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Bathymetric trends in the body size, and diet of *Astropecten americanus* in the northwest Atlantic Ocean

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ABSTRACT

Sea stars are major predators of marine invertebrates, in particular, mollusks. Data on the diet composition and the size structure of sea stars in the N.W. Atlantic Ocean are limited. Samples of sand star (*Astropecten americanus*) collected from three regions in the N.W. Atlantic Ocean were used to determine spatial and seasonal differences in diet and size structure. Samples were collected from ten stations during the 2009 spring and fall NMFS bottom trawl surveys. Four hundred and eighty-eight (488) prey items belonging to various taxa were identified from stomach contents of 524 sea stars of which 302 contained food. In terms of percentage contribution by number of prey items belonging to each taxon (Cn%), gastropods (40%), bivalves (22%) and crustaceans (21%) were the most important. Gastropods were more important in the diet of Southern New England (SNE) and Mid-Atlantic Bight (MAB) sea stars accounting for ~50% of the diet in each area, and were consumed by 35–42% of the sea stars, whereas crustaceans were more important in Georges Bank (GB) where they contributed ~83% of the diet, and were consumed by about 77% of the sea stars. There were more gastropods and foraminiferans in the stomachs of sea stars collected in fall, while crustaceans and bivalves were more common in spring samples. These differences may be due to spatial and seasonal differences in the abundance and composition of macrobenthic invertebrates. The size of sea stars decreased with depth, perhaps due to a reduction in prey abundance and higher sea star densities with depth. Additionally, length-weight relationships suggest that sea stars in GB were heavier at a given size (length) than those from SNE and MAB. This might have resulted from the latitudinal variation in the density and species composition of macrobenthic invertebrates that serve as prey for sea stars, such that densities were low on the continental shelf off Delaware-Virginia-North Carolina and relatively high in the region off southern Massachusetts and Rhode Island.

1. Introduction

The sea stars in the genus *Astropecten* are major predators of small marine invertebrates, especially mollusks and crustaceans (Lemmens et al., 1995; Turra et al., 2015). There have been a number of studies on the feeding ecology of members of this genus, including *A. irregularis* (Christensen, 1970; De Juan et al., 2007), *A. brasiliensis* (Caregnato et al., 2009), *A. aranciacus* (Ribi and Jost, 1978), *A. latespinosus* (Nojima, 1989), *A. articulatus* (Wells et al., 1961) and *A. marginatus* (Guilherme and Rosa, 2014). Few studies, however, have been conducted on the biology and ecology of *A. americanus*. The species is distributed between latitudes 35° and 41° N in the N.W. Atlantic Ocean from Cape Hatteras, North Carolina to Georges Bank (Franz et al., 1981; Hart, 2006; Pierdomenico et al., 2017). They are more common south of the Hudson Canyon and in deeper waters; and often form dense aggregations in waters deeper than 70 m (Hart, 2006).

Astropecten americanus predation is a significant factor regulating the recruitment of scallops (Hart, 2006). A significant negative correlation was observed between sea scallop recruitment and *A. americanus* abundance such that scallop recruitment decreased from peak levels at 60 m depth to very low recruitment at depths exceeding 75 m. Furthermore, *A. americanus* may compete for food resources with *Asterias* spp. as indicated by the fact that, in deep waters of the Mid-Atlantic where *A. americanus* abundance is high, the abundance of *Asterias* spp. is

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low (Hart, 2006).

Franz and Worley (1982) studied the feeding ecology of *A. americanus,* although the work was restricted to the Southern New England region of the N.E. continental shelf of the United States. Since there is a north-south gradient in the relative abundance and composition of benthic invertebrates in the northwest Atlantic Ocean (Wigley and Theroux, 1981), the diet information provided by Franz and Worley (1982) may not be reflective of prey consumption by *A. americanus* in the other areas of the northwest Atlantic. Moreover, since the early 1980s when the study was conducted, changes have occurred in the physical conditions, particularly temperature, of the Mid-Atlantic region. In fact, analyses of long-term datasets from the region suggest that 1999 to 2002 had some of the warmest bottom temperatures (Jossi and Benway, 2003). This might have affected not only the abundance, but also species composition of macrobenthic invertebrates that serve as food for sea stars.

The size of an organism is of physiological, ecological, and evolutionary importance (Peters, 1983). Several factors, including competition for resources, predation, recruitment, growth, longevity and size-related mortality singly or in combinations may influence body size (Van Voorhies, 1996). Latitudinal and depth-related variations in animal body size have been investigated in the marine environment, more so in deep-sea invertebrates (Thiel, 1979; McClain and Crouse, 2006) than in invertebrates inhabiting the continental shelf (e.g. Roy, 2002). The majority of these studies have reported a decrease in body size of the deep-sea invertebrate taxa with increasing depth of the ocean (Thiel, 1975; Sebens, 1987; Rex and Etter, 1998; Olabarria and Thurston, 2003; Rex et al., 2006). However, this pattern is not universal, as some studies have reported an increase in body size or no significant relationship of body size with depth (e.g. Fujita and Ohta, 1990; Roy, 2002; McClain and Crouse, 2006). Here we describe patterns in the diet of *A. americanus* collected from three regions (Georges Bank, Southern New England, and Mid-Atlantic Bight) of the Northwest Atlantic Ocean, compare the body sizes among the areas, and report on the relationship between the body size and depth in the northeast continental shelf (60–300 m) of the United States.

2. Study area and research methodology

2.1. Study area

Samples were collected from 10 randomly selected stations in Georges Bank (GB), Southern New England (SNE), and Mid-Atlantic Bight (MAB) areas of the northwest Atlantic Ocean (Fig. 1, Table 1). Seven stations were in the north of which 343, 227 were in GB; 197 and 184 in SNE Deep shelf; and 181, 163 and 168 in SNE nearshore areas, whereas three stations (28, 33 and 21) were located in the more southern waters of the MAB shelf (Chesapeake Bight). Five of these stations (343, 197, 181, 28 and 33) were sampled in the spring between March and June 2009. The other five stations (227, 184, 163, 168 and 21) were sampled in the fall months of September and October 2009.

2.2. Research methodology

2.2.1. Sample collection and preservation

Sea star samples were collected during the National Marine Fisheries Service (NMFS) trawl surveys on the *FSV Henry B. Bigelow*. Surveys were conducted using a 400 × 12, 4 seam bottom trawl that was fished with 550 kg, 22 m polyice oval trawl doors. Trawl durations and speed were 20 min and 3 knots, respectively. The catch was sub-sampled for sea stars and aggregated by species and sub-samples were removed, recorded, and preserved by freezing (see Hart, 2006). Samples were later sent frozen in iceboxes to the University of Maryland Eastern Shore (UMES) from NOAA Woods Hole Laboratory in October and December 2009 for processing, and upon arrival were stored in a freezer until thawed for processing.

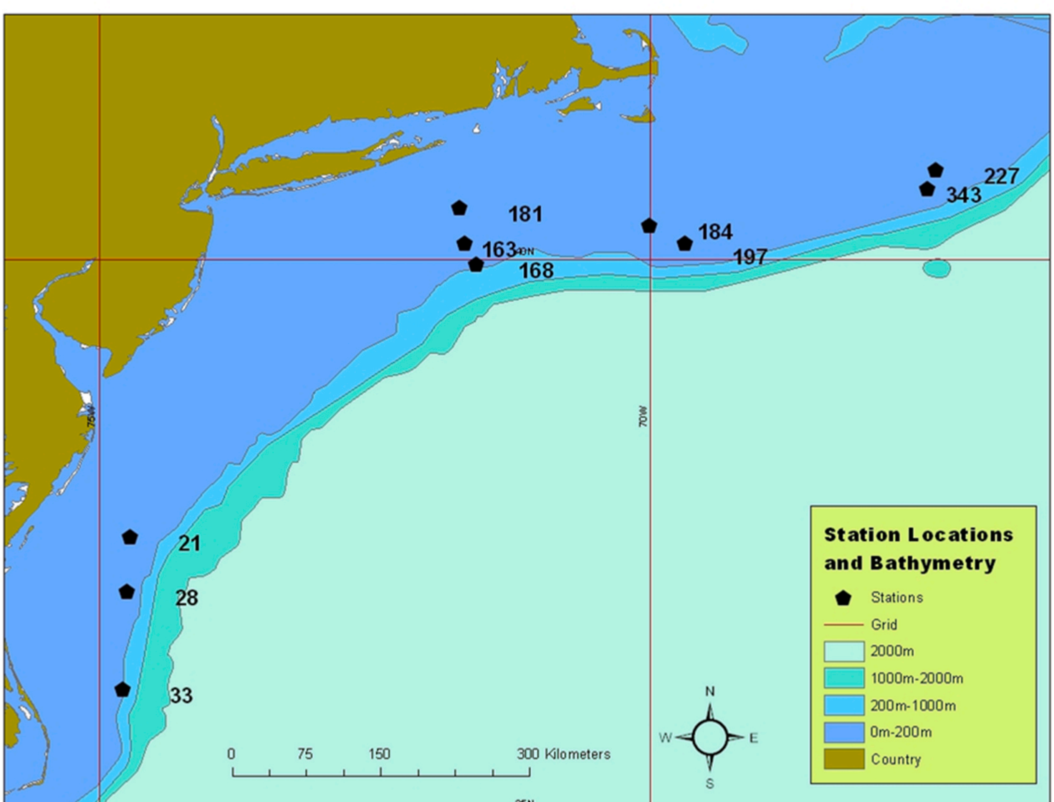


Fig. 1. Map of study area showing sampling stations.

Table 1
Sampling stations, Cartesian coordinates, depth and seasons during which samples were collected, and number of sea stars dissected and number with food in the gut.

Stations	Depth (m)	Latitude	Longitude	Season	Region	No. Dissected	No. with Food
28	84	36.9878	74.74005	Spring	MAB	58	34
33	278	36.10063	74.7794	Spring	MAB	66	48
181	66	40.4739	71.72032	Spring	SNE	53	29
197	92	40.15315	69.67913	Spring	SNE	64	13
343	96	40.64437	67.48327	Spring	GB	52	38
21	61	37.47571	74.7085	Fall	MAB	41	26
163	84	40.1504	71.6836	Fall	SNE	49	36
184	88	40.30826	69.9966	Fall	SNE	50	26
168	114	39.95989	71.5688	Fall	SNE	47	33
227	88	40.81307	67.3978	Fall	GB	44	19

2.2.2. Stomach content analyses and measurement of sea star sizes

A total of five hundred and twenty-four (524) *A. americanus* were examined. Individual sea stars were weighed to the nearest gram using a weighing balance, and the longest arms measured to the nearest millimeter with a meter ruler from the tip of the arm to the center of the disc. Samples were sub-divided into four size categories for further analysis (Little = 20–25 mm; Small = 26–30 mm; Intermediate = 31–35 mm and Large = >35 mm). Sea stars were dissected, and gut contents were examined under a dissecting microscope. Prey items were identified, counted, and preserved. Identifications of the prey to the lowest possible taxa were made by reference to Morris (1947) and Barnes (1987), and through the assistance of Toni Chute at the Northeast Fisheries Science Center. Diet data were expressed as percentage contribution by number (Cn%) and percent frequency of occurrence (FO%) of taxa (Hyslop, 1980).

2.2.3. Statistical analyses

The mean numbers of prey items in the stomachs of sea stars captured in spring and fall were compared using a *t*-test. Diet data were log (n+1)-transformed, and relationships between faunal, spatial and temporal variables were examined. Environmental variables used in analysis included depth (m), latitude and longitude coordinates of the various stations sampled.

The sizes of sea stars collected from GB, SNE, and MAB were compared using a one-way ANOVA. In addition, a regression analysis was used to examine the relationship between sea star mean size and depth. Furthermore, length-weight relationships of sea stars collected from GB, SNE and MAB were log-transformed and compared using ANCOVA to determine whether slopes of regression relationships were significantly different among sampling regions and between spring and fall.

3. Results

3.1. General description of sea star diet

A total of 131 out of 293 (44.7%) sea star stomachs examined in spring were empty, whereas 91 out of 231 (39.4%) stomachs collected in the fall were empty. The proportion of empty sea star stomachs increased with sea star size in spring from ~26% (20–25 mm) to about 78% (35–40 mm). In fall, 56.8% of 30–35 mm sea stars were empty whereas 37.0% and 31.2% of the sea stars measuring 35–40 mm and 25–30 mm were empty, respectively.

A total of 488 prey items belonging to 48 taxa (Table 2) were identified in the stomachs of 524 sea stars. When all data were pooled across stations and seasons, the major taxa contributing to the diet of *A. americanus* in terms of percentage contribution by number (Fig. 2) were gastropods (40%), crustaceans (21%), bivalves (22%), and protists, particularly foraminiferans (13%). The other prey types (e.g., scaphopods, fish, polychaetes, and other mollusks) were lumped together as miscellaneous items and contributed about 4% of the diet.

Table 2
Percent Contribution By Number of Prey items in the Diet of *Astropecten americanus*.

Taxonomic Group	% By Number
Annelida	
Onuphis sp.	0.20
Glycera americana	0.59
Arthropoda	
Amphipoda	6.08
Copepoda	0.20
Cumacea	3.14
Hutchisionella	0.20
Cancer sp.	2.94
Unidentified crustacean	8.43
Bivalvia	
Dosinia elegance	0.39
Astartes undata	2.35
Cerastoderma pinulatum	0.20
Clinocardium sp.	2.35
Trachycardium muricatum	1.57
Venus mecenaraia	0.20
Donax varaibilis	0.98
Cordakia orbicularis	0.20
Anatina lineate	0.20
Mactra sp.	0.20
Mulinia lateralis	8.82
Spisula solidissima	0.59
Pandora glasialis	0.20
Placopecten maggelanicus (scallop)	1.57
Periploma fragilis	0.39
Tellina magna	0.20
Pisces *Miscellaneous*	4.31
Cnidaria	
Epizanthus sp.	0.20
Foraminifera	12.94
Gastropoda	
Architectonica granulata	1.57
Busycon body part	0.39
Colus obesus	0.20
Hydrobia minuta	2.35
Janthia janthia	0.98
Littorina obtusata	0.20
Littorina littorea	0.20
Littorina saxatilis	0.59
Phasianella affinis	0.20
Alvania carinata	23.53
Skenea sp.	0.39
Terebra sp.	0.59
Magarites sp.	6.86
Litophoma americana	0.98
Turban operculum	0.20
Turbo castaneus	0.20
Lora sp.	0.20
Scaphopoda	
Scaphopoda: Dentalium sp.	0.78

Seventeen (17) gastropod taxa were reported in the stomachs of the sea stars (Table 2), the most abundant of which were *Alvania carinata* (23.5%) and *Magarites* sp. (6.9%). Arthropods were dominated by crustaceans, especially amphipods (6.1%) and unidentified crustaceans (8.4%), whereas *Mulinia lateralis* (8.8%) was the most important bivalve

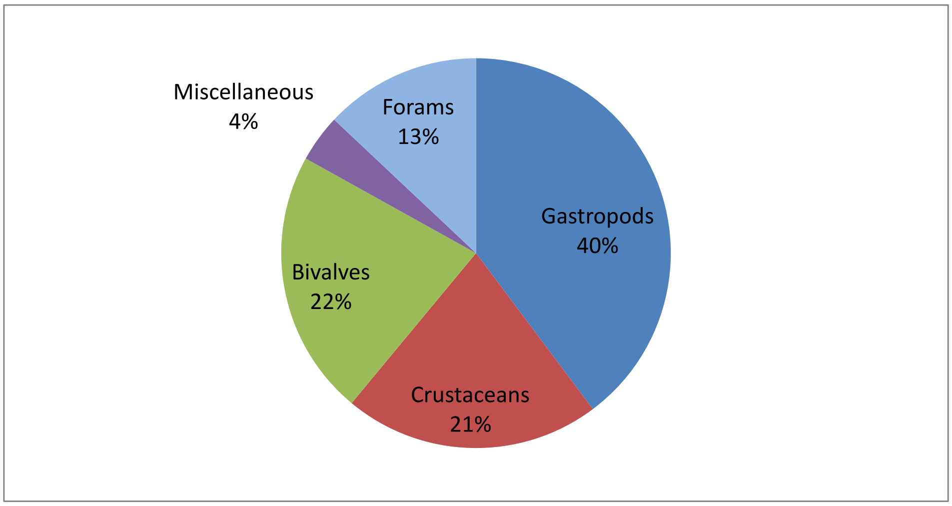


Fig. 2. Percentage contribution by number of major prey taxa in the diet of *A. americanus*. Data were based on the number of sea stars with prey in the stomach (n = 302).

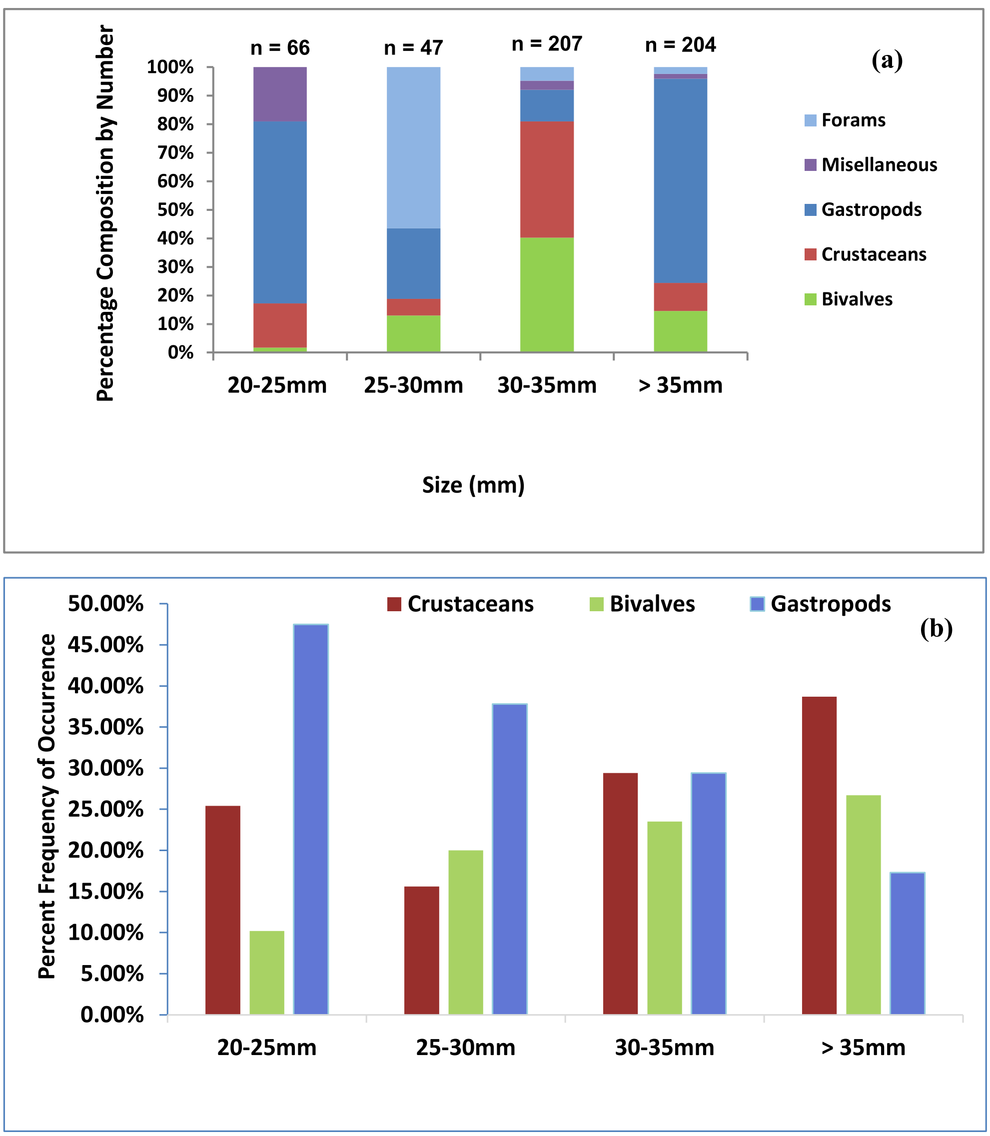


Fig. 3. Percent composition by number (a) and percent frequency of occurrence (b) of prey items in the diet of various size classes of *A. americanus* (number of sea stars examined in each size category is given).

prey in terms of contribution by number. There were 19 mollusk taxa in the stomachs of sea stars collected in spring, and 23 taxa in those collected in the fall. The percentage of prey consumed that was contributed by gastropods was higher in sea stars measuring >35 mm (71%) and 20–25 mm (65%) than in those measuring 25–30 mm (24%) and 30–35 mm (12%) (Fig. 3a). However, the percentage of sea stars that consumed gastropods decreased with size from 47.5% (20–25 mm), 37.8% (25–30 mm) to 17.3% (>35 mm) (Fig. 3b). The contribution by number of bivalves to the diet of sea stars was highest in the individuals measuring 30–35 mm (40%) and least in the size range of 20–25 mm (~2%) (Fig. 3a), and the proportion of sea stars that consumed bivalves increased from 10.2% (20–25 mm) to 26.7% (>35 mm) (Fig. 3b). The highest percentage by number (40%) of crustaceans consumed occurred in sea stars measuring 30–35 mm, whereas forams contributed significantly to the diet of 25–30 mm sea stars, accounting for 55% of the diet (Fig. 3a). About 29% of sea stars with arm length measuring 30–35 mm, and ~39% of those larger than 35 mm consumed crustaceans (Fig. 3b).

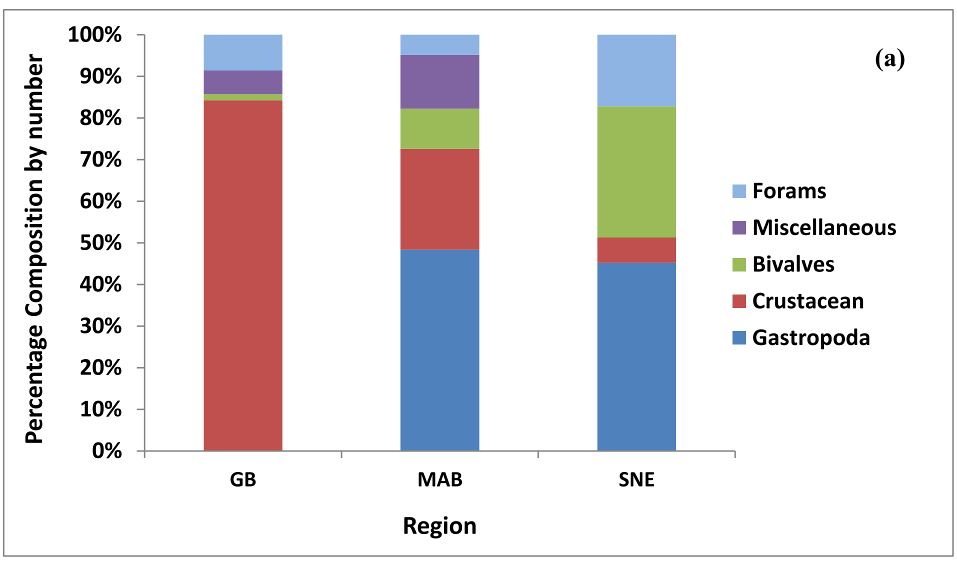
3.2. Spatial variation in the diversity of prey in the diet of A. americanus

The mean numbers (±SD) of prey items in the sea star stomachs in GB, SNE and MAB were 5.8 ± 14.8, 10.7 ± 20.7 and 6.9 ± 9.4, respectively. The number of prey taxa (species richness) found in gut contents of *A. americanus* increased along a longitudinal gradient (r^2 = 0.53, P = 0.02, n = 10), and the number of species consumed was significantly different among the 3 regions (GB, SNE and MAB), (ANOVA: $F_{(1,18)} = 26.54$, $P < 0.00007$, n = 10). Significant variations were also observed in prey diversity with latitude ($F_{(1,18)} = 311.33$, $P < 0.0001$) and depth ($F_{(1,18)} = 311.33$, $P < 0.0001$).

On a regional level, gastropods were important in the diet of SNE and MAB sea stars (Fig. 4) accounting for almost 50% of the diet in each area, but were very negligible in GB (Fig. 4a). Crustaceans were most important in GB in terms of percent contribution by number (83%) and percent frequency of occurrence (77%) but comparatively less important in MAB (20% by number; 24.7% by frequency of occurrence) and SNE (5% by number; 10% by frequency of occurrence) (Fig. 4a and b). Bivalves contributed 35% and foraminiferans 15% by number of prey consumed by SNE sea stars (Fig. 4a), but were negligible in sea stars from GB.

3.3. Seasonal variation in the diet of A. americanus

More prey items were found in the stomachs of sea stars collected in fall than those collected in spring (Fig. 5). An average of 1.4 prey items were extracted from 293 sea stars in the spring, whereas stomachs examined in the fall had on average 1.9 prey items. The number of prey items consumed by sea stars was different between the two seasons for gastropods (ANOVA: $F_{(1,18)} = 5.65$, P = 0.03, n = 10), but not for



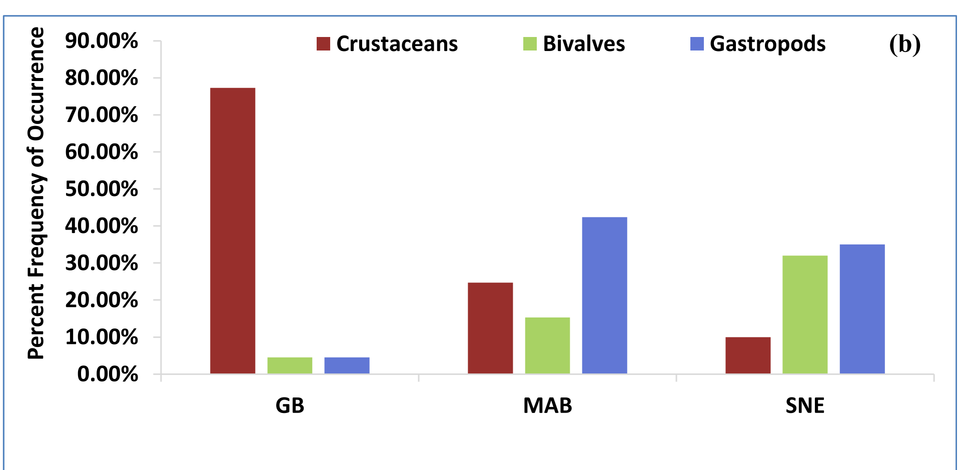


Fig. 4. Percent composition by number (a) and percent frequency of occurrence (b) of major prey taxa observed in the stomachs of *A. americanus* collected from various regions of the Northwest Atlantic Ocean. GB (Georges Bank), MAB (Mid-Atlantic Bight), SNE (Southern New England).

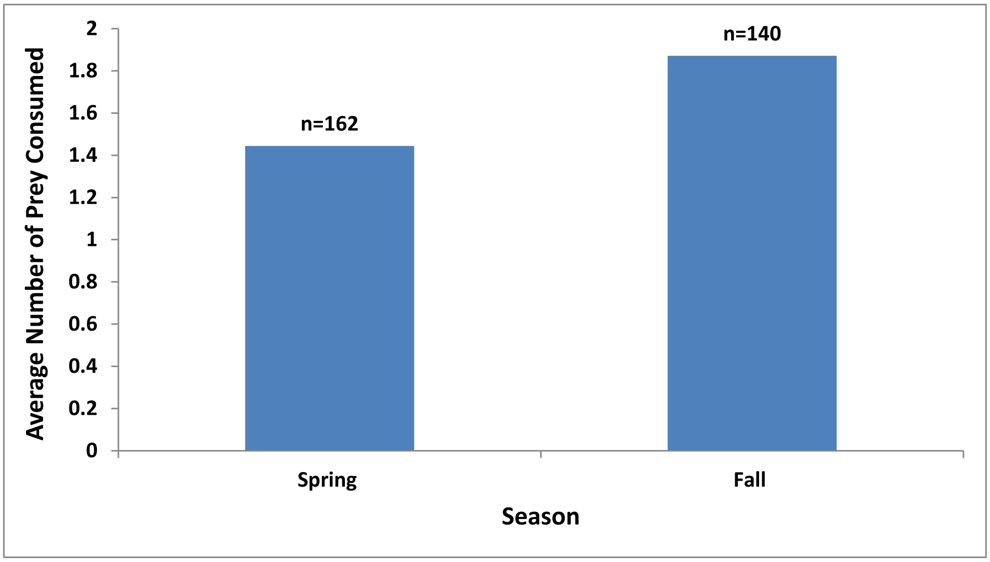


Fig. 5. Mean number of prey in all sea star stomachs collected in spring and fall that contained dietary items (n = the number of stomachs containing food).

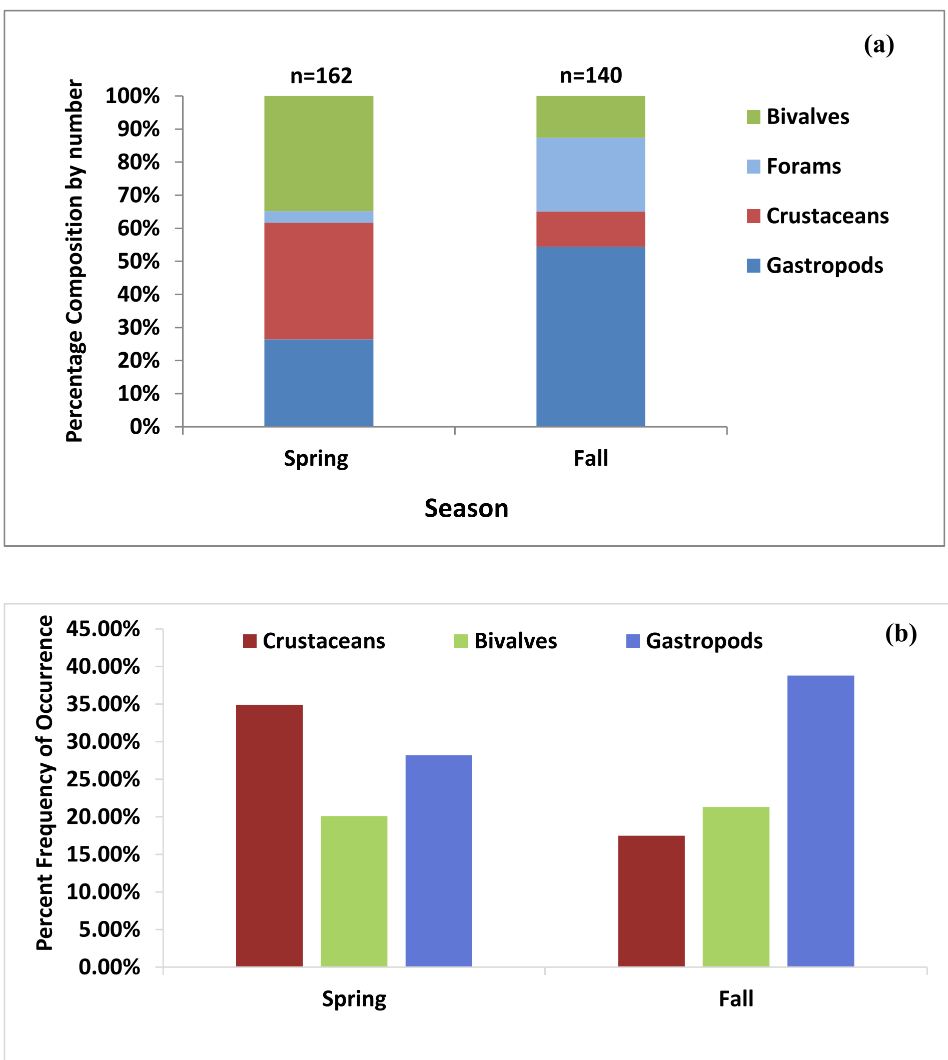


Fig. 6. Seasonal differences in the percent composition by number (a) and percent frequency of occurrence (b) of major prey taxa in the diet of *A. americanus* (n = number of stomachs containing food).

crustaceans (ANOVA: $F_{(1,18)} = 3.90$, $P = 0.06$, $n = 10$), bivalves (ANOVA: $F_{(1,18)} = 1.94$, $P = 0.18$, $n = 10$), and foraminiferans (ANOVA: $F_{(1,18)} = 1.20$, $P = 0.29$, $n = 10$).

There were more gastropods (55%) and forams (20%) in the stomachs of *A. americanus* samples collected in fall than there were gastropods (25%) and forams (4%) in the spring samples (Fig. 6a). Additionally, a higher percentage of sea stars consumed gastropods in fall (39%) than in spring (28%) as shown in Fig. 6b. Crustaceans (35%) and bivalves (35%) were relatively more common in the stomach contents of spring *A. americanus* samples than they were (crustaceans = 10% and bivalves = 10%) in fall samples (Fig. 6a). Furthermore, a higher percentage of sea stars consumed crustaceans in spring (35%) than in fall (18%), but the percentage of sea stars that consumed bivalves was similar in spring (20.1%) and fall (21.3%), Fig. 6b.

3.4. Size distributions of sea stars

The mean size (±SD) of sea stars (n = 414) measured in this study was 3.24 ± 0.86 cm with a range of 1.2–6.1 cm. Sea star size decreased with sampling depth ($r^2 = 0.84$, $p = 0.0001$, $n = 10$) (Fig. 7a). This pattern holds true even after data from the deepest station (Station 33) was eliminated ($r^2 = 0.43$, $p = 0.054$, $n = 9$). There was a steeper decline in the relationship between arm-length and depth for the fall (slope = −0.02; Fig. 7b) than spring (slope = −0.01; Fig. 7c) samples. Furthermore, a highly significant difference was observed between the mean size of sea stars collected in spring season (mean = 3.07 ± 0.91 SD, n = 273) and those collected in fall (mean = 3.56 ± 0.62 SD, n = 141) season (ANOVA: F = 33.02; $p < 0.00001$).

Mean size (cm) of sea stars differed among the three major regions, MAB (mean = 2.76 ± 0.84 SD, n = 130), SNE (mean = 3.51 ± 0.76 SD, n = 213) and GB (mean = 3.30 ± 0.78 SD, n = 71), (ANOVA: $F_{(411, 2)} =$

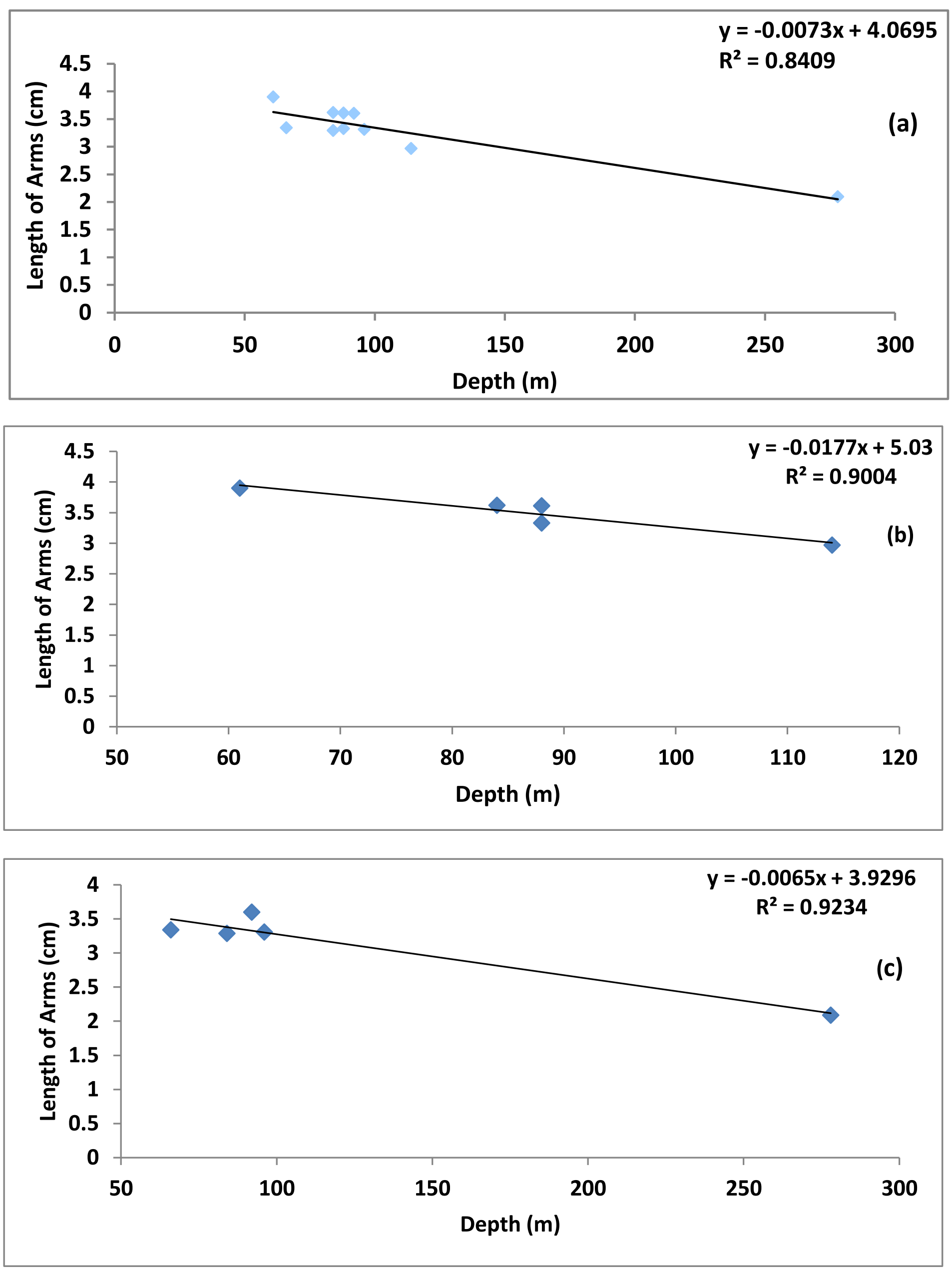


Fig. 7. (a). Mean length of *A. americanus* in relation to depth (data pooled for fall and spring); (b). Mean Length of *A. americanus* in relation to depth based on data collected in fall; (c). Mean Length of *A. americanus* in relation to depth based on data collected in spring.

36.53; P=<0.00001). ANCOVA results show a difference in slopes of the length-weight relationships of sea stars collected from GB, SNE and MAB (F = 2.843; P = 0.003), as well as in the intercepts (F = 12.470; p < 0.00001). A second model of length of sea star arms in relation to "depth" showed that both slopes and intercepts differed for the categorical variables "sample station" (slope: F = 2.59; P = 0.007; intercept: F = 1.07e+33; P < 0.00001), "regions" (slope: F = 246.9; P < 0.00001; intercept: F = 62.66; P < 0.00001) and "seasons" (slope: F = 46.36; P < 0.00001; intercept: F = 13.43; P = 0.0003).

Across the 3 regions (GB, SNE, and MAB), for a given arm length, the weight of sea stars seemed to be similar when arm length was small, but with an increase in arm length, sea stars from GB had higher weight values than those from the other two regions (Fig. 8a).

When arm length was modeled as the independent variable, and weight of sea stars the dependent variable and season in which specimens were collected the categorical factor, slopes of the ANCOVA model were not different (F = 1.8490; P = 0.17459), Fig. 8b.

4. Discussion

Four major groups: Arthropoda (46%), Annelida (21%), Mollusca (25%), and Echinodermata (4%) dominate the benthic invertebrates of the northwest Atlantic Ocean shelf in terms of numbers (Wigley and Theroux, 1981; Theroux and Wigley, 1998). By comparison, mollusks followed by crustaceans and foraminiferans were the most important dietary items found in the stomachs of *A. americanus* in this study, suggesting that, like other *Astropecten* species, *A. americanus* preferentially feeds on mollusks (Hayman, 1955; Christensen, 1970; Ribi and Jost, 1978; Franz and Worley, 1982; Wells and Lalli, 2003; De Juan et al., 2007; Brogger and Penchaszadeh, 2008). Christensen (1970) and Ribi et al. (1977) noted that crustaceans were not significant in the diet of *Astropecten irregularis* and *A. aranciacus*, respectively, but consistent with our findings, Franz and Worley (1982) reported that crustaceans were significant components of the diet of *A. americanus* in southern New England.

Gastropods were important in the diet of sea stars from SNE and MAB but rarely observed in the gut contents of sea stars from GB, whereas crustaceans were more important in sea stars from GB than in MAB and SNE. Bivalves were the second most important prey in the gut of sea stars from SNE but were surprisingly insignificant in the diet of sea stars from GB. Furthermore, the diversity of diets was lower in GB than in MAB and SNE. The relative abundance of macrobenthic invertebrates in the northwest Atlantic is related to latitude. Wigley and Theroux (1981) found that arthropods (62%) particularly amphipods, were dominant at higher latitudes (in Southern New England off southern Massachusetts and Rhode Island), but were of lesser importance in the New York-New Jersey region (42%) and in the Chesapeake Bight (21%). The reverse was the case for mollusks; their relative abundance decreased from

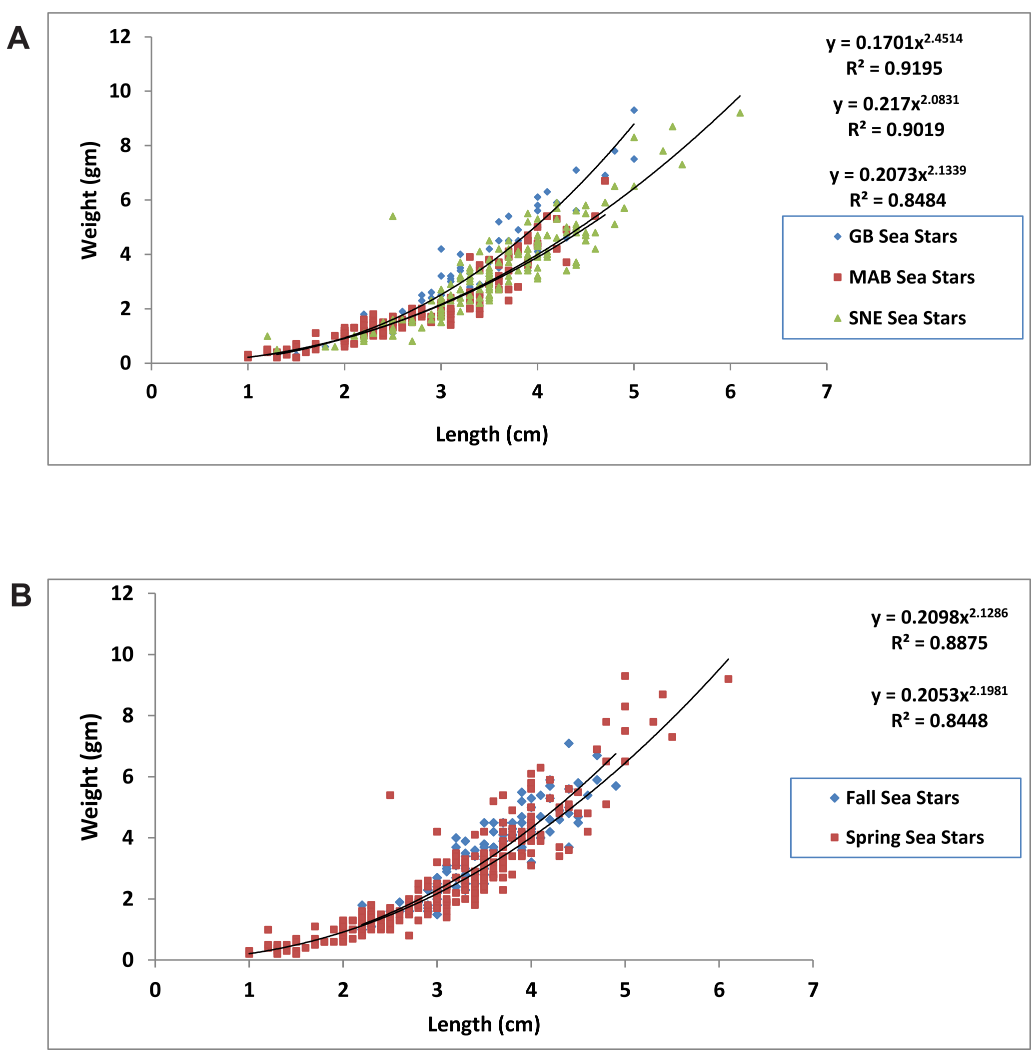


Fig. 8. a. Length-weight relationship of *A. americanus* collected from 3 regions (GB, SNE and MAB) in the Northwest Atlantic Ocean. Fig. 8b Length-weight relationship of *A. americanus* collected during spring and fall 2009 in the Northwest Atlantic Ocean.

Chesapeake Bight (57%) to New York Bight (18%) and Southern New England (10%). Thus, the spatial variations in the diet of *A. americanus* observed in this study correspond well with the relative abundance of potential prey in the environment. Although mollusks may be preferred prey for sea stars, perhaps the low density of mollusks in GB caused them to switch and feed on the much more abundant crustaceans in the area.

Gastropods were found in gut contents of sea stars from 7 out of 10 stations sampled. The three stations where no gastropods were found in the guts of sea stars are 227 and 343 in GB, and 181 in SNE. Several authors (Hayman, 1955; Ribi and Jost, 1978; Franz and Worley, 1982; Wells and Lalli, 2003; Brogger and Penchaszadeh, 2008) have suggested that sea stars consume gastropods because they are preferred prey. However, it is possible that the widespread distribution and greater gastropod availability in the bottom sediments may contribute to the occurrence of large numbers of gastropods in sea star diets. Alternatively, it may be that the hard-shells of mollusks make it harder for mollusk prey to be digested compared to soft-bodied invertebrate prey. Nevertheless, Franz and Worley (1982) noted that the ratio of gastropods to other prey in sediment samples was less than the ratio of gastropods to other prey in stomach contents, suggesting that *A. americanus* selectively prey on gastropods.

The number of prey consumed differed seasonally in this study, with more prey in stomachs of sea stars collected in fall than in spring, likely due to more active foraging with warmer temperatures. Our observations suggest a seasonal shift in the diet of *A. americanus*, with more bivalves and crustaceans consumed in the spring and more gastropods in the fall. This is consistent with results obtained by Franz and Worley (1982), who noted that the proportion of the bivalve *Arctica islandica* consumed by *A. americanus* declined from spring to fall; but whereas the proportion of crustaceans consumed increased from spring to fall in his work we found in our own study that more crustaceans were consumed in the spring than in the fall season.

The mean length of *A. americanus* decreased with depth in this study. The majority of the scientific literature on this subject has reported a decrease in animal body size with depth, but some authors have indicated that this pattern is not universal. Thurston (1979) reported a decrease in body-size with depth in lysianassid amphipods. Rex and Etter (1998) reported miniaturization with depth in their study on bathyal gastropods. Olabarria and Thurston (2003) also provide further evidence of decreasing body-size with depth (179–2245 m) in the gastropod *Troschelia berniciensi.* In contrast to the above studies, Pollini et al. (1979) reported no relationship between body size and depth (200–5000 m) for echinoderms, decapods and other macrofauna, although they noted that vertebrates such as fishes were bigger with depth.

Mechanistic models such as Thiel's (1975, 1979) size-structure hypothesis and Sebens (1982) optimality theory suggest decreasing body size with depth, but also permit selective environmental pressures to modify body size in ways that do not necessarily conform to model predictions. Physical (temperature and hydrostatic pressure, current/upwelling etc.), chemical (e.g., nutrient availability) and biological (predation, genetic variation, prey availability, competition etc.) factors vary across bathymetric gradients and may differentially impact growth and body-size among different oceanic taxa. Hence, several hypotheses have been postulated to explain the variation in body-size along a bathymetric gradient, including light intensity (Gilbert, 1991), oxygen concentration (Chapelle and Peck, 1999), food availability and local perturbations (Linse et al., 2006), ontogenetic migration (Stefanescu et al., 1992), and temperature, size-selective mortality, competition and depth (Olabarria and Thurston, 2003).

The most likely explanations for the reduction in average size of *A. americanus* with depth in this study are: (1) the relatively higher abundance at deeper than shallower stations (Hart, 2006), and (2) the decrease in the densities and biomasses of macrobenthic invertebrate prey from the inshore to offshore areas along a bathymetric gradient of the continental shelf (Wigley and Theroux, 1981; Theroux and Wigley, 1998). Both factors would be expected to decrease feeding and growth rates, leading to smaller mean sizes. In fact, Hart (2006) observed that *A. americanus* exhibited density-dependent growth such that at relative densities of more than 5000 per tow, the mean weight of the sea stars decreased with abundance.

Density-dependent growth has been reported in other echinoderm species. For *Astropecten brasiliensis,* an inverse relationship between body size and population density was observed such that body size was smaller and density higher at a shallower (30 m) than at deeper (45 m) depths (Ventura and Fernandes, 1995). Mean size of the brittle star (*Ophiura sarsii*) off the coast of Japan increased with depth (200–600 m), apparently related to the density of the brittle stars (Fujita and Ohta, 1990). This negative relationship between size and density of *Ophiura* sp. was interpreted to be due to intraspecific factors that might have occurred as a result of limitation in food and/or space.

Astropecten americanus samples collected at higher latitudes (Georges Bank) weighed more at larger sizes (lengths) > 2.7 cm than those from more southern areas (SNE and MAB). The latitudinal gradient in the densities of macrobenthic invertebrates in the area might have contributed to the observed pattern. Macrobenthic invertebrate densities were relatively low on the continental shelf off Delaware-Virginia-North Carolina, intermediate in the New York-New Jersey region and relatively high in the region off southern Massachusetts and Rhode Island (Wigley and Theroux, 1981; Theroux and Wigley, 1998). A latitudinal variation in body size has been reported in some taxa such that mean size increases with latitude (e.g. Olabarria and Thurston, 2003). Alternatively, the observed pattern may reflect density dependent growth; the density of *A. americanus* tends to decline with increasing latitude (Franz et al., 1981; Hart, 2006). The mean size of sea stars collected in spring season was smaller than the sea stars collected during fall season. This might have been related to the timing of their spawning and juvenile recruitment to the adult stage in addition to the seasonal changes in their migration in relation to temperature.

CRediT authorship contribution statement

Tunde Adebola: Data curation, Conceptualization, Formal analysis, Investigation, Validation, Visualization, Writing – original draft, Methodology. **Deborah Hart:** Investigation, Conceptualization, Writing – review & editing, Supervision. **Paulinus Chigbu:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Supervision, Visualization, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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