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POSSIBLE DEMOGRAPHIC CONSEQUENCES OF INTRASPECIFIC SHELTER COMPETITION AMONG AMERICAN LOBSTERS

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ABSTRACT

Pioneering work by J. Stan Cobb described how habitat architecture and body size scaling affect shelter-related behavior of American lobsters. Subsequent research suggested that shelter availability and competition could set local carrying capacity and demographics for this species. To determine how shelter spacing affects population density, the intensity of intraspecific competition and the distribution of body size for this species, I deployed sets of 10 identically sized artificial shelters spaced at distances of 2.5, 0.5, 1.0, 1.5 and 2.0 meters on otherwise featureless substrate at 10 m depth in mid-coast Maine, U.S.A. Five sets had two parallel strings of five opposing shelters and an additional linear string set 2 m apart without opposing shelters was the most widely separated treatment. Shelters spaced 1 m apart and closer had higher lobster population densities, more intraspecific competition and higher proportions of empty shelters. Surprisingly, lobsters there were also significantly smaller, declining from 62.7 mm to 50.8 on the carapace (CL) for 2 m linear to 0.25 m spaced shelters, respectively. Nearly all 932 lobsters measured in this study were juvenile (< 90 mm CL) and preharvestable (<83 mm CL) sized, so mate selection and fishing effects were unlikely. At the scale of the experiment, larger lobsters leave or avoid areas of high lobster population density and intense competition for areas of low population density and relaxed competition (called "demographic diffusion"). Scuba surveys in coastal zones found lobster population densities scale with shelter densities and were highest in boulder habitat where, like the experiment, more than half the shelters were vacant. Fisheries independent scuba and trawl surveys in Maine's shallow coastal zone repeatedly recorded declines of preharvestable lobsters larger than 60 mm CL in size and increases of those sizes offshore and in deep water. It is possible that this demographic diffusion is driven by behaviors associated with intraspecific shelter competition.

INTRODUCTION

> *"Not only is [the American lobster] found almost exclusively in areas where shelter is readily available, but there are a number of relatively complex behavior patterns associated with the choice . . . of a shelter."*
> Cobb 1971: 114

> *"Given the size range over which lobsters grow (up to 4 to 5 orders of magnitude in body mass) and their aggressive nature, it is possible crowding becomes important with greater size."*
> Cobb and Wahle 1994: 19

Carrying capacity is usually defined as the population that the resources of a habitat can support (Ricklefs, 1990). Pioneering work by J. S. Cobb (1971) described the American lobster's (*Homarus americanus* H. Milne Edwards, 1837) strong association with shelters and how habitat architecture, body size and shelter-related competitive behavior affect the carrying capacity of their environment. While many studies have shown that size and shape of habitable space affects the distribution, abundance and body size of marine species such as stomatopods (Steger, 1987), amphipods (Hacker and Steneck, 1990) and American lobsters (Wahle and Steneck, 1991), few have considered how behaviors associated with intraspecific competition could influence those patterns. Since lobsters seek and fight over shelters (O'Neill and Cobb, 1979), intraspecific competitive pressures should be most intense where population densities are high and shelter resources are limiting. Coastal Maine, USA, may be such a region.

Coastal Maine's shallow rocky habitats have the highest reported population density of lobsters (Butler et al., 2006). There, lobster population densities average over one per m^2 in boulder field habitats distributed over 200 km along Maine's southwestern outer coastal zone (Steneck and Wilson, 2001). The high population densities are driven by high rates of larval settlement (Cobb and Wahle, 1994; Palma et al., 1999; Steneck and Wilson, 2001; Wahle et al., 2004). As lobsters grow, they become less vulnerable to predators (Wahle, 1992, 2003), they begin active nocturnal foraging outside of their shelters (Cobb and Wahle, 1994; Cobb, 1995) and larger shelters become increasingly scarce (Caddy, 1986). Although lobster's nocturnal foraging and diurnal shelter-seeking behaviors are probably the result of evolving under conditions of high predator risk (Cobb, 1971, 1977), today large predators are functionally absent from coastal Maine (Witman and Sebens, 1992; Steneck, 1997; Steneck et al., 2004). This probably contributes to the low post-settlement mortality reported for this species (Wahle, 1992, 2003; Wahle and Steneck, 1992; Steneck, 1997; Palma et al., 1998) and ultimately results in its extremely high population densities (Butler et al., 2006).

Since shelter cohabitation is rare among American lobsters (Cobb, 1971; O'Neill and Cobb, 1979), the density and availability of shelters could limit local carrying capacity (Atema and Cobb, 1980) and population densities of larger preharvestable lobsters, (<83 mm carapace length or "CL") or even larger reproductive size lobsters (≥90 mm CL) for coastal Maine, Fogarty, 1995. If, mortality rates are low for competitively-displaced juvenile lobsters in habitats devoid of large predators then overall abundance may not be affected, they will only be redistributed (Cobb and Wahle, 1994; Butler et al., in 2006).

Shelter abundance and spatial distribution probably affects the size, population density and ultimately the local carrying capacity of larger lobsters. Because shelter-size specifically limits the maximum size of its occupants (Cobb, 1971, 1977), the density of larger shelters may well be most limiting to larger lobsters (Cobb, 1971, 1995; Caddy, 1986). Laboratory studies on shelter competition among American lobsters found that intraspecific competition was common, and that large individuals possessing both claws were competitively superior to smaller ones or those missing claws (O'Neill and Cobb, 1979). Thus, small lobsters would likely lose their shelters to large, competitively-dominant lobsters presumably displacing them to inferior habitats (Atema and Cobb, 1980). Given this, it is reasonable to expect that at high lobster population densities, intraspecific competition might result in an increased proportion of larger lobsters in shallow zones segregated from competitively subordinate lobsters.

In this paper, I ask whether intraspecific competition could be demographically important in nature. Unlike most past studies that were conducted under laboratory conditions, this research was entirely conducted in the field in coastal Maine, USA where lobster population densities are very high in shelter-rich boulder fields (Steneck and Wilson, 2001).

To examine these questions, I altered shelter densities while holding shelter size constant to determine if lobster population densities and intraspecific competition result in changes in lobster body size. I also drew from past and subsequent fisheries-independent field surveys, conducted throughout the region, of shelter density, lobster population density and body size to determine if demographic patterns seen locally in experiments reflect larger-scale patterns and thus could be regionally important.

MATERIALS AND METHODS

Local Shelter Manipulations and Occupancy

Study Site.—Shelter density manipulations were field-tested and methods perfected during the summers of 1988 to 1991 on the outer mid-coast of Maine near the Damariscotta River adjacent to Rutherford Island in an area called the Thread of Life (43.855°N, 069.551°W). Competition results reported here were for 1991 when replicate shelter arrays and the largest number of observations were recorded.

Size, Shape and Arrangement of Shelters.—Artificial lobster shelters were constructed from PVC pipes, cut longitudinally into hemicylindrical shelters. Shelter dimensions were based on Cobb's (1971) ratio for range of sizes found in the Maine study region (30-90 mm CL). Given that smaller lobsters can live in large shelters but not the reverse (Lawton and Lavalli, 1995), all shelters were 20.3 cm wide and 47.7 cm long (lobsters quickly modified the height of the shelters by excavating sediment). Each shelter was built with a back door constructed of a flap of tire inner tube rubber. Lobsters could escape through this back door but most faced out the front door most of the time (based on video and scuba observations).

Two sets of 10-shelter arrays were deployed on a featureless sediment and shell-hash substrate 10-20 m from an adjacent boulder and ledge habitat (Fig. 1). Each array set contained six sets of 10 artificial PVC shelters and each was deployed with a five-meter gap between adjacent arrays. Five of the arrays had two sets of five opposing shelters spaced so that adjacent and opposing front doors were 0.25, 0.5, 1.0, 1.5 and 2.0 m apart. The sixth array consisted of a linear set of 10 shelters set 2 m apart but without opposing shelters so lobsters occupying shelters were not facing other sheltered lobsters. Two sets of arrays were monitored a total of 23 times on 13 days between 28 June and 5 August 1991. The six shelter spacing treatments for each set of arrays was placed in random order (using a random number table) and checked once per observation day by scuba divers. Arrays were never surveyed on consecutive days. Incomplete shelter surveys, when not all array spacings were checked, were omitted from analysis and graphical representation. No diving was allowed in the region 12 hours prior to examining the shelters. All lobsters in the shelters were recorded for size (mm CL), sex, and number of claws.

Multivariate general linear hypothesis (MGLH) analysis was used for ANOVA and multivariate MANOVA statistical analyses. Assumptions of independence, homogeneity of variance and normality were examined and square root transformation was required for population density and body size data (Sokal and Rohlf, 1995). All proportion data were arcsine transformed prior to analysis. Bonferroni multiple comparison (Sokal and Rohlf, 1995) was used to determine significant differences among shelter spacing treatments at $P \leq 0.05$ level. Other statistical analyses are described where appropriate in the text.

Observing Lobster Behavior.—To observe lobster shelter and competitive behaviors with a minimum of human disturbance, I used a *Phantom 300* (Deep Ocean Engineering) remotely operated vehicle (ROV) and an ultra low light ultra high resolution Osprey Silicon Intensified Target (SIT) camera. The ROV and SIT cameras were operated from a houseboat moored over the site that had an AC electricity generator to power video cameras and recording devices. Video recorders set to long-play mode required changing videotapes every six hours. Continuous recordings began at first light and ran for eight hours each day. Clear water and continuous recordings allowed individual lobsters to be followed from prior to sunrise to after sunset. Lobster size and conspicuous features such as attached barnacles facilitated identification and observations of individual lobsters during the day.

Regional Surveys of Shelter Use

To quantify the relationship between shelter densities and lobster population densities, quantitative surveys of lobsters and their shelters were conducted in 1989 at 10 m depths in five regions in coastal Gulf of Maine with each region subsampled at four to six sites separated by at least one km. The regions were Nahant, Massachusetts (6 sites), York, Maine (6 sites), Pemaquid, Maine (4 sites), Mt. Desert Island, Maine (4 sites) and Jonesport, Maine, near the Canadian border (4 sites) (see Steneck and Wilson, 2001 for all study sites, sample sizes and demographic sampling methods).

At each site, at least 40 one-m^2 quadrats were placed haphazardly for depth-specific stratified sampling of boulder, ledge and sediment substrates (120 quadrats per site). Previous published research found that the minimum sufficient sample size per substrate to quantify lobster populations was 20 substrate-specific quadrats per site so our average number of quadrats was twice the necessary minimum (Steneck and Wilson, 2001). Each quadrat was first visually inspected for all conspicuous lobsters which were captured and measured to the nearest mm when found. Then a shelter-measuring tool was inserted in all crevices or potential shelters $\geq$ 2 cm in diameter. The tool measured shelter depth and width at the midpoint of the shelter's depth to the nearest cm. Following that, all boulders that could be moved were removed to capture the remaining adolescent or reproductive phase lobsters per quadrat ($\geq$ 40 mm CL, detailed methods in Steneck and Wilson, 2001).

Lobster size-frequency distributions in boulder habitat were quantified every year between 1985 and 1999 (Steneck and Wilson, 2001) but the most representative "snap-shot" was in June of 1987 for the Pemaquid region of Lincoln County, Maine from six sites separated by at least 1 km (n = 805 lobsters). The size frequency pattern that year was similar to those found other years but with lower sample sizes per region.

Fishery-independent trawl surveys were used to compare lobster size-frequency distributions below safe depths for scuba diving (data from Maine's Department of Marine Resources, Sherman et al., 2003 and from Chen et al., 2006, all trawl locations for each year are posted at: http://www.maine.gov/dmr/rm/trawl). Trawl data were used to compare lobster size structure in Maine's inshore water (within 5.6 km or 3 nautical miles from the nearest shore) with that found beyond that distance from shore throughout the Gulf of Maine. Maine inshore trawl data for 2001 were used to compare size structure of lobsters at similar distances from shore but stratified by depth.

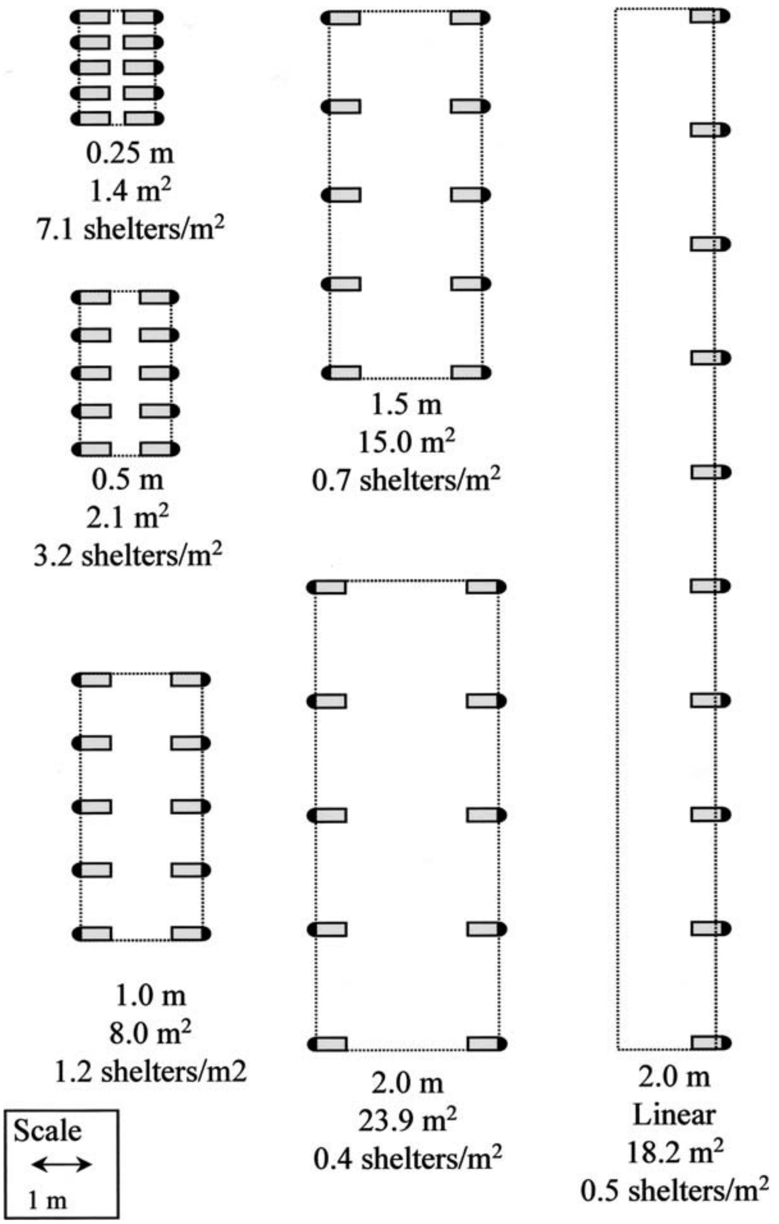

Fig. 1. Diagrammatic representation of the spacing for the six sets of 10 artificial shelters. Small shaded rectangles represent the 20.3 × 47.7 cm shelters made from hemicylindrical PVC pipe. The black circle at the distant edge of the shelter represents the rubber-flap back door attached to each shelter. Adjacent and opposing shelters were spaced as 0.25, 0.5, 1.0, 1.5, and 2.0 m blocks and one set of shelters set at 2.0 m in a linear format without opposing shelters. For each shelter spacing treatment, the relative "footprint" is illustrated by the dotted line rectangle surrounding each array. The footprint size and the shelter density within the perimeter rectangle are listed below each shelter spacing treatment. In the field, experiments were set at randomly assigned order in a linear pattern with at least 5 meters between adjacent sets of different shelter spacing.

RESULTS

Shelter Spacing and Density Manipulations

There were no significant differences between the two sets of shelter arrays (Table 1), so their results were pooled to simplify graphical representation. Among all shelter spacing treatments, there were no significant differences in the sex ratio (Friedman ANOVA χ^2 (N = 78, *d.f.* = 5) = 6.33, $P < 0.275$) that skewed slightly towards males with 44.1% of the 932 lobsters recorded being female. Specifically, the percent female was 44.8, 37.0, 41.2, 47.6, 47.6, 46.7 for shelter spacing of 0.25, 0.5, 1.0, 1.5, 2.0 and 2.0 linear, respectively (see Fig. 1). The percent of lobsters recorded in the experiment having two claws averaged 84.3% with the only significant difference occurring between lobsters in shelters spaced 1.0 m apart (78.5% two clawed) and those in shelters spaced 0.25 m apart (83.9% two clawed) (Friedman ANOVA $\chi^2 = 23.69$, $P < 0.00025$; N = 87, *d.f.* = 5). Thus, the sequence of lobsters having two claws varied but without trend relative to shelter spacing (83.9, 80.9, 78.5, 87.4, 83.5 and 83.8 percent two clawed for the closest to farthest spacings) and had no differences between any of the other shelter spacings (sign test $P > 0.05$).

With decreasing shelter spacing and thus increasing shelter density (Fig. 2), lobster population density increased (Fig. 2a, $F_{1,5} = 77.04$, $P < 0.01$) but shelter occupancy declined (Fig. 2b, $F_{1,5} = 21.57$, $P < 0.01$) (Table 1). About 80% of shelters spaced 1.5 m or more apart were occupied with lobsters, however, at closer spacings occupancy dropped by half to below 40% at 0.25 m spacings (Fig. 2b).

To determine why more shelters were vacant when densely spaced (Fig. 2b), video recordings were made of densely and distantly spaced shelters (0.5 and 2.0 m spacing, respectively) during morning hours when lobsters returned to shelters after their nocturnal foraging. The average number of lobsters seen, and the average number of lobsters entering a shelter per day for shelter spacing treatment (0.5 and 2.0 m) were not significantly different (Table 2). However, there were significantly more competitive confrontations per shelter per day in the densely spaced shelters (Table 2). Most confrontations were aggressive postures (meral spread) and lunges (see Atema and Cobb, 1980 for a description of these and other agonistic behaviors). Although the average number of lobsters seen and the rate at which they entered shelters did not change with shelter density (Table 2), the frequency of competitive confrontations increased (Table 2) and the percent of occupied shelters declined (Fig. 2b). The competitive behavior may have inhibited occupancy or have evicted lobsters from shelters. Such evictions were observed in ROV videos in other lobster-shelter experiments (discussed below).

While it is likely that intraspecific competition increases with decreasing spaces between shelters and with increasing shelter-driven population densities (Fig. 2a, b), surprisingly, the average size of the remaining lobsters was significantly smaller ($F_{1,5} = 13.10$, $P < 0.01$) and the proportion of larger lobsters was significantly lower (Fig. 2c-e). Specifically, lobsters larger than 60 mm CL steadily increased in abundance with increasing spacing among shelters (Fig. 2d, $F_{1,5} = 17.68$, $P < 0.01$). Lobsters larger than 70 mm CL were least prevalent when shelters were most closely spaced and were most abundant in the 2 m spacing without opposing shelters (Fig. 2e, $F_{1,5} = 8.63$, $P < 0.01$). The increase in average and large sized lobsters at the widest spacing without opposing shelters (Fig. 2c-e) indicates the orientation of shelters relative to each other is important to the observed patterns.

Lobsters recorded in this study averaged about 56 mm CL (14-93 mm CL range; Fig. 2f). However, the mode and distribution and abundance of body sizes shifted from small left leaning distributions at 0.25 m spacing to large right leaning distributions at 2.0 m spacing (Fig. 3). Interestingly, the small mode size for lobsters in the densest shelter spacing (~ 35 mm CL) is nearly absent for lobsters found simultaneously at the 2.0 m linear spacing.

Shelter-related behavior and associated competitive interactions observed in video tapes conformed to those of previous laboratory studies (Atema and Cobb, 1980) with one big difference. Almost all of the lobsters observed in the shelter experiments were juvenile lobsters considerably smaller than 90 mm CL, the size when 50% of females sexually mature in the study area (Fig. 2f; Fogarty, 1995). Water clarity at the study site allowed individual lobsters to be observed continuously as they entered and left shelters or interacted with other lobsters. The typical pattern observed was that lobsters would return to shelters just prior to sunrise (about 04:00 h during the summer in Maine). Usually there was a period of about two hours of low activity after lobsters settled into their shelters. Then lobsters would venture out of their shelters with their claws apart (in a meral spread) to confront lobsters. I observed lobsters moving a meter to evict lobsters. Most such encounters resulted in the smaller lobster leaving the shelter without contact. Occasionally, lobsters were observed lunging, or in one case, literally pulling a subordinate lobster to extract it from the artificial shelter (see Atema and Cobb, 1980 for more complete behavioral descriptions). Clearly, larger lobsters won most competitive battles as described from previous studies (O'Neill and Cobb, 1979). After numerous successful bouts, competitively dominant lobsters were occasionally observed in videotapes exiting the arena and walking out of the field of view.

Table 1. Two way ANOVA comparisons of A. lobster population density, B. shelter occupancy, C. average body size, D. proportion of lobsters over 60 mm CL and E. proportion of lobsters over 70 mm CL from two spatially replicated sets of six differently-spaced sets of 10 equal sized artificial shelters, i.e., Fig. 1, "Shelter Arrays". Proportions were arcsine transformed for analyses.

Source	*d.f.*	SS	MS	*F*	*P*
A. Population Density					
Shelter Array	1	0.14	0.14	0.26	0.611
Spacing	5	76.37	76.37	138.09	< 0.01
Error	135	74.66	0.55		
B. Shelter Occupancy					
Shelter Array	1	0.008	0.008	0.23	0.63
Spacing	5	1.87	1.87	54.83	< 0.01
Error	135	4.60	0.34		
C. Average Body Size					
Shelter Array	1	48.40	48.40	1.55	0.21
Spacing	5	2038.57	2038.57	65.37	< 0.01
Error	135	4210.20	31.18		
D. Proportion Over 60 mm CL					
Shelter Array	1	0.05	0.05	1.74	0.188
Spacing	5	2.24	2.24	86.06	< 0.01
Error	135	3.53	0.03		
E. Proportion Over 70 mm CL					
Shelter Array	1	0.05	0.05	4.12	0.044
Spacing	5	0.53	0.53	40.37	< 0.01
Error	135	1.78	0.013		

Patterns of Shelter Use in Nature

In field surveys at 10 m depth in five widely spaced coastal regions in the Gulf of Maine, lobster population densities scaled with shelter densities but with different slopes (Fig. 4a). At sites with the highest lobster density, habitat space should be most limiting, i.e., Nahant region of Massachusetts in 1989 (Fig. 4a). As expected, large shelters were much less abundant than small shelters (Fig. 4b; Caddy, 1986). Although lobsters larger than 60 mm CL were found in the region (Fig. 4c), unoccupied shelters were common at nearly every shelter diameter (Fig. 4b) leaving less than half (40 percent) of all shelters occupied (Fig. 4d).

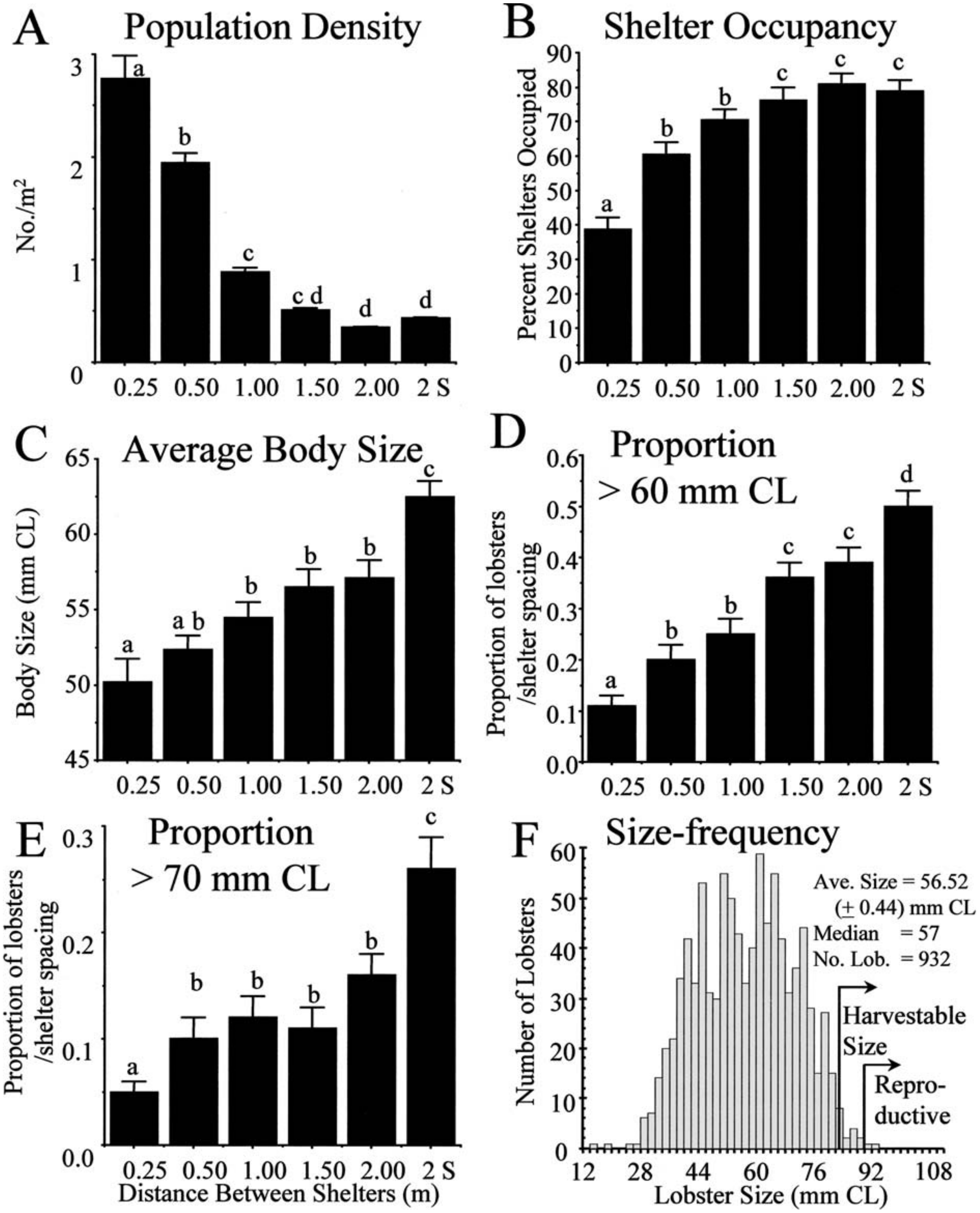

Fig. 2. Demographic responses of lobsters to variously spaced, identically sized PVC shelters. Abscissas for A-E are distance in meters between five opposing and adjacent shelters. "2S" refers to the linear string of shelters set 2 m apart without opposing shelters (Fig. 1). Bonferroni multiple comparison (Sokal and Rohlf, 1995) was used on square root transformed data to determine significant differences (indicated by lower case letter) among shelter spacing treatments at $P \leq 0.05$ level (averages of daily observations with variance expressed as + standard error). Data from two sets of arrays were analyzed individually (without significant differences; Table 1) and pooled for these figures. All shelters in all arrays were surveyed a total of 23 times. A. Population density, B. Shelter occupancy, C. Average body size, D. Proportion of lobsters > 60 mm CL, E. Proportion of lobsters > 70 mm CL, F. Size-frequency distribution of all lobsters.

Table 2. Summary results of lobster behavior in the field from video observations of 0.5 and 2.0 m spaced shelter arrays over a four-day period during which time a total of 126 lobsters were observed. Total duration of videos was 32.9 and 33.5 h, for 0.5 and 2.0 m spacings, respectively. Viewing area for both was 1.6 m^2. Averages are given and variance is one standard deviation of the mean (SD).

	Shelter spacing				
	0.5 m		2.0 m		
Event	Ave.	SD	Ave.	SD	χ^2 *P*
# Lobsters per 8 h observation period	20.0	8.8	11.3	6.1	$P > 0.05$
# Lobsters entering a shelter per day	1.9	1.4	3.8	4.0	$P > 0.05$
# Confrontations per shelter per day	0.7	0.3	0		$P < 0.05$

Population Size-frequency Distribution

Visual scuba surveys revealed relatively small lobsters dominated shallow boulder fields in coastal zones with a mode and median size around 60 mm CL and well below the minimum harvestable size (Fig. 5a). The same lobster size structure was recorded in larger-scale fisheries-independent trawl surveys conducted near shore in Maine state waters (Fig. 5b). In both cases, the smallest lobsters were undoubtedly underrepresented due to the methods used but lobsters larger than 60 mm CL should be more reliably sampled. While trawling under samples lobster population densities relative to scuba surveys, especially in rocky habitats, the body size structure of trawled lobsters 60 mm CL and larger is likely a reasonable estimate of the population at very large sample sizes, e.g., 26,196 lobsters measured in Maine's inshore trawl surveys for 2000-2002 (Fig. 5b). In fact, federal and state stock assessments use trawl surveys to determine the abundance of lobsters within one to two molts of the minimum harvestable size (83 mm CL) to determine risks of overfishing (ASMFC, 2000). Thus, the decline in abundance of preharvestable lobsters ranging in size from 60 to 83 mm CL in shallow coastal zones was evident in scuba (Fig. 5a) and inshore trawl surveys (Fig. 5b).

Using identical trawl survey conducted offshore (Fig. 5c) and inshore at depths greater than 60 m (Fig. 6) revealed increasing abundance from 60 to 83 mm CL and larger harvestable-sized lobsters. Population densities were also lower offshore and at depth (Chen et al., 2006). The offshore trawl surveys were mostly beyond Maine's state jurisdictional boundary and range from 6 to 300 km from the nearest land (Steneck, 2006). The low abundance of lobsters 83 mm CL and greater in inshore waters could result from fishing, but that is an unlikely explanation for the decline of preharvestable lobsters ranging from 60 to 83 mm CL in size (Figs. 2f, 4c, 5a, 6a). While larger harvestable lobsters may accumulate offshore due to lower fishing pressure there, that explanation is less compelling for lobsters of that size range in Maine's heavily fished inshore waters deeper than 60 m (Fig. 6b; ASMFC, 2000).

DISCUSSION

This study highlights several distinct but unexplained demographic patterns evident in populations of American lobsters in Maine. For example, the consistent decline of larger preharvestable lobster from shallow coastal zones (Figs. 4c, 5a, b, 6a) and the increase of lobster of that size in deep water coastal (Fig. 6b) and offshore sites (Fig. 5c) has not been adequately addressed. This is unlikely the result of fishing in shallow coastal zones because most lobsters there were preharvestable size lobsters and poaching of undersized lobsters is rare in Maine (Acheson and Steneck, 1997). While shelter space may limit local lobster population densities (Cobb, 1971) and larger shelters necessary for larger lobsters may be most limiting (Caddy, 1986; Cobb and Wahle, 1994), field surveys found that even in high density, large shelter-limited habitats, over half the large shelters remained unoccupied (Fig. 4d). How can shelters be both a limiting and under utilized resource? The agonistic and competitive behavior of lobsters is conspicuous and well studied, but if competition is most intense when population and shelter densities are highest as exists in coastal zones in Maine (Steneck and Wilson, 2001) then why aren't the remaining preharvestable lobsters large (O'Neill and Cobb, 1979)? Questions such as these and the larger

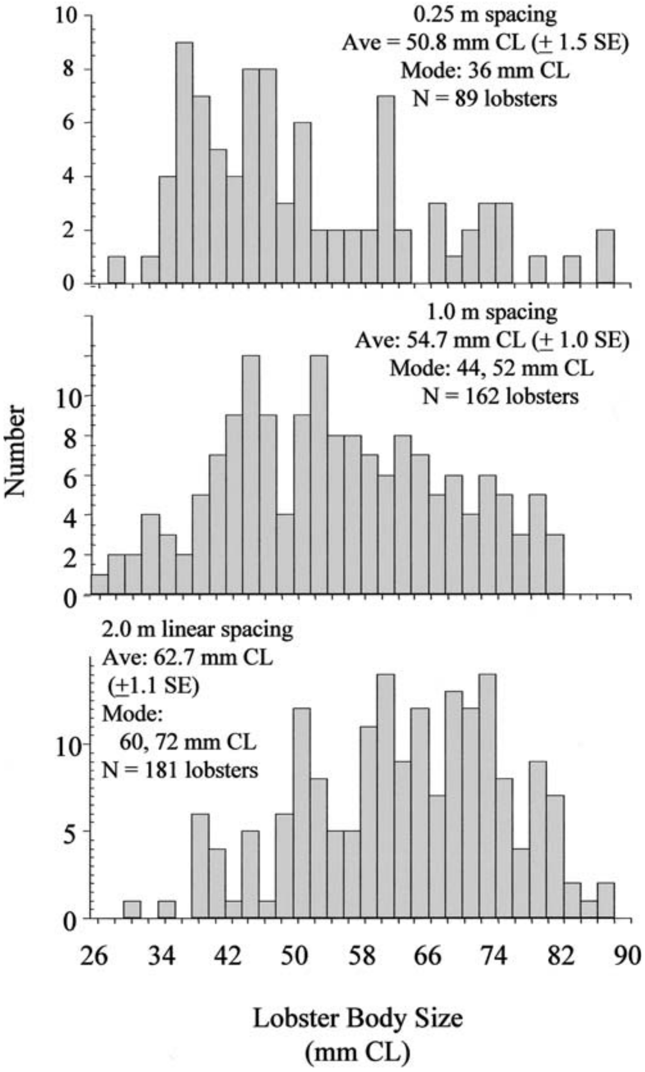

Fig. 3. Size-frequency distribution of lobster from shelter arrays set at 0.25, 1.0 and 2.0 m (linear) spacings. Average size differences are significant (See Fig. 2c).

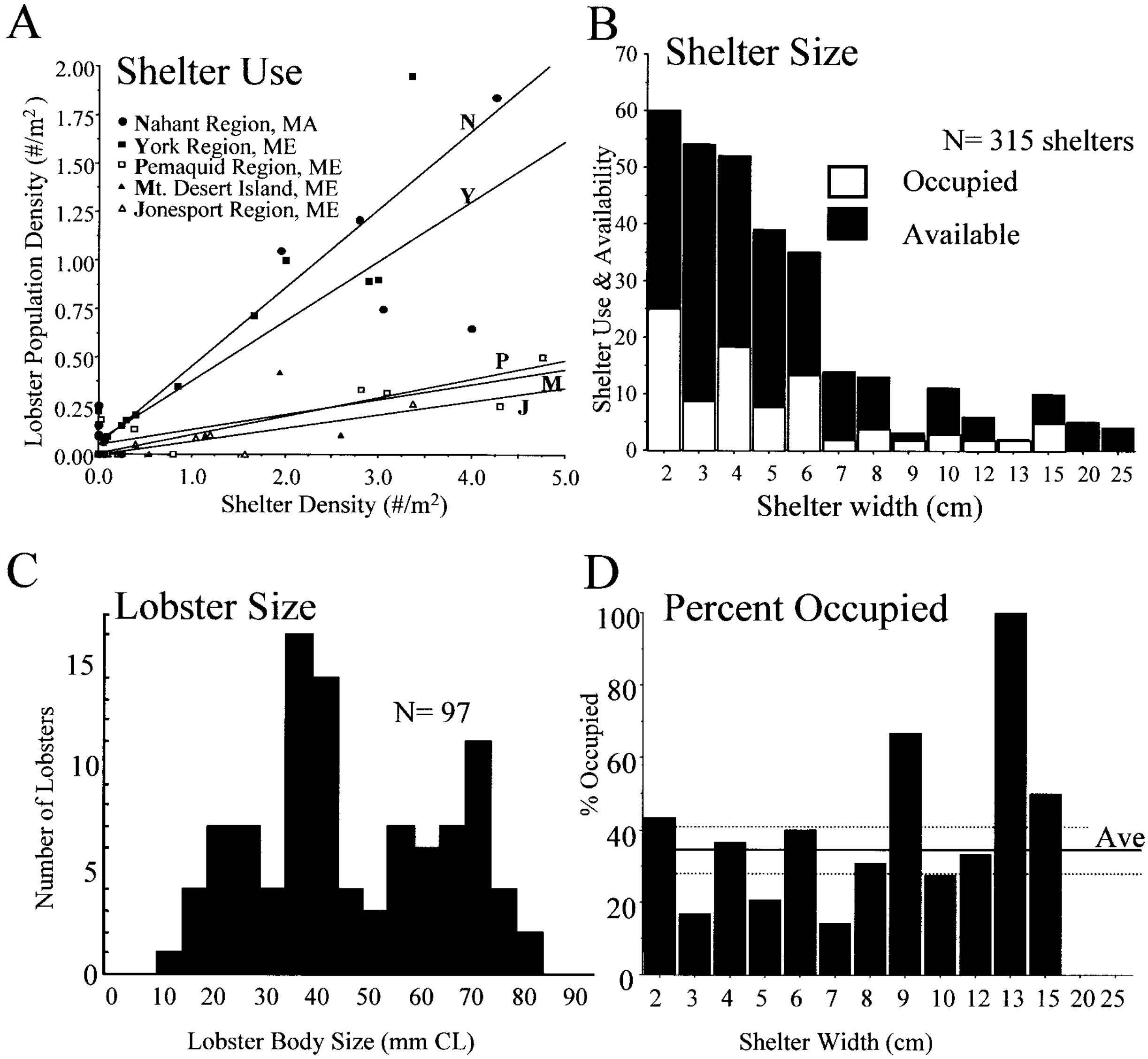

Fig. 4. Lobster population densities and shelter relationships. A. Lobster population density as a function of shelter density at five regions throughout coastal Gulf of Maine in 1989. All regressions are significant ($P \leq 0.01$) $R^2 = 0.78$, 0.86, 0.74, 0.49, 0.80 for Nahant (line with steepest slope), York, Pemaquid, Mt. Desert and Jonesport (line with shallowest slope) regions, respectively. Each regression line is signified by the 1st letter of the region. B. Shelter size-frequency distribution of occupied and unoccupied shelters C. Lobster sizes recorded. D. Percent of shelters that were occupied. All data for B-D were from six sites in the Nahant, Massachusetts region where lobster densities were greatest. Note that large shelters that are most limiting (especially for larger lobsters) are not fully occupied.

question of whether there are broader demographic consequences to intraspecific competition had not been explored and thus were the impetus for the shelter spacing experiment.

The shelter spacing experiment produced clear, but in some ways, counter-intuitive results. At uniform depths and substrate over several hundred meters, the spacing of randomly assigned sets of identical shelters influenced the body size, population density and shelter use of this species (Fig. 2). Large lobsters were significantly less abundant where shelter and population densities were high, and competition was intense (Fig. 2, Table 2). Thus, at the scale of the shelter spacing experiment, large, competitively-dominant lobsters chose to live in habitats where population densities and competitive pressures were low despite greater shelter availability in adjacent closely spaced shelters. As a result, the greatest proportion of unoccupied shelters (i.e., 60%) was found where shelters were most closely spaced (0.25 m apart; Fig. 2b).

The patterns of population density, body size and shelter use between field (Fig. 4) and experimental (Fig. 2) studies were remarkably similar. In both cases at high population densities only about 40% of the shelters were occupied and largest preharvestable lobsters were relatively rare. Other factors such as predation, fishing effects and reproduction can be ruled out because the size of lobsters most affected were either too big for most coastal predators (Wahle and Steneck, 1992; Steneck, 1997), or below the size where they would be vulnerable to fishing or sexually mature. Since lobsters forage primarily nocturnally over a range of several

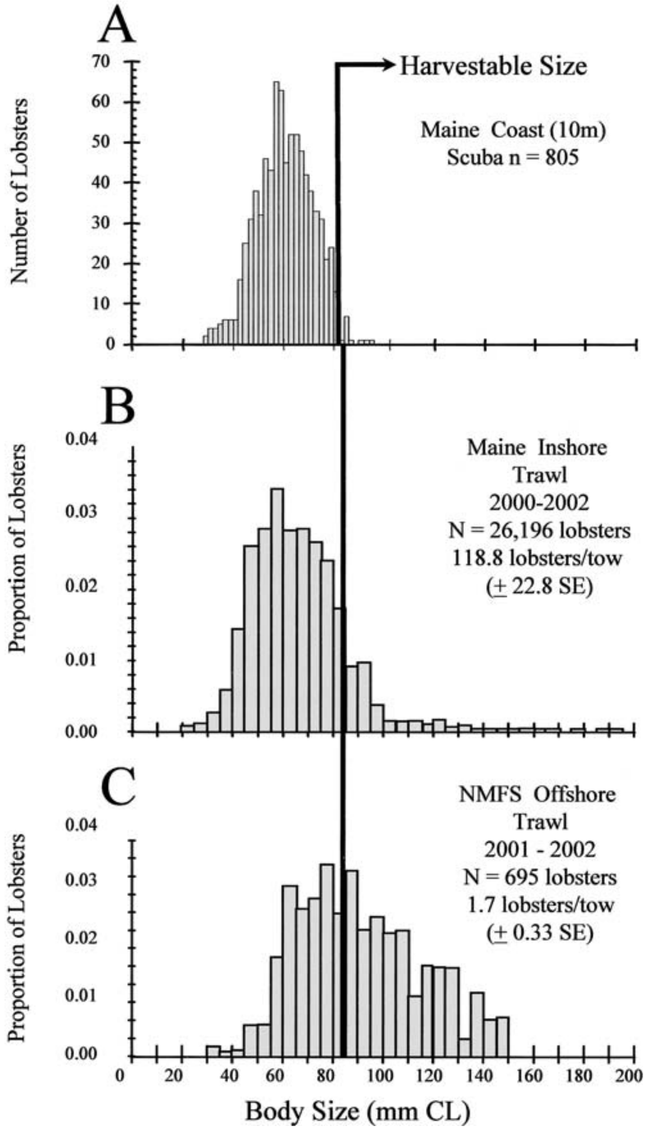

Fig. 5. Size frequency distribution of lobsters in shallow coastal boulder fields in the Pemaquid region of Maine 1987 (A) and from inshore Maine (B), and offshore US federal waters (data from National Marine Fisheries Service) (C). Trawl-survey data for 2000-2002 (from standardized tows) is from Chen et al. (2006). The heavy vertical line indicates the minimum harvestable size (81 for A and 83 mm CL for B and C).

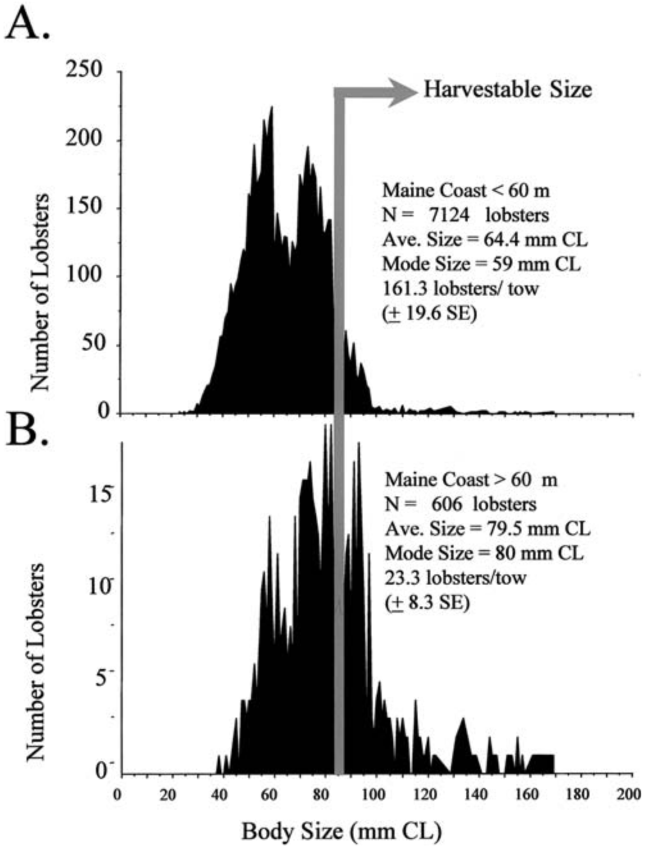

Fig. 6. Size frequency distribution of inshore lobsters (i.e. within 5.6 km of the coast) stratified by depths less than (A) and greater than (B) 60 m. Data from Autumn 2001 trawl surveys (from standardized tows described in Chen et al., 2006) (available at: http://www.maine.gov/dmr/rm/trawl).

hundred meters (Cooper and Uzmann, 1980), it is unlikely that food availability contributed to the pattern seen among these randomly placed shelter spacing experimental treatments. This leaves intraspecific competition for shelter space as the dominant ecological process for this species in shallow coastal habitats.

A Case for Competition-driven "Demographic Diffusion"

Within the shelter spacing experiment, larger lobsters choose habitats where shelter and lobster population densities (Fig. 2) and frequency of encounters with other lobsters (Table 2) were low. I call this "demographic diffusion". Demographic diffusion occurs when an identifiable segment of the population moves from habitats of high population density to habitats of low population density. The phrase connotes the typical chemical properties of diffusion in which compounds move from a region of high, to a region of low concentration. In this case, large American lobsters segregate from smaller individuals living at high population densities under relatively intense intraspecific competition for space.

Intraspecific competition prevented lobsters from occupying every shelter—especially at high lobster population densities (Fig. 2a, b, Table 2, O'Neill and Cobb, 1979). This was also evident in field data showing that population densities scaled with shelter availability (Fig. 4a) but fewer than half the shelters were occupied in shelter-rich boulder habitats (Fig. 4d). It is unclear when large preharvestable lobsters exit the shelter dense coastal zones. During the shelter experiments, competitively successful large lobsters were observed leaving shelter arrays in video monitored treatments. Whether the observed departures represented demographic diffusion is not known but the end result of smaller body size and lower proportion of large lobsters at high population densities (Figs. 2, 3) is consistent with that interpretation.

A simple behavioral energetic model involving the costs and benefits of aggression could explain demographic diffusion among American lobsters. This model suggests that costs of aggression increase linearly, whereas the benefits level off once the essential resource is acquired (Huntingford and Turner, 1987). In this case, the American lobster would benefit from the cost of obtaining a single shelter because that would serve as a refuge from predators and a safe location in which to molt (Cobb, 1971; Cobb and Tamm, 1975; Cobb et al., 1982). However, American lobsters often continue their aggression against all other lobsters within their range of detection (Atema and Cobb, 1980), as I have observed in videos, and probably result in the high shelter vacancy under high population densities (Figs. 2b, 4b, d). Thus, considerably more energy may be spent competing under high population densities than is gained in shelter-related benefits.

In regions where high rates of post-larval settlement result in high lobster population densities (Wahle and Incze, 1997; Palma et al., 1999; Steneck and Wilson, 2001), larger lobsters faced with constant battles with myriad smaller lobsters, may choose to leave regions of high population densities to regions of lower population densities resulting in the segregation of large lobsters due to "demographic diffusion". Aggression is energetically costly and except for mating, there is no evidence that dominant lobsters can turn off their agonism against the subordinate lobsters they detect (Atema and Cobb, 1980). This is likely why lobsters of this species rarely cohabitate shelters as is commonly in spiny lobsters (Butler et al., 2006) and why empty shelters are common at high population densities. As lobsters grow, their range of detection increases (Atema, 1986). Therefore, remaining in shallow, heavily lobster-populated coastal zones may be maladaptive for larger preharvestable lobsters due to the higher costs of aggression there without associated benefits. In this light, demographic diffusion may be an adaptive solution for larger lobsters living in lobster-rich coastal zones.

We do not know the scale at which demographic diffusion operates. However, the large-scale, near-shore, dominance of small lobsters in shallow coastal zones (Figs. 5 and 6) is consistent with demographic diffusion if larger sexually immature preharvestable lobsters move to offshore or near-shore deepwater habitats where population densities are lower (Figs. 5c, 6b; Chen et al., 2006). It also serves as a plausible explanation for why large competitively dominant preharvestable lobsters (70-80 mm CL) do not displace competitively inferior (Cobb, 1971; O'Neill and Cobb, 1979) smaller size classes from habitats having high population densities (Fig. 2). That is, if competitively dominant preharvestable lobsters displace smaller lobsters then size-frequency distributions would be right-skewed with a mode just below harvestable size of 83 mm CL and an abrupt decline at larger sizes presumably due to demographic effects of harvesting. Instead, most size frequency distributions show declines of preharvestable lobsters from 60 mm to 83 mm CL in size (Fig. 5a, b). This was also shown for near-shore trap-caught lobsters in 1972 and 1973 (Krouse and Thomas, 1975; using ventless traps) and has been observed repeatedly using fisheries independent sampling methods in the Gulf of Maine's coastal habitats for nearly 20 years, e.g., 1987 Fig. 5a; 1988, Steneck (1989); 1989, Fig. 4c; 1991 Fig. 2f, 2001, Fig. 6.

The preharvestable decline of larger lobsters in shallow near-shore habitats is matched by increases in larger lobsters in near-shore deepwater and offshore sites (Figs. 5c, 6) in Maine state and U.S. federal waters. A well-known segregation between juvenile and adult lobsters also occurs around Canada's Grand Manan Island in the mouth of the Bay of Fundy. There, a large migratory population of large reproductive lobsters move into shallow zones in northern bays of Grand Manan that are otherwise devoid juvenile lobsters (Campbell and Pezzack, 1986). In the southern portion of that island, lobster population densities are high and the size structure is small (mostly juvenile lobsters). Other places dominated exclusively by large reproductive lobsters are well offshore from the coastal Gulf of Maine on Georges and Browns Banks (Skud and Perkins, 1969; Campbell and Pezzack, 1986; Butler et al., 2006). Although this demographic segregation has been known for a long time, no theories have been advanced explaining what may have caused them. Large lobsters were thought to have accumulated in the absence of fishing but at several of these sites few if any juvenile lobsters had been found. How could populations of primarily very large lobsters (mode size 120 mm CL on Corsair Canyon; Skud and Perkins, 1969; reviewed in Butler et al., 2006) persist if they had not migrated from shallow nursery habitats?

The hypothesis that intraspecific competition may contribute to ontogenetic habitat segregation requires further examination. However, several alternative hypotheses such as predation, the effects of harvesting and long-distance movements related to reproduction are unlikely. This is because predation rates on tethered lobsters over 60 mm CL in coastal Maine were virtually zero (Steneck, 1997; Butler et al., 2006). Also, lobsters between 60 and 80 mm CL are well below the minimum harvesting size and the median reproductive size (83 and 90 mm CL, respectively). Although lobster's seasonal range of movement increases with body size (Butler et al., 2006), no alternative explanations have been proposed to explain why larger preharvestable lobsters do not remain in shallow coastal zone habitats where food and warmer summer water temperatures are more favorable.

With distance offshore, the area extent of shelter-rich boulder fields declines. Nevertheless, lobster populations find and congregate in discrete shelter-rich habitat patches (Steneck, personal observation from submersible studies). Within such patches, relatively intense local competition could contribute to demographic diffusion even in areas of regionally low lobster population densities. If so, demographic diffusion could be a weak but relatively constant force shaping larger scale patterns of distribution, abundance and body size of lobsters.

Finally, the ultimate evolutionary explanation for demographic diffusion may prove to be even more elusive. If lobsters evolved in a world with large predators (Steneck et al., 2002, 2004), would not demographic diffusion have resulted in higher mortality rates and thus have been maladaptive? Possibly, but it is likely that only under the relatively recent conditions of low or functionally absent predation (Steneck et al., 2004), that lobster population densities have become so great (as they have in Maine;

Steneck and Wilson, 2001) that shelter space, competition and demographic diffusion are important. Also, larger lobsters have probably always been relatively immune to predation (Wahle, 2003).

Management Considerations

There are some potential management implications to demographic segregation resulting from demographic diffusion. If settlement drives near shore, coastal demography (Wahle and Incze, 1997; Palma et al., 1999), then strong benthic recruitment years or periods, may result in significant increases in coastal population densities and possibly drive larger lobsters to offshore habitats. This has apparently happened. Beginning in the 1980s, the population density of juvenile early benthic phase lobsters increased throughout coastal Maine (Wahle et al., 2004; Steneck, 2006) and Canada (Lawton, personal communciation). Then, in the 1990s, large reproductive-phase lobster abundances began increasing offshore throughout the Gulf of Maine (Jacobson, 2001). Between 1990 and 2000 large, reproductive phase lobsters doubled in abundance from what they had been in the 1980s (Steneck, 2006).

If demographic diffusion results in larger lobsters migrating offshore, and if fishing pressure there is less than that it is in coastal zones (ASMFC, 2000), a reduction in overall fishing mortality rates could result. Thus, demographic diffusion could effectively contribute to the protection of reproductive phase lobsters and the resilience of this species. This may help explain why *H. americanus* has withstood over 150 years of targeted fishing pressure but remains today a vibrant fishing industry.

If periodic waves of large lobsters offshore result from periods of high larval/postlarval recruitment to shallow coastal zones (Wahle et al., 2004), then it follows that absent high recruitment, larger lobsters may remain in coastal zones where they are most vulnerable to fishing pressure. Thus, it may make sense to preserve large lobsters offshore by setting a maximum size over which they cannot be harvested just as exists today in Maine. This way, periodic waves of large lobsters would be protected for their future reproductive contribution should current juvenile densities decline.

Conclusions

Although it is well known that lobsters compete for shelters, the larger demographic consequences of competition are not yet fully understood. As Cobb (1971) pointed out, lobster behaviors are complex and in nature they may differ considerably from those observed under laboratory settings. This will be particularly evident if competitively mediated demographic diffusion, evident at the scale of the shelter spacing experiment, functions at the scale of kilometers to segregate larger lobsters from smaller juvenile populations.

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