Abstract.–Seasonal distributions and relative abundances of the Atlantic rock crab *Cancer irroratus*, Jonah crab *C. borealis*, northern lady crab *Ovalipes ocellatus*, and coarsehand lady crab *O. stephensoni* were determined from fish trawl and clam dredge surveys on the continental shelf from Nova Scotia to Cape Hatteras, North Carolina during 1978–87. Rock crabs have the broadest distribution, which includes coastal waters of the Gulf of Maine and depths of 6–456m from Georges Bank to Cape Hatteras. Jonah crabs are more widely distributed in the Gulf of Maine and on Georges Bank than rock crabs. They occur most frequently in the northern and offshore zones of the middle Atlantic from south of Georges Bank to off Delaware, at depths to over 400m. Northern lady crabs occur primarily in the inner strata of the middle-Atlantic shelf in depths <27m, and on shallower portions of Georges Bank. Coarsehand lady crabs occur from southern New Jersey to Cape Hatteras, to over 200m. *Cancer* spp. occur mainly at 3–18°C, while *Ovalipes* spp. occur mainly at 11–24°C. Sex ratios in rock and Jonah crab catches deviated from 1:1 by season and gear; males dominate in spring trawl surveys, females in summer dredge and fall trawl surveys. Trawl catches of all species were significantly larger at night or twilight than during the day, suggesting more nocturnal activity. Temperature, depth, and their interaction significantly affected the catches of these crabs.

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Distribution and Abundance of Four Brachyuran Crabs on the Northwest Atlantic Shelf

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The most common species of brachyuran crabs on the northwest Atlantic continental shelf are the Atlantic rock crab *Cancer irroratus* (subsequently referred to as rock crab), Jonah crab *C. borealis*, northern lady crab *Ovalipes ocellatus*, and coarsehand lady crab *O. stephensoni*. Knowledge of their distributions is incomplete, largely because previous surveys were geographically limited, survey stations were sparse, or surveys were conducted in one season only (Musick and McEachran 1972; Shotton 1973; Haefner 1976, 1977, 1985; Williams and Wigley 1977; Bigford 1979; Williams 1984). No documented information was available on interannual fluctuations in abundance for any of the crabs.

This study was undertaken to investigate shelf-wide seasonal distributions and abundance fluctuations of the four crab species over a ten-year period. Our goals also included providing information about sediments on which the crabs occur, depth ranges, water temperature preferences, size frequencies, sex ratios, and diel catches.

Methods

Data were obtained from groundfish trawl and clam dredge surveys conducted by the Northeast Fisheries Center (NEFSC), National Marine Fisheries Service, over the continental shelf from the northern Gulf of Maine to Cape Hatteras, for the ten-year period 1978 through 1987. The data set consisted of 11,211 stations: 8776 trawls and 2435 dredges. Station locations were selected using a stratified-random design based primarily on depth (Grosslein and Azarovitz 1982, Murawski and Serchuk 1989). Density of trawl stations was 1/500 km^2 for inshore strata (depth <27m) and 1/1000 km^2 for offshore strata (depth ≥27m). Clam dredge stations were spaced at 1/460 km^2.

The area covered by trawl surveys in late February–May, designated as spring, and September–November, designated as fall, included the shelf and its upper slope between Nova Scotia and Cape Hatteras. Tow depths in spring and fall were 6–456 m. Trawl surveys in January–February, designated as winter, and July–August, designated as summer, were limited to depths of 6–203m. Spring and fall trawl surveys were conducted in each of the ten years, winter trawl surveys in 1978 and 1981, and summer trawl surveys from 1978 through 1981. Clam dredge surveys were conducted during winter in December, January, and February (1978–80) and summer in July and August (1978–86) from Georges Bank to Cape Hatteras at depths of 9–110m (Table 1). Bottom water temperatures were taken at all stations.

In our analysis, the shelf was divided into Gulf of Maine, Georges Bank, and middle-Atlantic subareas (Fig. 1).

Table 1
Groundfish trawl and clam dredge surveys by the NMFS Northeast Fisheries Science Center from Nova Scotia to Cape Hatteras, used in this study. Number of stations (offshore/inshore) used for analysis, and total number of crabs collected, by species, corrected for net or dredge size.

	Trawl				Dredge	
Year	Winter	Spring	Summer	Fall	Winter	Summer
1978	0/[a]78	[a]317/[a]72	168/105	435/77	[b]233/[b]71 [b]75/[b]47	
1979		[a]348/[a]89	145/102	429/89	97/36	
1980		[a]305/[a]100	162/103	270/89	142/62	148/47
1981	86/0	[a]240/[a]90	104/60	255/89		
1982		247/91		285/91		230/69
1983		275/93		308/92		268/128
1984		260/93		341/92		338/110
1985		254/93		266/102		
1986		256/93		262/88		256/78
1987		261/77		236/86		
Total	86/78	2790/891	579/370	3087/895	547/216	1240/432
Rock	340	22916	626	3038	2129	2343
Jonah	8	876	223	883	68	242
Northern lady	0	110	571	3653	1087	936
Coarsehand lady	0	10	47	204	66	185

[a]#41 trawl used; other cruises used #36 trawl.
[b]1.22 m dredge used; other cruises used 1.52 m dredge.

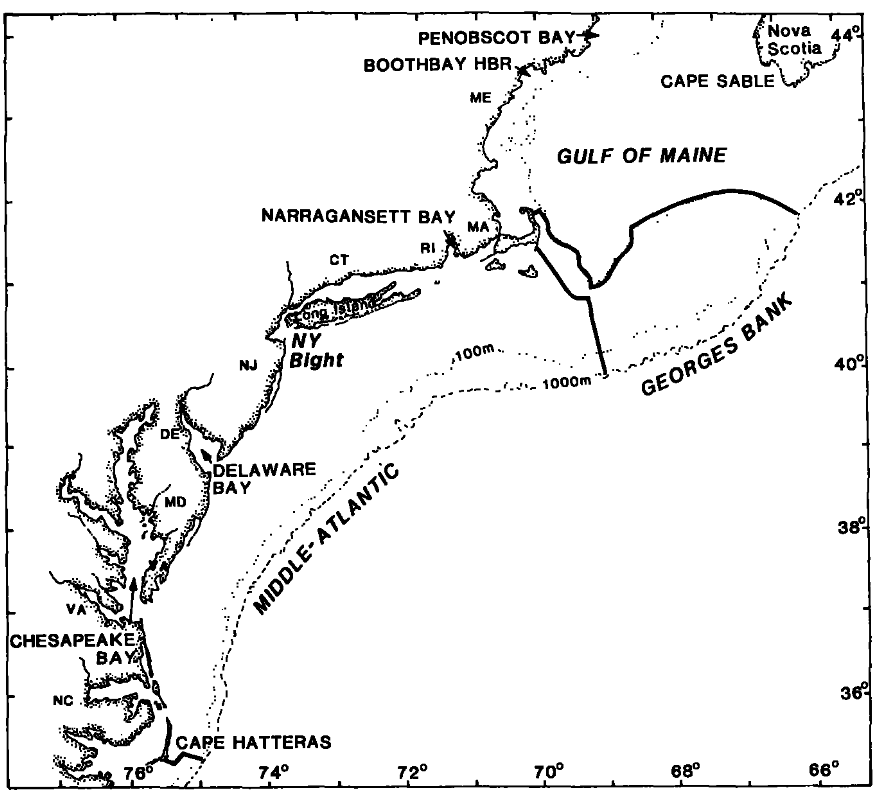

Figure 1
Northwest Atlantic coast and continental shelf with subarea locations mentioned in text.

Locations of stations occupied in the study are plotted by season and gear, cumulatively for all years, in Figures 2a–e. Fall trawl stations were similar in location and number to spring and were not plotted.

The trawlnets used were the #36 and #41 commercial-type otter trawls. The #41 Yankee trawl was used only in spring 1978–81. The #36 Yankee trawl has an opening width of 10.4 m, while the #41 Yankee has an opening width of 11.8 m. In both nets, the mesh size is 12.7 cm stretched with a codend liner of 1.25 cm stretched mesh. Rollers at the front edge of the nets reduce snagging on the bottom. The nets are towed at 6.3 km/hour for 30 minutes per station on a 24-hour basis. Additional details on gear, methods, and sampling area for trawl surveys are described by Grosslein (1969), Grosslein and Azarovitz (1982), Sissenwine et al. (1983), and Survey Working Group, NEFSC (1988).

Crab catches in clam dredge surveys in 1978–86 were used to supplement the trawl data. Dredges used in 1978 were 1.22 m wide; since 1979, they have been 1.52 m wide. Both have 5 cm mesh bags (Murawski and Serchuk 1989). The dredges employ jets of water at their openings to loosen sediments, and are towed at 2.7 km/hour for 4 minutes (1.22 m dredge) or 5 minutes (1.52 m dredge) per station, on a 24-hour basis.

Catchability factors were used to standardize the catches for the two trawlnets and the

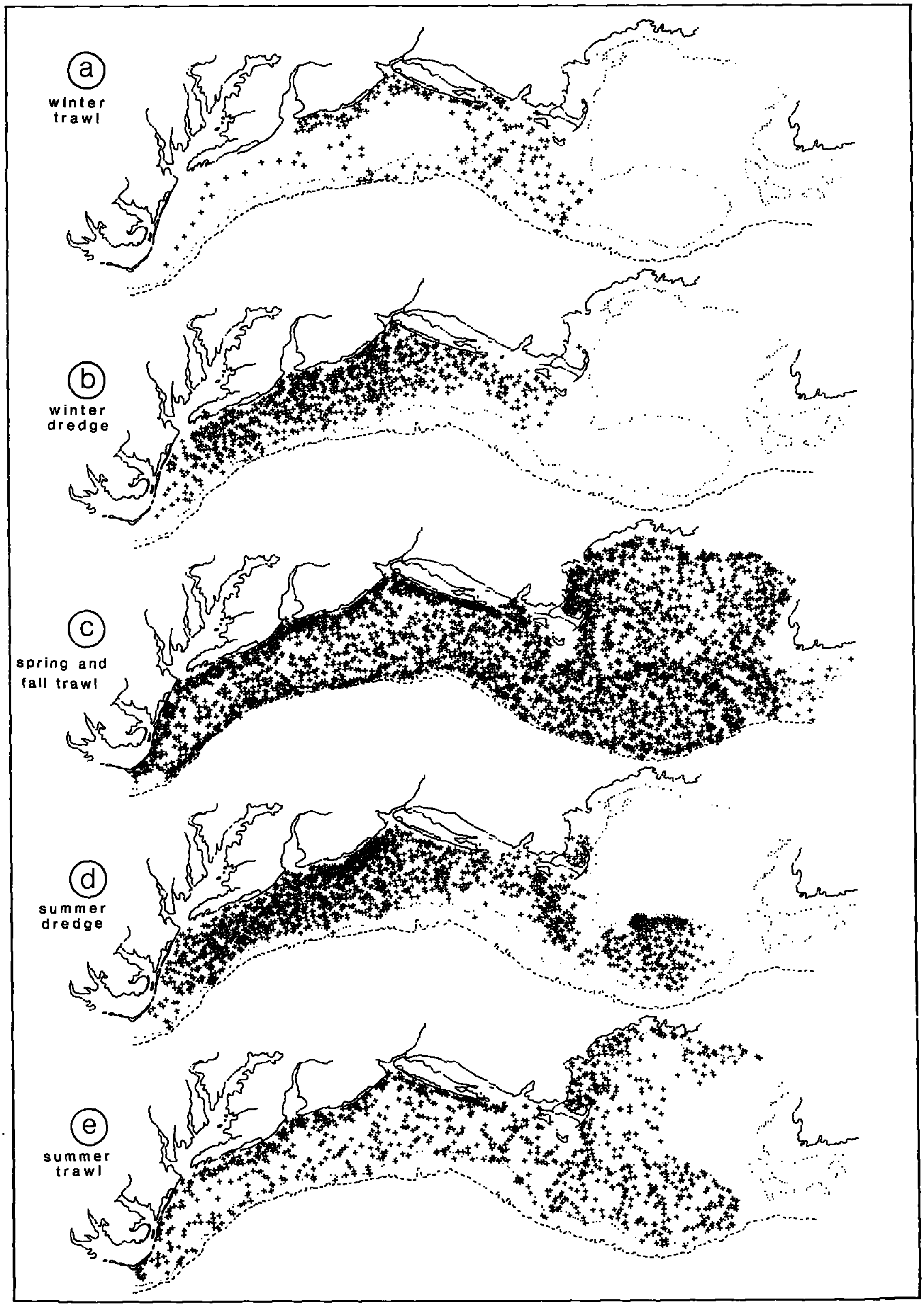

Figure 2
Cumulative station locations: (a) winter trawl, (b) winter dredge, (c) spring trawl (fall trawl similar but not shown), (d) summer dredge, (e) summer trawl.

two clam dredges used. The #41 trawl catches were divided by 1.79, the ratio of catch-per-tow of *Cancer* spp. by the #41 net to the #36 net on the RV *Albatross IV* (Sissenwine and Bowman 1978), to equate them to the #36 trawl catches. The 1.22m dredge catches were multiplied by 1.56 [(1.52/1.22)(5/4)] (S.A. Murawski, NMFS Woods Hole Lab., Northeast Fish. Sci. Cent., Woods Hole, MA, pers. commun., Oct. 1987) to make them comparable with catches of the 1.52m dredge.

Carapace widths, measured between the tips of the anterolateral spines, were determined at sea for all specimens. When occasional collections totaled more than 100 crabs of one species, a random subsample of about 100 was measured and sexed, and the results expanded to estimate total catch. Width frequencies are presented from trawl collections only, because dredge collections included few crabs <5cm.

Data on sex were available for rock crabs and Jonah crabs from all surveys. Sexes of northern lady crabs and coarsehand lady crabs were available from winter dredge surveys only.

For analysis of the relative abundance of crabs, the survey area was divided into five strata, i.e., Gulf of Maine offshore and inshore, Georges Bank, and middle-Atlantic offshore and inshore. The mean and variance of catch-per-tow in each stratum were estimated using the delta distribution, which considers the lognormally transformed catch at positive tows, i.e., tows with crabs (Pennington 1983). Estimates for the five strata were combined by weighting by stratum area in km^2 using equations for stratified mean and variance (Survey Working Group, NEFSC 1988). Trawl and dredge data were handled separately. Weighted estimates of abundance were obtained by sex, time of capture, and bottom temperature for each species of crab. Relative abundances in numbers and weight were calculated by year from fall surveys, because the same size net was used each year.

To examine diel variability in catch, the stations were divided into four groups, i.e., dawn, day, dusk, and night, using the starting time of tow. For each season, two 4-hour periods of low light were defined, and the remaining hours were full light and full dark. For example, for dawn in winter the earliest and latest times of sunrise were determined for all months and latitudes of the survey, and 1 hour was added before and after, to yield a 4-hour period. For winter surveys, periods were, in hours: dawn 0501–0900, day 0901–1500, dusk 1501–1900, night 1901–0500. For spring and fall surveys, hours: dawn 0401–0800, day 0801–1600, dusk 1601–2000, and night 2001–0400. For summer surveys, hours: dawn 0301–0700, day 0701–1700, dusk 1701–2100, and night 2101–0300. Weighted estimates of abundance by time period were compared by analysis of variance for unequal sample size (the GT2 multiple comparison method in Sokal and Rohlf 1981).

For rock and Jonah crabs, sex ratio was calculated by dividing the weighted mean abundance of males by that of females. The mean abundances of each sex were compared by t tests.

We used stepwise regression analysis to fit linear models of abundance (all species) and sex ratio (rock and Jonah crabs) by the independent variables of depth, temperature, and their interaction, using the method of least squares (SAS Institute Inc. 1985). The dependent variables were transformed to logarithms as ln [abundance + 1] and ln [abundance of males/abundance of females]. The data were fit by seasons and subareas.

Results and discussion

Distribution and abundance

Rock crabs Rock crabs were distributed throughout the shelf, with their center of abundance extending from Georges Bank to Cape Hatteras in depths of 6–456m (Figs. 3a–b, 4a–d). The principal sediments in that area are sand and sand/gravel (Uchupi 1963, Schlee 1973). Previous studies found rock crabs also on rocky (Scarratt and Lowe 1972) and muddy (Krouse 1980) sediments, and on blue mussel *Mytilus edulis*, (Reilly and Saila 1978), oyster *Crassostrea virginica*, and shell beds (C.L. MacKenzie Jr., unpubl. data).

Seasonal distribution patterns of rock crabs in the middle-Atlantic subarea show that they migrate across much of the shelf, moving inshore during cold months and offshore during warm months. Winter surveys show rock crabs concentrated in depths <40m, with only scattered occurrences farther offshore (Fig. 3a–b). In spring, their distribution remained essentially unchanged (Figs. 4a, 5). In spring trawl surveys, inshore stations averaged 22.3 crabs per tow whereas offshore stations averaged only 1.1 crabs per tow (Table 2). Later in the year, part of the population moves offshore, resulting in a more even distribution on the shelf during summer and fall (Figs. 4b–d, 5). Catch-per-tow during the fall trawl surveys averaged 1.2 crabs at inshore stations and 0.9 crabs at offshore stations (Table 2).

In the Gulf of Maine, rock crabs occurred only in coastal zones from spring through fall (Fig. 4a–d; Table 2). We have no data on the winter distribution of rock crabs in that subarea, but Krouse (1972, 1976, 1980) reported that they occupy coastal zones year-round in Maine.

Triggering cues for seasonal migrations in the middle-Atlantic are unknown, but they are apparently related to seasonal cooling and warming. Terretta

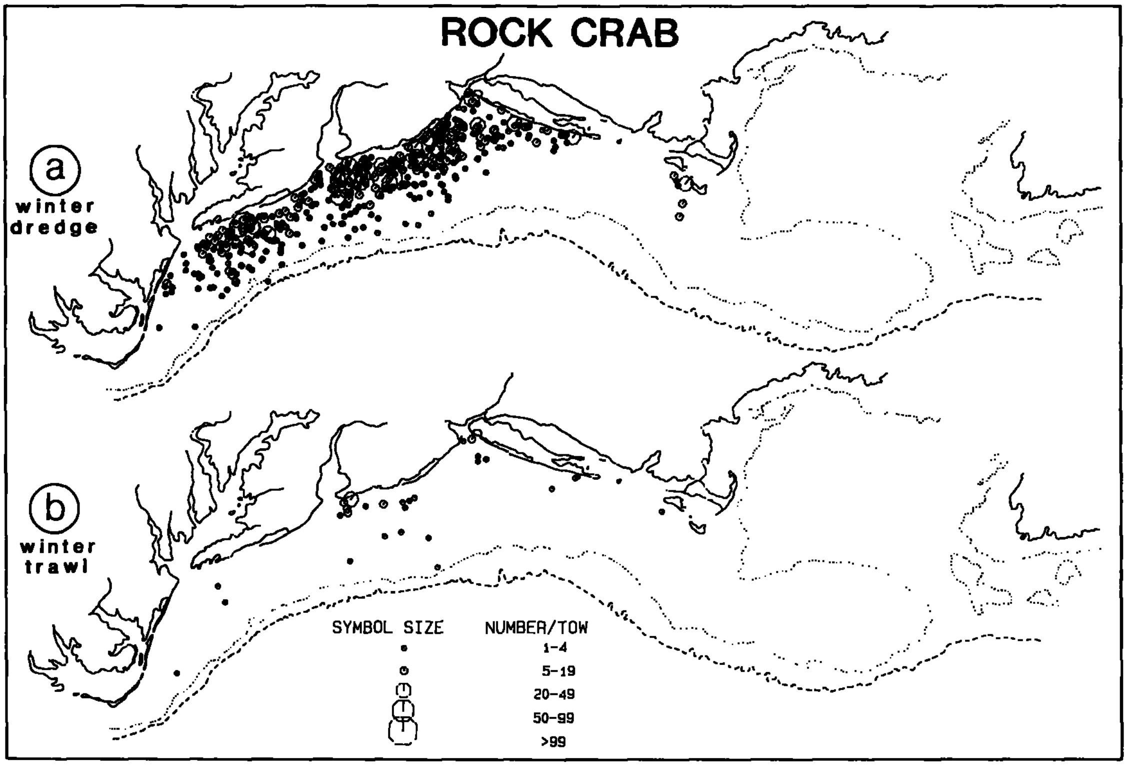

Figure 3
Rock crab distribution from winter dredge and winter trawl surveys.

(1973) reported that rock crabs enter Chesapeake Bay in the fall, when temperatures are below 12°C, and exit in the spring before they rise to 12°C. Although rock crabs have been caught at temperatures as high as 25°C (Williams and Wigley 1977), our data show that they tend to avoid temperatures above 18°C (Fig. 6). They were most abundant in spring in temperatures of 4–7°C, and in fall at 8–18°C. In previous trawl surveys, most rock crabs were caught at 0–14°C (Musick and McEachran 1972, Haefner 1976), but less sampling was done at higher temperatures.

Mean catch-per-tow by number and weight in fall varied among years (Fig. 7). The year of peak catches, 1986, produced nearly 20 times more rock crabs than in the lowest catch year, 1978. However, the decadal data set revealed no consistent trend in abundance. The highest catches by weight were in 1981 and 1986; the year 1986 was unusual in that 60% of the crabs were ≤5 cm carapace width. The mean weight per crab was 35 g in 1986, but averaged 63 g in all other years combined.

Size frequencies of rock crabs differed by subarea and sex (Fig. 8). Modal carapace widths of males and females in the Gulf of Maine and middle-Atlantic peaked at 7–9 cm. The largest crabs in both subareas were males. On Georges Bank, they were smaller; widths of both sexes peaked at 4 cm.

Weighted mean catch-per-tow of rock crabs by trawls was highest at night in spring and at twilight in summer and fall (Table 3). We assume that crabs on the bottom can be caught by trawls, but crabs buried in sediments can be captured only by clam dredges. Nocturnal activity in rock crabs was reported by MacKenzie (1981), who observed that rock crabs are buried at times during the day, but not at night. Fogarty (1976) and Rebach (1987) found that rock crabs exposed to artificial photoperiods are more active in dark than in light periods. Dredge catches of rock crabs also fluctuated by time of day, but the effect of light upon catchability of crabs by dredges is unknown.

Abundances of males and females were significantly different for all gears and seasons (Table 4). Males outnumbered females in spring and summer trawl surveys, whereas females outnumbered males in fall trawl and all dredge surveys. In contrast, Shotton (1973) and Haefner (1976) found that males usually outnumbered females in late-spring and fall surveys off Virginia.

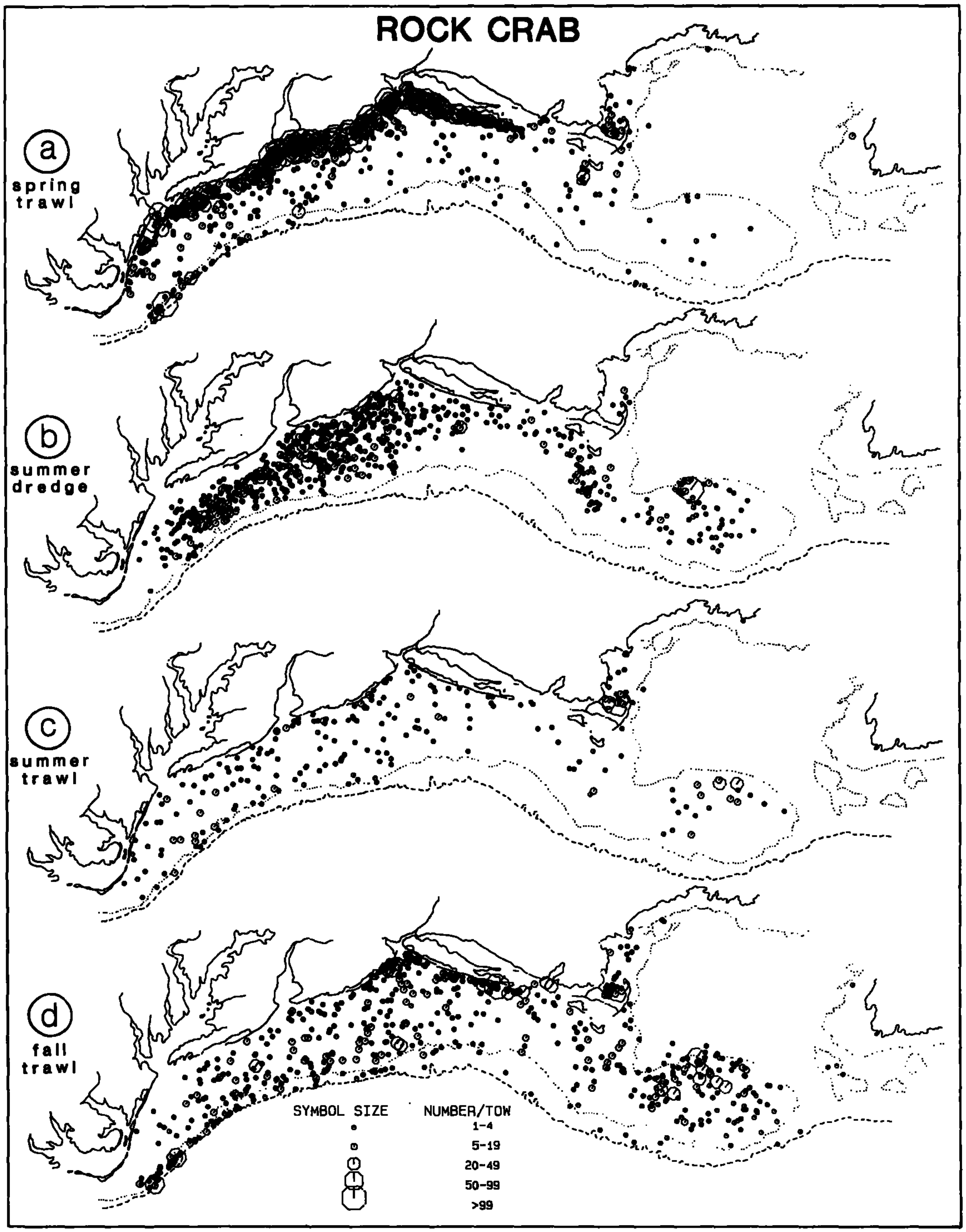

Figure 4
Rock crab distribution from spring trawl, summer dredge, summer trawl, and fall trawl surveys.

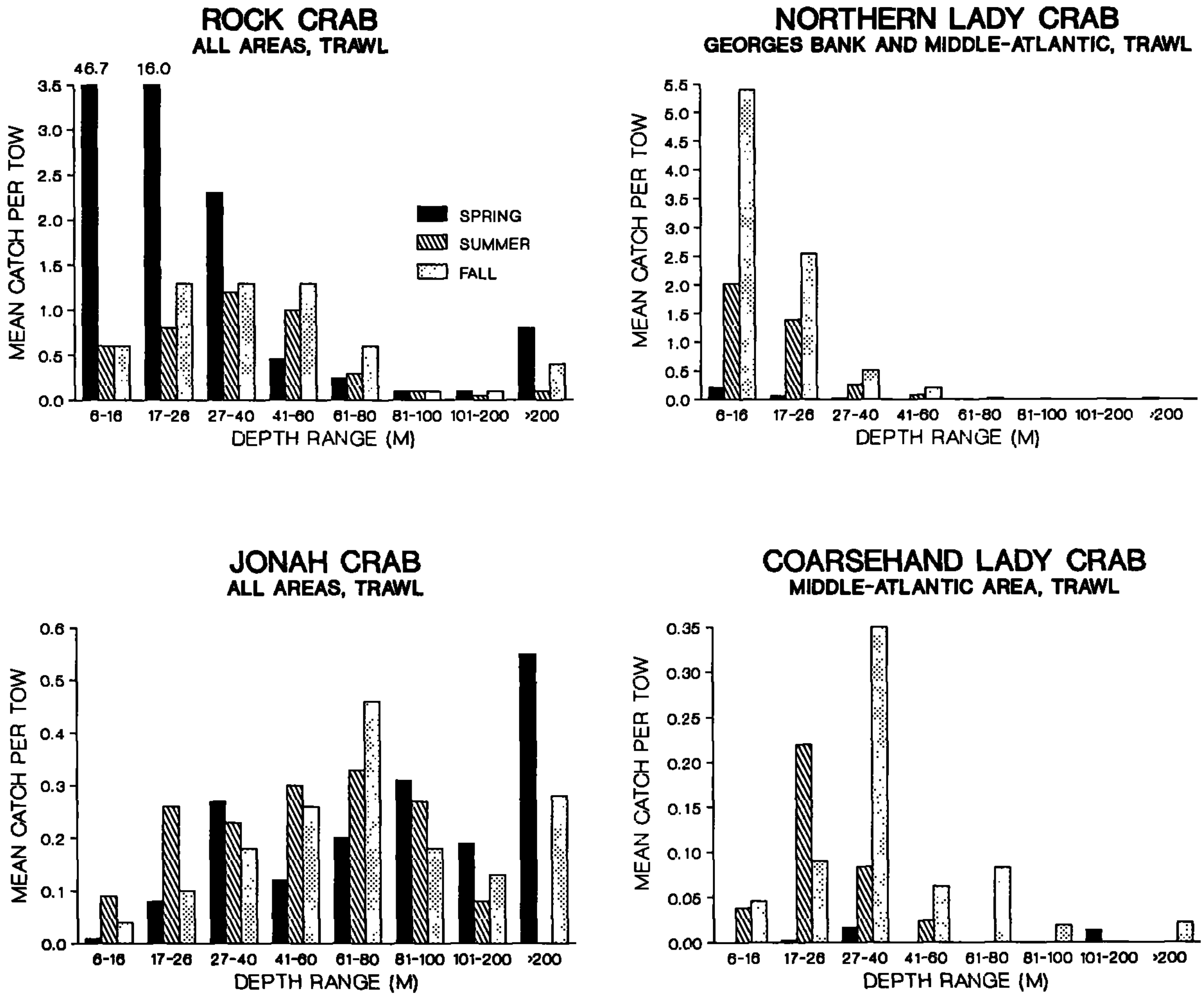

Figure 5

Mean catch-per-tow (unweighted) at depth ranges for rock, Jonah, northern lady, and coarsehand lady crabs in spring, summer, and fall trawl surveys. The first two depth ranges, 6–16 and 17–26m, are within inshore strata of the trawl surveys.

In the middle-Atlantic, male rock crabs were distributed closer to shore than females. A larger proportion of males occurred inshore than offshore in spring and summer trawl surveys, and a larger proportion of females occurred offshore than inshore in dredge surveys (Fig. 9). Males are also dominant in estuaries such as lower Delaware Bay (Winget et al. 1974) and lower Chesapeake Bay (Terretta 1973), where they overwinter (Haefner and Van Engel 1975), and along the Virginia coast (Shotton 1973).

While different migratory patterns of the sexes might partially account for the unequal sex ratios in rock crab catches in this study, we consider differences by sex in availability to sampling gear to be largely responsible. Comparing catches of rock crabs in winter dredge surveys with spring trawl surveys, both of which were conducted during the cold season, significantly more females were caught than males by dredges, whereas significantly more males than females were caught by trawls (Table 4). This suggests that females bury more than males. The two summer surveys showed the same phenomenon. Our spring trawl data showed the ratio of males to females was lowest at night (Fig. 10), from which we conclude that diel activity rhythms at that season may be different by sex, and that females are more active at night than by day. They would be buried when inactive during daylight hours.

Inactivity of females may be related to the reproductive cycle. Females extrude eggs in fall, which are

Table 2

Catch-per-tow (delta mean and standard error) of each crab species, 1978–87, by gear, quarter, and strata (Off = offshore, In = inshore), and weighted delta mean and standard error for all strata. Corrected for #41 trawlnet and 1.22 m clam dredge. All stations except winter trawl included.

		Trawl						Dredge			
		Spring		Summer		Fall		Winter		Summer	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Rock crab											
Gulf of Maine	Off	0.03	(0.010)	0.05	(0.030)	0.02	(0.006)	no stations		no stations	
	In	2.24	(0.849)	1.24	(0.403)	0.84	(0.179)	no stations		no stations	
Georges Bank	Off	0.07	(0.013)	0.67	(0.216)	0.56	(0.689)	no stations		0.59	(0.096)
Middle Atlantic	Off	1.12	(0.130)	0.83	(0.091)	0.93	(0.071)	2.25	(0.195)	1.61	(0.079)
	In	22.34	(2.215)	0.58	(0.072)	1.15	(0.133)	5.27	(0.536)	0.76	(0.071)
All strata		2.64	(0.004)	0.61	(0.002)	0.56	(0.001)	2.88	(0.007)	1.22	(0.001)
Jonah crab											
Gulf of Maine	Off	0.10	(0.014)	0.10	(0.042)	0.06	(0.010)	no stations		no stations	
	In	0.33	(0.154)	0.26	(0.121)	0.29	(0.078)	no stations		no stations	
Georges Bank	Off	0.13	(0.020)	0.14	(0.040)	0.13	(0.014)	no stations		0.22	(0.049)
Middle Atlantic	Off	0.44	(0.041)	0.34	(0.059)	0.48	(0.041)	0.09	(0.019)	0.14	(0.021)
	In	0.08	(0.024)	0.21	(0.064)	0.09	(0.017)	0.08	(0.048)	0.08	(0.026)
All strata		0.23	(0.0003)	0.23	(0.001)	0.23	(0.0002)	0.09	(0.001)	0.15	(0.0004)
Northern lady crab											
Georges Bank	Off	no crabs		0.07	(0.029)	0.10	(0.021)	no stations		0.28	(0.065)
Middle Atlantic	Off	<0.01	(0.003)	0.17	(0.052)	0.11	(0.023)	0.17	(0.039)	0.12	(0.018)
	In	0.11	(0.018)	1.53	(0.180)	3.36	(0.351)	3.01	(0.688)	1.43	(0.163)
All strata		0.03	(0.0001)	0.38	(0.002)	0.62	(0.001)	0.76	(0.005)	0.36	(0.001)
Coarsehand lady crab											
Middle Atlantic	Off	0.01	(0.004)	0.07	(0.035)	0.13	(0.026)	0.10	(0.023)	0.15	(0.025)
	In	<0.01	(0.001)	0.08	(0.034)	0.06	(0.014)	0.05	(0.025)	0.08	(0.028)
All strata		0.01	(0.0001)	0.07	(0.001)	0.11	(0.001)	0.09	(0.001)	0.10	(0.0004)

carried until hatching in spring (Krouse 1972). Conversely, perhaps some of the more active males avoid a slowly towed dredge but cannot avoid a trawl because it is too large. Haefner's (1976) trawl surveys, which showed significantly more males than females, must have caught the active males and missed the buried females.

There are a few possibilities as to why rock crabs in the middle-Atlantic migrate inshore in fall and remain until spring. Perhaps they do so to feed when potential competitors for prey, such as the blue crab *Callinectes sapidus* and northern lady crab, both of which occur inshore, are dormant in winter. Rock crabs are the only brachyurans in the subarea which molt in winter (Haefner and Van Engel 1975), and it is possible that they migrate inshore to avoid fishes which could prey on them while they are in the vulnerable soft and paper-shell stages. The latter stage in adults persists for two to three months (Haefner and Van Engel 1975). Another possibility is that their larval stages survive better in coastal zones when released in spring.

The environmental variables that accounted for the largest proportion of the variance of rock crab abundance in the middle-Atlantic subarea were depth in spring and temperature in summer and fall (Table 5). The slope of the regression of depth upon abundance was negative in that subarea in all seasons and was strongest in spring (compare with Figure 5). Temperature was also negatively correlated with rock crab abundance in that subarea. In the Gulf of Maine, depth and the cross-product, depth * temperature, had the

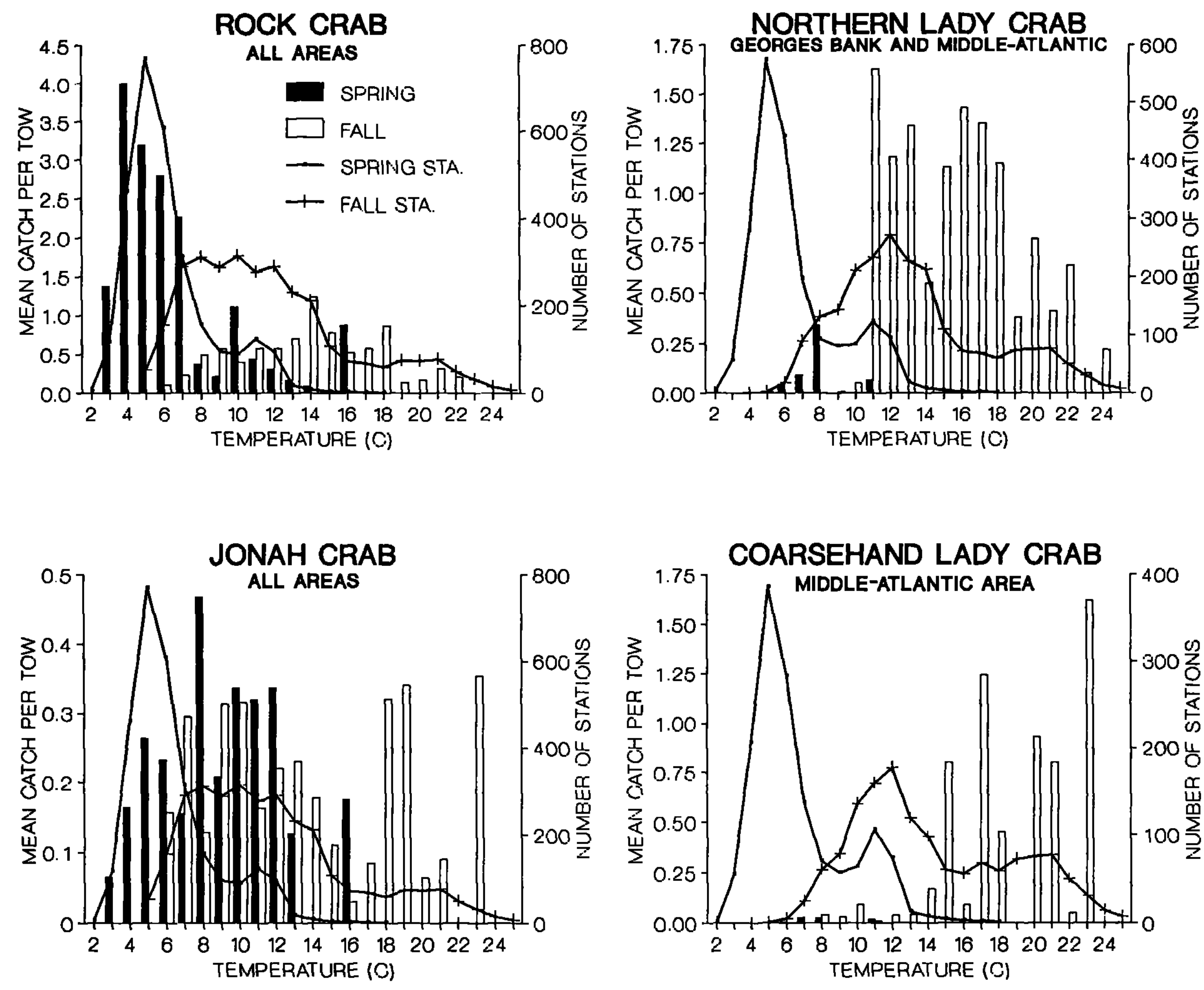

Figure 6

Mean abundance (unweighted) at bottom-water temperatures from spring and fall trawl surveys, with number of stations (lines) at each temperature.

highest partial correlation with abundance. On Georges Bank, the most important variable was temperature in summer and fall. In both subareas, temperature was positively correlated with rock crab abundance. Sex ratio was significantly associated with depth*temperature (R, −0.355) and depth (R, +0.245) in fall; however, no variables were significant in spring or summer.

Jonah crabs Jonah crabs were distributed on the shelf and its upper slope from Penobscot Bay, Maine, and Cape Sable, Nova Scotia, southward to Cape Hatteras, but were sparse south of Delaware (Fig. 11a–d). Jonah crabs were less abundant than rock crabs on Georges Bank and in the middle-Atlantic. They occurred in all surveyed depths, but were least abundant in 6–16 m (Fig. 5). The sediment where most Jonah crabs occur is silty sand (Uchupi 1963, Schlee 1973). They have also been collected on gravel and rocky sediments (Jeffries 1966, Krouse 1980).

A comparison of distributions in Figure 11 suggests that Jonah crabs migrate toward the offshore edges of the shelf in Georges Bank and the middle-Atlantic subarea in winter and into their central portions in summer. Observations in the coastal zone of Maine (Krouse 1980) and in Narragansett Bay (Jeffries 1966), where Jonah crabs were present in summer but not in winter, confirm that seasonal migrations probably occur. However, data on offshore and inshore catch-per-tow (Table 2) and depth range (Fig. 5) show that migrations may

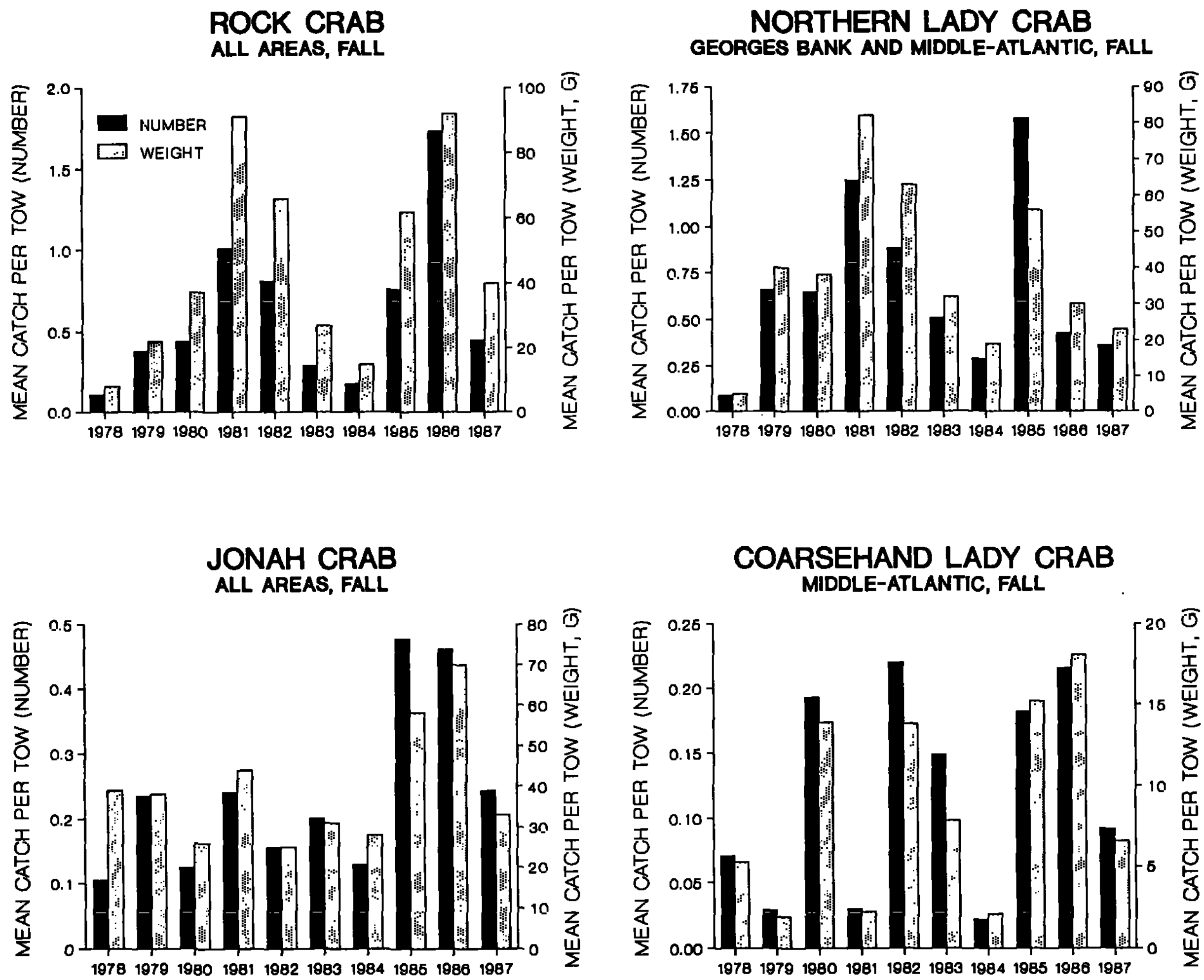

Figure 7

Weighted mean catch-per-tow by number and weight (g), by year. Data are from fall trawl surveys.

be minor, and much less extensive than in the rock crab.

Jonah crabs were collected at temperatures of 3–23°C (Fig. 6). Similarly, Haefner (1977) collected Jonah crabs in the middle-Atlantic over a temperature range of 6–24°C at depths of 150–400 m, while maximum abundance of the species was from 8–14°C. Krouse (1980) concluded that Jonah crabs have a narrower temperature tolerance than rock crabs. We found no difference in the annual temperature ranges of the two species. However, in spring, the majority of rock crabs occurred at 3–7°C when they were concentrated inshore, while the majority of Jonah crabs occurred at 8–12°C because they were mostly offshore.

The scarcity of Jonah crabs off the coasts of Maryland, Virginia, and North Carolina (Fig. 11) may be due to unfavorably high temperatures. Average bottom temperatures in that area in August and September are 18–23°C. At those latitudes, Jonah crabs were more abundant on the outer shelf and slope, where temperatures are mostly 14–18°C during those months (Mountain and Holzwarth 1989).

Mean catch-per-tow by number and weight varied among years (Fig. 7). It was roughly similar during 1978–84 and in 1987. However, it was nearly twice as high in the years 1985 and 1986.

Carapace widths of Jonah crabs differed by sex. In all three subareas, males had a broad range of widths, while females had sharp modal peaks of 10, 12, and 8 cm, in the Gulf of Maine, Georges Bank, and middle-Atlantic, respectively (Fig. 8). Few females attained widths of >13 cm. These size ranges correspond to

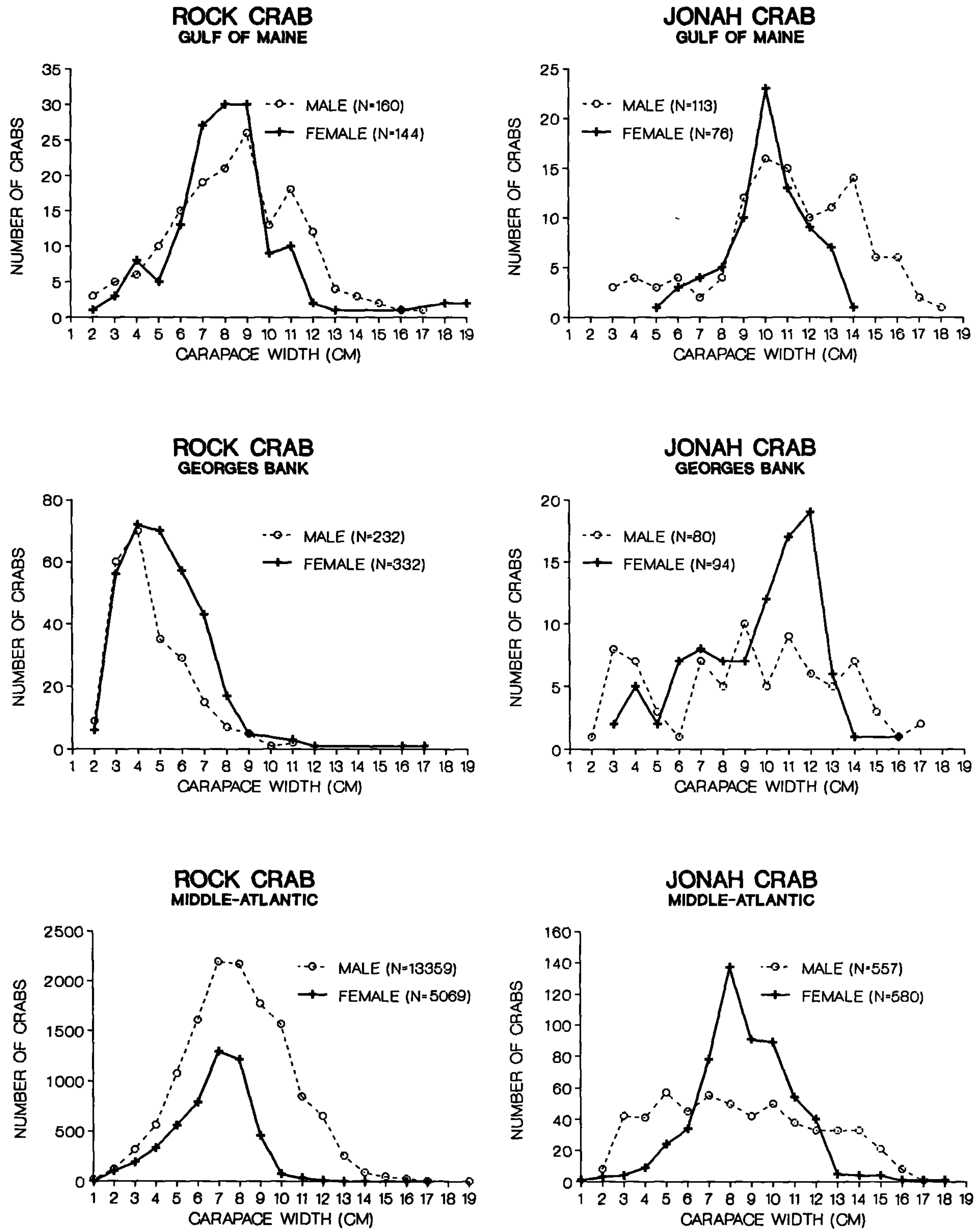

Figure 8
Carapace width-frequency distributions of combined spring and fall trawl-caught rock, Jonah, northern lady, and coarsehand lady crabs.

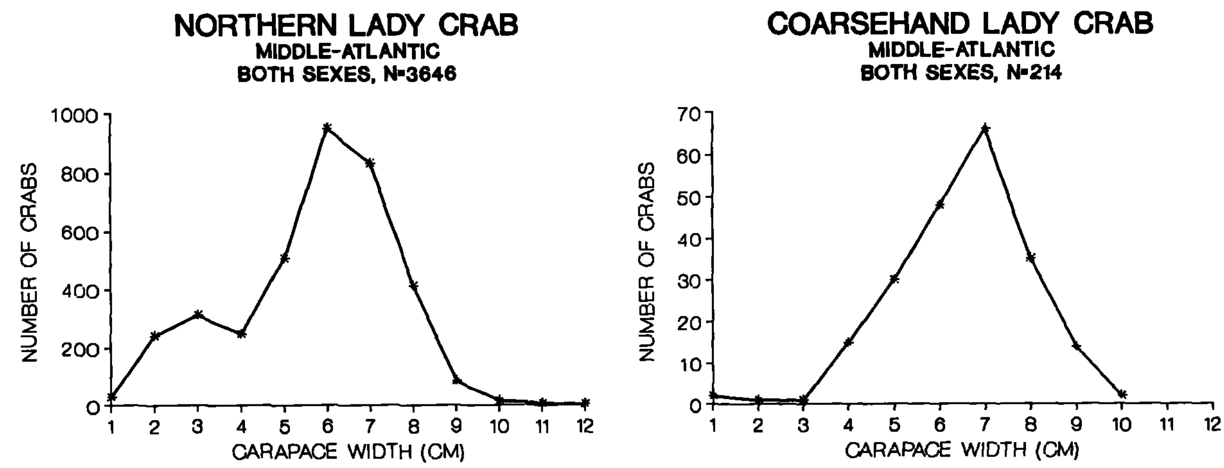

Figure 8 (continued)

Table 3

Catch-per-tow (weighted delta means and standard errors) of crabs by time of day, with number of crabs included. Time periods as defined in Methods. Day, night, and twilight catch-per-tow were significantly different by GT2 multiple comparison tests ($P<0.05$) within species, gear, and season, in all cases except two: in rock and Jonah crabs in winter, two groups were not statistically different and are noted with superscripts a and b. Number of stations as in Table 2.

	Trawl						Dredge			
	Spring		Summer		Fall		Winter		Summer	
Species/period	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Rock crab										
Day	2.25	(0.0112)	0.612	(0.0047)	0.375	(0.0011)	4.84	(0.072)	1.26	(0.0032)
Night	3.20	(0.0102)	0.460	(0.0053)	0.636	(0.0015)	[a]3.78	(0.032)	1.04	(0.0045)
Twilight	2.31	(0.0103)	0.727	(0.0067)	0.647	(0.0018)	[a]3.74	(0.045)	1.31	(0.0043)
No. crabs	22916		626		3038		2163		2343	
Jonah crab										
Day	0.206	(0.0008)	0.241	(0.0025)	0.200	(0.0007)	[b]0.129	(0.0064)	0.163	(0.0011)
Night	0.300	(0.0010)	0.291	(0.0056)	0.253	(0.0008)	0.088	(0.0016)	0.178	(0.0020)
Twilight	0.190	(0.0006)	0.183	(0.0021)	0.229	(0.0007)	[b]0.144	(0.0064)	0.112	(0.0009)
No. crabs	876		223		883		53		242	
Northern lady crab (Georges Bank and middle-Atlantic subareas only)										
Day	0.013	(0.0001)	0.376	(0.0054)	0.272	(0.0012)	0.447	(0.0118)	0.344	(0.0016)
Night	0.027	(0.0003)	0.499	(0.0077)	0.797	(0.0044)	0.748	(0.0106)	0.372	(0.0037)
Twilight	0.019	(0.0002)	0.329	(0.0040)	0.891	(0.0044)	0.820	(0.0185)	0.393	(0.0028)
No. crabs	110		571		3653		447		936	
Coarsehand lady crab (Middle-Atlantic subarea only)										
Day	0.004	(0.0001)	0.016	(0.0007)	0.030	(0.0004)	0.051	(0.0034)	0.118	(0.0011)
Night	0.014	(0.0003)	0.057	(0.0025)	0.140	(0.0014)	0.116	(0.0031)	0.188	(0.0031)
Twilight	0.001	(0.0001)	0.151	(0.0062)	0.155	(0.0018)	0.132	(0.0046)	0.107	(0.0015)
No. crabs	10		47		204		49		185	

Figure 9 (facing page)

Sex ratios (abundance males:abundance females) of rock and Jonah crabs, by season and offshore/inshore strata, middle-Atlantic subarea.

Figure 10 (facing page)

Sex ratios (abundance males:abundance females) of rock and Jonah crabs by time of day, all subareas combined.

Table 4

Catch-per-tow (weighted delta means and standard errors) of male and female rock and Jonah crabs, by gear and season, significance (S) ($P<0.01$) by t tests, sex ratio (male:female), and total number of crabs sexed (corrected for net and dredge size). Number of stations sampled as in Table 2.

	Trawl						Dredge			
	Spring		Summer		Fall		Winter		Summer	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Rock crab										
Males	1.211	(0.0019)	0.229	(0.0010)	0.235	(0.0002)	0.711	(0.0020)	0.402	(0.0005)
Females	0.457	(0.0005)	0.196	(0.0009)	0.275	(0.0003)	1.603	(0.0051)	0.782	(0.0010)
Significance	S		S		S		S		S	
Sex ratio	2.6:1		1.2:1		1:1.2		1:2.2		1:1.9	
No. crabs	16666		432		2657		2126		2226	
Jonah crab										
Males	0.119	(0.0002)	0.072	(0.0005)	0.087	(0.0001)	0.041	(0.0004)	0.045	(0.0002)
Females	0.073	(0.0001)	0.074	(0.0005)	0.121	(0.0002)	0.027	(0.0003)	0.103	(0.0003)
Significance	S		NS		S		S		S	
Sex ratio	1.6:1		1:1.0		1:1.4		1.5:1		1:2.3	
No. crabs	718		144		783		54		234	

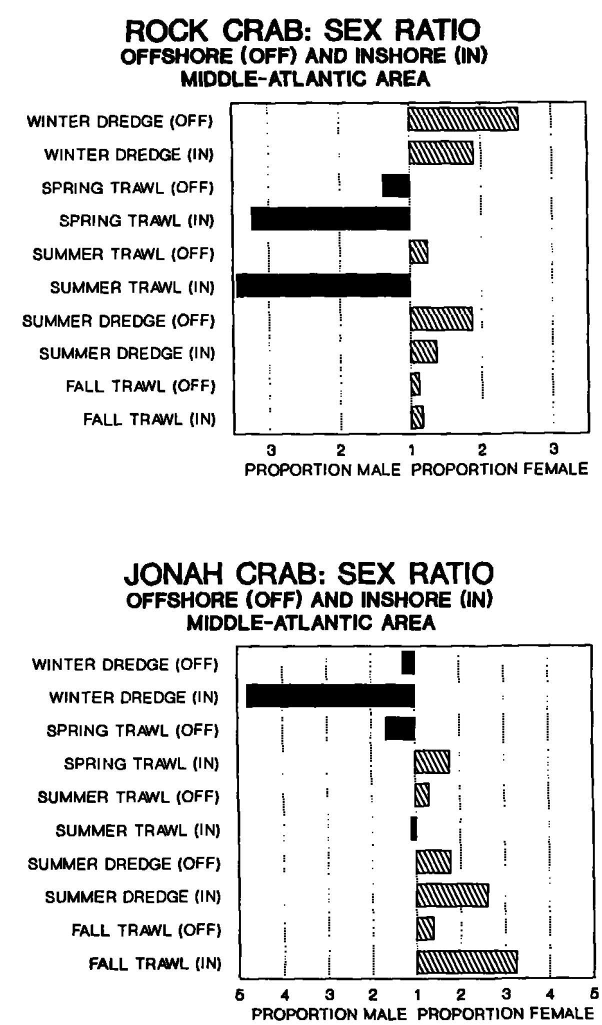

Figure 9

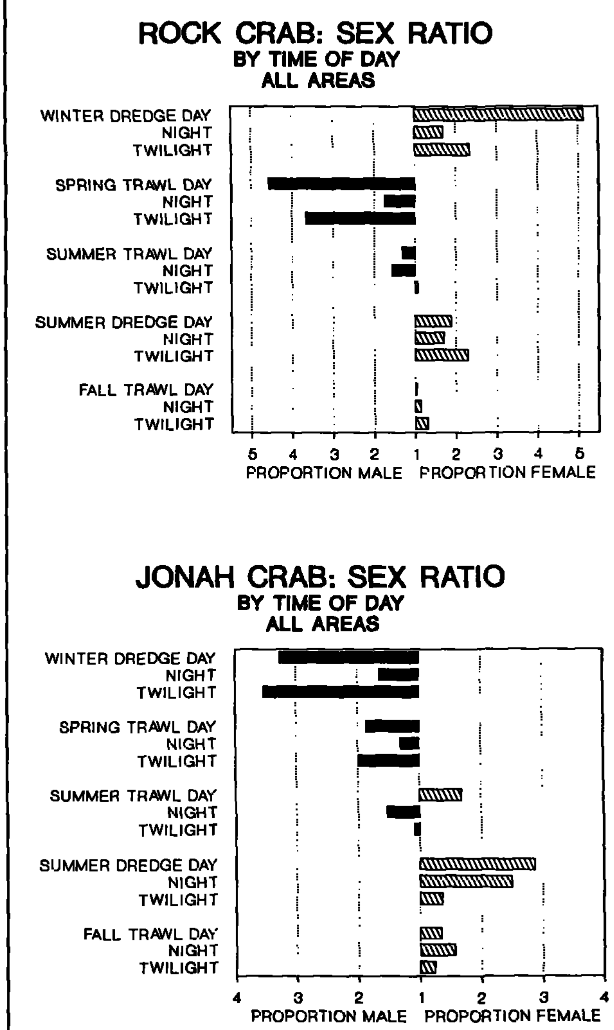

Figure 10

Table 5

Partial correlation coefficients (R) and model R^2 of depth, temperature, and their interaction upon abundance of crabs, determined by regression analysis. Shown when significant to $P<0.05$; dashes = not significant. Slope of R is positive unless sign is negative. Data are from spring, summer, and fall trawl surveys, Gulf of Maine (GM), Georges Bank (GB), and middle-Atlantic (MA); a = no crabs.

	Spring			Summer			Fall		
	GM	GB	MA	GM	GB	MA	GM	GB	MA
No. stations	817	590	2877	161	187	881	893	746	3069
Rock crab									
Depth	-0.230	—	-0.316	—	—	-0.140	0.259	0.098	-0.093
Temperature	0.162	—	-0.225	—	0.319	-0.185	0.119	0.232	-0.129
Depth * Temperature	—	—	0.129	-0.350	—	0.089	-0.240	-0.126	—
Model R^2	0.079	—	0.167	0.122	0.102	0.062	0.139	0.079	0.025
Jonah crab									
Depth	—	—	0.319	-0.198	—	0.186	0.074	—	0.099
Temperature	—	—	—	—	0.158	—	0.120	—	-0.182
Depth * Temperature	—	0.200	-0.131	—	—	—	-0.066	—	—
Model R^2	—	0.040	0.119	0.039	0.025	0.034	0.024	—	0.043
Northern lady crab									
Depth	a	a	-0.093	a	0.202	-0.365	a	0.162	0.072
Temperature			—		0.265	0.165		0.222	0.271
Depth * Temperature			0.067		—	—		-0.078	-0.147
Model R^2			0.013		0.124	0.167		0.082	0.101
Coarsehand lady crab									
Depth	a	a	—	a	a	—	a	a	—
Temperature			—			0.161			0.080
Depth * Temperature			—			—			—
Model R^2			—			0.026			0.006

those reported earlier for the Gulf of Maine (Krouse 1980) and middle-Atlantic (Haefner 1977).

Trawl catches of Jonah crabs were highest at night in spring, summer, and fall, suggesting diel activity cycles similar to those of rock crabs (Table 3). Under artificial photoperiods, Jonah crabs are active only in the dark period, with peak activity at dusk (Fogarty 1976). Our data also show differences in sex ratio by time of day, especially in spring (Fig. 10), suggesting differences in diel activity between the sexes.

Male Jonah crabs were significantly more abundant than females in spring trawl surveys, whereas females were significantly more abundant in fall (Table 4). These results are very similar to the findings of Haefner (1977) for Jonah crabs off Virginia. Males dominated the dredge catch in winter, though sample size was small; females dominated the dredge catch in summer. Seasonal changes in sex ratio may be due to limited single-sex migrations or differences in catchability reflective of the reproductive cycle.

In the Gulf of Maine, from a limited number of individuals in this study, the sex ratio in spring trawl collections was 4.5:1 males and in fall 1.2:1 females. Krouse (1980) found that in coastal Maine, males dominated the catch in lobster pots in July and females in August and September. He concluded that female Jonah crabs occupy shallow zones during the latter two months to molt and copulate.

Differences in sex ratios of Jonah crabs offshore and inshore in the middle-Atlantic were unlike those of rock crabs (Fig. 9). Considering spring and fall, when sample size was largest, the ratio of females to males was higher inshore than offshore. In contrast, in depths greater than 200 m, males outnumbered females in both seasons. In contrast, in Haefner's (1977) fall survey, sex ratios favored males from 41–60 m depths and females from 61 m to the survey limit of 260 m.

Most of the partial correlation coefficients of the environmental variables versus the catches in numbers were lower for Jonah crabs than for rock crabs (Table 5). Perhaps this was because Jonah crabs were distributed rather evenly across all temperatures and depths (Figs. 5, 6). In the middle-Atlantic, their abundance was

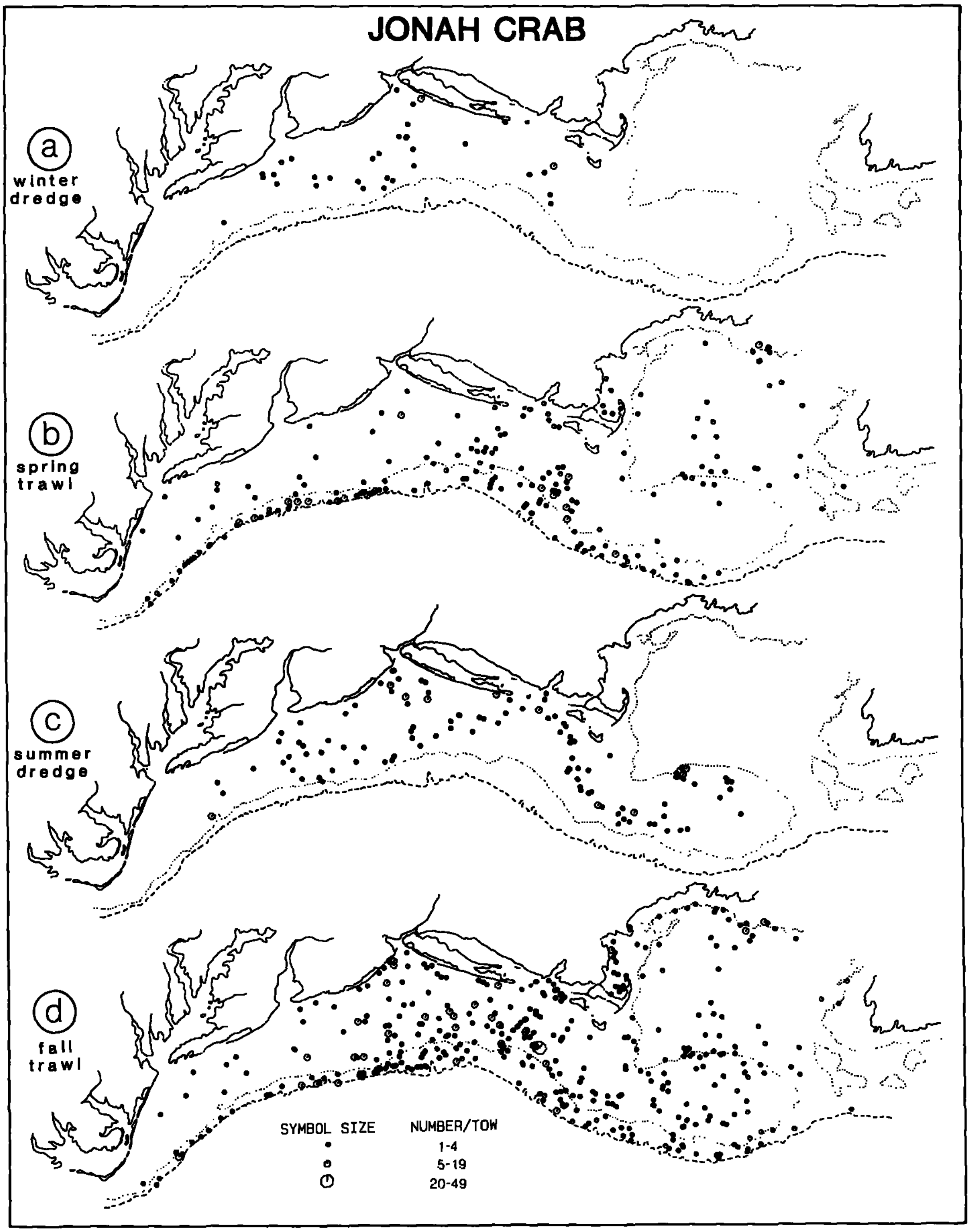

Figure 11
Jonah crab distribution, from winter dredge, spring trawl, summer dredge, and fall trawl surveys.

most highly correlated with depth in spring, but positively, unlike that of rock crabs. In that subarea, their abundance was negatively correlated with temperature in fall, with a minor effect of depth. No significant associations were found between the sex ratios and environmental variables.

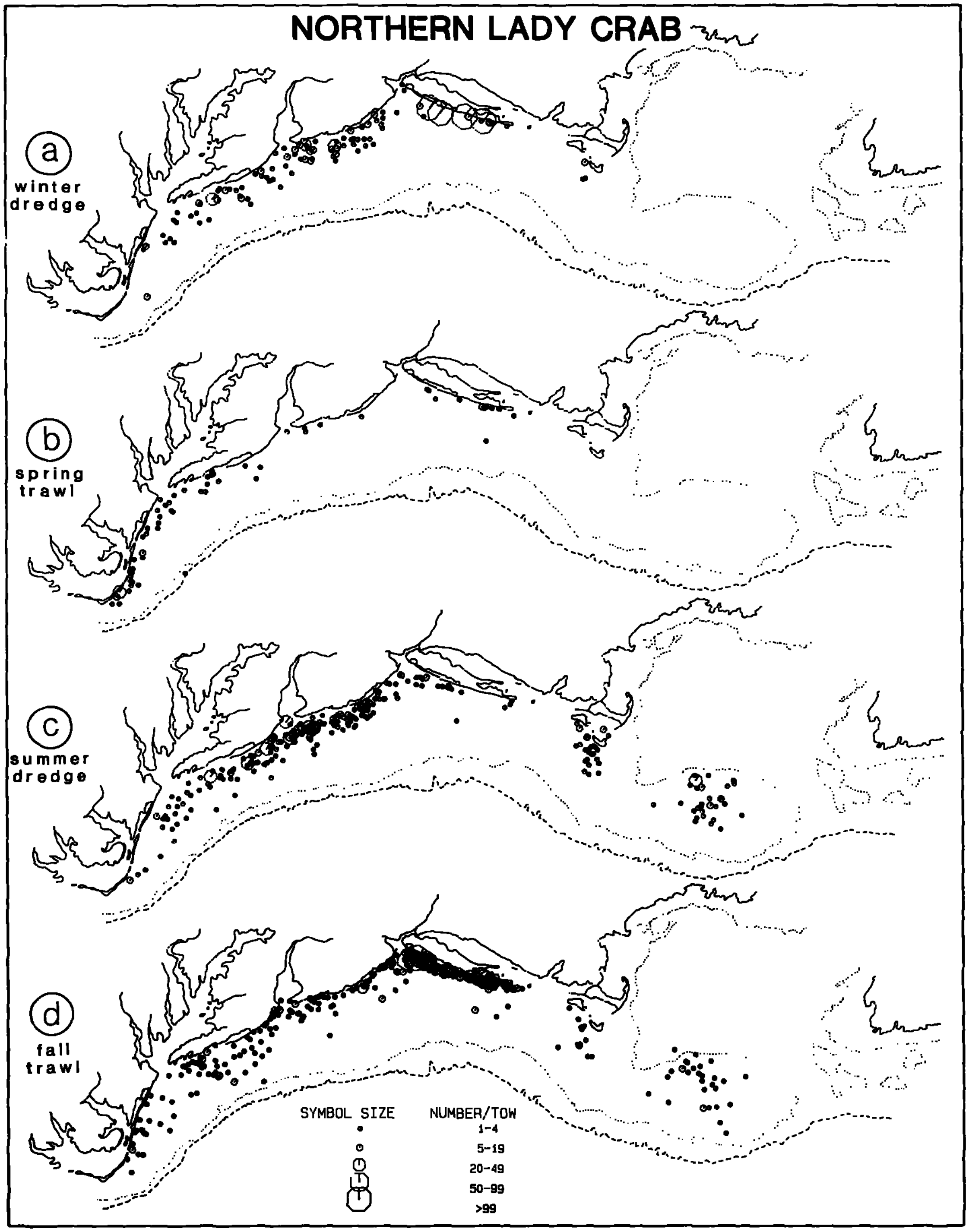

Figure 12
Northern lady crab distribution, from winter dredge, spring trawl, summer dredge, and fall trawl surveys.

Northern lady crabs Northern lady crabs were distributed on the inner middle-Atlantic shelf and Georges Bank, mostly in depths <27 m (Figs. 5, 12a–d). They were concentrated on the inner shelf from the eastern tip of Long Island southward. Two other pockets of concentration in summer and fall were on the shoals south of Nantucket Island, and on the shallow portion of Georges Bank. Catch-per-tow was highest on the inshore stratum of the middle-Atlantic, where it was over ten times offshore catch-per-tow (Table 2). Northern lady crabs have been observed in densities as high as 3-4/m^2 within 2km of the New Jersey coast (MacKenzie et al. 1985). The sediments where northern lady crabs are found are fine-to-medium sand or gravelly sand (Uchupi 1963). Williams (1984) found this species on a variety of sediments, mostly sand.

This study supports the speculation by Musick and McEachran (1972) that northern lady crabs may be inactive or buried in winter. As stated above, we hypothesize that dredges catch buried crabs that trawls do not. In our 1978 winter trawl survey in the middle-Atlantic, which included 78 stations, no northern lady crabs were collected, but in the 1978 winter dredge survey in the same area, which included 133 stations, 240 were collected. Moreover, in spring trawl surveys, during which water temperatures had not risen appreciably since winter, this crab was rarely collected.

Northern lady crabs were caught with trawls where temperatures were 4-24°C; 96% were caught where temperatures were 11.0°C and above (Fig. 6). Along the New Jersey coast, Grant (1987) found northern lady crabs were abundant in summer but absent when temperatures dropped below 18°C. This crab was not found in the Gulf of Maine; temperatures there are mostly 4-10°C (Mountain and Holzwarth 1989).

Mean catch-per-tow varied substantially among years. The catch was relatively low in 1978; in contrast, the mean weight of crabs was about 16 times higher in 1981, the peak year (Fig. 7). In 1985, the mean weight per crab was 29g, when an unusually large number of small crabs were present on Georges Bank and in the middle-Atlantic. For all other years combined, the mean weight per crab was 58g.

The modal carapace width of northern lady crabs was 6cm (Fig. 8). From winter dredge surveys, for which sex information was available, modes were 7cm in males and 6cm in females. The ratio of abundance of males to females was 1.1:1 (*N* 427) at that time.

The abundance of northern lady crabs was significantly different by time of day, i.e., highest at night or twilight in trawl surveys (Table 3). Similarly, in a laboratory study this species was most active at dusk and night (Sponaugle and Lawton 1990).

The abundance of northern lady crabs was negatively correlated with depth in spring and summer in the middle-Atlantic (Table 5). In summer and fall, it was positively correlated with temperature. In fall, depth had a weak, positive partial correlation with catches, although if considered alone, depth correlated negatively. On Georges Bank, the abundance of northern lady crabs was positively correlated with temperature and depth in summer and fall.

Coarsehand lady crabs Coarsehand lady crabs were distributed across the middle-Atlantic from southern New Jersey to Cape Hatteras in depths to 293m (Fig. 13a-d). The range of this species was reported previously as from Accomac County, Virginia, to Biscayne Bay, Florida (Wenner and Read 1982, Williams 1984, Haefner 1985). The principal sediment from New Jersey to Cape Hatteras is sand (Uchupi 1963). Williams (1984) also reported that this crab occurs on sand.

The distributions of coarsehand and northern lady crabs overlapped, but coarsehand lady crabs were distributed farther offshore (Fig. 5), as Musick and McEachran (1972) and Williams (1984) reported. Abundance of coarsehand lady crabs peaked at depths of 27-40m. Coarsehand lady crabs were less abundant than northern lady crabs in the middle-Atlantic inshore stratum (Table 2), as Dudley and Judy (1971) observed off the North Carolina coast. Both species were about equally abundant in the offshore stratum.

Coarsehand lady crabs were collected at temperatures of 6-23°C, but only about 5% occurred at temperatures below 14°C (Fig. 6). The temperature range of this species is narrower than that of the northern lady crab.

As in the other crabs, interannual variations in mean catch-per-tow of coarsehand lady crabs were large. In the years 1979, 1981, and 1984, only about a tenth as many crabs were collected per tow as in the years 1980, 1982, 1985, and 1986 (Fig. 7).

Size frequencies of coarsehand lady crabs (sexes not distinguished) peaked at 7cm (Fig. 8). Wenner and Wenner (1989) reported coarsehand lady crabs from North Carolina to Florida, in depths of 4-20m, with average carapace widths of only 3-4.5cm. Our data showed that in the inshore stratum (<27m), 69% of the crabs were >5cm.

Catches of coarsehand lady crabs were highest at night or twilight in all trawl surveys (Table 3), indicative of nocturnal or crepuscular activity.

According to regression analysis, only temperature was significantly correlated with abundance of coarsehand lady crabs caught by trawl (Table 5). The correlations were smaller than those of northern lady crabs, possibly reflecting the more even distribution of the coarsehand lady crab within its range.

Conclusion

The four most common crab species on the northwest Atlantic shelf have spatial and temporal distributions that are quite different. *Cancer* species occur at higher

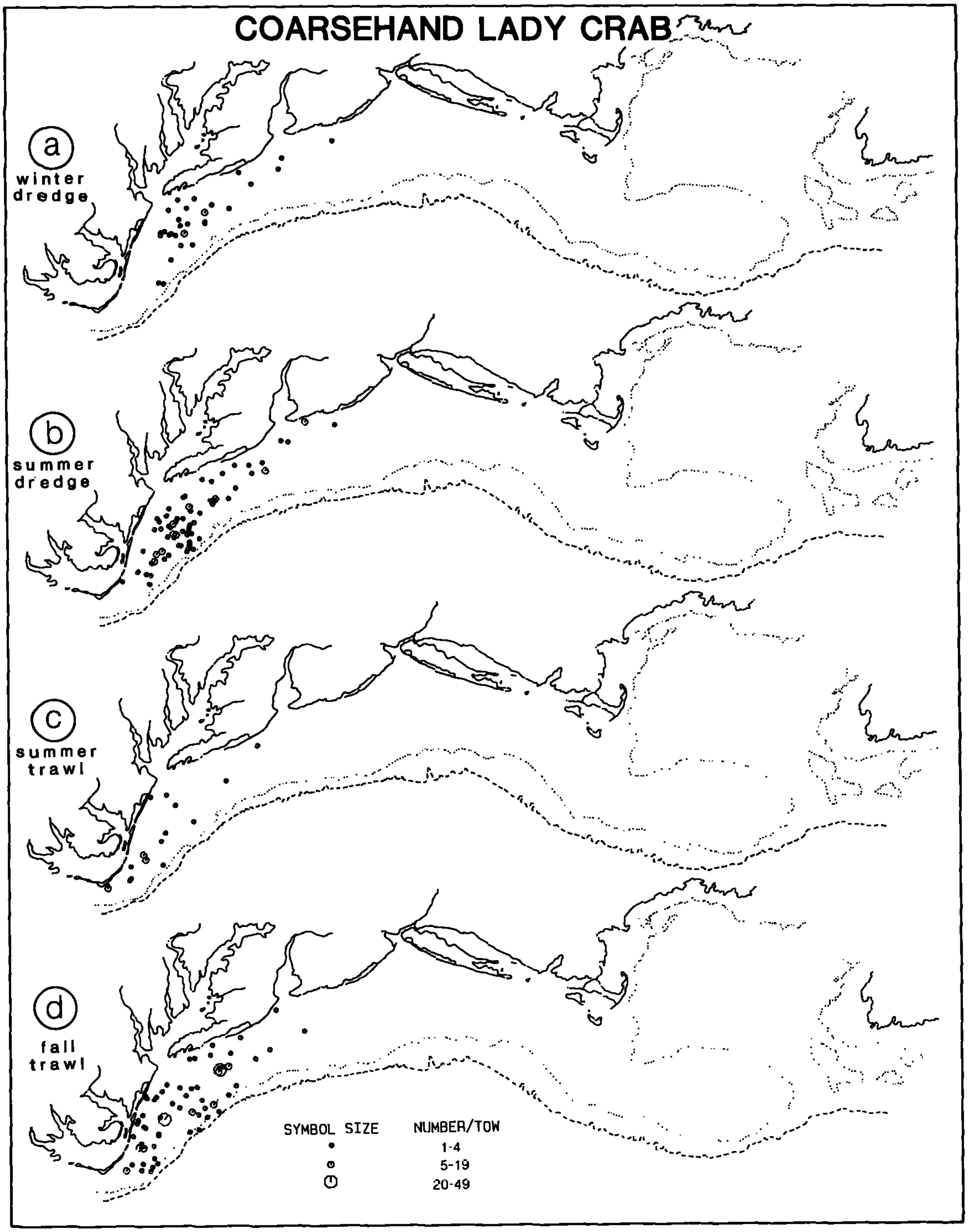

Figure 13
Coarsehand lady crab distribution, from winter dredge, summer dredge, summer trawl, and fall trawl surveys.

latitudes and lower temperatures than *Ovalipes* species. Rock and northern lady crabs are most abundant at inshore strata, but rock crabs are active throughout the year, whereas northern lady crabs are inactive in the winter. Jonah and coarsehand lady crabs are more sparsely distributed in the study area and their abundances are seasonally consistent within each stratum. Depth or temperature, or their interaction, were significantly correlated with abundances of all four crab species.

Substantial gaps in the knowledge of these crabs remain. Temperature appears to affect distributions and migrations, but data to identify critical threshold temperatures are generally lacking. Besides depth and temperature, other factors such as food availability probably affect distribution, but are poorly known. The mean size at maturity for each species, the time of egg release, and locations of settlement and foods of juvenile crabs are scarcely known. Mortality rates of these crabs from fish predation are not known, and a comparison of the relative importance of the crabs with fishes as predators of benthic infaunal invertebrates has not been made.

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