

MASSIVE PREY RECRUITMENT AND THE CONTROL OF ROCKY SUBTIDAL COMMUNITIES ON LARGE SPATIAL SCALES

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Abstract. What drives community change on large spatial scales? An opportunity to address this fundamental question was provided by a massive subtidal recruitment of the mussel, *Mytilus edulis*, across the southwest Gulf of Maine (GOM), USA, in 1995. Since *M. edulis* is consumed by many predator species, we hypothesized that the episodic increase in food resources had a bottom-up effect on populations of mussel consumers. The mussel recruitment event was unprecedented in its large spatial extent, high coverage of the sea floor, and depth of penetration into the rocky subtidal zone. During 1995–1997 we tracked mussels and their consumer populations in the area to document what happened. Surveys across a 120-km marine landscape revealed that juvenile mussels covered 33–91% of the bottom (8–12 m depth) at 13 of 17 sites between October 1995 and June 1996. The cover of mussel prey in June 1996 explained significant variation in the density and biomass of mussel predators, the sea stars *Asterias* spp. and rock crabs *Cancer* spp., at 16–17 sites 10, 13, and 23 months after mussel recruitment. These results are consistent with the hypothesis that the extensive mussel recruitment had a bottom-up effect on the subtidal food web. Levels of *Asterias* spp. recruitment, biomass, and density following mussel recruitment were the highest recorded at two monitored sites in 16–18 years. One year after the large pulse of mussel food resources, *Asterias* spp. recruitment was positively related to the percent cover of mussels, suggesting a feedback between food supply and consumer recruitment on a large spatial scale. Crab size-structure data supported the interpretation that recruitment contributed to the high densities of rock crabs recorded in July 1997. We suggest that the bottom-up effects observed in consumer populations were produced by increased growth, elevated reproduction and recruitment, and possibly by immigration.

Coupling between bottom-up and top-down control was observed after a lag of 12–14 months post-mussel recruitment when predation by sea stars, rock crabs, and sea urchins eliminated extensive beds of juvenile mussels across the study region. The elimination of *Mytilus* prey triggered cannibalism in the sea star *Asterias vulgaris*, which contributed to density-dependent population declines in sea stars between 1996 and 1997. A key assumption of a consumer reproduction and recruitment response—that some of the larvae produced by local adult stocks of consumers could be retained in the study region—was tested by investigating the potential larval dispersal of sea stars and crabs in a simulated three-dimensional flow field of the southwest GOM. The simulation supported the assumption as 15–75% of particles released below 1-m depth were retained in the region over 2–5 week periods approximating the larval life-span of the consumers. Furthermore, the degree of retention increased dramatically between the surface (1 m) and 15-m depth, implying that the extent of large-scale connectivity by passive larval dispersal is highly dependent on depth. In this study, massive prey recruitment stimulated coupling between bottom-up and top-down forces, resulting in broad-scale changes in local consumer populations that persisted after the prey-recruitment signal was removed, underscoring the importance of episodic events in marine community dynamics.

Key words: bottom-up vs. top-down; cannibalism; connectivity; current modeling; density dependence; large-scale research; larval-dispersal modeling; marine food webs; *Mytilus edulis*; predation; recruitment; rocky subtidal communities.

INTRODUCTION

The foundation of community ecology has been constructed from studies conducted on small spatial scales

(Levin 1992, Brown 1995, Lawton 2000). For the most part, the building blocks of the foundation have been analyses of species tolerances to environmental requirements (Gleason 1926, Whittaker 1967) and species interactions at local sites (Connell 1961, Paine 1966). Local sites (scale of meters to few kilometers) within larger landscapes (20–200 km) and regions

Manuscript received 23 August 2001; revised 16 May 2002; accepted 21 May 2002. Corresponding Editor: J. E. Duffy.

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(200–4000 km, Mittelbach et al. 2001) are connected by wind, water runoff, and ocean currents transporting nutrients, food, and reproductive propagules of the next generation of organisms (Dayton and Tegner 1984, Roughgarden et al. 1988, Greene and Johnson 1995, Noller, *in press*). Thus, communities living at local sites are interconnected to some extent on larger spatial scales. Understanding the extent and scale of such connectivity is essential not only for the growth of community ecology as an intellectual endeavor, but also for predicting how local biota will be modified in response to the elimination of source populations and by variation in climate. Considerable progress has been made toward developing a broader spatial context for intertidal (Bustamente et al. 1995, Menge et al. 1997, Broitman et al. 2001, Connolly et al. 2001) and coral-reef (Hughes 1994, Cornell and Karlson 1996, Edmunds and Bruno 1996, Hughes et al. 1999) communities since the importance of expanding the spatial scale of marine ecological research was emphasized by Dayton and Tegner (1984) nearly two decades ago. Little is currently known about the role of large-scale processes in regulating the local dynamics of rocky subtidal communities, where historical factors (Witman and Sebens 1992, Estes and Duggins 1995, Smith 2001) and oceanographic climate are known to be important (Dayton et al. 1999).

Recruitment is one process that can link populations across large spatial scales in marine ecosystems where many bottom-dwelling species have planktonic larvae that colonize multiple sites from the water column (Thorson 1950, Caley et al. 1996). Because it represents increased prey for consumers (predators, herbivores), recruitment of lower trophic-level species may stimulate changes in consumer populations at higher trophic levels. Such changes driven by increased resources (nutrients, food) at lower trophic levels are termed “bottom-up effects” (McQueen et al. 1989), which have been demonstrated by increased abundance, reproduction, and/or growth rates of consumer populations in lakes (McQueen et al. 1989, Carpenter and Kitchell 1993), oak forests (Hunter 1992), kelp forests (Duggins et al. 1989), rivers (Power et al. 1995), and rocky intertidal habitats (Bosman et al. 1987, Menge 1992, Metaxas and Scheibling 1993, Bustamente et al. 1995, Leonard et al. 1998, Nielsen 2001). Current theory recognizes that bottom-up and top-down (predatory control) effects are coupled, and therefore should be integrated (Hunter and Price 1992, Osenberg and Mittelbach 1996, Polis and Strong 1996). Linkage between bottom-up and top-down processes occurs when increased food at basal trophic levels (i.e., bottom-up influence) leads to elevated predation from higher trophic-level predators (i.e., top-down control).

Bottom-up–top-down linkages created by the recruitment of prey species may be characterized by high temporal and spatial variability because recruitment is notoriously variable in plants (Silvertown 1980), marine invertebrates (Thorson 1950), and fish (Sale et al.

1984). A type of highly variable recruitment, termed “masting,” occurs in many temperate and tropical trees that episodically produce unusually large seed crops (Janzen 1978, Silvertown 1980). Masting may trigger strong bottom-up–top-down linkages, such as when a mast production of acorns led to an increase in populations of mice that subsequently controlled herbivores (Jones et al. 1998). Although the importance of high recruitment is recognized (Menge 1992, Robles 1997, Leonard et al. 1998), the trophic consequences of large recruitment events remain virtually unstudied on landscape and regional spatial scales (i.e., >20 km maximum distance between sites, Mittelbach et al. 2001) in marine benthic ecosystems. This is partly due to the need to track populations for many years to detect unusual events, and to the inherent difficulty of working on large spatial scales in marine ecosystems (Underwood and Petraitis 1993).

In this paper we first document the scale of mussel recruitment across a subtidal landscape offshore of a 120-km-long coastline. We then test a key prediction of bottom-up theory—that consumer abundance should be correlated with the food resources that are increased (Power 1992, Forkner and Hunter 2000). Specifically, we regressed the abundance of mussel recruits (prey) against the average biomass and density of four species of consumers at 16–17 sites. Tracking mussels and their consumer populations across the area during 1995–1997 enabled us to document top-down control and food limitation among consumers in the form of sea star cannibalism after the mussel prey were consumed. Long-term data on sea star abundance and recruitment at two of the sites were analyzed to place the magnitude of the sea star population increase into perspective. Finally, an oceanographic-current model was used to test a critical assumption of a large-scale bottom-up effect, that larvae of predators produced in response to increased food resources (mussels) could be retained within the study region, thus explaining part of the subsequent predator population increase. Our results suggest that massive recruitment of marine species, analogous to seed masting on land, may synchronize predator population dynamics at local sites across large landscapes. This in turn generates bottom-up and top-down linkages in marine benthic communities.

METHODS

Study region

This study was conducted at 17 subtidal sites located in the southern Gulf of Maine (Fig. 1). The area extended from off Cape Elizabeth, Maine, USA, in the north to south of Cape Ann, Massachusetts, USA. The body of water between these two Capes is known as the “Bigelow Bight.” Oceanographic conditions in Bigelow Bight are characterized by tidal mixing and general northeast–southwest coastal current flow driven by the Eastern Maine Coastal Current (Lynch et al. 1997). Three southern sites off Cape Ann were located

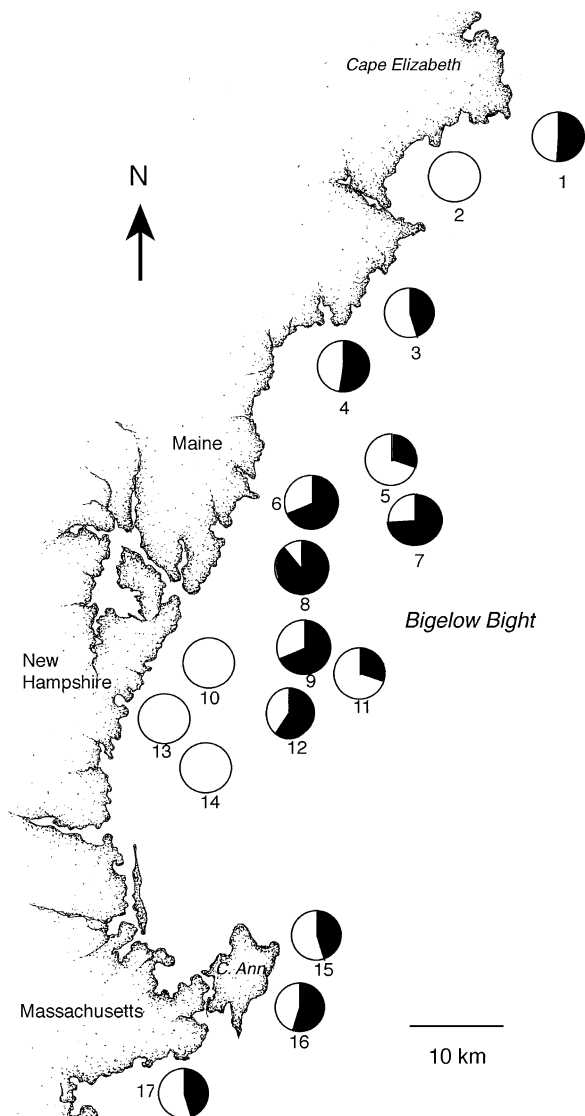


FIG. 1. Map of southern Gulf of Maine (USA) region showing the mean percent cover of mussel (*Mytilus edulis*) recruits at 8–12 m depth in June 1996 as blackened sectors of pie diagrams. Clear circles indicate no *Mytilus* recruitment at a site. The sites (with abbreviations) are: (1) East Hue and Cry Ledge, EH, (2) Stratton Island, SI, (3) Goosefare Bay Rocks, GR, (4) Kennebunk Ledge, KL, (5) Spouting Shoal, SS, (6) York Ledge, YL, (7) Boon Island, BI, (8) Murray Rock, MR, (9) Duck Island, DI, (10) Gunboat Shoal, GS, (11) Star Island, STI, (12) White Island, WI, (13) Hampton Rock, HRK, (14) Hampton Shoal Ledge, HSL, (15) Dry Salvages, DS, (16) Londoner Ledge, LL, and (17) Halfway Rock, HR.

at the transition between the Bigelow Bight and Massachusetts Bay (Fig. 1).

Study sites were located either on the submerged sides of islands or on rocky ledges. The study was conducted at the depth range where massive mussel recruitment was initially observed at Murray Rock in October 1995 (8–12 m). The substrate consisted of large expanses of horizontal-sloping, granite bedrock

ledge at all sites. The benthic communities were predominantly large areas of coralline algal flats interspersed with small beds of horse mussels, kelp, and foliose red algae as described in Witman (1985, 1987), Sebens (1986a, b), and Ojeda and Dearborn (1989). All 17 sites were highly exposed to wave action, with flow forces similar to those reported at two of the sites, Murray Rock and Star Island (Witman 1987).

Mussel recruitment

The percentage of the rocky bottom covered by blue mussel recruits was determined by photographing quadrats (0.25-m² area) with a quadrapod camera framer (Witman 1985) at random marks along transects randomly dropped at 8–12 m depth. Thirty-two to forty quadrats were photographed per site for a total of 613, 557, and 577 quadrats sampled in June 1996, October 1996, and July 1997, respectively. The random sampling of quadrats occurred in approximately 500–1000 m² area of bottom at each site. The cover of mussel recruits in the photo quadrats was determined by the random-dot technique (Menge 1976), where the organism in 200, 2-mm-diameter circles (dots) was identified and enumerated on a projected image of each quadrat (as in Witman and Grange [1998]). If aggregations of predators covered mussels in the photo quadrats, they were removed after an initial photograph was taken, and the bottom was rephotographed to reveal the primary substratum. Samples of mussel recruits were collected to track cohorts by size frequency analysis during the initial observation of massive recruitment at Murray Rock, and subsequently from all sites in June 1996 by scraping all mussels off the substratum in two randomly dropped 0.01-m² quadrats per site. The shell lengths of more than 250 *Mytilus edulis* from each site were measured under a microscope equipped with an ocular micrometer.

To track the persistence of the mussel cohorts, permanent quadrats measuring 0.25 m² in area were set up on areas of ledge dominated by *Mytilus edulis* recruits at five sites (Murray Rock, York Ledge, Boon Island, Duck Island, Halfway Rock) at 10–12 m depth. The corners of 10 quadrats per site were marked with underwater epoxy (Koppers splash zone compound [Kop-Coat, Pittsburgh, Pennsylvania, USA]) and numbered tags that served as alignment points for the quadrapod. The quadrats were photographed 5 to 9 times over a 2-yr period. Changes in the percent cover of mussels in the permanent quadrats were determined by converting the quadrat slides to a PICT (picture format image) file with a 35-mm slide scanner and measuring the area covered by mussels with Adobe Photoshop software (Adobe Systems International San Jose, California, USA). Areas of the bottom delineated as permanent quadrats were fully accessible to consumers, enabling predation on mussels by sea stars, sea urchins, whelks, and crabs to be documented.

Consumer populations

Blue mussels are important prey of many species of predators including the sea stars, *Asterias vulgaris* and

Asterias forbesi (Menge 1976, 1979, Lubchenco and Menge 1978, Hulbert 1980, Harris et al. 1998), rock crabs, *Cancer borealis*, *C. irroratus*, (Menge 1983, Moody and Steneck 1993), green crabs, *Carcinus maenus* (Elner 1978, Menge 1983), sea urchins, *Strongylocentrotus droebachiensis* (Briscoe and Sebens 1988), lobsters, *Homarus americanus* (Elner and Campbell 1987), small fish, *Tautoglabrus adspersus* (Edwards et al. 1982, Ojeda and Dearborn 1991), and the snails *Nucella lapillus* (Menge 1976) and *Buccinum undatum* (J. D. Witman, unpublished data). We hypothesized that the large pulse of mussel prey would have a bottom-up effect on the subtidal food web by increasing the abundance, growth and/or recruitment of populations of mussel consumers. Region-wide surveys of the 17 sites were conducted 3 times (June 1996, October 1996, and July 1997) to determine the abundance of mussel consumers and the percent cover of mussel recruitment. Consumer abundance was measured both as the density of individuals in random photo quadrats (taken in mussel cover surveys, as above), in band transects, and also as biomass. Biomass may be a more relevant metric than density for estimating bottom-up effects because it responds directly to increased food resources and equates the effects of body size differences among consumers (Petraitis 1995, Osenberg and Mittelbach 1996). We determined the biomass of consumer species from size-mass regressions using body sizes measured in the photo quadrats and in band transects (Appendix). Maximum body sizes were determined for both sea star species, *A. vulgaris* and *A. forbesi*, as the distance from the center of the disc to the tip of the longest arm, referred to as the "radius." Maximum diameters of the body (test [calcified body of a sea urchin]) were used for the sea urchin *S. droebachiensis*, while maximum carapace widths were measured for two species of crabs, *Cancer borealis* and *C. irroratus*. Shell lengths were used to classify body sizes of the whelk *Buccinum undatum*. Sea star and crab sizes were obtained by measuring individuals in the photo quadrats. Additionally, sizes and abundance of the more mobile crabs and whelks were assessed in three replicate, randomly placed 25.0 × 1.0 m band transects at each site.

The procedure for estimating the biomass of consumers consisted of collecting sea stars, urchins, crabs, and whelks from the sites, measuring them for maximum body dimension, and weighing them as wet biomass after they were drained on towels for 10 minutes until dry. Size-mass regressions were computed using natural log-transformed linear regressions of body size on wet biomass. Biomass per quadrat (0.25 m²) or per band transect (25.0 m²) was then predicted from the size-mass regression equations by using the sizes of each individual consumer measured in quadrats or transects as independent variables in the equations, and then summing the predicted biomass of all individual consumers per sampling unit. Average biomass per site was calculated from the replicate quadrats or transects

for each species and standardized to per 0.25 m² area. Collections for size-mass regressions were made in June 1996 and July 1997. Biomass estimates for October 1996 were based on the June 1996 size-mass regressions. To avoid depleting their populations, crabs were collected for size-mass regressions from only two sites each year. All regressions were highly significant (Appendix).

Variability in the recruitment of *Asterias* spp. sea stars over time and in relation to the abundance of mussel food resources was investigated from two sources of data. First, small sea stars (1.5–15.0 mm radius) were counted in a time series of random photo quadrats taken with a quadrat at Murray Rock and Star Island prior to the 1995 mussel recruitment, and again from quadrat photos at all sites during the 1996–1997 surveys. The resolution of the photo quadrats was high enough to detect small *Asterias* spp. sea stars because they were white and conspicuous against the dark substrate. Sea stars in this size range were likely produced during the summer reproductive season, as a growth experiment (below) suggested that they are ≤4–5 mo old. These summer recruits were also counted from photo quadrats taken at 16 sites in October 1996 to discern a potential effect of increased mussel food supply during 1995–1996 on the size of the 1996 sea star cohort. Balch and Scheibling (2000) used a similar size range of 1 to ≤10 mm radius to classify the recently settled juvenile cohort of *Asterias* spp. off Nova Scotia. *Asterias* populations in the Gulf of Maine (GOM) spawn in late spring to early summer (May–June, Galtsoff and Loosanoff 1939, Menge 1986; C. W. Walker, personal communication). The planktonic trophic larvae are thought to disperse in the water column for 2–5 weeks (Galtsoff and Loosanoff 1939). *Asterias* recruits in the 1.5–15 mm size range could be detected in photo quadrats from June to November. A second source of information on sea star recruitment was provided by the regressions of mussel cover vs. sea star density and biomass as a size class of juvenile *Asterias* spp. (>15 to ≤50 mm radius), representing individuals that were ~6–12 mo old. It was not possible to distinguish between the two species of small *Asterias*, so *A. vulgaris* and *A. forbesi* were probably both represented here as *Asterias* spp. recruits.

To interpret the age of juvenile *Asterias*, a sea star growth experiment was conducted in the sea water system at the Marine Science Center, Nahant, Massachusetts (USA) during September–December 1997 (S. Altman and J. D. Witman, unpublished manuscript). Thirty *Asterias vulgaris* measuring 5.0–10.0 mm radius were collected from Murray Rock and fed over the same temperature regime as in the field. The 10 *Asterias* raised on an unlimited diet of *Mytilus* recruits grew an average 3.6 mm per month (S. Altman and J. D. Witman, unpublished manuscript), supporting our interpretation that the 1.5–15 mm size class represents a "young-of-the-year" sea star recruit that is less than 4–5 mo old.

Cancer spp. crabs in the GOM spawn in May to July and typically appear as recruits (<10-mm carapace width) in July or later (Palma et al. 1998, McNaught 1999; R. Wahle, *personal communication*). The cryptic coloration of small rock crabs made it difficult to census crab recruits smaller than 10.0-mm carapace width in photo quadrats. Rock crab recruitment was assessed from small crabs measured in the replicate band transects (as above), and as crabs >10.0-mm carapace width in the photo quadrats. We estimated that one-yr-old crabs were >10.0- to \leq 30.0-mm carapace width (Reilly and Saila 1978; R. Wahle, *personal communication*). This size range was used to designate the 1995 cohort sampled at the end of June 1996, and the 1996 cohort sampled in July 1997.

Sea star cannibalism

We predicted that the large populations of mussel consumers would be food limited after the juvenile mussels were no longer available. Consequently, we quantified the extent of sea star cannibalism in the photographic surveys of mussel and consumer abundance since *Asterias vulgaris* and *A. forbesi* are occasionally cannibalistic (Lubchenco and Menge 1978, Menge 1979, Harris et al. 1998). This was done by examining all feeding aggregations of sea stars in the randomly located 0.25-m² photo quadrats during surveys in June 1996, October 1996, and July 1997. Cannibalism was detected as groups of 2–8 *A. vulgaris* wrapped around each other in a ball-shaped aggregation (Fig. 2). The aggregations were pulled apart and mortality from cannibalism was scored if the central region of a sea star (i.e., containing the mouth) was completely enveloped by the stomach of a conspecific. In all instances, the central region of the sea star being consumed was digested. This distinguished cannibalism from nonlethal, intraspecific predation that produced lesions on the aboral surface of *A. vulgaris* (J. D. Witman and S. J. Genovese, *unpublished data*). Mortality from cannibalism was expressed as the percentage of the total *A. vulgaris* at a site killed by cannibalism. The percentage of the total *A. vulgaris* population involved in cannibalistic feeding aggregations was also calculated. Cannibalism was not observed in populations of *A. forbesi* or *Cancer* spp. crabs.

Wave-height data for 1995–1996 were obtained from NOAA National Data Buoy station number 44007 located in northern Bigelow Bight (43.53 N latitude, 70.14 W longitude) near East Hue and Cry Ledge (Fig. 1).

Oceanographic-current model

To test the likelihood that the newly hatched larvae of consumers (sea stars, crabs) would be retained in the study area, we examined Lagrangian drift pathways in a simulated three-dimensional flow field. The flow was represented as the climatological mean tide (M2) plus subtidal residual circulation (including seasonal wind, tidal rectification, barotropic and baroclinic effects), calculated as in Lynch et al. (1996, 1997) with

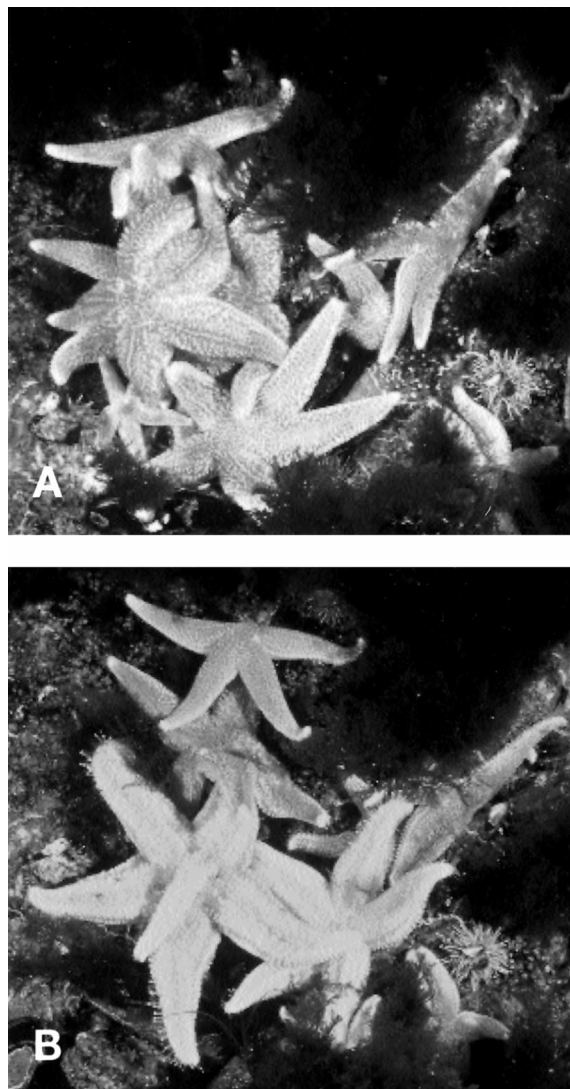


FIG. 2. Cannibalistic feeding aggregation of seven *Asterias vulgaris* at Murray Rock in October 1996. (A) The aggregation as it was initially encountered. (B) The same aggregation after the sea stars were turned over to reveal an arm of an individual *A. vulgaris* protruding from a conspecific's mouth at lower left. The central region of the victim sea star (not in view) was being digested in the predator's stomach.

the QUODDY finite-element model. Since sea star and crab larvae are primarily dispersed during the summer months, climatological mean forcing representative of July and August was used. The mesh and domain of the model used in this study have enhanced resolution relative to the model presented in Lynch et al. (1997), and has been verified through field study.

Particle positions were integrated in these fields using a fourth-order Runge-Kutta method (DROG3D, Blanton 1995). We assumed that the larvae behaved as passive particles, so the integration was done without dispersive effects. A single particle was released from each of the 13 study sites where mussels recruited (Fig.

1) at depths of 1, 5, 10, and 15 m at weekly intervals bracketing the 2–5 wk larval life-span of *Asterias* spp. (Galtsoff and Loosanoff 1939) and the dispersive phase of *Cancer* spp. zoea and megalopae (Sastry 1977). Each of the four temporal simulations (i.e., 2, 3, 4, and 5 wk) included all four depths.

Since the launching time relative to the tidal cycle affects the particle's ultimate path, a sensitivity analysis of starting times equally spaced through the tidal cycle was performed. This analysis showed the effects of varying launch times to be negligible (J. McLaughlin, unpublished data). The resulting trajectories were plotted in Matlab (The MathWorks, Natick, Massachusetts, USA) and evaluated by calculating the percentage of particles that remained within the bounds of the study area. Reasoning that a passive particle could travel past a site and return to it on a complete tidal excursion, we used the downstream distance that a particle would travel on one tidal excursion as the outer boundary of the study area.

RESULTS

Mussel recruitment

Mussel recruitment was first observed as a "pavement" covering over 2 km² of rocky ledge at 8–12 m depth below mean low water at Murray Rock (MR; Gulf of Maine, USA) in October 1995. The average cover of mussel recruits at MR in October was 91.0 ($\pm 7.1\%$ (mean ± 1 SD, $n = 33$ [0.25-m²] photo quadrats). Recruitment was apparently not substrate specific as juvenile mussels were observed covering all substrates including rock ledge, horse mussels, rock crabs, foliose algae, and the stipes and holdfasts of kelp. Since the mean shell length of mussels in October was 2.3 ± 0.97 mm (mean ± 1 SD, Fig. 3), and 1-mo-old *Mytilus edulis* are ~ 1.0 -mm shell length (Seed 1969), we estimated that settlement occurred in August–September 1995. The size and percent cover of mussel cohorts were tracked over the winter at MR and at two other sites until surveys could be initiated in June 1996 to assess the spatial extent of the recruitment. The June 1996 survey indicated that the recruitment phenomenon was widespread, with *Mytilus* recruits covering, on average, 33–89% of the bottom at 13 of the 17 sites (Fig. 1). The highest coverage of mussel recruits occurred in the central area of the study region (Fig. 1).

The 4.1–7.1 mm range in mean shell length from all sites in June 1996 contained the mean size of the 1995 cohort at MR in June 1996 (6.57 mm, Fig. 3), strongly suggesting that the small mussels sampled at other sites also settled in 1995. The 1995 cohort is also evident from the modes (2.0–4.0 mm) in the size distributions of mussels sampled in early 1996 at York Ledge and Halfway Rock (Fig. 3). Although *M. edulis* frequently settles at the intertidal–subtidal fringe (Menge 1979), and occasionally in small patches (tens of square meters area) down to depths of 5 m (Hulbert 1980, Briscoe and Sebens 1988; J. Witman, personal observations),

there are no data indicating that juvenile blue mussels covered large areas of the bottom at 5- to 12-m depths prior to 1995.

Resource abundance and consumer populations

Regression analyses indicated significant, positive relationships between *Mytilus* cover and the mean biomass and density of sea stars and rock crabs in June 1996, eight months after the mussel recruitment event was detected (Fig. 4, Table 1). Given the large number of processes potentially influencing populations at multiple sites spanning the 120-km distance, we were surprised that the abundance of a food resource could explain 57.4–68.2% of the variation in the biomass of sea stars and crabs at this time (Fig. 4, Table 1). The percentage variation in sea star and crab density explained by mussel cover was less than for biomass, but the regressions were significant nonetheless (Table 1). Relationships between mussel cover and whelk or urchin biomass in June were nonsignificant (Fig. 4C and D). Photography of permanent quadrats at five sites and observations at several other sites indicated that mussel recruits persisted at 54–93% cover from November 1995 through June 1996, (Fig. 5A) and were preyed on by sea stars, crabs, and urchins. Aggregations of sea stars were observed denuding the substrate of mussels at all of the sites (Fig. 6). Sea urchins were observed grazing mussels off the substratum (Fig. 6D), but they were not as widely distributed as sea stars, with five sites lacking urchins (Fig. 4D) in June 1996. Rock crabs cleared patches in the mussel beds as they fed (J. D. Witman, S. J. Genovese, and J. F. Bruno, personal observations, J. D. Witman, unpublished photographs).

The complete elimination of extensive beds of small *Mytilus* from three of the sites (Murray Rock, York Ledge, and Boon Island) by 1 October 1996 was unexpected, however, and prompted us to re-survey 13 more of the original sites. Mussel cover and consumer abundance and sizes were assessed using the same methods as in June. The random photo transects indicated that the juvenile blue mussels previously covering the bottom were absent from all 13 mussel sites by mid-October 1996 when the survey was completed. We ascribed the elimination of the large-scale recruitment pattern to predation, since high levels of predation on mussels was witnessed at all mussel sites over the year. An alternative hypothesis for the disappearance of the subtidal *Mytilus* beds was that they were dislodged during periods of high wave action. However, wave action was not a viable alternative explanation because the mussel beds survived rough seas during the winter and were eliminated during the calmest months of the year (May–September) when surface waves in the Bigelow Bight were generally < 1.0 m high (Fig. 5B).

Mussel coverage in June 1996 was still a significant predictor of sea star and crab abundance across the region in October 1996 and again in July 1997 (Figs. 7–8, Table 1). There was a weak, significantly positive

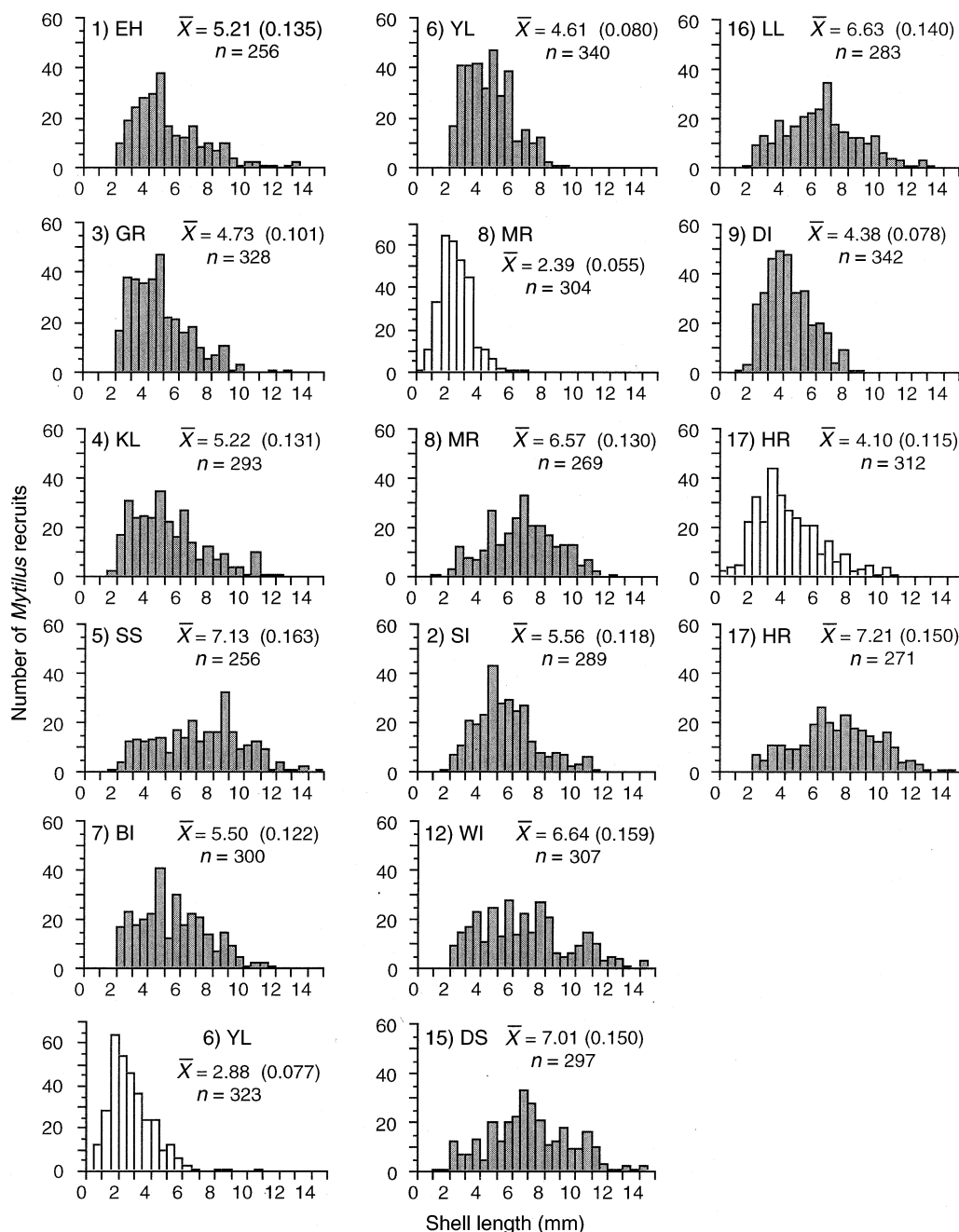


FIG. 3. Size frequency distributions of *Mytilus* recruits (see Fig. 1 for north-to-south location order and numbered site codes). The shell length (mean with 1 SE in parentheses) is reported above each distribution, as is the sample size. Plots with shaded bars are from June 1996. Plots with clear bars are from October 1995 (Murray Rock), January 1996 (York Ledge), and March 1996 (Halfway Rock).

relation between the biomass of whelks, *Buccinum undatum*, in July 1997 and mussel cover one year before (Table 1) that may reflect a delayed bottom-up response.

Analysis of covariance (ANCOVA) revealed temporal changes (1996–1997) in the relation between consumer abundance and mussel cover for both sea star and crabs (Table 1, Figs. 4, 7, and 8). The elevations

of the sea star vs. mussel cover regression lines were significantly higher in June 1996 than in October 1996 and July 1997 for both density and biomass (Table 1), indicating a regional decrease in the density and biomass of *Asterias* populations after the increase in 1996. Significant differences in the slopes of the regression lines revealed the opposite pattern for crab densities, which were significantly higher in July 1997 than in

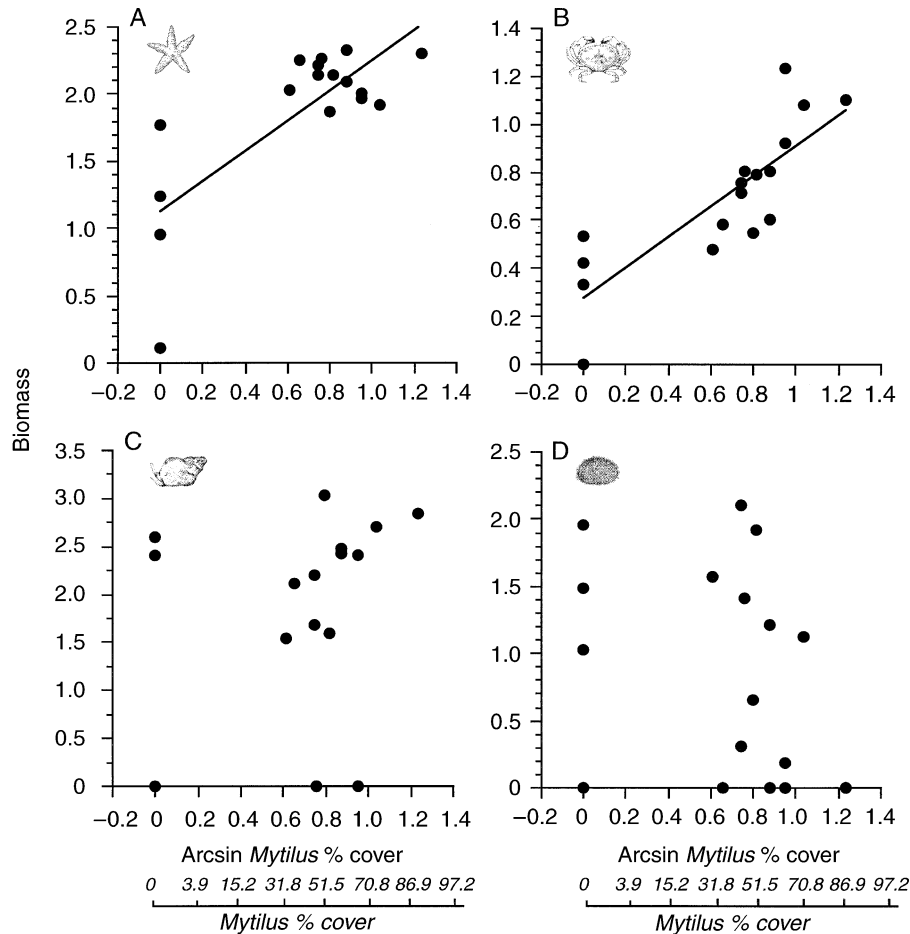


FIG. 4. Regressions of average mussel percent cover on the average biomass of (A) sea stars (*Asterias* spp.), (B) rock crabs (*Cancer* spp.), (C) whelks (*Buccinum undatum*), and (D) sea urchins (*Strongylocentrotus droebachiensis*) in June 1996. Solid circles represent the average values per site. Biomass was measured as grams per 0.25 m² and is presented as $\log(x + 1)$. Although the analyses were performed on transformed data, the untransformed percent cover values are reported in italics below the x-axis for clarity. Regression lines were plotted if they were significant at $P \leq 0.05$ (A, B). Regression equations are reported in Table 1.

June and October 1996 (Table 1). Elevations of the crab biomass regression lines were significantly greater in October 1996 than in June 1996 and July 1997, due to the large sizes of crabs in October.

The abundance of sea stars 10–11 months after the mussel recruitment event was the highest recorded in 16–18 years at two of the study sites where long-term monitoring data were available (Fig. 9). Analysis of variance (ANOVA) and Tukey-Kramer post hoc tests used to compare mean abundances over time indicated that *Asterias* biomass at Star Island (STI) in June 1996 was significantly greater than biomass in October 1996, which was significantly greater than all remaining dates (Fig. 9). Mean *Asterias* densities at STI in June and October 1996 were significantly higher than densities on all other sampling dates (Fig. 9). ANOVA on mean *Asterias* biomass at Murray Rock revealed the same temporal patterns as density at STI, while average *Asterias* densities in June 1996 were significantly greater than on all other dates (Fig. 9).

The null hypothesis that the size-specific biomasses of the most widely distributed sea star, *A. vulgaris*, did not differ at sites of high (>50%), low (<35%), and no *Mytilus* cover was tested by ANCOVA. The log-transformed size vs. log-transformed biomass regressions of *A. vulgaris* available from 16 sites in June 1996 were used for the analysis. Significantly greater elevations at high vs. low, or vs. no-mussel-cover sites would indicate heavier sea stars of a given size, suggesting a bottom-up effect by greater growth in biomass at sites with abundant mussel food resources. Data from all high-cover sites (EH, KL, YL, MR, BI, DI, WI, LL [see Fig. 1 for site codes]) were pooled since slopes and elevations of these size vs. biomass regressions did not differ. Since the overall ANCOVA comparing regressions from pooled high-cover sites to all other sites indicated that the slopes were heterogeneous ($F = 8.69$, $df = 7, 1286$, $P \leq 0.001$), the Johnson-Neyman test (Huitema 1980) was used to compare elevations. This test indicated that the elevations of size vs. mass re-

TABLE 1. Results of linear regression analysis of the percent cover of mussel recruits in June 1996 against density and biomass of three consumer species together with ANCOVA and other results testing the null hypothesis that the slopes or elevations of sea star or crab regression lines did not differ by sampling date.

Date	Regression†			ANCOVA F_{\ddagger}	Parameter compared	Tukey or Johnson- Neyman ranking§
	Equation	F	r^2			
Sea stars (<i>Asterias</i> spp.)						
Density						
June 1996	$y = 0.692 + 0.772x$	14.0**	0.484	19.9***	elevations	June 1996 > October 1996 > July 1997
October 1996	$y = 0.640 + 0.414x$	6.73**	0.325			
July 1997	$y = 0.229 + 0.595x$	17.8***	0.561			
Biomass						
June 1996	$y = 1.144 + 1.072x$	20.28***	0.574	12.4***	elevations	June 1996 > October 1996 > July 1997
October 1996	$y = 0.916 + 0.971x$	23.55***	0.627			
July 1997	$y = 0.531 + 1.092x$	15.82***	0.530			
Crabs (<i>Cancer</i> spp.)						
Density						
June 1996	$y = 0.0029 + 0.043x$	7.9**	0.346	5.10*	slopes and elevations	July 1997 > October 1996, June 1996
October 1996	$y = 0.0056 + 0.033x$	11.7**	0.455			
July 1997	$y = 0.0168 + 0.092x$	37.9***	0.730			
Biomass						
June 1996	$y = 0.276 + 0.635x$	32.2***	0.682	6.95**	slopes	July 1997 > October 1996, June 1996
October 1996	$y = 0.557 + 0.694x$	17.6***	0.557			
July 1997	$y = 0.133 + 0.912x$	54.8***	0.792		elevations	
Whelks (<i>Buccinum undatum</i>)						
Biomass						
July 1997	$y = -0.888 + 1.23x$	6.075*	0.302	

* $P \leq 0.05$; ** $P \leq 0.01$; *** $P \leq 0.001$.

† Regression equations represent $\log(y + 1)$ average density or biomass per 0.25 m² vs. mussel cover (arcsine square-root transformed) in June 1996. For regressions, $df = 1, 16$ for June and $df = 1, 15$ for other months. Significant positive regressions are consistent with a bottom-up effect of mussel recruitment on consumer abundance.

‡ ANCOVA tests resulting in F values all had $df = 2, 45$.

§ Tukey's multiple-comparison tests after ANCOVA indicate which dates differed significantly ($P \leq 0.05$), with the inequality sign indicating the direction. Dates separated by a comma were the same. Slopes of sea star regressions did not differ by sampling date, so elevations were compared. The Johnson-Neyman test allows elevations to be compared when slopes are significantly different (Huitema 1980) and was used for comparison of crab regressions.

|| Whelk regressions for June and October 1996 were not significant.

gressions from the pooled high-cover sites were significantly greater ($P \leq 0.05$) than those at a no-mussel-cover site (HRK) and a low-mussel-cover site (SS), supporting the alternate hypothesis of greatest mass gain at sites where *Mytilus* recruits were most abundant. Regression equations for sites that differed were: pooled high-cover sites, $y = -6.27 + 2.34x$, $r^2 = 0.93$; HRK, $y = -5.08 + 1.68x$, $r^2 = 0.75$; SS, $y = -3.67 + 1.97x$, $r^2 = 0.90$. A similar approach was used to compare *A. forbesi* size vs. biomass regressions among three sites. ANCOVA indicated that the elevations of *A. forbesi* regression lines were greater at high (LL) and intermediate (DS) mussel-cover sites than that of a low-cover site (SS), ($P \leq 0.05$ for all, Johnson-Neyman test; regression equations in Appendix).

Recruitment of consumers

Sea stars.—*Asterias* recruitment increased to an all-time high of 12.5–25.2 recruits 0.25 m² at MR and STI

in October 1996 and remained high in 1997 (Fig. 9). ANOVA indicated that the average density of *Asterias* recruits at STI in October 1996 was significantly greater than all other sampling dates (Fig. 9). At Murray Rock, average recruitment densities in October 1996 and July 1997 were statistically indistinguishable, but were significantly greater than all other sampling dates (Fig. 9). Sea star recruitment in October 1996 was high at other sites in addition to the two long-term monitoring sites, ranging from average densities of 7.5 (Hampton Shoal Ledge) to 34.7 (Kennebunk Ledge) juvenile sea stars/0.25 m². These average densities from October 1996 were 4.7–21 times higher than average *Asterias* recruitment densities at Murray Rock (1.58 ± 0.53 individuals [mean ± 1 SE]) prior to the *Mytilus* recruitment event. The October 1996 range of average *Asterias* recruitment was also 3.7–17 times higher than *Asterias* recruitment at Star Island (2.03, 0.25 standard error) averaged over the years before 1995. The abun-

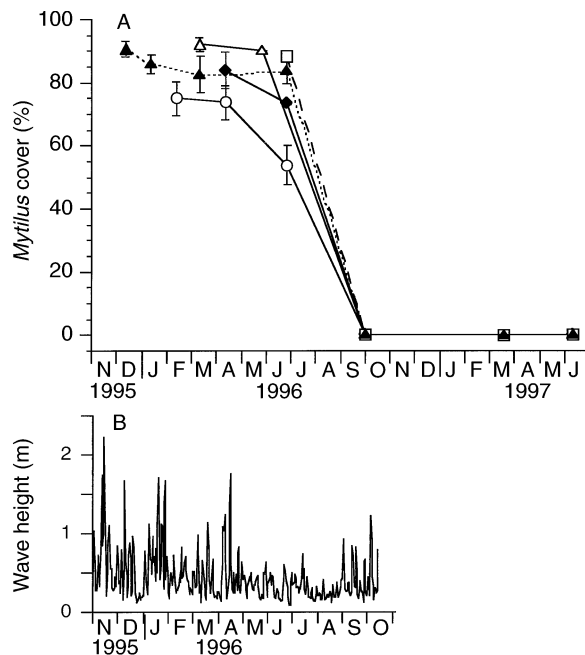


FIG. 5. Mussel cover and wave activity. (A) Trends in mean percent cover of mussels, *Mytilus edulis*, in permanent 0.25-m² quadrats ($n = 10$ quadrats per site) at five of the study sites. Data are means ± 1 SE. Site code: Δ = York Ledge (6), \square = Boon Island (7), \blacktriangle = Murray Rock (8), \blacklozenge = Duck Island (9), \circ = Halfway Rock (17). Predators eliminated the mussel cover by October 1996. (B) Maximum daily wave heights, 1 November 1995–15 October 1996, at Portland, Maine, USA, NOAA weather buoy (number 44007), located adjacent to site 1, East Hue and Cry Ledge (Fig. 1). Note that the mussel cover persisted during the period of high wave action (November–April) but was eliminated during the calmest months.

dance of *Asterias* recruits across the study region in October 1996 was positively related to the abundance of mussel food resources in June 1996 by the regression equation: y (\log_{10} average sea star recruit density per 0.25 m²) = $-1.0 + 0.26x$ (arcsine square-root average *Mytilus* cover), $r^2 = 0.29$, $F = 5.94$, $P \leq 0.028$, $df = 1, 15$. The comparatively low (29%) variation in average sea star recruit density explained by mussel cover is due to large (greater than threefold) variability in the average density of sea star recruitment at high-mussel-cover sites.

Crabs.—The cumulative frequency of *Cancer* spp. crab sizes is shown in Fig. 10. Compared to the 1996 distribution, the July 1997 size distribution was shifted to the right, indicating a greater proportion of small crabs in the 1997 population. For example, 50.0% of the July 1997 population was comprised of the 1996 cohort (≤ 30 -mm carapace width) and it contained the highest proportion (7%) of young-of-the-year recruits (≤ 10 mm, Fig. 10). The number of crabs in the 10–30 mm size range was 51.0% higher in 1997 than in 1996. The June 1996 population was composed of a smaller proportion (30.0%) of crabs ≤ 30.0 mm in carapace width.

Cannibalism.—The percentage of *A. vulgaris* mortality from cannibalism showed a significant, sixfold increase after the *Mytilus* beds were eliminated, reaching a maximum of 3.02% average mortality across the region in July 1997 (Table 2). Individual site values of cannibalism mortality ranged from 0% at Gunboat Shoals and Hampton Rock (all sampling periods) to a maximum of 7.04% at Murray Rock in July 1997. Regression analysis revealed that percentage cannibalism mortality was unrelated to average *A. vulgaris* density in October (Table 2), largely due to a high percentage of cannibalism at one of the sites with relatively low sea star density (HR), and high cannibalism at MR with intermediate sea star density. By July 1997, however, there was a significant positive relation between mortality from cannibalism and sea star density, with mean density explaining 50% of the mortality (Table 2). The percentage of *A. vulgaris* populations at a site involved in cannibalistic aggregations was higher than the percentage mortality from cannibalism, attaining maxima of 5.9% and 17.9% at MR in October 1996 and July 1997, respectively. Further, as suggested by a significant positive regression between $\log N_{1997}$ (population in 1997) and $\log N_{1996}$, the *Asterias* population decline between June 1996 and July 1997 was density dependent ($F = 13.5$, $P \leq 0.0027$, $df = 1, 15$, $\log N_{1997} = 0.047 + 0.48 \log N_{1996}$, Turchin 1995).

Dispersal model.—The results of the simulated particle-dispersal study are shown in Fig. 11 and Table 3. The model showed striking depth differences in the particle trajectories for all 2–5 wk durations of model runs. The common pattern was that the percentage retention of particles increased dramatically from the surface down to 15-m depth, while none of the particles released at the surface (1-m depth) were retained in the study region (Fig. 11, Table 3). Particles at the surface were also advected farther offshore than particles released at depth (Fig. 11). There was some evidence of subsurface eddy circulation in the southern Bigelow Bight, involving York Ledge and Murray Rock (Fig. 11B and C), which would increase retention of passive larvae in this area. Retentive eddies were also identified in the model runs at 10 m (Fig. 11B and C) and 15-m depth (not shown) for three sites around Cape Ann (DS, LL, HR). Assuming that sea star and crab larvae behave as passive particles in the flow field, the model results imply that 53.8 to 23.0% of larvae released from the depth of abundant mussel food resources (10 m) and drifting at this depth for 2 to 5 wk, respectively, would be retained in the study region (Table 3). The percentage retention of larvae released from 5 m, or ascending immediately to this depth from 10 m decreases to 30.7 to 15.3% over the 2–5 wk period. The maximum percentage retention in the study region was 75% for larvae dispersed at 15 m for 2 wk (Table 3).

DISCUSSION

Mechanisms of bottom-up response

The bottom-up effect on mussel consumers observed in this study may have been produced by (1) a growth

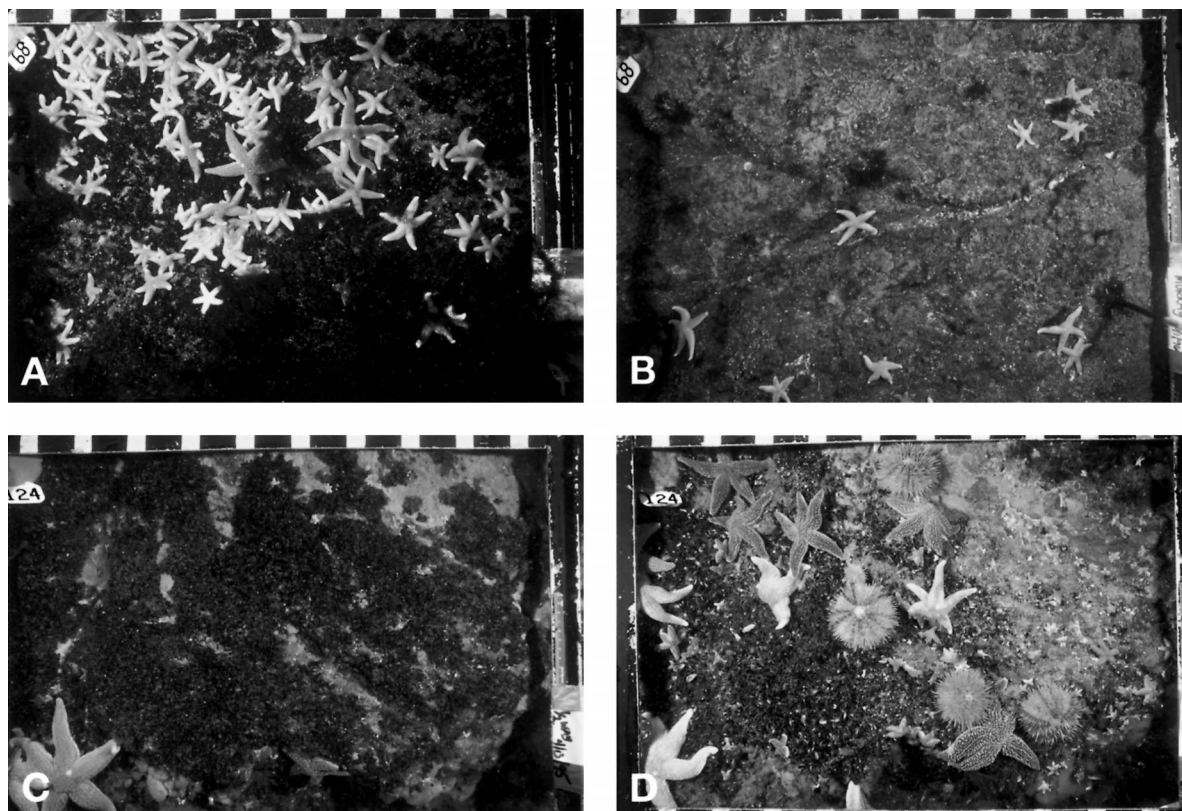


FIG. 6. Representative time-series photographs illustrating predation on *Mytilus edulis* recruits in permanent photo quadrats from (A and B) Murray Rock in the central study region (Gulf of Maine, USA) and (C and D) Halfway Rock at the southern end of the region. Black areas of the photos in (A)–(C) are *Mytilus*. (A) In one quadrat in June 1996 *Asterias vulgaris* is feeding on the mussels whereas (B) in the same quadrat in October 1996 the same area of bottom is devoid of mussels. (C) In April 1996 few predators are seen in a quadrat at Halfway Rock, but (D) by June 1996 half of the mussel cover has been consumed by sea stars *Asterias forbesi* (at the center–upper left of the quadrat), *A. vulgaris* (on the left side of the quadrat), and sea urchins *Strongylocentrotus droebachiensis* (in the center of the quadrat). Light increments at the top and bottom of the quadrat frames are 2 cm wide, and a centimeter ruler is on the right side of the frame.

response, (2) a consumer reproduction and recruitment response, (3) an immigration response, or some combination of the three. The three mechanisms are not, however, mutually exclusive explanations for the significant positive relationships between mussel cover and predator abundance (density, biomass) across the study region. All three mechanisms were apparently operating to increase sea star abundance. By June 1996, juvenile mussels had been an abundant food source for subtidal predators for 10–11 months. Evidence that this resulted in enhanced growth of *Asterias vulgaris* at the sites where mussels were most abundant came from significantly higher elevations of the size–biomass regressions of *A. vulgaris* at high-mussel-cover sites than from a low-cover site, and from a site lacking mussels. Similarly, the elevations of the size–biomass regressions of *A. forbesi* were significantly higher at two sites of high-to-moderate mussel cover than at a low-mussel-cover site. Heavier sea stars at abundant-mussel sites can account for part of the significant positive relationships between mussel cover and sea star biomass

in June 1996, but cannot explain the significant relationships between mussel cover and sea star density.

That *Asterias* recruitment increased to historically high levels at two sites in 1996–1997 is suggestive of a reproduction and recruitment response, where the reproductive output of *Asterias* populations was increased throughout the Bigelow Bight by the large pulse of mussel food resources in 1995–1996. Although we lack information on sea star fecundity to establish a direct link between food resources and reproductive output, Menge (1986) found that gonad size was positively related to body size (biomass) in New England *A. vulgaris* and *A. forbesi*. The body sizes (biomass) of these sea stars were largest when feeding on *Mytilus* beds (Menge 1979, 1986), indicating that reproductive output was closely related to the availability of mussels (Menge 1986). Thus, it is likely that the large increase in mussels led to a reproductive response in the sea star populations. Our interpretation that sea star recruitment was enhanced across the study region was supported by the high (compared to historical recruit-

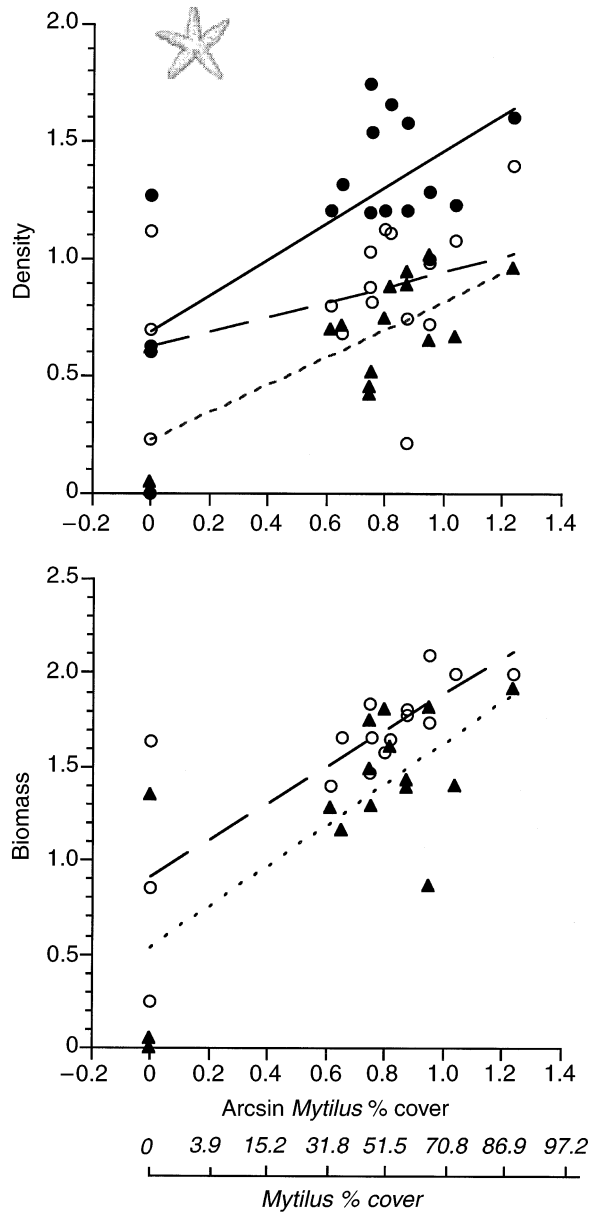


FIG. 7. Relationships between the average density (top) and biomass (bottom) of sea stars at 2–3 sampling periods and the percent cover of mussels in June 1996. Biomass was measured as grams per 0.25 m² and is presented as $\log(x + 1)$; density was measured as the number of individuals per 0.25 m² and is presented as $\log + 1$. Although the analyses were performed on transformed data, the untransformed percent cover values are reported in italics below the x-axis for clarity. Solid regression lines fit through site values (●) represent June 1996 densities, dashed regression lines and ○ depict densities or biomass from October 1996, while the stippled lines and ▲ illustrate data from July 1997. The relationship between sea star biomass and mussel cover in June 1996 is shown in Fig. 4A. Regression equations are reported in Table 1.

ment record) average densities of *Asterias* spp. recruits at 16 sites in October 1996.

The significant relation between mussel cover in June and the density of *Asterias* recruits in October 1996 suggests that a positive feedback occurred between food supply and the recruitment of this mussel consumer on a large spatial scale. It is difficult to discern from the present data if this result was caused by a greater input (production of larvae and settlement) of *Asterias* to sites with abundant mussels or by greater survival of juvenile sea stars after they settled at mussel

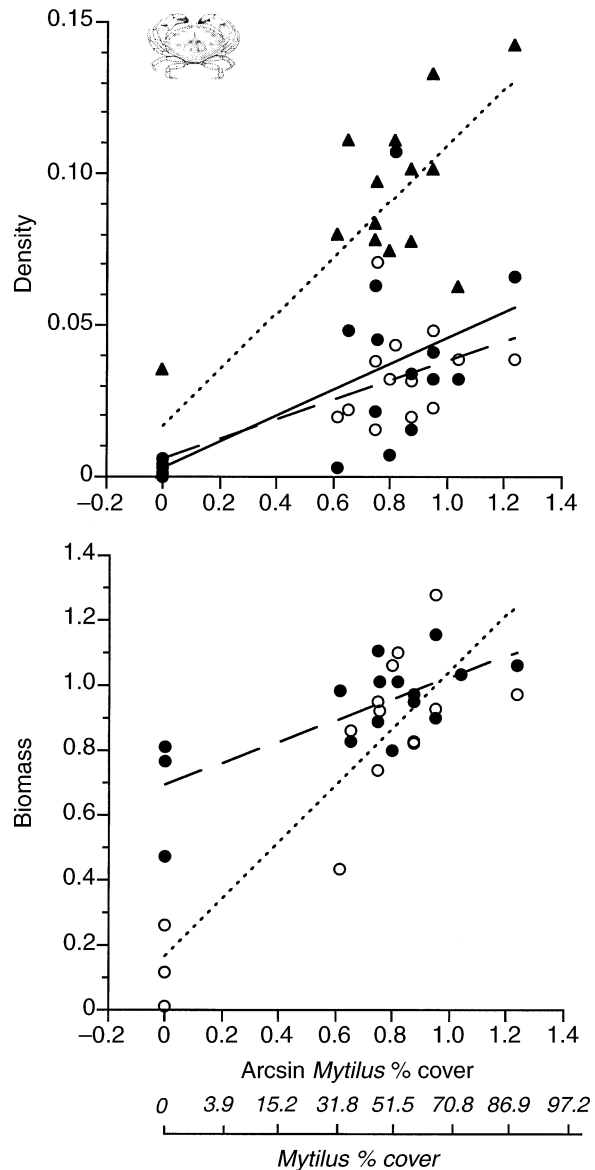


FIG. 8. Relationships between the average density (top) and biomass (bottom) of rock crabs at 2–3 sampling periods and the percent cover of mussels in June 1996. Symbols and format notation are as in Fig. 7. The relationship between crab biomass and mussel cover in June 1996 is depicted in Fig. 4B. Regression equations are reported in Table 1.

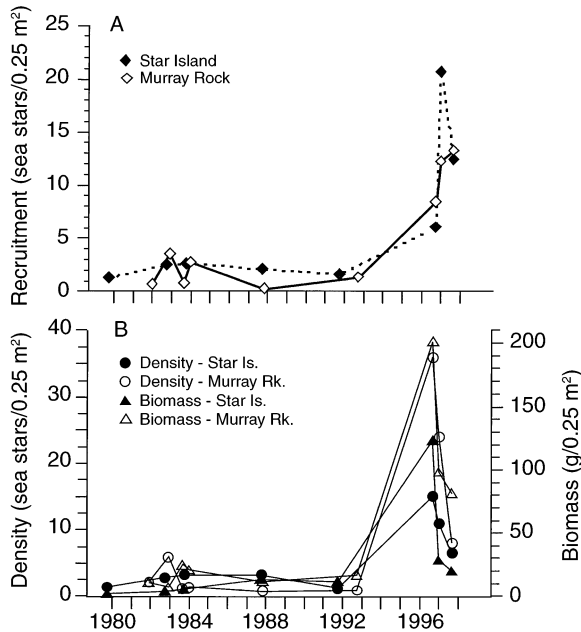


FIG. 9. Long-term trends in (A) recruitment and (B) abundance of *Asterias* spp. populations at 8–10 m depth at Star Island (STI) and Murray Rock (MR), Gulf of Maine, USA. Data are averages per 0.25-m² quadrat, $n = 28$ –40 photo quadrats per sampling; error bars are omitted here for clarity. The 1996 recruitment data are from July and October. Note the striking increase in sea star abundance following the fall 1995 mussel recruitment, and elevated levels of sea star recruitment. Comparisons of mean sea star density, density, and recruitment by sampling date were made by one-way ANOVA (log-transformed data) since random quadrats were sampled over time.

ANOVA results for the STI site (all with $df = 7, 253$), were as follows. Biomass: $F = 32.5$, $P < 0.001$; post hoc Tukey-Kramer (TK) tests ($P < 0.05$ used for all) indicated that June 1996 biomass was significantly greater than October 1996 biomass, which was greater than the biomass at all remaining dates; also, July 1997 biomass was greater than biomass at all pre-1996 dates except August 1987. Density: $F = 36.5$, $P < 0.001$; TK tests revealed no significant difference between densities in June 1996 and October 1996, but densities at these times were significantly greater than at all other dates; density was also significantly greater in July 1997 than in August 1979 or August 1991. Recruitment: $F = 101.3$, $P < 0.001$; TK tests showed the October 1996 recruitment was significantly greater than all other dates and that July 1997 recruitment was significantly greater than at all other dates except October 1996; also, July 1996 recruitment was significantly greater than recruitment at all prior dates.

ANOVA results for the MR site (all with $df = 8, 266$) were as follows. Biomass: $F = 27.2$, $P < 0.001$; TK tests indicated that June 1996 and October 1996 biomasses did not differ significantly but that biomass at these dates was significantly greater than at July 1997; also, biomass at all three of these dates was significantly greater than at all pre-1996 dates. Density: $F = 48.8$, $P < 0.001$; TK tests revealed that June 1996 density was significantly greater than all pre-1996 densities, that October 1996 density was greater than that at all prior dates except June 1996, and that July 1997 density was greater than that at all dates before 1996. Recruitment: $F = 66.8$, $P < 0.001$; TK tests revealed that recruitment did not differ between October 1996 and July 1997, but that recruitment at both of these dates was significantly greater than at all prior dates; also, recruitment in July 1996 was significantly greater than in August 1992, August 1987, July 1983, and August 1981.

sites. Nonetheless, it was surprising that spatial variation in sea star recruitment was even loosely coupled to the abundance of food across the region, as *Asterias* sea stars have open populations with a larval phase that drifts in the water column for weeks (Loosanoff 1964). A study of invertebrate larval supply and recruitment from 1996 to 1998 along the coast of York, Maine, USA, ~4.1 and 7.8 km from two of our study sites (York Ledge and Murray Rock, respectively; sites 6 and 8 in Fig. 1), also reported unusually high recruitment of *A. vulgaris* in 1996 (McNaught 1999). A significant regression between the density of *Asterias* larval supply and recruitment across all of McNaught's (1999) sites indicated that sea star recruitment was principally driven by larval supply. This finding is consistent with our interpretation that the high levels of sea star recruitment resulted from greater reproductive output (i.e., larval production).

Populations of *A. vulgaris* and *A. forbesi* are known to aggregate in response to mussel prey (Menge 1979, Hulbert 1980, Sloan and Aldridge 1981, Campbell 1983, Harris et al. 1998). Some of the changes in the density of *Asterias* populations over the three survey periods may have been caused by an immigration response, with sea stars immigrating from other sites or from outside of the ~1500-m² area surveyed within sites at 8–12 m depths. Immigration of *Asterias* spp. to areas of high mussel cover likely explains some of the positive relation between sea star density and mussel cover. However, at sites with extremely high mussel cover, like York Ledge, Boon Island, Murray Rock (MR), and Duck Island, where mussel recruits covered several square kilometers of bottom (J. D. Witman, S.

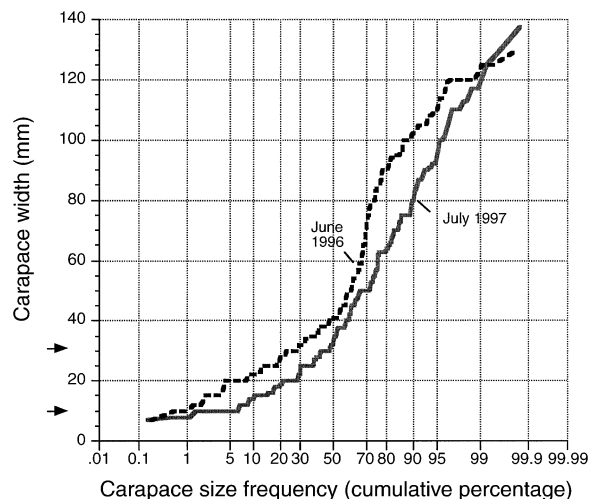


FIG. 10. Cumulative size frequency of *Cancer* spp. carapace widths in June 1996 (stippled curve, $n = 260$ crabs, pooled from all sites) and July 1997 (solid curve, $n = 320$ crabs). Arrows on the y-axis indicate the 10–30 mm range of carapace widths of crabs considered to be approximately one year old. Note the greater percentage of crabs in this size range in 1997 than in 1996.

TABLE 2. Regressions of log-transformed average *Asterias vulgaris* density per 0.25-m² quadrat (X) vs. arcsine square-root transformed percentage of *Asterias* cannibalized (Y).

Date	Regression†				Mortality due to cannibalism (%)‡
	Equation	P	F	r ²	
October 1996	$y = 0.056 - 0.002x$	NS	0.0038	0.002	0.50 ± 0.12
July 1997	$y = 0.045 + 0.177x$	0.0021	14.08	0.50	3.02 ± 0.47

† A significant relation indicates that cannibalism is density dependent. For both analyses, $df = 1, 14$. NS indicates not significant.

‡ The average percentage mortality per site due to cannibalism (mean ± 1 SE) is reported in the last column with $n = 16$ sites. No cannibalism was observed in June 1996. The percentage cannibalism mortality varied among June 1996, October 1996, and July 1997 (one-way ANOVA on arcsine-transformed data; $F = 29.73$, $P < 0.001$, $df = 2, 45$). Tukey-Kramer post hoc tests indicated that average cannibalism mortality was significantly greater in July 1997 than in October or June 1996.

J. Genovese, J. F. Bruno, and B. Pavlin, *personal observations*), effectively blanketing the entire shallow subtidal zone, it probably was not necessary for resident sea stars to move far to locate mussel prey. After the mussels were consumed, the feeding aggregations dissipated and sea star densities declined gradually, but large emigrations of sea stars out of the monitored study areas was not observed. A subsequent study of *A. vulgaris* movement was conducted at one site (MR) during the warm season (August–October) in 1997 when sea star activity was higher than other periods of the year (S. Altman and J. D. Witman, *unpublished manuscript*). Sea stars moved an average distance of 0.12 ± 0.07 m/d [mean ± 1 SD] $n = 36$ sea stars) to 0.44 ± 0.17 m/d standard deviation $n = 38$ sea stars) per trial and stayed within the study area for the duration of the three-month study (S. Altman and J. D. Witman, *unpublished manuscript*). These rates are lower than those reported by Hulbert (1979) at 8- and 18-m depths at the Star Island (STI) site in summer (1.09 and 0.72 m/d, respectively). Even at these higher rates of movement, emigration of large numbers of sea stars off the local sites does not seem likely. We suggest that the three mechanisms of bottom-up response in sea stars occurred at different temporal scales, possibly beginning with an immigration response to the prey patches in 1995, followed by a growth response during 1995–1996, leading to a recruitment response in 1996–1997.

Comparison of sea star abundance in the time series of random photo quadrats taken at STI and MR suggested that the abundance of *Asterias* spp. after the

1995 mussel recruitment event was the highest on record. Additional support for this interpretation comes from a comparison of data in Hulbert (1980) indicating that the average biomass of *A. vulgaris* from 1977 to 1979 at the STI site (8-m depth) was 10.2 g/0.25 m². The current study documented an average biomass of *A. vulgaris* that was 10, 2.4, and 1.8 times higher at Star Island in June 1996, October 1996, and July 1997, respectively.

Fewer data were available to reconstruct potential mechanisms of bottom-up enrichment for crabs than for sea stars, as data on size–mass regressions were not available from enough sites to investigate a growth response. Several lines of evidence suggest that the recruitment and/or post-settlement survival of crabs was increased by the high availability of mussel prey during 1995–1996. For instance, the size of the 1996 cohort, as revealed by sampling in July 1997, was more than >50% larger than the 1995 cohort (Fig. 10). The increased density of crabs in 1997 was also indicated by the significantly greater slope of the mussel cover vs. crab density regression in 1997 vs. 1996. Our finding of high rock crab recruitment in 1997 was corroborated by a separate recruitment study at nearby sites off York, Maine. McNaught (1999) found that post-settlement densities of *Cancer irroratus* on standardized Astroturf substrates were ~7–20 times higher in 1997 than in 1996, representing the highest crab recruitment of his three-year study. The fact that the larval supply of rock crabs matched the temporal pattern of crab recruitment (McNaught 1999) at sites close to ours supports the interpretation that increased produc-

FIG. 11. Maps of simulated particle trajectories for particles released from the 13 sites with *Mytilus* recruits to examine the potential for passively dispersed sea star and crab larvae to be retained in the study region. Sites are numbered as in Fig. 1. The outer boundary of the region is depicted by the dashed line. (A) Trajectories of particles released at the surface (1-m depth) after a duration of 2 wk. (B) Trajectories resulting from a release at the depth of mussel cover (10 m) after 2 wk. (C) Trajectories 5 wk after release from 10-m depth. Retention was scored if the particle path ended inside or at the dashed boundary line. Data from all the model runs are shown in Table 3. Note that none of the particles released at the surface were retained in the study region (A), but that considerable retention occurred when particles were released from the 10-m depth for either 2 or 5 wk (B and C; Table 3). Retentive eddy circulation is associated with sites 6 and 8 (York Ledge and Murray Rock) and sites 15–17 (Dry Salvages, Londoner Ledge, and Halfway Rock).

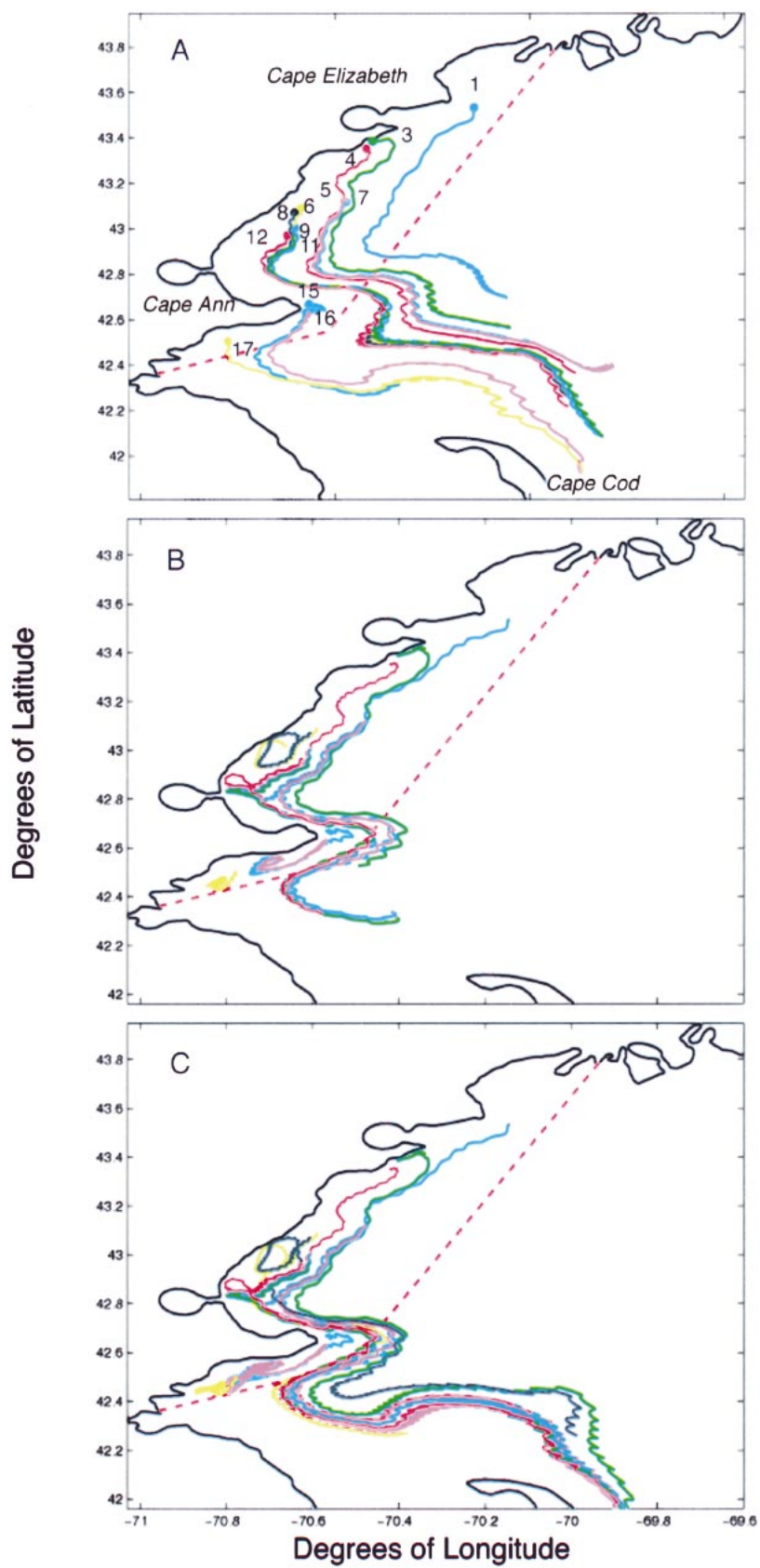


TABLE 3. Results of dispersal modeling for the newly hatched larvae of consumers (sea stars, crabs), reporting the percentage of particles (drogues) released from the 13 mussel-recruitment sites that remained in the study area (Fig. 11).

Depth (m)	Retention (%)			
	2 wk	3 wk	4 wk	5 wk
1†	0	0	0	0
5	30.76	15.38	15.38	15.38
10	53.84	30.76	23.07	23.07
15	75.0	50.0	41.66	41.66

Notes: One of the 15-m drogues collided with the bottom so the calculations of percentage at 15 m are based on a total of 12 sites, rather than 13 as at other depths. Particle release was weekly, bracketing the 2–5 wk larval life-span of *Asterias* spp. and the dispersive phase of *Cancer* spp. zoea and megalopae.

† Surface.

tion of crab larvae (i.e., reproductive output) could account for the 1996–1997 increase of small *Cancer* crabs shown in Fig. 10.

Rock crabs are more mobile than sea stars, and some of the changes in density may have been caused by immigration or emigration from areas where mussels were abundant. In our present study, peak densities of rock crabs (*C. irroratus* and *C. borealis* combined) occurred in July 1997, nine months after the mussels were consumed. At this time, average densities of rock crabs at Star Island were 2.3 times greater than in September 1982 (Witman 1985). Crab densities in July 1997 at White Island, another site at the Isles of Shoals, were 3.5 times greater than recorded in July 1994 (Gibeault 1995). Similarly, long-term monitoring of subtidal *Cancer* crab populations at a rocky-ledge control site off southern New Hampshire indicated a more than twofold increase in density of *C. borealis* and a more than fourfold increase in *C. irroratus* caught in traps (adjusted for catch per unit effort) from 1996 to 1997 (NAI 2000). The 1997 catches of *C. irroratus* were the third highest recorded during 1991–1999 (NAI 2000).

Aggregative responses of predators to prey (Hassell and May 1974) are well known and involve immigration of predators to areas of high prey abundance. Demonstrations of strong bottom-up effects on food webs, including exploitation of bud-burst phenomenon by insects and birds (Perrins 1990, Forkner and Hunter 2000), consumption of mast seed production by mammals (Jones et al. 1998), and elevated zooplankton consumption by fish (McQueen et al. 1989) all have involved highly mobile predators. Bottom-up responses of mobile predators to increased prey apparently commences with an aggregative response, which may be the only effect to account for an increase in predator population numbers in short-term studies not continued long enough to discern changes in predator growth or recruitment. Aggregative (immigration) responses represent a spatial population response as opposed to the temporal responses of growth and recruitment (Harri-

son and Cappuccino 1995). In marine benthic communities, where prey recruitment often occurs as an influx of larvae from the overlying water column, bottom-up effects may also occur in consumer species that are sessile, slow moving (e.g., sea stars), or highly mobile.

Potential dispersal and stock-recruitment feedback in consumer populations

In coastal marine systems with strong alongshore advection, upstream populations of adults are an important source of recruits for benthic populations downstream (Possingham and Roughgarden 1990, Lynch et al. 1996, Roberts 1997, Wing et al. 1998). In our present study it is possible that some of the sea stars and crabs that recruited to sites in the northeast Bigelow Bight in particular originated from adult populations upstream of the study region that may have been unaffected by the pulse of mussel food resources. However, the three-dimensional simulation of larval dispersal indicated that roughly 15–75% of particles released from mussel sites remained within the study region if they stayed below 1-m depth. This model result supports the interpretation that a feedback between consumer populations and enhanced recruitment is a feasible explanation for some of the increases in sea star and crab populations 10–23 months after the mussel-recruitment event. This result establishes the possibility that local population dynamics and regional processes are coupled via consumer recruitment. Clearly, this hypothesis should be verified by empirical studies of the dispersal of sea stars and crabs.

There is currently an important debate about whether marine populations with pelagic larval stages are open, with long-distance dispersal, or closed, with some retention of larvae near adult stocks (Cowen et al. 2000). Our results suggest that the extent to which a population is open or closed is greatly influenced by the depth of larval dispersal. Populations releasing larvae or propagules that dwell at or near the surface disperse longer distances and are more open (or connected) than populations releasing larvae that remain even 5 m below the surface.

Localized retention of some larvae released from adult stocks implies a relationship between the size of the adult stock and the magnitude of recruitment (Ricker 1975). Although stock-recruitment relationships were originally demonstrated in fish (Cushing 1973), several recent studies have documented or predicted localized propagule retention in blue crabs (Lipcius and VanEngel 1990), scallops (Peterson and Summerson 1992), corals (Wolanski et al. 1989, Black et al. 1991, Hughes et al. 2000), abalone (McShane et al. 1988), and kelp (Reed et al. 1998). These studies indicate that local production influences subsequent recruitment more commonly than previously thought, and may be an overlooked mechanism of bottom-up response in marine consumers.

Our simulation of larval dispersal only estimates the *potential* for sea star and crab larvae to be retained in the study region. The model is simplistic in assuming that the larvae can be modeled as passive particles, with no behaviors to actively change their position in the water column, and no larval mortality. Larval behaviors such as swimming or vertical migration would influence dispersal and the degree of retention predicted by the model (Morgan 2001). The assumption that the weakly swimming bipinnaria–brachiolaria larvae of *Asterias* spp. are unable to locomote against the coastal current and therefore are passively dispersed is probably valid (Young 1995). The assumption may be less tenable for crab larvae. Like many species of brachyuran crabs, *Cancer* spp. may be capable of swimming against slow currents to achieve vertical or horizontal migration in some circumstances (Sulkin 1984). Thus, the predicted retention for larvae of crabs is best viewed as a rough estimate of their actual retention, which could be less if they ascended from the depth of the *Mytilus* beds (10–15 m) to the surface. Nonetheless, Clancy and Cobb (1997) concluded that substantial numbers of *Cancer irroratus* larvae are passively dispersed by wind and tides in southern New England. The degree of retention predicted by our simulation may be conservative, as Cowen et al. (2000) found that a Lagrangian model overestimated the distance of larval–fish transport, compared to a model with larval mortality and diffusion.

Population regulation in sea stars

Broad-scale changes in populations of predatory sea stars (*A. vulgaris*, *A. forbesi*) and their mussel prey indicated an unusual degree of reciprocal influence between predators and prey for open marine populations. Following Osenberg and Mittelbach's (1996) definitions of population limitation and regulation, we suggest that the sea star populations were regulated by food limitation. For instance, a numerical response in sea star populations after the dramatic increase of mussel food resources suggests that the populations were food limited prior to 1995. The density-dependent decrease in sea star populations after the mussels were consumed was associated with widespread cannibalism in *A. vulgaris* populations, supporting the interpretation that food limitation occurred again between 1996 and 1997. Population regulation was evident since density dependence (Osenberg and Mittelbach 1996) was documented both in the significant regressions of log population sizes in 1997 vs. 1996 (Turchin 1995) and in the regressions of mean *A. vulgaris* density vs. percentage cannibalism mortality in July 1997. Several studies have discussed the potential for food limitation in *Asterias* populations, including Menge's (1979) conclusion that occasional, but not chronic, food limitation occurs in local *Asterias* populations in New England. Both Menge (1979) and Harris et al. (1998) described a low incidence of cannibalism in either *Asterias forbesi* or *A. vulgaris* pop-

ulations, accounting for 1.6% of 124 *A. forbesi* (Menge 1979) feeding observations and <0.01% of *A. vulgaris* feeding observations (Harris et al. 1998). The average of 3.02% cannibalism mortality in July 1997 is apparently the highest cannibalism observed in *A. vulgaris*. We observed that cannibalism was particularly common within the intermediate size classes of *A. vulgaris* (5.0–15 cm radius), which may be especially vulnerable to food limitation since they cannot feed on large horse mussels like the largest size classes of *Asterias* can (Hulbert 1980, Witman 1987).

Cannibalism clearly contributed to the overall reduction of *Asterias* spp. populations after the elimination of *Mytilus* (Table 1, Fig. 3), but it is difficult to predict the degree of reduction from the static percentages obtained during the surveys because the rates of mortality are poorly known. To better understand the rate of cannibalism, two cannibalistic aggregations of *A. vulgaris* were marked at MR in October 1997. Both of the victim sea stars were consumed within a week, but the actual duration of cannibalism may have been longer because the length of time that the sea stars had been feeding when they were first encountered was unknown. A simple illustration of the potential for cannibalism to influence sea star densities assumed a constant rate of 0.5 or 3.0% mortality per 10 d, between October 1996 and July 1997, and a closed population. In that simulation, mortality was 12–75% over the 252-d period, a range that encompasses the 25% reduction observed in average sea star densities between 1996 and 1997. A more sophisticated, yet preliminary, effort to model the contribution of cannibalism to population changes in *A. vulgaris* using a nonlinear matrix model with exogenous levels of recruitment and density-dependent cannibalism based on this study (F. Hill, J. D. Witman, and H. Caswell, *unpublished manuscript*), revealed that even a low per capita cannibalism rate of 0.025 (i.e., half the October 1996 average) produced complex fluctuations in sea star populations. The amplitude of the population fluctuations were damped by high levels of sea star recruitment (M. Hill, *personal communication*).

Other factors potentially causing sea star population declines were not specifically considered here, so there are alternative hypotheses to cannibalism as a primary cause of the reduction in sea star population density between 1996 and 1997. For example, *Asterias* spp. are subjected to diseases (Menge 1979), and shallow populations are affected by storm-generated physical disturbance (Menge 1979, Witman 1996). No diseased individuals were observed during any of the surveys (J. D. Witman, S. J. Genovese, J. F. Bruno, and B. I. Pavlin, *personal observations*), so it is unlikely that disease contributed to the population decline. Sea stars living at shallow depths (<5 m) are occasionally cast ashore on the coast of the Gulf of Maine during severe winter storms. Populations of sea stars at the 8–12 m study depths are less vulnerable to physical disturbance than their intertidal or shallow subtidal counterparts as

the impact of physical disturbance and the magnitude of flow speed decreases with depth. (Witman and Dayton 2001; C. Siddon and J. Witman, *unpublished data*). Consequently, it is unlikely that physical disturbance was a key factor contributing to the reduction of sea stars between 1996 and 1997.

Anthropogenic influence

Relaxed predation from large predatory fish is a potential alternative explanation to a bottom-up influence of mussels for the population increases of sea stars and crabs because the abundance of large fish has been reduced in the Gulf of Maine by hundreds of years of overfishing (Baird 1874, Witman and Sebens 1992, Steneck and Carlton 2001). While small sea stars are probably consumed indirectly by some predators biting benthic substrata, we are unaware of any significant subtidal predators of *Asterias* spp. (other than their congeners) in the Gulf of Maine (Menge 1979, Hulbert 1980, Sebens 1986a, Witman 1996). Thus, it is improbable that sea star populations responded to overfishing of predatory fish. One hypothesized effect of overfishing of cod on benthic communities is to release populations of crabs and other cod prey from high fish-predation pressure (Witman and Sebens 1992). However, the reduction of cod predation pressure on crab populations in the coastal Gulf of Maine began long before the abrupt changes in the abundance of mussel prey, sea stars, and crabs documented during 1995–1997 in this study. For example, the decline in coastal cod stocks was noted by Baird (1874), and landings of cod in coastal Maine waters dropped substantially between 1927 and 1998 (Steneck and Carlton 2001). Subtidal surveys conducted in 1982–1983 at one of the sites in the present study (Star Island) ranked cod second to last in terms of fish abundance (Witman 1985). Cod were absent from this and other coastal subtidal sites in 1987–1988 (Witman and Sebens 1992). Our interpretation is that the influence of overfishing, and bottom-up forces on crab populations have occurred on different temporal scales, with the 1995–1997 changes associated with massive mussel recruitment superimposed on a longer term trend of increasing coastal crab populations over the last three centuries of overfishing.

Although the cause of the large mussel recruitment of 1995 was not the focus of this study, exceptionally high recruitment to the bottom may have been caused by a (1) greater production of mussel larvae, (2) greater survival of mussel larvae in the water column, or (3) lower post-settlement mortality of mussels. We speculate that factors associated with greater output and/or pre-settlement survival of mussel larvae had a greater influence than changes in post-settlement mortality of mussel recruits to cause such a massive settlement over sites spanning a 120-km-long area. Oceanographic conditions in the Bigelow Bight during 1995 are being investigated to search for conditions related to explanations 1 and 2. A reduction of post-settlement mortality seems an unlikely cause because extensive mus-

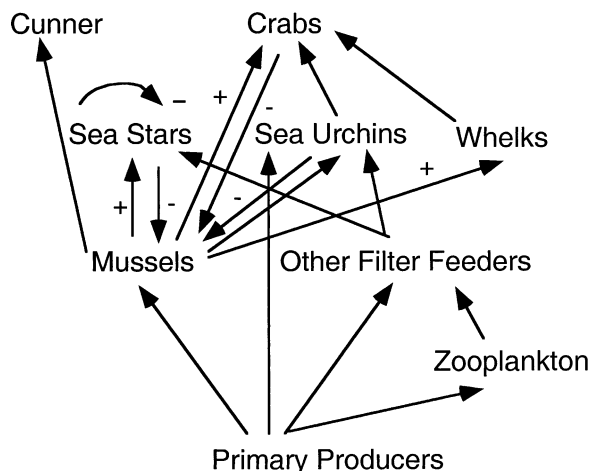


FIG. 12. Simplified connectedness food web (sensu Paine 1980) for shallow rocky subtidal communities in the coastal Gulf of Maine constructed from feeding observations. Bottom-up (+) and top-down (-) effects triggered by the massive recruitment of mussels are indicated. A loop back to the same group indicates cannibalism (-).

sel recruitment occurred at sites previously characterized by high predation pressure from sea stars, sea urchins, and crabs (Halfway Rock, Sebens 1986a, b, Witman and Dayton 2001; Star Island, Witman 1985, 1987; Murray Rock, Witman 1987).

Recruitment and linkages in bottom-up and top-down control

Recent studies in rocky intertidal communities have revealed that bottom-up and top-down effects are linked, particularly at sites influenced by upwelling currents (Menge et al. 1997, 1999). Little is known, however, about the ubiquity of linkages between bottom-up and top-down control in marine communities. As in other ecosystems, the important questions to address in marine communities concern the factors influencing the degree of coupling between bottom-up and top-down forces and the spatial and temporal scales of the linkages (Power 1992). Top-down control may be decoupled from strong bottom-up effects of food resources in intertidal communities by physical factors (Bustamente et al. 1995, Leonard et al. 1998) and by the feeding preferences of consumers (Nielsen 2001). Flow speed was the physical factor controlling the relative importance of bottom-up and top-down forces in estuarine rocky intertidal communities (Leonard et al. 1998). Top-down effects of crab predation on mussels were prevented in high-flow regimes, which inhibited crab feeding (Leonard et al. 1998). In contrast, we observed that bottom-up and top-down forces were interrelated at these rocky subtidal sites (Fig. 12). Flow measurements at three of the sites (Witman 1987; C. Siddon and J. Witman, *unpublished data*) and observations from many dives indicated that all of the sites were fully exposed to wave action and should be con-

sidered high-flow sites. Ultimately, flow was not high enough at the 8–12 m study depths to inhibit predation on mussels by sea stars, sea urchins, and crabs, which were able to remove the mussels from large areas of bottom over 10–12 months.

The spatial scale of the linkage between bottom-up and top-down forces was dictated by the spatial scale of the prey (mussel) recruitment. It was a landscape–regional scale effect, because the mussel recruitment occurred throughout the southwestern Gulf of Maine region, at least. The temporal scale of the bottom-up effect of massive mussel recruitment fits the description of a rapidly decreasing resource (Price 1980), but one that is episodic rather than seasonal. The temporal scale of the top-down effects of the consumer populations depends on their mobility (Harrison and Cappuccino 1995) and their generation times relative to the persistence of the enhanced food resources (Price 1980). In this case, the juvenile mussel beds apparently persisted long enough for the iteroparous sea stars and crabs to achieve a reproduction and recruitment response. It appears that the frequency of subtidal recruitment of blue mussels in New England has increased since the 1995 event reported at 13 offshore sites here and at 2 offshore sites by Harris et al. (1998). For example, massive *Mytilus* recruitment was observed in summer 2000 at the Isles of Shoals, Gulf of Maine (D. McNaught, C. Siddon, and J. Witman, *personal observations*, L. Harris, *personal communication*) in Narragansett Bay, Rhode Island (A. Altieri, *personal communication*), and in Long Island Sound (J. Stachowicz, *personal communication*). The factors causing such large *Mytilus* recruitment events are unknown, but clearly deserve further study since they greatly impact benthic food webs. In southern California, high *Mytilus californianus* recruitment events, at approximately 3-yr intervals, dictates the nature of biological interactions in the rocky intertidal zone (Robles 1997).

In our present study, inferences about bottom-up and top-down control of subtidal communities were established without the benefit of manipulative experiments to identify causal relationships. We adopted a descriptive and mensurative experimental approach (i.e., sampling, monitoring, modeling, *sensu* Hurlbert 1984) to investigate the influence of episodic mass recruitment on spatial and temporal scales that we considered large enough and long enough to reveal fundamental insight into the dynamics of the system (Wiens 1989). Our inferences about bottom-up effects were also supported by long-term data indicating that the documented predator abundances and recruitment levels (sea stars) were unusual, widespread, and coupled to growth responses in sea stars. Top-down effects on mussels were directly observed as advancing fronts of sea stars and as small-scale predation by sea urchins, crabs, and sea stars in permanent quadrats. Although desirable, manipulations of predator densities by caging would have been difficult to carry out successfully at 13 sites spanning 120

km in this subtidal system because the important mussel consumers (sea stars, crabs, and urchins) would have likely recruited or emigrated into predator-exclusion cages before they could be removed during regular maintenance. We agree with Underwood and Petraitis (1993) that a refined understanding of local community dynamics will come from approaches that integrate sampling over large spatial and temporal scales with smaller scale experiments.

There are many parallels between the bottom-up effects of massive mussel recruitment and the effects of mast seed production in plants (Kelley 1994). Both phenomena can occur on large spatial scales, involve episodes of synchronous, massive recruitment, and may have bottom-up effects on consumer populations (Jones et al. 1998). While predator swamping is one of the selective advantages hypothesized for mast seed production in plants (Kelley 1994), the mussels exhibiting massive recruitment in this study were not able to escape predation. Masting phenomena in plants may serve as a good conceptual model for investigating the bottom-up effects of large-scale recruitment of marine prey species.

In conclusion, prey recruitment triggered both bottom-up and top-down control in rocky subtidal communities on a large spatial scale. We suggest that strong linkages between bottom-up and top-down forces are especially likely when prey have episodic recruitment and consumers experience food shortages. Because massive recruitment episodes have been observed in algae (Hoffman 1987), and in many species of benthic invertebrates and fish (Caley et al. 1996), large recruitment pulses are likely to stimulate bottom-up effects on large spatial scales in other marine ecosystems. Although unusual episodic events are difficult to detect, they may leave long-lasting signatures on ecological communities and provide insight into large-scale processes that couple the dynamics of local populations.

ACKNOWLEDGMENTS

We thank E. Westheimer, A. Hartman, J. Rantanen, and S. Altman for help in analyzing many photo quadrats and mussel samples. Thanks to Captains P. Pelletier, K. Houtler, D. Currier, and J. Gingrich for enabling large-scale logistics to run smoothly, and to S. Grace, F. Smith, and P. Ewanchuk for diving assistance. D. Lynch generously allowed us to use his fine-scale coastal circulation model of the Gulf of Maine and offered helpful advice. We are grateful to P. Levin, R. Etter, M. Hill, J. E. Duffy, and two anonymous reviewers for improving earlier drafts of the manuscript with their critical comments. This research was supported by SGER grant (OCE-9614216) from the Biological Oceanography Program of the NSF, The Andrew Mellon Foundation, and a NOAA grant to D. Lynch at Dartmouth College entitled “Program in Interdisciplinary Marine Modeling and Management.” This is contribution number 352 of the U.S. GLOBEC Program.

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APPENDIX

Size–mass regression equations used to predict biomass of consumer species are available in ESA's Electronic Data Archive: Ecological Archives M073-005-A1.