Effects of sea stars and crabs on sea scallop *Placopecten magellanicus* recruitment in the Mid-Atlantic Bight (USA)

Deborah R. Hart*

National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole,
Massachusetts 02543, USA

ABSTRACT: Relationships between recruitment of the Atlantic sea scallop *Placopecten magellanicus* and the abundances of 3 types of invertebrate predators, the sand star *Astropecten americanus*, the common sea stars *Asterias* spp. and the crabs *Cancer* spp., were investigated using data from large-scale scallop surveys in the Mid-Atlantic Bight (USA). Both asteroid groups appeared to reduce sea scallop recruitment, with significantly lower recruitment in areas where the sea stars were in high abundance. No significant effect of *Cancer* spp. crabs on scallop recruitment was detected. Very high densities of *A. americanus*, no sea scallop recruitment, and low *Asterias* spp. densities were observed in all stations with depths >85 m, and in many stations between 65 and 85 m. *Astropecten americanus* may be a dominant component of the deep-water (>75 m) benthic community in the Mid-Atlantic Bight that is capable of excluding both sea scallops and *Asterias* spp. from areas where *A. americanus* are highly abundant.

KEY WORDS: Recruitment · Predation · Scallop · Sea star · *Placopecten magellanicus* · *Asterias* spp. · *Astropecten* spp. · *Cancer* spp.

INTRODUCTION

Recruitment is an important determinant of the population dynamics of most benthic organisms with planktonic larvae. Yet, despite intensive study, there is still limited understanding of the factors that determine the spatio-temporal patterns of recruitment (Ólafsson et al. 1994, Gosselin & Qian 1997, Hunt & Scheibling 1997, Fraschetti et al. 2003). While the supply of larvae can influence the level of recruitment, much variation in recruitment cannot usually be explained by this factor. This implicates processes occurring soon after settlement as important determinants of recruitment. During the first 4 mo after settlement, mortality of benthic invertebrates is typically greater than 80% and often exceeds 98% (Gosselin & Qian 1997). Processes that may contribute to this mortality include predation, starvation, competition for food or space, disease, toxic algae, temperature extremes and physical disturbance. Of these, predation has been best documented, and

often appears to be responsible for the bulk of post-settlement mortality. For example, juvenile surf clams *Spisula solidissima* occur at densities of 2500 m^{-2} or more early after settlement, but these clams can suffer mortality approaching 100% within 9 mo, mainly due to crab predation (MacKenzie et al. 1985). Even in cases where larval supply may limit recruitment, such as with the bay scallop *Argopecten irradians*, predation on juveniles can strongly affect the spatio-temporal patterns of recruitment (Peterson & Summerson 1992, Bishop et al. 2005).

Like most other benthic invertebrates, juvenile Atlantic sea scallops *Placopecten magellanicus* suffer high mortality. McGarvey et al. (1992) estimated the probability of survival on Georges Bank of a sea scallop egg to Age 2 to be 1.26×10^{-7}, and the probability of survival from the larval stage to Age 2 to be 9.2×10^{-6}. While considerable mortality occurs during the pelagic larval stage, survivorship during the early post-settlement stage must also be low. Short-term

survival of seeded juvenile scallops in enhancement experiments range from 1 to 40%, with the majority of the mortality due to predation (Cliche et al. 1994, Barbeau et al. 1996). Merrill & Edwards (1976) observed small (<10 mm) juvenile sea scallops at densities of over 2000 m^{-2} on a navigation buoy. By comparison, the mean densities of 2 yr old sea scallops in surveyed US scallop grounds is several orders of magnitude lower, about 0.05 m^{-2}, corresponding to about 100 recruits tow^{-1} (assuming 43% dredge efficiency, Gedamke et al. 2004). The present paper relates the spatial patterns of sea scallop recruitment to abiotic factors such as depth and to the abundances of 3 types of potential predators: the sand star *Astropecten americanus*, the common sea stars *Asterias* spp., and the crabs *Cancer* spp. In particular, I test the hypothesis that scallop recruitment is negatively related to the abundances of *Cancer* spp. and the 2 sea star groups.

The sea star *Astropecten americanus* is a common inhabitant of soft-bottom areas of the NW Atlantic, ranging along the continental shelf and slope from Cape Hatteras to the southern flank of Georges Bank (Boesch 1979, Franz et al. 1981). *Astropecten* spp. forage on the sediment surface, swallow their prey whole through their mouth, and then bury themselves in the sediment while digesting their prey. Their diet consists primarily of small invertebrates, and they are typically generalist feeders, although they often show preferences for certain prey items, usually small mollusks (Christensen 1970, Sloan 1980, Franz & Worley 1982, Lemmens et al. 1995). The stomach contents of *A. americanus* indicate that this species consumes primarily small mollusks and crustaceans (mostly <3 mm, and all <12 mm), including juvenile sea scallops (Franz & Worley 1982, Smereka 2003). The subtropical *A. articulatus*, whose distribution overlaps that of *A. americanus* near Cape Hatteras (Boesch 1979, Franz et al. 1981), is a predator of juvenile calico scallops *Argopecten gibbus* off North Carolina (Schwartz & Porter 1977).

The sea stars *Asterias* spp. (*A. forbesi* and *A. vulgaris* = *A. rubens*, Franz et al. 1981) are widely distributed in the Mid-Atlantic Bight area (Boesch 1979, Franz et al. 1981), and consume a wide variety of prey, including scallops and many other bivalves (Sloan 1980). *Asterias* spp. can consume much larger prey items than *Astropecten* spp. by prying open their prey and everting their stomach. However, they also can consume

smaller prey such as juvenile scallops (Smith 1940, Vevers 1949, Sloan 1980, Barbeau et al. 1996). The introduced sea star *A. amurensis* was shown to reduce the post-settlement survivorship of the bivalve *Fulvia tenuicostata* in Tasmania (Ross et al. 2002).

Cancer spp. (the rock crab *C. irroratus* and the Jonah crab *C. borealis*) are also common inhabitants of the NW Atlantic, and can prey on juvenile sea scallops (Elner & Jamieson 1979). *C. irroratus* was the most important predator on juvenile scallops during seeding enhancement trials in Canada, although *Asterias* spp. predation was also a significant contributor to seeded scallop mortality (Cliche et al. 1994, Barbeau et al. 1996, 1998).

MATERIALS AND METHODS

Study area. Samples (Fig. 1) were taken in the Mid-Atlantic Bight area, a portion of the eastern North American continental shelf, between 36° 30′ and 41° N, and 71° 30′ and 74° 50′ W, in depths between 27 and 104 m. This area has temperate water temperatures (Table 1) and sandy sediments often mixed with shells, with occasional patches of sandy gravel and sandy silt (Boesch 1979, Wigley & Theroux 1981). Samples taken from a more northeasterly region (Georges Bank and vicinity), between 40° 24′ and 42° 10′ N, and 66° 25′ and 69° 50′ W, were used for comparative purposes.

Fig. 1. Example catches from National Marine Fisheries Service (NMFS) sea scallop survey. In (a) catch was dominated by *Placopecten magellanicus*, many of them small 'recruit' scallops; in (b) catch was dominated by sea star *Astropecten americanus*

Table 1. Bottom temperatures (°C) from CTD casts during March and September 1998 to 2002 (near seasonal minimum and maximum temperatures) in the Mid-Atlantic Bight study area as a function of depth

Depth (m)	March Mean	March Range	September Mean	September Range
27–39	6.3	3.7–10.3	16.7	9.6–23.5
40–54	6.6	4.2–10.2	11.6	8.2–20.6
55–69	7.8	4.2–13.6	10.5	7.8–18.7
70–84	9.5	5.2–13.6	10.4	7.7–16.8
85–104	10.5	4.8–13.9	12.7	8.3–14.4

Sampling protocol. Samples were taken aboard the RV 'Albatross IV' during 2000 to 2002 on the annual summer National Marine Fisheries Service (NMFS) sea scallop survey (Fig. 1). The survey followed a random-stratified design, using a 244 cm wide modified New Bedford scallop dredge with 5.1 cm rings and a 3.8 cm mesh plastic liner (Serchuk & Wigley 1986, NEFSC 2004). Tows were conducted for 15 min at a speed of 7.04 km h^{-1}. Scallops, finfishes and *Cancer* spp. were removed from the catch and recorded. Sea scallops were measured in 5 mm size-bins; the raw size-frequency was then adjusted to take into account the selectivity of the liner (NEFSC 2004). After adjustment, the survey dredge had similar efficiency as a commercial dredge for larger scallops, and (unlike unlined commercial scallop dredges with 8.8 cm rings) was able to retain scallops with similar efficiency down to the 3.8 cm mesh-size of the liner (NEFSC 2004). Sea scallop 'recruits' were identified as those between 40 and 69 mm (a 40 mm scallop in the Mid-Atlantic would grow to 69 mm in 1 yr according to the growth curve of Serchuk et al. 1979), roughly corresponding to the year class spawned 2 yr prior to the survey (Thouzeau et al. 1991). *Cancer* spp. were counted and weighed in aggregate, and in some selected stations in 2001 and 2002, they were counted and weighed by species. Substrate and a number of invertebrate taxa were assessed qualitatively by noting whether they were absent, present or a dominant component of the catch. Most fine-grained substrate (e.g. sand) will not be retained by the liner, so its absence from the catch does not necessarily indicate its absence from the bottom sediment, especially in deep-water stations where the longer haul-back time causes more of the substrate to be washed out of the dredge.

At pre-determined stations (n = 335 over the 3 yr, about half of all stations in the Mid-Atlantic Bight), the catch was subsampled for sea stars. After removal of scallops, crabs and finfishes, the remainder of the catch was quantified by shoveling into 46 l baskets. Random subsamples of the baskets were collected to fill a 5 l bucket. Sea stars were sorted into *Astropecten* spp.

and *Asterias* spp. and counted from the subsample, and each was weighed in aggregate. The total number and weight of the 2 asteroid types could then be calculated by expanding the subsample by the total quantity in the baskets. No attempt was made to further separate the sea stars by species on deck, although all *Astropecten* spp. samples that were examined closely on deck or frozen and later examined were *A. americanus*, while both *Asterias forbesi* and *A. vulgaris* were common, with *A. vulgaris* tending to occur in deeper and more northerly waters than *A. forbesi.* Other genera of sea stars, such as *Henricia*, *Luidia* and *Leptasterias* were occasionally observed at low densities in the subsamples, but were not included in this study. All data reported here are only from those stations in the Mid-Atlantic Bight where sea star subsampling occurred. Similar data was also collected on Georges Bank and neighboring areas, and will be used herein for comparative purposes.

Data analysis. As initial exploratory techniques, Pearson correlation coefficients between variables were computed, and relationships between abundances $\ln(x + 1)$-transformed and depth or latitude were plotted and fitted using linear or quadratic regression as well as lowess smoothers with stiffness of 0.75 (Chambers et al. 1983). More detailed analyses were performed using backward stepwise linear regression (variables were removed if they were not statistically significant at p = 0.05). Response variables (e.g. scallop recruitment) were $\ln(x + 1)$-transformed to obtain approximately normal residual patterns. Initial ANCOVA analysis indicated that the results did not significantly depend on the sampling year, sediment type observed (e.g. sand, gravel, mud), or on the absence, presence, or dominance of sand dollars in the catch. These factors were therefore not further considered in the analysis. We used 2 sample *t*-tests, $\ln(x + 1)$-transformed in order to meet the requirements of approximate normality and homogeneity of variances, to compare scallop recruitment at high and low predator densities. All statistical analyses were performed using the software package Statistica 6.1 (StatSoft).

RESULTS

Scallop recruitment was strongest south of Hudson Canyon and in intermediate depths (Figs. 2 & 3a,b). *Astropecten americanus* were always highly abundant in the deeper stations (>75 m, Figs. 2a & 3c,d). They tended to be more common in the southern areas, and were often absent from shallow northerly stations. Note the spatial partitioning of high *A. americanus* and sea scallop catches. *Asterias* spp. were more common in shallower depths and at higher latitudes (Figs. 2b &
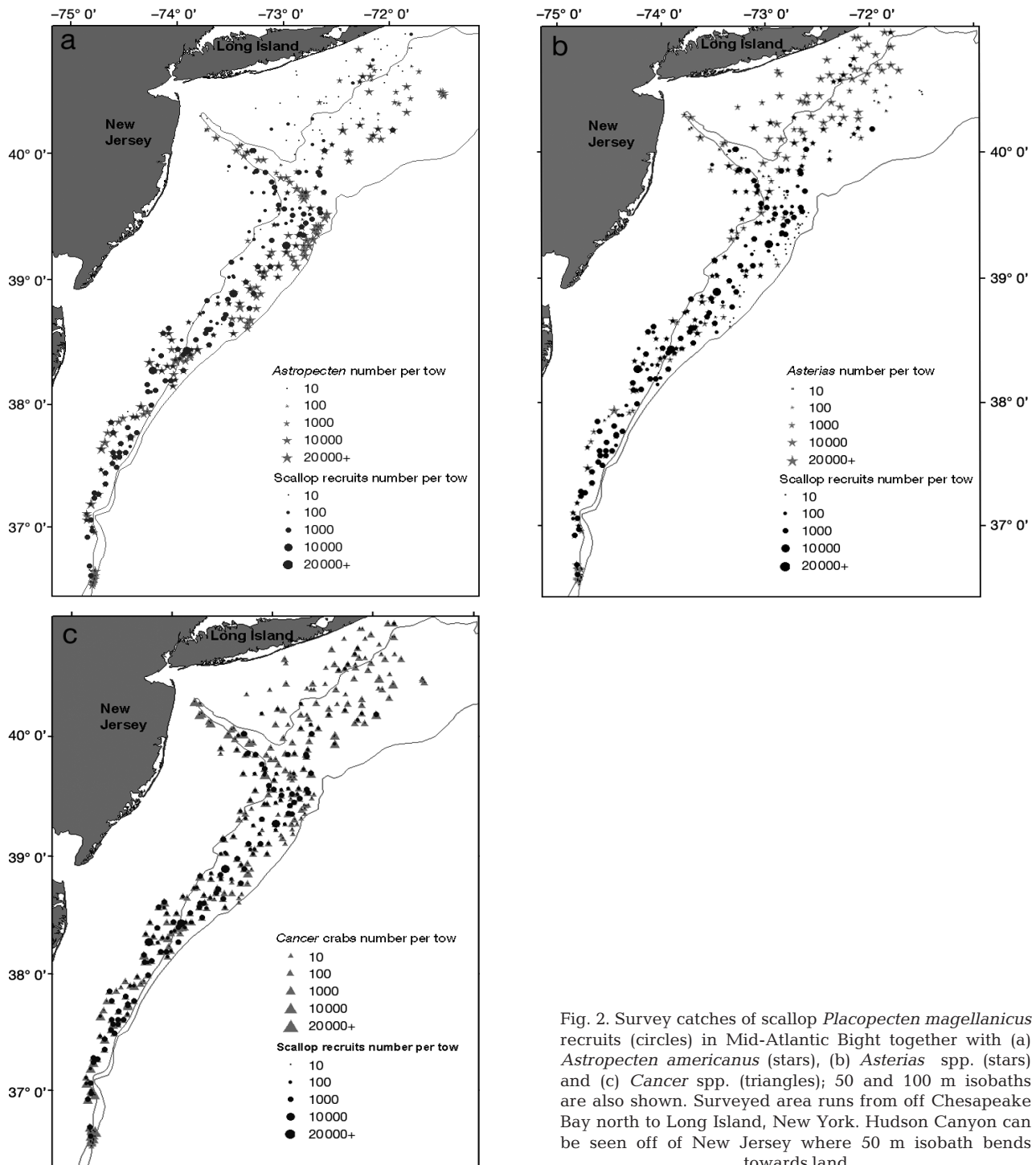
Fig. 2. Survey catches of scallop *Placopecten magellanicus* recruits (circles) in Mid-Atlantic Bight together with (a) *Astropecten americanus* (stars), (b) *Asterias* spp. (stars) and (c) *Cancer* spp. (triangles); 50 and 100 m isobaths are also shown. Surveyed area runs from off Chesapeake Bay north to Long Island, New York. Hudson Canyon can be seen off of New Jersey where 50 m isobath bends towards land

3e,f), *Cancer* spp. were slightly more common in the southern latitudes and at moderate depths (Figs. 2c & 3g,h). Of the crabs that were identified to species (about 47% of the total), 78% were *C. irroratus*, with the remainder *C. borealis*.

Bivalve shells (most commonly those of *Placopecten magellanicus* and the clams *Arctica islandica*, *Spisula solidissima*, *Ensis* spp., and *Astarte* spp.) and sand were the most commonly observed components of the substrate (Table 2). The sand dollar *Echinarachnius parma* often dominated the catches in the shallower stations (Table 3). Other common invertebrates observed included sea urchins, sponges, gastropods (e.g. the whelks *Buccinum* spp., and the moon shell *Lunatia*
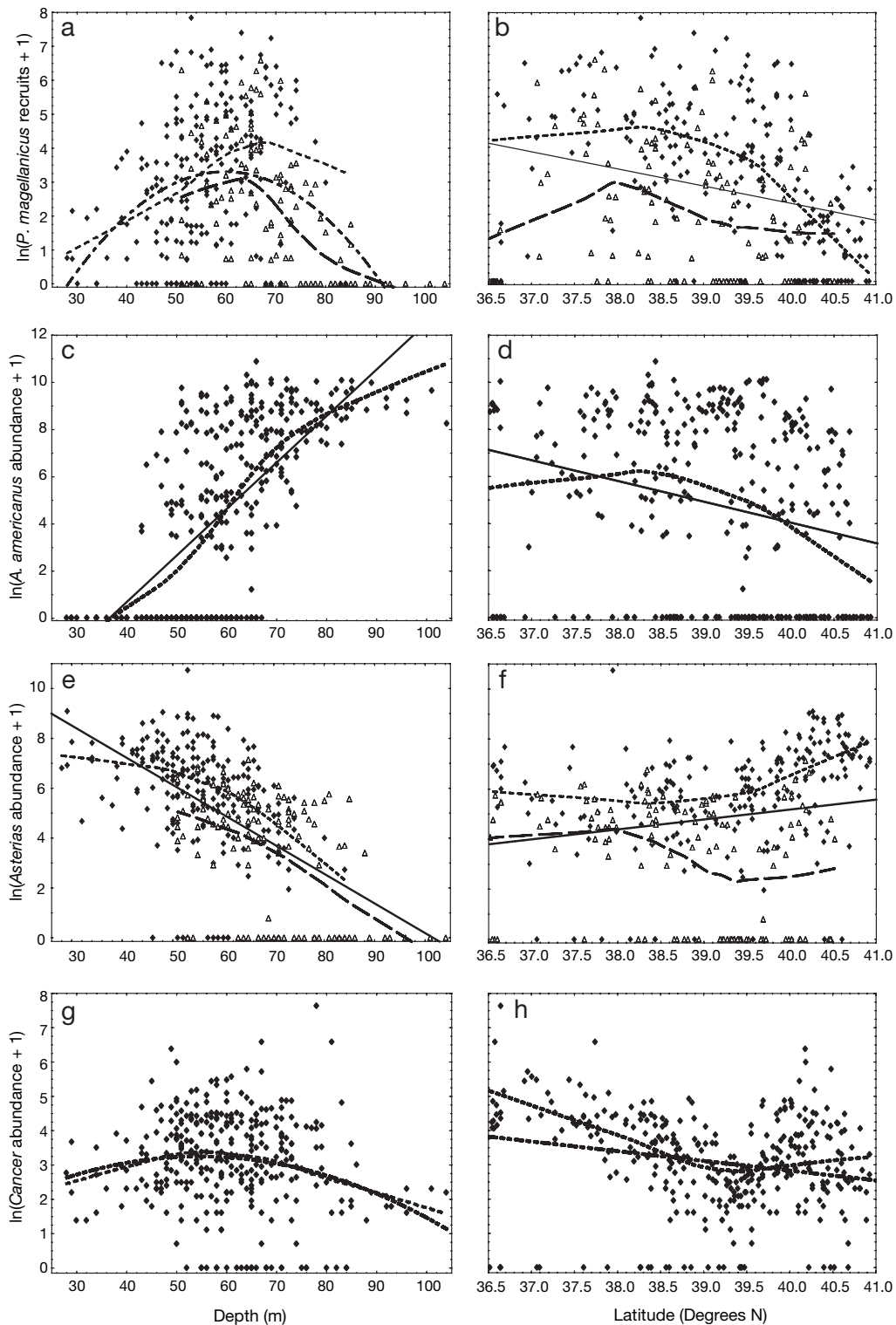
Fig. 3. Distribution of survey catches (nos. tow^{-1}) in the Mid-Atlantic Bight of (a,b) *Placopecten magellanicus* recruits, (c,d) *Astropecten americanus*, (e,f) *Asterias* spp., and (g,h) *Cancer* spp. as a function of depth (a,c,e,g) and latitude (b,d,f,h). All response variables were ln(x + 1)-transformed. Simple linear regression fits to all data points (continous lines) or, in graphs for *P. magellanicus* (a) and *Cancer* spp. (g) vs. depth, quadratic regression fits (dashed line), as well as lowess-smoothed lines (stiffness = 0.75; dashed line) are also shown. Data points in *P. magellanicus* (a,b) and *Asterias* spp. (e,f) graphs are separated into stations where *A. americanus* biomass was high (>10 kg tow^{-1}, △), and low (<10 kg tow^{-1}, ◆). In these cases, lowess smoothers are given for both high (long-dashed line) and low (short-dashed line) *A. americanus* stations, with the regression fit to all data

Table 2. Percentage of stations in 2000 to 2002 NMFS (National Marine Fisheries Service) scallop surveys containing various substrates as a function of depth. *: category that was frequently dominant component of substrate

Depth (m)	Bivalve shells	Gastropod shells	Sand	Gravel/ cobble	Mud/ clay
27–39	100*	90	87*	0	0
40–54	97*	81	61*	10	4
55–69	100*	77	60*	9	7
70–84	100*	61	45*	4	11
85–104	100*	74	43	9	4

Table 4. Major finfishes in catch (mean no. tow^{-1}) during 2000 to 2002 NMFS scallop surveys as a function of depth

Depth (m)	Skates	Flounder	Hakes	Goosefish
27–39	44.7	10.0	1.9	0.8
40–54	15.6	7.9	11.6	2.2
55–69	12.9	11.8	22.6	2.5
70–84	2.9	12.7	8.2	2.2
85–104	1.1	12.7	3.3	1.2

heros) and worms (e.g. the polychaete *Aphrodite* sp.). Skates, primarily the little skate *Leucoraja erinacea*, were the most common demersal finfishes observed (Table 4). Flounder (mostly the gulfstream flounder *Citharichthys arctifrons* and the fourspot flounder *Paralichthys oblongus*), hakes (primarily the spotted hake *Urophycis regia* and the red hake *U. chuss*), and goosefish *Lophius americanus* were other common demersal finfishes in the study area.

As a preliminary exploration of the relationships among scallops, sea stars and crabs, a correlation matrix was computed (Table 5), relating abundance and mean weight of *Astropecten americanus*, *Asterias* spp. and *Cancer* spp., with latitude, depth, and sea scallop recruits. There were significant negative correlations between *A. americanus* abundance, *A. americanus* mean weight, *Asterias* spp. number and sea scallop recruitment. Abundances of both sea star groups as well as sea scallop recruits were significantly correlated with depth, and abundances of all biotic groups were significantly correlated with latitude.

To further examine the effects of predation and other factors on sea scallop recruitment, a multiple regression was performed using *Astropecten americanus*, *Asterias* spp. and *Cancer* spp. abundance and mean weight, together with latitude, depth and depth-squared (in order to account for the apparent non-linear relationship of sea scallop recruitment with depth; Fig. 3a) as predictors of *Placopecten magellani-*

cus recruitment, ln $(x + 1)$-transformed. Of the independent variables examined, 6 were significant predictors of sea scallop recruitment: *A. americanus* and *Asterias* spp. abundance, *A. americanus* mean weight, latitude, depth and depth-squared, with all but depth negatively associated with scallop recruitment. After the non-significant variables were eliminated via a backward stepwise procedure, the latitude variable was no longer significant, and the final regression, with the remaining 5 significant predictors (Table 6a; see also Fig. 4), had a combined R^2 of 0.37.

Because depth is correlated with abundance of both *Astropecten americanus* and *Asterias* spp., there is some confounding of these variables in the multiple regression. This creates some uncertainty as to whether the reductions in sea scallop recruitment at depth extremes is mainly due to sea star predation or to some other effect related to depth (e.g. temperature). To help separate the effects of depth from those of sea stars, sea scallop recruitment was binned by depth categories (27 to 39, 40 to 54, 55 to 69, 70 to 84 and 85 to 104 m; n = 12, 95, 151, 64 and 13, respectively), and by low or high sea star abundance or biomass (Fig. 5; see also Fig. 3a). *A. americanus* was separated by biomass (= abundance × mean size) categories rather than by abundance, because both *A. americanus* abundance and mean size appear to affect scallop recruitment.

Mean sea scallop recruitment increased with increasing depth down to 70 m, and declined thereafter at both high and low *Astropecten americanus* and *Asterias* spp. densities. At each depth range, sea scallop recruitment was greater in the low sea star categories (except in cases where there were no observations). Sea scallop recruitment was significantly greater at the low *A. americanus* stations in the 55 to 69 m (Student's $t = 2.1$, p = 0.04) and 70 to 84 m ($t = 4.1$, p < 0.001) depth ranges, and at the low *Asterias* spp. stations at 40 to 54 ($t = 3.9$, p < 0.001) and 55 to 69 m ($t = 3.0$, p = 0.003) depths.

Table 3. Percentage of stations in 2000 to 2002 NMFS scallop surveys containing live invertebrates as a function of depth. *: category that was frequently dominant component of catch

Depth (m)	Sand dollars	Sea urchins	Sponges	Gastro-pods	Ascid-ians	Anem-ones	Barn-acles	Worms
27–39	65*	45	74	81	32	3	0	42
40–54	58*	67	70	73	35	2	6	46
55–69	43*	51	63	74	39	4	5	45
70–84	14	15	48	58	20	4	4	33
85–104	9	9	52	48	39	17	0	30

Table 5. *Astropecten americanus*, *Asterias* spp. and *Cancer* spp. Pearson correlation coefficients between predator abundances and their mean weights (wt), *Placopecten magellanicus* recruitment, ln(x + 1)-transformed, latitude and depth in the Mid-Atlantic Bight. *p < 0.05, **p < 0.01, ***p < 0.001

	1	2	3	4	5	6	7	8	9
1. *A. americanus* abundance	1.00	−0.34***	−0.14*	0.15*	0.12*	0.03	−0.19*	0.45**	−0.24*
2. *A. americanus* mean wt		1.00	0.08	0.03	0.04	0.13	0.21**	−0.18**	−0.15*
3. *Asterias* spp. abundance			1.00	−0.10	−0.03	0.07	0.12***	−0.22***	−0.13**
4. *Asterias* spp. mean wt				1.00	0.03	−0.08	−0.10	0.06	0.00
5. *Cancer* spp. abundance					1.00	−0.17**	−0.25**	0.05	−0.03
6. *Cancer* spp. mean wt						1.00	0.41***	0.11	−0.19**
7. Latitude							1.00	−0.25*	−0.27**
8. Depth								1.00	−0.12*
9. *P. magellanicus* recruits									1.00

It is illuminating to compare the depth distributions of *Placopecten magellanicus* recruits and *Asterias* spp. from the Mid-Atlantic Bight with those of individuals collected to the north, on Georges Bank, Nantucket Shoals and the Great South Channel, since *Astropecten americanus* is rare in the latter areas (Franz et al. 1981). *A. americanus* was observed in only 26 of the 257 stations in Georges Bank and vicinity where sea star samples were taken, mostly in the deep-water stations on the southern edge of Georges Bank and Nantucket Shoals. At only 6 of these stations was *A. americanus* biomass greater than 10 kg tow^{-1}. Of these 6 stations, sea scallop recruits and *Asterias* spp. were each absent from 4, and scallop recruits were present in low numbers in the other 2, similar to the pattern observed in the Mid-Atlantic Bight. Sea scallop recruitment in Georges Bank and neighboring areas was greatest between 60 and 90 m, and declined more gently at depth extremes than in the

Table 6. Results of multiple regression of (a) significant predictors of sea scallop *Placopecten magellanicus*, recruitment ln(x + 1)-transformed, and (b) significant predictors of *Asterias* spp. abundance ln (x + 1)-transformed. Coeff: raw predictor values; Std. coeff: results after independent variables were standardized to achieveunit standard deviations and zero means

Predictor	Coeff	SD	p-value	Std. coeff	SD
(a)					
Intercept	−3.7	3.3	0.26		
Astropecten americanus abundance	−0.00011	0.00002	<10^{-6}	−0.35	0.06
Astropecten americanus mean wt	−0.25	0.04	<10^{-6}	−0.32	0.06
Asterias spp. abundance	−0.00047	0.00013	0.0004	−0.21	0.06
Depth	0.33	0.095	0.0007	1.64	0.48
Depth-squared	−0.0029	0.00068	0.00003	−2.02	0.47
(b)					
Intercept	11.5	0.6	<10^{-6}		
Astropecten americanus abundance	−0.00006	0.00002	0.003	−0.15	0.05
Depth	−0.11	0.01	<10^{-6}	−0.52	0.05

Mid-Atlantic (Fig. 6a). *Asterias* spp. abundance declined slightly at most with increasing depth (Fig. 6b), and were common in most deep-water stations, in contrast to the situation in the Mid-Atlantic.

The negative correlation between *Astropecten americanus* and *Asterias* spp. abundance suggests that there may be an antagonistic interaction between these 2 types of asteroids. To explore this further, *Asterias* spp. abundance, ln(x + 1)-transformed was regressed against depth and *Astropecten americanus* abundance. Both these variables were significant (Table 6b, Fig. 7), with a total R^2 of 0.36. *A. americanus* mean weight was not a significant third predictor when added to the other 2 variables in the regression.

Astropecten americanus mean weight did not appear to be related to abundance in the cases where its abundance was less than about 5000 tow^{-1} (Fig. 8). However, there was a substantial decline in mean weight as its abundance increased beyond this point. When stations at which there were <5000 *A. americanus* were removed, linear regression indicated that *A. americanus* abundance was a significant predictor of its mean weight (t = −4.6, p < 0.001, R^2 = 0.21). Depth was not a significant second predictor of mean weight when it was added to the regression (t = −1.0, p = 0.31). Regressions also indicated that *Asterias* spp. mean weight (log-transformed) was significantly related to *Asterias* spp. (t = −2.2, p = 0.03) and *A. americanus* (t = 3.0, p = 0.003) abundance, although the explanatory power of these variables was low (R^2 = 0.06). *Cancer* spp. mean weight (log-transformed) was significantly related to its abundance (t = −3.5, p < 0.001), depth (t = −2.2, p = 0.03) and depth-squared (t = 2.5, p = 0.01).
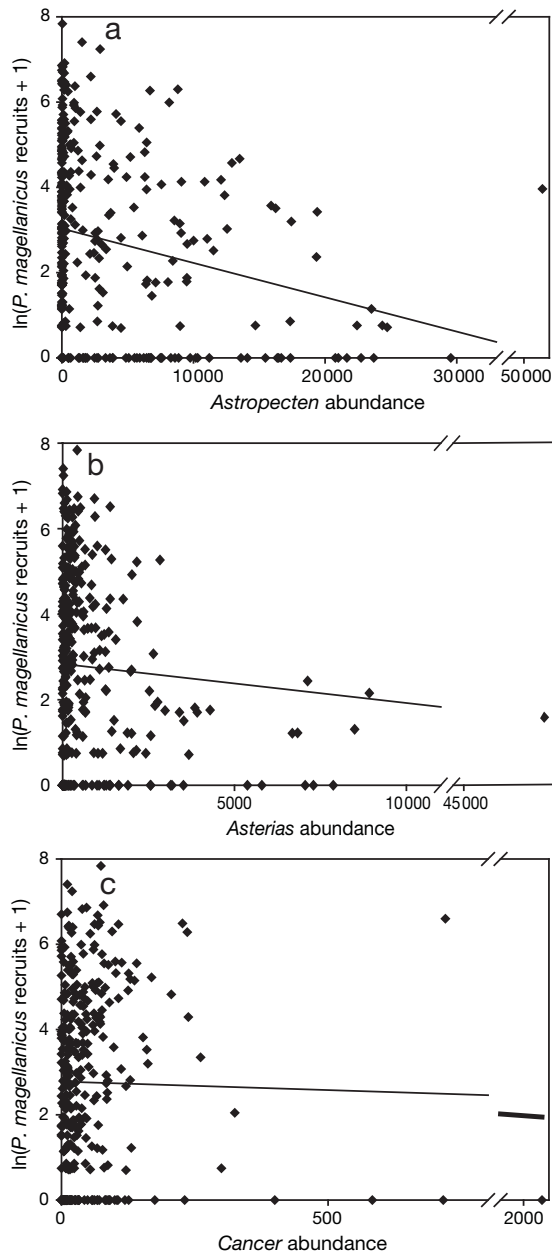
Fig. 4. *Placopecten magellanicus* recruitment vs. (a) *Astropecten americanus*, (b) *Asterias* spp., and (c) *Cancer* spp. abundance (nos. tow^{-1}) in the Mid-Atlantic Bight. Simple linear regression lines are also shown. Data are ln(x+1)-transformed

Fig. 5. *Placopecten magellanicus.* Box- and whisker plots showing mean (small inner square), SE of mean (outer box) and 95% confidence interval (whiskers) for scallop recruitment in the Mid-Atlantic Bight in 5 depth categories (27 to 39, 40 to 54, 55 to 69, 70 to 84 and 85 to 104 m) at stations with (a) low and high *Astropecten americanus* biomass, and (b) low and high *Asterias* spp. abundance. ND: no observations. Data are nos. tow^{-1}, ln(x+1)-transformed

DISCUSSION

Sea scallop recruitment in the Mid-Atlantic Bight is significantly related to depth and to the abundances of *Astropecten americanus* and *Asterias* spp. The reduction in scallop recruitment at shallower depths is probably related to maximum bottom temperatures, which can approach or exceed the upper temperature at
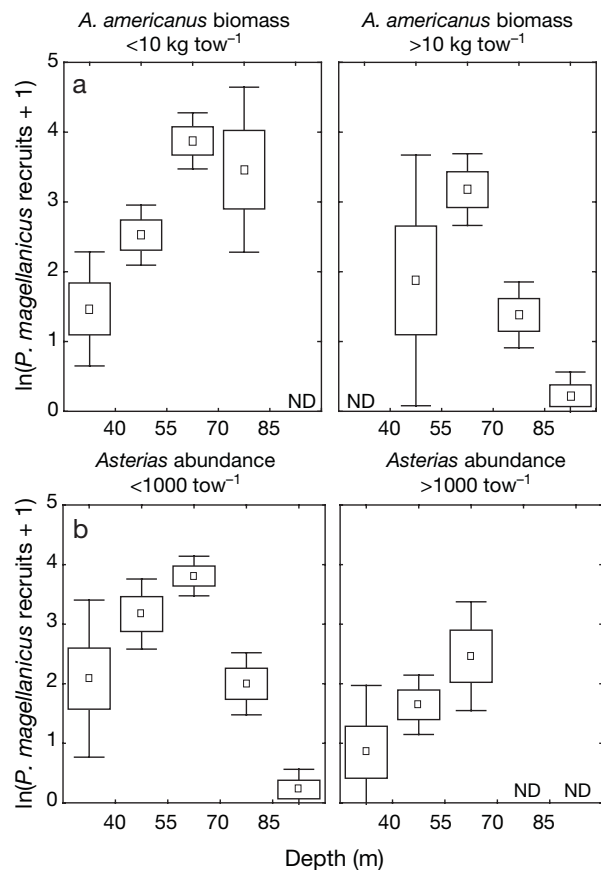
which sea scallops can survive (about 21°C, Hart & Chute 2004); the relatively high abundance of *Asterias* spp. in shallow waters probably also contributed to this pattern.

Sea scallop growth is typically slower in deep water, probably due to food limitation from reduced phytoplankton density (Schick et al. 1988, Thouzeau et al. 1991). Sea scallop recruitment would therefore be expected to decrease with increasing depth, since the spat will experience the high mortality suffered by small scallops for a longer period. However, the decline with increasing depth would be expected to be gradual were food limitation the main cause of this relationship, as was observed on Georges Bank. In the Mid-Atlantic Bight, sea scallop recruitment rapidly declined from a peak at about 60 m depth, to very low recruitment beyond 75 m, and no observed recruitment deeper than 85 m. Strong sea scallop recruitment
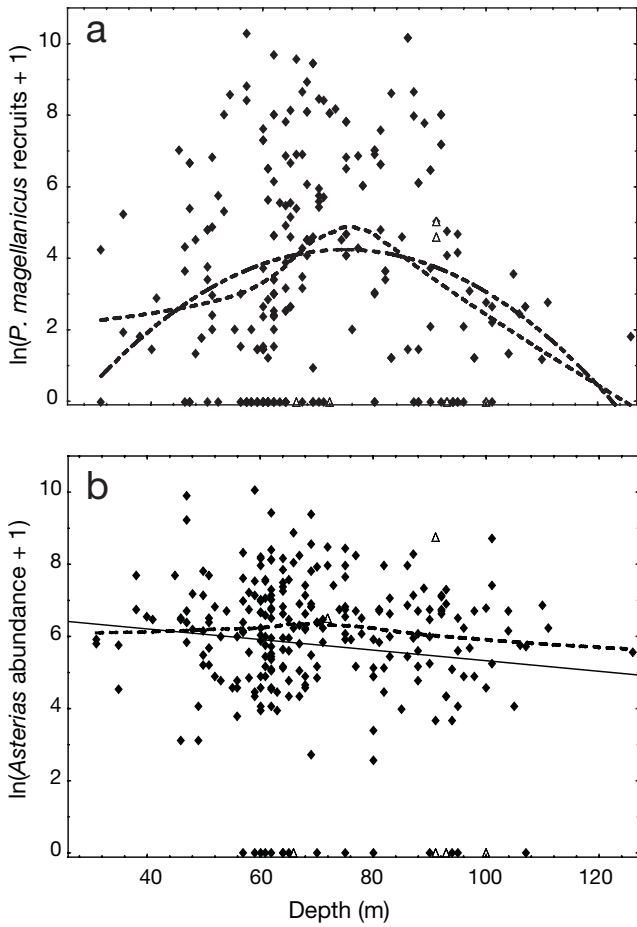
Fig. 6. Distribution of (a) *Placopecten magellanicus* recruitment, and (b) *Asterias* spp. abundance as a function of depth in areas surveyed NE of the Mid-Atlantic Bight (Georges Bank, Nantucket Shoals and Great South Channel); (nos. tow^{-1}) data are ln(x+1)-transformed. (△) Six stations where *Astropecten americanus* biomass was >10 kg tow^{-1}. Simple linear regression (continous line). In (a) quadratic regression (dot-dashed line) was used, in (b) lowess-smoothed (dashed lines; stiffness = 0.75) curves are also shown

was observed at >90 m depth on Georges Bank, and sea scallops have been observed in even deeper water in the Gulf of Maine (Schick et al. 1988), so the absence of sea scallop recruits from deep-water in the Mid-Atlantic Bight is due to a factor not operating in these more northerly areas. Since *Astropecten americanus* is rare or absent on Georges Bank and in the Gulf of Maine, but common in deep water in the Mid-Atlantic Bight, it is probably the cause of the differential distribution of scallop recruits between these regions. Indeed, *A. americanus* was always observed at high abundance beyond 75 m, and at even higher densities beyond 85 m, corresponding well to the points where sea scallop recruitment strongly declined, and was then absent.
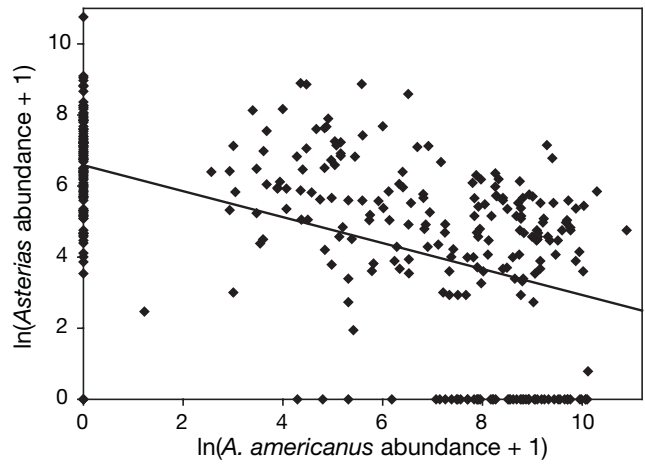

Fig. 7. *Asterias* spp. abundance vs. *Astropecten americanus* abundance (both in nos. tow^{-1}), in the Mid-Atlantic Bight; data are ln(x+1)-transformed; simple linear regression line is shown
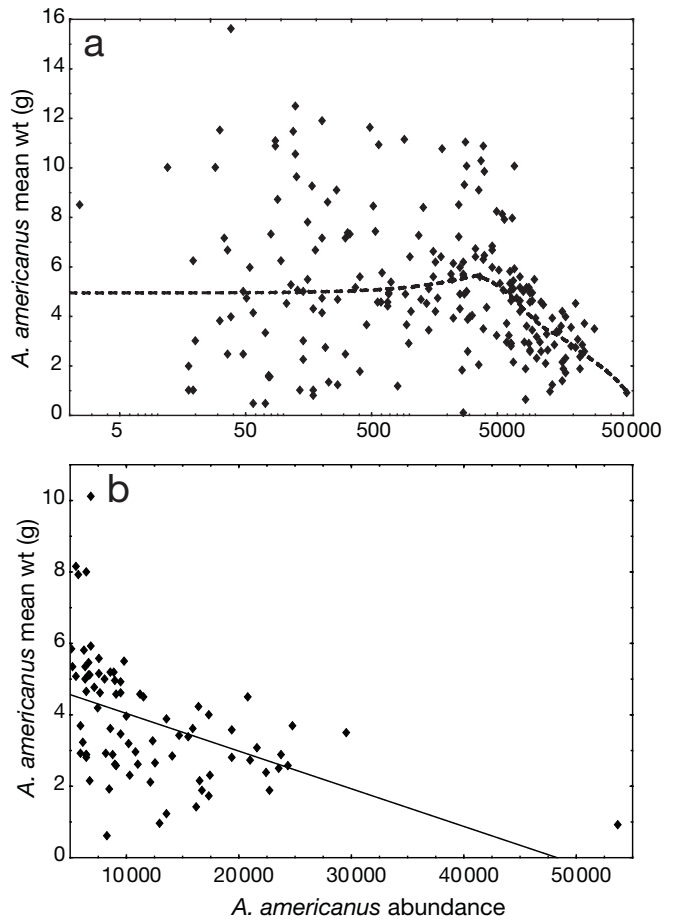

Fig. 8. *Astropecten americanus.* Mean weight (g) vs. abundance (nos. tow^{-1}) in the Mid-Atlantic Bight for (a) all stations where *A. americanus* were caught (note log scale on *x*-axis) together with lowess line (stiffness = 0.75), and (b) stations where >5000 *A. americanus* were caught (linear regression line shown)

In contrast to what has been observed during sea scallop enhancement experiments, no significant relationship was observed between *Cancer* spp. and sea scallop recruitment, although there was a hint of a negative correlation. It is possible that the densities of *Cancer* spp. in the Mid-Atlantic region were too low for them to make a substantial impact on scallop populations. Also, the mobility of *Cancer* spp. may mean that high density areas do not persist on an annual time scale, making it difficult to detect interactions involving *Cancer* spp. using the methodology of this study.

Finfishes do not appear to have a substantial influence on scallop recruitment in the Mid-Atlantic Bight. The most common benthic fish observed, the little skate *Leucoraja erinacea*, consumes mostly crustaceans and polychaetes (Collette & Klein-MacPhee 2002). Of over 50 000 prey items found in the stomachs of little skates recorded in the NEFSC (Northeast Fisheries Science Center) food-habits database (Link & Almeida 2000), no scallops were identified, although about 2% of the items were unidentified bivalves. Also, the other benthic fishes (e.g. flounder and hakes) observed in this area rarely, if ever, consume scallops (scallops comprised <0.1% of the prey items in the stomachs of spotted and red hake, and no scallops were observed in the stomachs of fourspot and gulfstream flounder, from the NEFSC food-habits database), and their depth distributions are not negatively correlated with that of sea scallops.

Studies in Canadian waters have indicated that sea scallop densities and recruitment are considerably higher in gravel or gravel-sand bottoms than in sand bottoms (e.g. Thouzeau et al. 1991). The level of sea scallop recruitment observed in this study in the Mid-Atlantic Bight, with almost entirely sand bottoms, is comparable or greater to that observed in harder bottom further north. It is possible that the nearly universal presence of shell substrate in the Mid-Atlantic Bight can substitute for gravel, providing sufficient attachment sites for settlement and possibly also some protection from predators, as has been noted for the Iceland scallop *Chlamys islandica* (Guay & Himmelman 2004). Additionally, sea scallops may preferentially settle in gravel bottoms when available, as in Canada, but have no alternative but to settle in sand bottoms in the Mid-Atlantic Bight.

Sea scallop spawning-stock biomass and egg production in the Mid-Atlantic Bight were well above historical means during the 2000 to 2002 study period, and (possibly not coincidently) recruitment was also well above average (NEFSC 2004). However, recruitment remained low at depth extremes during this period. Moreover, the relationships observed here were consistent over the 3 yr period,

whereas larval settlement patterns tend to be highly variable (Fraschetti et al. 2003). These considerations suggest that larval supply is not responsible for the observed distribution of sea scallop recruitment with depth.

Franz & Worley (1982) found 20 sea scallops (modal size 0.7 mm) in the stomachs of 106 *Astropecten americanus* collected in November on Nantucket Shoals. Smereka (2003) found 38 scallops (shell heights 5 to 12 mm) in the stomachs of 282 *A. americanus* collected in the Mid-Atlantic Bight during July 2002 in the NMFS sea scallop survey that was a part of this study. Combining the frequency of sea scallops in their stomachs with the high abundances of *A. americanus* (often 10 000 to 20 000 tow^{-1} or higher compared to a tow path of about 4500 m^2) indicates that direct predation of scallop spat by *A. americanus* is capable of impacting sea scallop recruitment.

Sea scallop pediveligers are capable of delaying settlement for at least a few days if bottom conditions are unsatisfactory for settlement (Culliney 1974), and post-settlement juveniles may swim short distances to escape sea star predation. Thus, it is possible that some of the effects observed here were due to predator avoidance rather than direct predation. However, the nearly ubiquitous distribution of *Astropecten americanus* in deep water would make it difficult for juvenile scallops to avoid this sea star at these depths. The fact that sea scallops are often seen in the stomachs of *A. americanus* and the numerous observations of consumption of scallops by *Asterias* spp., imply that avoidance behavior can at most be only a partial explanation for the observed patterns.

Sea scallop recruits in the 40 to 69 mm range are about 2 yr old, and thus would have been only subject to *Astropecten americanus* predation for 18 to 22 mo previously. The hypothesis that the negative relationship observed between *A. americanus* and sea scallop recruits was due to predation requires an assumption that aggregations of *A. americanus* are persistent, so that high abundances of these sea stars observed in a given year correspond to high densities 2 yr previously. In deep water (>75 m), *A. americanus* appear always to be at high density, so the persistence criterion would be met in these locations. To test persistence in shallower water, 2 stations on the 2000 survey where *A. americanus* were unusually abundant (depths of 68 and 65 m) were resampled in 2001 and 2002. *A. americanus* catches in 2000 to 2002 at the first site were 20 600, 20 160, and 17 504, respectively, and were 17 316 in 2000 and 16 120 in 2002 at the second site (a photograph of the catch at this site in 2001 showed that it was dominated by *A. americanus*, but due to an oversight, no sea star subsample was taken), indicating that aggregations of these sea stars can per-

sist for several years. Boesch (1979) sampled a number of fixed stations in the Mid-Atlantic several times a year during 1975 to 1977, and similarly found little temporal variation in catches of *A. americanus* and *Asterias* spp.

Some species of *Astropecten* may seasonally migrate (Pabst & Vicentini 1978, Nojima 1983, Lemmens et al. 1995, Freeman et al. 2001). The populations in each of these cases were near-shore, where the environment can change substantially, with horizontal movements on the order of hundreds of meters. *A. araniacus*, whose maximum size is much larger than that of *A. americanus*, typically move about 10 m d^{-1} (Burla et al. 1972), suggesting that it would be able to migrate <2 km in 6 mo. Bottom temperatures or other environmental variables are unlikely to change much on the scale of a few kilometers offshore, making seasonal migrations of *A. americanus* unlikely. As indicated above, aggregations of *A. americanus* appear to persist at a location for several years.

The time-lag between *Astropecten americanus* predation and observed scallop recruitment is likely to be at least one of the reasons why *A. americanus* mean weight was a statistically significant predictor of sea scallop recruitment. Though asteroid growth is highly variable, there still should be a correlation between size and age. *A. americanus* <2 yr old would not have had the opportunity to consume the observed scallop recruits because they would have settled after the scallops. This may explain the outlier station in Fig. 4b, where over 50 000 *A. americanus* along with moderate scallop recruitment were observed; the mean weight of the *A. americanus* at this station was among the lowest of all stations (<1 g, Fig. 8).

Astropecten americanus were confined to deeper water at higher latitudes, consistent with the idea that they are limited by winter minimum temperatures (Franz et al. 1981). The pattern of abundance of *Asterias* spp., which declines strongly with increasing depth in the Mid-Atlantic Bight, cannot be as simply explained by temperature limitation. Indeed, bottom temperatures at 70 to 110 m depth in the Mid-Atlantic are well within the tolerance of *A. forbesi* and, with the possible exception of the most southern areas, *A. vulgaris* as well (Smith 1940, MacKenzie 1969, Sloan 1980, Franz et al. 1981, Barbeau & Scheibling 1994). *A. vulgaris* was commonly observed at these depths in the samples taken on Georges Bank and neighboring areas, and can occur to depths of 400 m or more (Vevers 1949). Because neither temperature limitation nor direct depth effects can explain the reduced number of *Asterias* spp. in deep water in the Mid-Atlantic, it appears that the high density of *Astropecten americanus* in deeper water is at least in part responsible for the low *Asterias* spp. abundance. Confirming this idea

is the fact that *Asterias* spp. were absent from the majority of the Georges Bank stations with high *Astropecten americanus* abundance even although they were common in most other deep-water stations in this area.

A negative interaction between *Astropecten americanus* and *Asterias* spp. may appear surprising, since adults of these 2 groups do not directly compete, with *Asterias* spp. mainly preying on items too large for *A. americanus* to consume. The fact that *A. americanus* abundance is a significant positive predictor of *Asterias* spp. weight suggests that *A. americanus* are reducing the number of juvenile *Asterias* spp. *A. americanus* may be outcompeting young *Asterias* spp. for food when these juveniles' diet is similar to that of adult *A. americanus*. It is possible that *A. americanus* is consuming newly settled *Asterias* spp., although no *Asterias* spp. have been found in the stomachs of *A. americanus* (Franz & Worley 1982, Smereka 2003). *A. americanus* may also be reducing the number of *Asterias* spp. due to what may be termed 'preemptive competition', whereby *A. americanus* consume most of the potential prey items of *Asterias* spp. before they can grow to a size normally taken by this genus. While preemptive competition is an unusual concept, it may be an important process in many systems of organisms with complex life-histories and large ontogenetic changes in size and diet, as is common in marine ecosystems. *A. americanus* may be an unusual type of dominant predator that structures the benthic invertebrate community by removing large quantities of juvenile invertebrates as well as effectively competing against other predators.

The mean weight of *Astropecten americanus* appears to be unrelated to its abundance at densities of less than about 5000 tow^{-1}, but drops sharply at higher densities. As discussed above, migration is an unlikely explanation for this phenomenon. Asteroid growth is highly variable, depending on food supply, and they can survive long periods with little or no food by growing slowly or even reducing their size (Vevers 1949, Hancock 1958, Christensen 1970). At *A. americanus* densities of <5000 tow^{-1}, it appears that their growth rate (and probably their consumption rate) does not depend on their density, suggesting that they are feeding near their maximum rate. At *A. americanus* densities >5000 tow^{-1}, mean size declines rapidly with abundance, probably because of decreased growth (and possibly also increased mortality) due to food limitation. A similar pattern was noted for *Asterias vulgaris* populations in Canada (Smith 1940). The data from the present study suggest that density-dependent processes may also be occurring for *Asterias* spp. and *Cancer* spp., although the effects appear much weaker, probably because of lower densities.

In an observational study such as that presented here, there is always some uncertainty as to the mechanisms that produced the observed relationships. While direct predation is the most likely explanation for the negative associations between sea scallop recruits and sea stars, it is possible that predator avoidance by settling pediveligers or by post-settlement juveniles was also a contributing factor. While there is some uncertainty as to the mechanism by which *Astropecten americanus* is excluding *Asterias* spp., it is clear that high levels of *A. americanus* do reduce *Asterias* spp. abundance. This study has demonstrated how the patterns of recruitment of an important commercial species can be fitted into an ecosystem context.

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