scale differences in consumer pressure

We documented that adult abundances of the blue mussel increased with experimental consumer exclusion, particularly in the two southernmost estuaries. This finding suggests that consumers play a strong role overall in structuring mussel populations in Narragansett Bay and Long Island Sound, but not Casco Bay. We expected to see many active predators where we quantified the strongest consumer pressure (i.e., in Long Island Sound), and high abundance of predators where mussel cover was low (i.e., in Casco Bay). Neither of these predictions was borne out in our survey data: predator densities were consistently low across the study region, with the exception of the whelks *U. cinerea* and *N. lapillus*. The low numbers of intertidal predators, and the lack of consumer effects in Casco Bay in particular, were not consistent with patterns of consumer abundances or effects observed by others in New England rocky shores, where predators have been found to be more abundant, and predation rates higher, at sites characterized by lower wave exposure or tidal flow (Menge 1976, Leonard et al. 1998).

We suspect that many predators present at our sites were not captured by the intertidal surveys. For example, subtidal seastars and crabs such as *Cancer borealis* that forage at high tide were not captured in the surveys because we were only able to survey at low tide. However, from observation and preliminary field experiments of predation on tethered mussels (H. M. Leslie et al., *unpublished data*) we know that crabs are a major influence in this system (see also Leonard et al. 1998, Bertness et al. 1999, Leonard et al. 1999). Crabs can also have indirect effects on mussels through direct predation on other mussel consumers, such as whelks. Crab predation on grazers, such as *Littorina littorea* (Ellis et al. 2007, Perez et al. 2009), also has been shown to alter surface rugosity, and thus mussel recruitment, by effecting grazing activity (Petraitis 1990). In addition, ducks and gulls can have both direct and indirect effects on mussel populations. For example, gulls prey heavily on crabs in the Gulf of Maine, especially during summer months (Ellis et al. 2005). By consuming crabs, gulls can have indirect trophic impacts on other invertebrates, including *M. edulis* as well as *N. lapillus* and *L. littorea* (Ellis et al. 2007). Moreover, seasonal variation in bird predation on mussels (particularly by eiders) has been found to affect the size distribution of mussels remaining in a community, thereby affecting which consumers are most effective in subsequent mussel predation (Boudreau and Hamilton 2012). Given the surprising lack of predation effects we documented in Casco Bay, the few predators we were able to observe, and the important role predation and other sources of mortality play in structuring population dynamics (Persson and De Roos 2013), the identity, roles, and interactions of intertidal predators at these sites warrant further attention.

While the focus of our consumer exclusion experiment was on spatial variation in predation intensity rather than size-specific effects, previous investigations have shown that not only does mussel size or stage influence predation rates, but so does the composition of the predator assemblage (and their relative sizes and foraging strategies). Dominant consumers at northwest Atlantic rocky shore sites include gulls, ducks, crabs, whelks, and seastars (Menge 1976, Petraitis 1990, Ellis et al. 2005, 2007, Boudreau and Hamilton 2012). Here we synthesize what is known about the species- and size-specific effects of these predators on mussel populations. Boudreau and Hamilton (2012), on mildly to moderately wave-exposed rocky shores in Canada's Bay of Fundy, documented that eider ducks ingested mussels ranging from 2–60 mm in length (i.e., both newly recruited juveniles and adults), whereas crabs tended to forage on 30–42 mm long mussels, and whelks consumed 25–50 mm long mussels, although they preferred individuals closer to 25 mm in length. Hunt and Scheibling (1998), working on wave-exposed rocky shores in Nova Scotia, found that even one of the smallest size classes ($\geq$5 mm shell length) of the whelk *N. lapillus* could significantly affect mussel cover. In a companion laboratory study, as the size of these post-recruit whelks increased, so too did the mean size of mussels consumed (Hunt and Scheibling 1998). Also in the laboratory, DeGraaf and Tyrrell (2004) observed that *C. maenus* ate significantly fewer mussels that were large (15–21 mm shell length) than those that were small (5 mm shell length).

As the cage-controls likely excluded most birds (as shown by Wootton 1993, Boudreau and Hamilton 2012), but not whelks and the other benthic consumers, they also may be thought of as 'bird exclusions.' If this was the case, the lack of significant differences between the controls and cage-controls throughout the experiment suggest that birds, as a group, exerted little consumer pressure on mussel abundances. Further observational and experimental studies at these sites are needed to verify this finding, as well as to investigate the relative contributions of individual predatory species on mussel populations, and how those effects may vary geographically. By employing a series of cages similar to Boudreau and Hamilton (2012), and coupling this experiment with more comprehensive intertidal and subtidal surveys, it should be possible to distinguish between species-specific consumer effects of birds, crabs, whelks, and seastars at these sites. Relatedly, addition of another nested set of estuarine sites north of Cape Cod would improve the spatial coverage of the comparative-experimental study and enable more robust inferences of the regional-scale variation in recruitment, adult abundances, and consumer pressure that we documented.

Within-estuary variation in mussel recruitment, adult abundance, and consumer pressure

Finally, we observed that ambient adult abundances, mussel recruitment, and consumer pressure varied on the within-estuary scale. In initiating this study, we specifically selected sites within each estuary so as to examine the possible influence of location (inner vs. outer bay) on mussel population dynamics. We hypothesized that adult abundances, recruitment rates, and consumer pressure would be elevated at inner bay sites, in keeping with previous investigations where enhanced nutrients and primary productivity have been shown to fuel increased biomass and reproduction of primary consumers like mussels and barnacles, and to contribute to more rapid succession and intensified species interactions (e.g., Bertness et al. 1991, Menge et al. 2003, Leslie et al. 2005).

Our findings provided equivocal support for this 'bottom-up' hypothesis. While ambient adult mussel abundances were higher at the inner bay sites than at the outer bay sites in Long Island Sound, this was not the case in the two more northern estuaries (Fig. 2B). Similarly, the higher mussel recruitment at the inner bay sites in Casco Bay was not matched by the patterns in the other two estuaries (Fig. 3B). And finally, while consumer pressure was higher at the inner bay sites in Narragansett Bay, we documented the opposite pattern in Long Island Sound: there, our experimental results indicated that consumer pressure was higher at the outer bay sites (Fig. 5B). Given the extent of coastal development in the two southern estuaries, we suspect that the Narragansett Bay and Long Island Sound sites may experience more consistent and greater land-based nutrient loading (and thus higher primary productivity conditions) through time than the Casco Bay sites. However, currently available environmental data at the scale of our study sites do not enable us to test this hypothesis. We do, however, have a site-level proxy for land-based impacts: human population density. Higher human population densities are known to contribute to greater inputs of land-based nutrient pollution and associated coastal marine changes, including coastal eutrophication and hypoxia (Valiela et al. 1992, National Research Council 2000, Boesch et al. 2001, Nixon et al. 2008). Inner bay sites tended to be adjacent to areas of higher human population density (Appendix: Fig. D1). Again, however, the resolution of the available environmental data is coarser than the human population data, which precludes robust comparisons of these variables at the regional scale.

Conclusions

In summary, *M. edulis* populations varied in ways consistent with some but not all of the hypotheses presented in this paper. First, we hypothesized that mussel abundance and recruitment would be greater at the more southerly sites due to warmer temperatures and increased metabolic rates, which could result in more rapid transition to the juvenile stage and thus reduced exposure to predation risk in the plankton (Rumrill 1990). Instead we documented a strong decoupling between these two variables, such that recruitment rates were highest in the northernmost estuary, Casco Bay, and ambient adult abundances were highest in the southernmost estuary, Long Island Sound. Second, we hypothesized that mussels would be more abundant at sites with fewer predators. Instead, we found very few predators at the 18 sites where we conducted surveys, and the distribution of these predators was not associated with the intensity of consumer effects, as measured experimentally. Nevertheless, we found that consumer effects significantly impacted mussel populations in Narragansett Bay and Long Island Sound. Further study of the identities, feeding modes and size-selectivity, and relative effects of the consumer species responsible would be productive, both to advance system-specific knowledge and to explore the effects of stage-structured population dynamics on population and community processes. Finally, we hypothesized that mussel responses differed between inner and outer bay sites due to increased nutrient loading (and thus greater primary production and food resources for filter feeding invertebrates) at the inner bay sites. While the available environmental data are consistent with the logic of this comparison, the data on mussel recruitment, abundances, and responses to consumer pressure did not suggest strong support for the influence of bottom-up forcing on these estuarine mussel populations.

Overall, our results confirm the roles of both top-down and bottom-up forces in structuring rocky shore populations of *Mytilus edulis* (e.g., Menge 1992, Leonard et al. 1998, Worm et al. 2002, Vinueza et al. 2006). However, a number of puzzles remain, including the spatial decoupling of recruits and adults on a regional scale and the lack of consumer effects in Casco Bay. These findings illustrate the value of further comparative-experimental studies of wave-protected estuarine rocky shores, particularly given these coastal ecosystems' vulnerability to both local and global scale anthropogenic impacts, including those arising from proximity to coastal urban centers.

ACKNOWLEDGMENTS

Many thanks to the individuals who enabled us to access rocky shore sites from Maine to New York, including A. Romer, B. Purciaseppe, D. Goodkind, D. Beutel, K. Nordstrom, J. Smith, J. Carey, J. Garber, L. Churchill, T. Goodchild, S. Nordwall, J. Zuke, D. Anderson, and S. Hale. We also thank K. Gedan, N. Chu, S. Crosby, L. Watka, B. Black, C. Brisson, A. Tomasso, A. Austin, L. Zipf, J. Leibovic, J. Hakam, H. Booth, C. Sullivan, and I. Rich for help in the field and lab. We thank the Friends of Casco Bay, RI Dept. of Environmental Management, Univ. of Rhode Island, Univ. of Connecticut, and CT Dept. of Environmental Protection for sharing environmental data, and K. Cortes, L. Carlson, and J. Witman for assistance with data synthesis and analyses. This manuscript benefitted from comments by two anonymous reviewers and J. Witman. Research support was provided to H. M. Leslie by RI EPSCoR and Brown University's Department of Ecology and Evolutionary Biology, Institute at Brown for Environment and Society, and ADVANCE Program (NSF Grant #0548311).

Literature Cited

Airamé, S., J. E. Dugan, K. D. Lafferty, H. Leslie, D. A. McArdle, and R. R. Warner. 2003. Applying ecological criteria to marine reserve design: a case study from the California Channel Islands. Ecological Applications 13:S170–S184.

Altieri, A. H., and J. D. Witman. 2006. Local extinction of a foundation species in a hypoxic estuary: integrating individuals to ecosystem. Ecology 87:717–730.

Bayne, B. L., editor. 1976. Marine mussels: their ecology and physiology. Cambridge University Press, Cambridge, UK.

Bernhardt, J. R., and H. M. Leslie. 2013. Resilience to climate change in coastal marine ecosystems. Annual Review of Marine Science 8:371–392.

Bertness, M. D., S. D. Gaines, D. Bermudez, and E. Sanford. 1991. Extreme spatial variation in the growth and reproductive output of the acorn barnacle *Semibalanus balanoides*. Marine Ecology Progress Series 75:91–100.

Bertness, M. D., G. H. Leonard, J. M. Levine, P. R. Schmidt, and A. O. Ingraham. 1999. Testing the relative contribution of positive and negative intercations in rocky intertidal communities. Ecology 80:2711–2726.

Boesch, D. F., R. H. Burroughs, J. E. Baker, R. P. Mason, C. L. Rowe, and R. L. Siefert. 2001. Marine pollution in the United States. Pew Oceans Commission, Arlington, Virginia, USA.

Boudreau, M. R., and D. J. Hamilton. 2012. Seasonal variation in effects of multiple predators on an intertidal mussel bed: implications for interpretation of manipulative experiments. Marine Ecology Progress Series 465:137–153.

DeGraaf, J. D., and M. C. Tyrrell. 2004. Comparison of the feeding rates of two introduced crab species, *Carcinus maenus* and *Hemigrapsus sanguineus*, on the blue mussel, *Mytilus edulis*. Northeastern Naturalist 11:163–167.

Ellis, J. C., W. Chen, B. O'Keefe, M. J. Shulman, and J. D. Witman. 2005. Predation by gulls on crabs in rocky intertidal and shallow subtidal zones of the Gulf of Maine. Journal of Experimental Marine Biology and Ecology 324:31–43.

Ellis, J. C., M. J. Shulman, M. Wood, J. D. Witman, and S. Lozyniak. 2007. Regulation of intertidal food webs by avian predators on New England rocky shores. Ecology 88:853–863.

Gedan, K. B., J. Bernhardt, M. D. Bertness, and H. M. Leslie. 2011. Substrate size mediates thermal stress in the rocky intertidal. Ecology 92:576–582.

Helmuth, B., N. Mieszkowska, P. Moore, and S. J. Hawkins. 2006. Living on the edge of two changing worlds: forecasting the responses of rocky intertidal ecosystems to climate change. Annual Review of Ecology, Evolution, and Systematics 37:373–404.

Helmuth, B. S. T., and G. E. Hofmann. 2001. Microhabitats, thermal heterogeneity, and patterns of physiological stress in the rocky intertidal zone. Biological Bulletin 201:374–384.

Hughes, T. P., A. H. Baird, E. A. Dinsdale, N. A. Molchaniwskyj, M. S. Pratchett, J. E. Tanner, and B. L. Willis. 2000. Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. Ecology 81:2241–2249.

Hunt, H. L., and R. E. Scheibling. 1998. Effects of whelk (*Nucella lapillus* (L.)) predation on mussel (*Mytilus trossulus* (Gould), *M. edulis* (L.)) assemblages in tidepools and on emergent rock on a wave-exposed rocky shore in Nova Scotia, Canada. Journal of Experimental Marine Biology and Ecology 226:87–113.

Hunt, H. L., and R. E. Scheibling. 2001. Patch dynamics of mussels on rocky shores: integrating process to understand pattern. Ecology 82:3213–3231.

Le Corre, N., A. L. Martel, F. Guichard, and L. E. Johnson. 2013. Variation in recruitment: differentiating the roles of primary and secondary settlement of blue mussels *Mytilus* spp. Marine Ecology Progress Series 481:133–146.

Leonard, G. H. 1999. Positive and negative effects of intertidal algal canopies on recruitment and survival of barnacles. Marine Ecology Progress Series 178:241–249.

Leonard, G. H., M. D. Bertness, and P. O. Yund. 1999. Crab predation, waterborne cues, and inducible defenses in the blue mussel, *Mytilus edulis*. Ecology 80:1–14.

Leonard, G. H., J. M. Levine, P. R. Schmidt, and M. D. Bertness. 1998. Flow-driven variation in intertidal community structure in a Maine estuary. Ecology

79:1395–141.

Leslie, H. M., E. N. Breck, F. Chan, J. Lubchenco, and B. A. Menge. 2005. Barnacle reproductive hotspots linked to nearshore ocean conditions. Proceedings of the National Academy of Science 102:10534–10539.

Lesser, M. P., M. Bailey, D. Merselis, and J. R. Morrison. 2010. Physiological response of the blue mussel *Mytilus edulis* to differences in food and temperature in the Gulf of Maine. Comparative Biochemistry and Physiology Part A 156:541–551.

Menge, B. A. 1976. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. Ecological Monographs 46:355–393.

Menge, B. A. 1992. Community regulation: under what conditions are bottom-up factors important on rocky shores? Ecology 73:755–765.

Menge, B. A., C. Blanchette, P. Raimondi, T. Freidenburg, S. Gaines, J. Lubchenco, D. Lohse, G. Hudson, M. Foley, and J. Pamplin. 2004. Species interaction strength: testing model predictions along an upwelling gradient. Ecological Monographs 74:663–684.

Menge, B. A., and G. M. Branch. 2001. Rocky intertidal communities. Pages 221–252 *in* M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine community ecology. Sinauer, Sunderland, Massachusetts, USA.

Menge, B. A., B. A. Daley, P. A. Wheeler, E. Dahlhoff, E. Sanford, and P. T. Strub. 1997. Benthic-pelagic links and rocky intertidal communities: bottom-up effects on top-down control? Proceedings of the National Academy of Sciences USA 94:14530–14535.

Menge, B. A., J. Lubchenco, M. E. S. Bracken, F. Chan, M. M. Foley, T. L. Freidenburg, S. D. Gaines, G. Hudson, C. Krenz, H. Leslie, D. N. L. Menge, R. Russell, and M. S. Webster. 2003. Coastal oceanography sets the pace of rocky intertidal community dynamics. Proceedings of the National Academy of Sciences USA 100:12229–12234.

Miller, L. P., and B. Gaylord. 2007. Barriers to flow: The effects of experimental cage structures on water velocities in high-energy subtidal and intertidal environments. Journal of Experimental Marine Biology and Ecology 344:215–228.

Minnesota Population Center. 2011. National Historical Geographic Information System: Version 2.0. University of Minnesota, Minneapolis, Minnesota, USA.

Morgan, S. G. 2001. The larval ecology of marine communities. Pages 159–182 *in* M. D. Bertness, S. D. Gaines, and M. E. Hay, editors. Marine community ecology. Sinauer, Sunderland, Massachusetts, USA.

National Research Council. 2000. Clean coastal waters: understanding and reducing the effects of nutrient pollution. National Academy Press, Washington, D.C., USA.

Navarrete, S. A., and T. Manzur. 2008. Individual and population-level responses of a keystone predator to geographic variation in prey. Ecology 89:2005–2018.

Navarrete, S. A., and B. A. Menge. 1996. Keystone predation and interaction strength: interactive effects of predators on their main prey. Ecological Monographs 66:409–429.

Negishi, J. N., and Y. Kayaba. 2010. Size-specific growth patterns and estimated longevity of the unionid mussel (*Pronodularia japanensis*). Ecological Research 25:403–411.

Nixon, S. W., B. Buckley, S. L. Granger, L. A. Harris, A. J. Oczkowski, R. W. Fulweiler, and L. W. Cole. 2008. Nitrogen and phosphorous inputs to Narragansett Bay: past, present, and future. Pages 101–175 *in* A. Desbonnet and B. A. Costa-Pierce, editors. Science for ecosystem-based management: Narragansett Bay in the 21st century. Springer, New York, New York, USA.

Paine, R. T. 1966. Food web complexity and species diversity. American Naturalist 100:65–75.

Paine, R. T. 1994. Marine rocky shores and community ecology: an experimentalist's perspective. Pages 1–152 *in* O. Kinne, editor. Excellence in Ecology. Volume 4. Ecology Institute, Oldendorf/Luhe, Germany.

Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs 57:858–873.

Palumbi, S. R. 2004. Marine reserves and ocean neighborhoods: The spatial scale of marine populations and their management. Annual Review in Environment and Resources 29:31–68.

Perez, K. O., R. L. Carlson, M. J. Shulman, and J. C. Ellis. 2009. Why are intertidal snails rare in the subtidal? Predation, growth and the vertical distribution of *Littorina littorea* (L.) in the Gulf of Maine. Journal of Experimental Marine Biology and Ecology 369:79–86.

Persson, L., and A. M. De Roos. 2013. Symmetry breaking in ecological systems through different energy efficiencies of juveniles and adults. Ecology 94:1487–1498.

Petes, L. E., B. A. Menge, and G. D. Murphy. 2007. Environmental stress decreases survival, growth, and reproduction in New Zealand mussels. Journal of Experimental Marine Biology and Ecology 351:83–91.

Petraitis, P. S. 1987. Factors organizing rocky intertidal communities of New England: herbivory and predation in sheltered bays. Journal of Experimental Marine Biology and Ecology 109:117–136.

Petraitis, P. S. 1990. Direct and indirect effects of predation, herbivory and surface rugosity on mussel recruitment. Oecologia 83:405–413.

Petraitis, P. S. 1991. Recruitment of the mussel *Mytilus-edulis*-L on sheltered and exposed shores in Maine, USA. Journal of Experimental Marine Biology and Ecology 147:65–80.

Petraitis, P. S. 1995. The role of growth in maintaining spatial dominance by mussels (*Mytilus edulis*). Ecology 76:1337–1346.

Raby, D., M. Mingelbier, J. J. Dodson, B. Klein, Y. Lagadeuc, and L. Legendre. 1997. Food-particle size and selection by bivalve larvae in a temperate embayment. Marine Biology 127:665–672.

Robles, C., R. Sherwood-Stephens, and M. Alvarado. 1995. Responses of a key intertidal predator to varying recruitment of its prey. Ecology 76:565–579.

Rumrill, S. S. 1990. Natural mortality of invertebrate larvae. Ophelia 32:163–198.

Suchanek, T. H. 1981. The role of disturbance in the evolution of life history strategies in the intertidal mussels *Mytilus edulis* and *Mytilus californianus*. Oecologia 50:143–152.

Sukhotin, A. A., D. Abele, and H. O. Portner. 2002. Growth, metabolism and lipid peroxidation in Mytilus edulis: age and size effects. Marine Ecology Progress Series 226:223–234.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biological Reviews 25:1–45.

Valiela, I., et al. 1992. Couplings of watersheds and coastal waters: sources and consequences of nutrient enrichment in Waquoit Bay, Massachusetts. Estuaries 15:443–457.

Vinueza, L. R., G. M. Branch, M. L. Branch, and R. H. Bustamante. 2006. Top-down herbivory and bottom-up El Niño effects on Galápagos rocky-shore communities. Ecological Monographs 76:111–131.

Widdows, J., P. Fieth, and C. M. Worrall. 1979. Relationships between seston, available food, and feeding activity in the common mussel *Mytilus edulis*. Marine Biology 50:195–207.

Witman, J. D., S. J. Genovese, J. F. Bruno, J. W. McLaughlin, and B. I. Pavlin. 2003. Massive prey recruitment and the control of rocky subtidal communities on large spatial scales. Ecological Monographs 73:441–462.

Wootton, J. T. 1993. Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. American Naturalist 141:71–89.

Worm, B., H. K. Lotze, H. Hillebrand, and U. Sommer. 2002. Consumer versus resource control of species diversity and ecosystem fundtioning. Nature 417:848–851.

Supplemental Material

Appendix A

Table A1. Geographic coordinates of all rocky shore study sites.

Estuary	Site	Location	Coordinates (°N, °W)
Casco Bay	Mackerel Cove	Outer	43.728, −69.998
	Lookout Point	Outer	43.808, −69.995
	Maine Yacht Club (MYC)	Inner	43.679, −70.250
	Willard Beach	Inner	43.647, −70.226
	Falmouth Foreside	*Outer*	*43.733, −70.204*
	Martin Pt.	*Inner*	*43.690, −70.246*
Narragansett Bay	Gooseneck Cove	Outer	41.455, −71.335
	GSO	Outer	41.494, −71.421
	Mt. Hope Farm	Inner	41.668, −71.237
	Portsmouth	Inner	41.593, −71.286
	Ft. Adams	*Outer*	*41.472, −71.336*
	Common Fence Pt.	*Inner*	*41.655, −71.221*
Long Island Sound	Stony Creek	Outer	41.262, −72.750
	Seaview	Outer	41.297, −72.252
	Larchmont	Inner	40.916, −73.748
	Davenport	Inner	40.894, −73.769
	Pleasure Beach	*Outer*	*41.308, −72.148*
	Rye Town Beach	*Inner*	*40.960, −73.678*

Notes: Italics indicates sites where only intertidal surveys were conducted. Location is as in Table 2.

Table A2. Geographic coordinates of all environmental monitoring stations, from north to south.

Estuary	Station name	Location	Coordinates (°N, °W)	Data source(s)
Casco Bay	Little Iron Island	Outer	43.82, −60.97	FoCB
	Fort Gorges	Inner	43.66, −70.22	FoCB
	Portland	. . .	43.66, −70.25	NOAA
Narragansett Bay	URI GSO Dock	Outer	41.49, −71.42	RI DEM FSMN/URI GSO
	Mt. Hope Bay	Inner	41.68, −71.22	RI DEM FSMN/URI GSO
	Quonset	. . .	41.59, −71.41	NOAA
Long Island Sound	Eastern Sound	Outer	41.26, −72.07	MYSound
	Execution Rocks	Inner	40.88, −73.73	MYSound
	Kings Point	. . .	40.81, −73.76	NOAA

Note: Data sources are as in Tables 1 and 2.

APPENDIX B

Fig. B1. Here we show a representative block (n = 8) from the consumer exclusion experiment deployed at the 12 sites, nested within three estuaries. The marked control plot is outlined with the red dotted line. The cage control is on the left.

APPENDIX C

Table C1. Tukey HSD post-hoc comparisons among all site × treatment combinations for mussel abundance in August 2011 as measured in the consumer exclusion experiment.

Level: [Estuary] Site, treatment	Tukey HSD connecting letter report				
[NB] Portsmouth, cage	A				
[LI] Seaview, cage	A	B			
[NB] GSO, cage		B	C		
[LI] Davenport, cage		B	C	D	
[LI] Stony Creek, cage			C	D	E
[LI] Larchmont, cage			C	D	E
[LI] Davenport, cage-control			C	D	E
[NB] Gooseneck, cage			C	D	E
[LI] Larchmont, cage-control			C	D	E
[NB] Mt. Hope Farm, cage			C	D	E
[CB] Willard Beach, control			C	D	E
[LI] Seaview, cage-control				D	E
[NB] GSO, cage-control				D	E
[NB] Portsmouth, cage-control				D	E
[LI] Stony Creek, cage-control				D	E
[CB] MYC, cage				D	E
[NB] Portsmouth, control				D	E
[CB] Willard Beach, cage				D	E
[NB] Gooseneck, cage-control					E
[CB] Lookout Point, cage					E
[CB] Mackerel Cove, cage					E
[CB] Willard Beach, cage-control				D	E
[CB] MYC, cage-control					E
[CB] Mackerel Cove, cage-control					E
[CB] Lookout Point, cage-control					E
[CB] MYC, control					E
[CB] Mackerel Cove, control					E
[CB] Lookout Point, control					E
[NB] GSO, control					E
[NB] Mt. Hope Farm, control				D	E
[LI] Seaview, control					E
[NB] Gooseneck, control					E
[NB] Mt. Hope Farm, cage-control				D	E
[LI] Davenport, control					E
[LI] Larchmont, control				D	E
[LI] Stony Creek, control				D	E

Notes: Levels not connected by the same letter are significantly different. Estuary is as in Table 1.

Table C2. Results of pair-wise linear contrasts between sites, comparing mussel abundance within the cage treatment in August 2011.

Site	MC	LP	MYC	WB	GC	GSO	MTF	PM	SC	SV	LM	DP
Casco Bay												
Mackerel Cove	. . .											
Lookout Point	1.00	. . .										
Maine Yacht Club	0.69	0.69	. . .									
Willard Beach	0.89	0.89	0.84	. . .								
Narragansett Bay												
Gooseneck Cove					. . .							
GSO					**0.001**	. . .						
Mt. Hope Farm					0.44	<**0.001**	. . .					
Portsmouth					<**0.001**	<**0.001**	<**0.001**	. . .				
Long Island Sound												
Stony Creek									. . .			
Seaview									<**0.001**	. . .		
Larchmont									0.83	<**0.001**	. . .	
Davenport									0.28	<**0.001**	0.17	. . .

Notes: Each value is the p-value returned from pair-wise linear contrasts between sites. Ellipses indicate that no test was done. For clarity, values are only shown below the diagonal (i.e., values above the diagonal in blank cells are identical). Significant differences appear in boldface. Abbreviations are: MC, Mackerel Cove; LP, Lookout Point; MYC, Maine Yacht Club; WB, Willard Beach; GC, Gooseneck Cove; GSO, University of Rhode Island Graduate School of Oceanography; MTF, Mt. Hope Farm; PM, Portsmouth; SC, Stony Creek; SV, Seaview; LM, Larchmont; DP, Davenport.

APPENDIX D

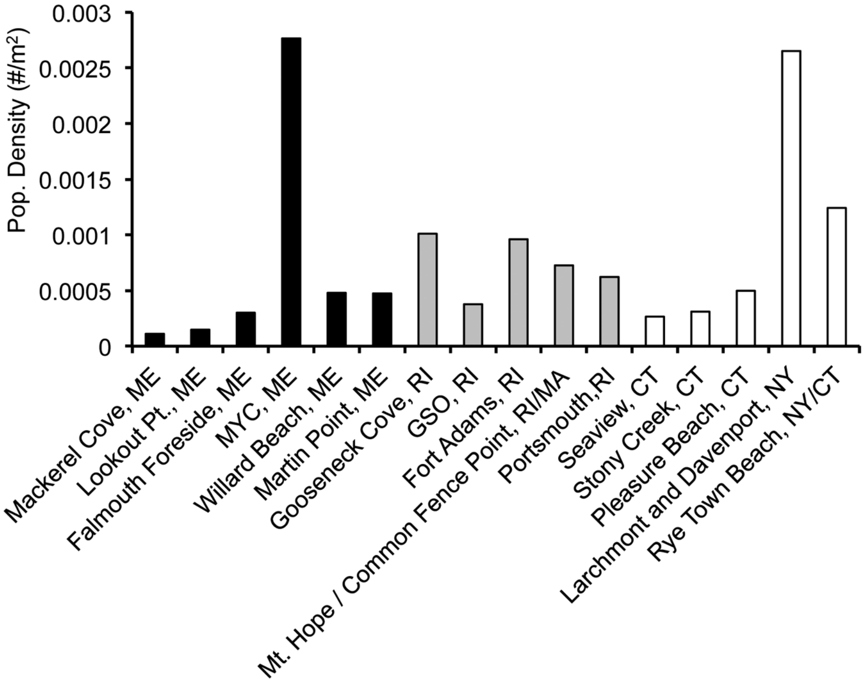

Fig. D1. Population density (number of people per square meter) of each study site (n = 18). Black: Casco Bay, Gray: Narragansett Bay, White: Long Island Sound. Human population densities were significantly higher at the inner bay sites vs. the outer bay sites ($F_{1,14} = 6.872$, $p = 0.020$), but did not vary among the estuaries ($F_{2,14} = 1.052$, $p = 0.375$) [ANOVA with estuary (n = 3) and location within estuary (n = 2)]. Note that Larchmont and Davenport and Mt. Hope Farm and Common Fence Point are shown together, as these pairs of sites are within the same watersheds and thus have equivalent values. Data are from the 2010 US Census (Minnesota Population Center 2011); see *Methods: Environmental data* for details.