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SKEWED SEX RATIO IN AN ESTUARINE LOBSTER (*HOMARUS AMERICANUS*) POPULATION

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ABSTRACT   A total of 19,485 lobsters were caught at eight sites in the estuarine and coastal waters of New Hampshire from 1989 to 1992, and their size and sex were determined. The sex ratio of lobsters caught farthest from the coast, in Great Bay, was heavily skewed in favor in males. Sex ratios in other estuarine and river sites were also skewed toward males, and there was a tendency for the number of males per female to decline as one moved down the estuary toward the coast, where the sex ratio was nearly 1:1. The single offshore site was dominated by females, with about 0.6 males for each female. There were also seasonal trends in the sex ratios in the upper estuarine sites, where the number of males per female tended to decline from summer through autumn. In general, differences in the sex ratios between sites were those of primarily adult lobsters larger than 80 mm carapace length (CL). At all sites, the sex ratio of lobsters smaller than this size was close to 1:1, whereas in the upper estuary the mean sex ratio of lobsters greater than 80 mm CL was more than 14:1. These data, in conjunction with seasonal variations of sex ratios, suggest that differential movements of adult male and female lobsters is the primary cause of skewed sex ratios in the Great Bay Estuary.

KEY WORDS: Estuary, lobster, *Homarus americanus*, sex ratio

INTRODUCTION

The American lobster, *Homarus americanus* (Milne-Edwards), is broadly distributed in the western north Atlantic from Labrador to North Carolina (Squires 1990). Within this range, the species supports important commercial and recreational fisheries, particularly in New England and the Canadian Maritime provinces. Because of their commercial importance, lobsters have received a considerable amount of attention from the scientific community (see reviews by Cobb and Phillips 1980a, Cobbs and Phillips 1980b, Factor 1995). Not surprisingly, most of these studies have focused on coastal and off-shore populations where lobsters are most abundant.

Although lobsters are considered to be stenohaline, and generally limited to marine ($\geq$25 ppt salinity) habitats (Dall 1970), there are smaller exploited populations found in estuarine habitats (Thomas 1968, Thomas and White 1969, Munro and Therriault 1983, Reynolds and Casterlin 1985, Vetrovs 1990). The physiological ecology and population structure of these lobsters is poorly understood. In recent years, we have been studying one such population located in the Great Bay Estuary of New Hampshire, USA (Jury et al. 1994a, Jury 1994b, Jury et al. 1995, Crossin et al. 1998, Watson et al. 1999). This system, located in the southeastern portion of the state, is characterized by extensive mudflats separated by deep (10–20 m) channels, strong tidal mixing and flushing, and marked seasonal changes in temperature and salinity. Monthly mean temperatures can vary from 0–18°C at the coast, and from 0–25°C in the upper estuary (Loder et al. 1983). The system receives freshwater from seven rivers that drain an area of approximately 2400 km². Salinities in the upper estuary may drop to 10–15 ppt in the spring, as freshets associated with snow and ice melt, and heavy rains enter the system. At the coastal terminus, average salinities are much more stable, typically ranging from 30–33 ppt (Loder et al. 1983).

Among the data we have gathered is information on sex ratio by location, season, and size class. The sex ratio of many geographically separate American lobster populations has been reported. Although most coastal lobsters populations that have been examined approximate the expected 1:1 ratio (Cooper 1970, Stew-

art 1972, Krouse 1973, Cooper et al. 1975, Pecci et al. 1978), there are several instances where skewed ratios have been observed. These include reports of populations with more males than females (Briggs and Mushacke 1979, Munro and Therriault 1983, Karnofsky et al. 1989), as well as reports of populations with more females than males (Skud and Perkins 1969, Estrella and McKiernan 1989). Explanations for these skewed sex ratios have included differential catchability (Krouse and Thomas 1975, Fogarty and Borden 1980, Miller 1990, Tremblay and Eagles 1997), segregation of the sexes by depth (Skud and Perkins 1969, Briggs and Mushacke 1979), differences in migratory behavior (Munro and Therriault 1983), physiological and behavioral differences between the sexes (Jury et al. 1994a, Jury et al. 1994b), and fisheries regulations that protect some females (Estrella and McKiernan 1989). In this paper, we report consistent spatial differences in lobster sex ratio within a New England estuary, and differences in sex ratio between size classes of lobsters found in upper estuarine areas.

MATERIALS AND METHODS

The Great Bay estuarine system lies in the southeastern corner of New Hampshire, USA. It receives freshwater from seven rivers, which mixes with saltwater entering from the western Gulf of Maine. Lobsters were sampled at eight sites in the estuarine and coastal waters from 1989 to 1992 (Fig. 1). These spanned a distance (by water) of approximately 37 km, ranging from Great Bay proper, which is about 26 km inland, to the Isles of Shoals, which lie 11 km offshore. The eight sites fall into three broader spatial categories, which we have arbitrarily designated as "estuarine" (Great Bay, Little Bay, Bellamy River), "riverine" (upper, mid-, and lower Piscataqua River), and "coastal" (Coast, Isles of Shoals). Along this line of sites, physical and chemical characteristics vary from those of a typical New England estuary (greatly fluctuating temperature and salinity, strong tidal mixing, soft substrate) to those of a typical New England coast (relatively stable temperature and salinity, less tidal current, and harder substrates of cobble and rock).
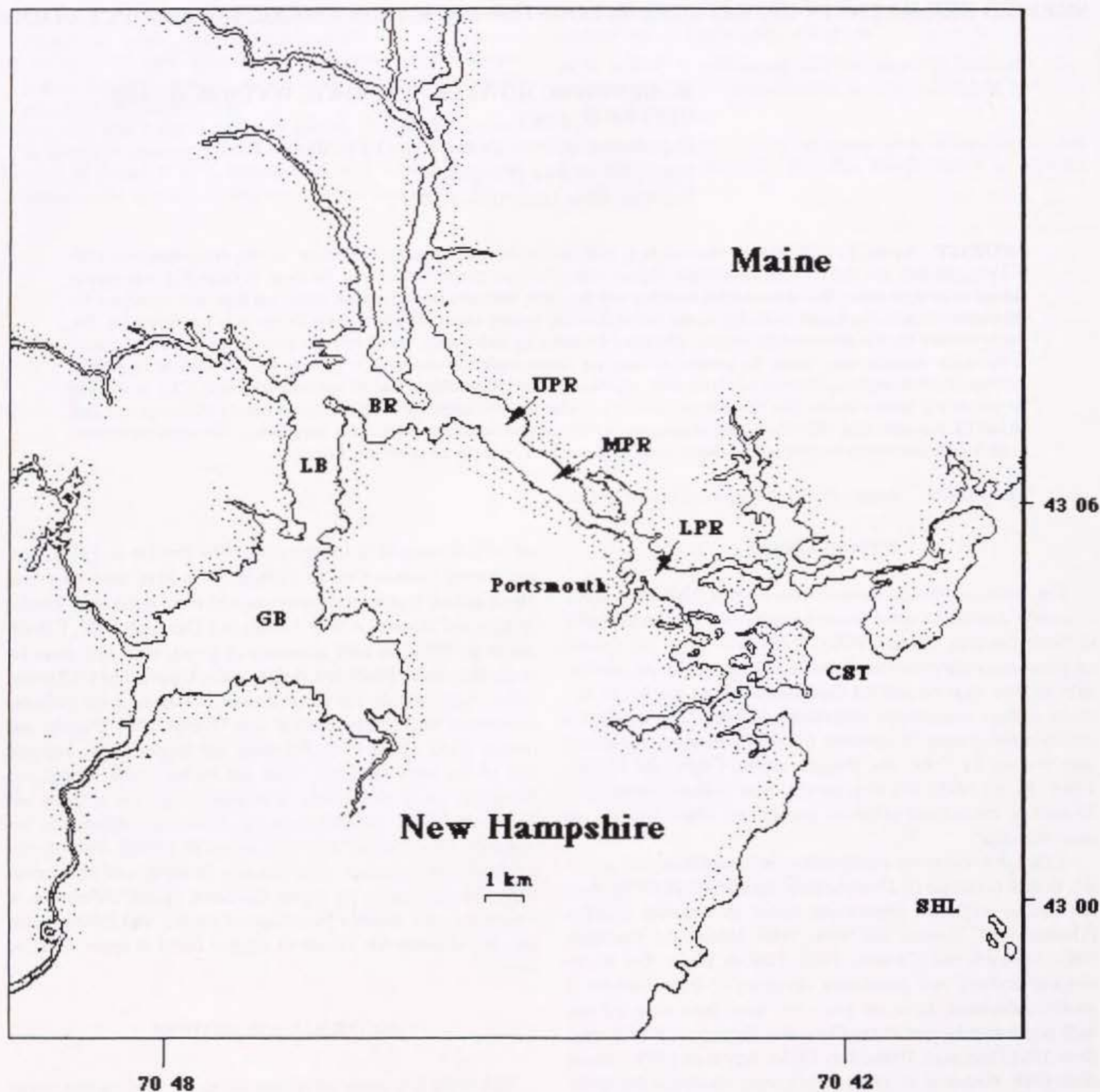
Figure 1. Location of the study sites within the estuarine and coastal waters of New Hampshire. GB (Great Bay), LB (Little Bay), BR (Bellamy River), UPR (Upper Piscataqua River), MPR (Middle Piscataqua River), LPR (Lower Piscataqua River), CST (Coast), SHL (Shoals).

All lobsters were caught in traps baited with herring and tended two to three times per week. Most were caught in our own traps as part of a larger study on estuarine lobsters, but many were caught by commercial lobstermen with whom we fished, and a small number were caught by the New Hampshire Department of Fish and Game. All traps from which we collected data were made of vinyl-coated wire, equipped with one or two escape vents (1 7/8" H × 6" W), and had either a single (research traps) or double parlor (commercial traps). Although winter sampling was limited because of upper estuarine ice cover and general lack of commercial fishing activity, we were able to sample all sites adequately during the spring (April–June), summer (July–September), and autumn (October–December) in most years. All lobsters had their carapace length (CL) and abdomen width measured to the nearest millimeter, all were molt-staged using external shell criteria and/or pleopods (Aiken 1973, Aiken 1980), and all were sexed by examining the first pair of pleopods (Templeman 1944). Most were also tagged, before release, with numbered modified sphyrion tags (Scarratt 1970), because in another part of the study, we were examinine movement and growth (Watson et al. in press).

At each study site, except the Shoals, both temperature and salinity (YSI Meter Model 33) were measured at the surface each time our traps were hauled. In 1991, data were collected from surface and bottom waters. There was always <2°C and 2 ppt difference between surface and bottom values because of extensive vertical mixing (Loder et al. 1983).
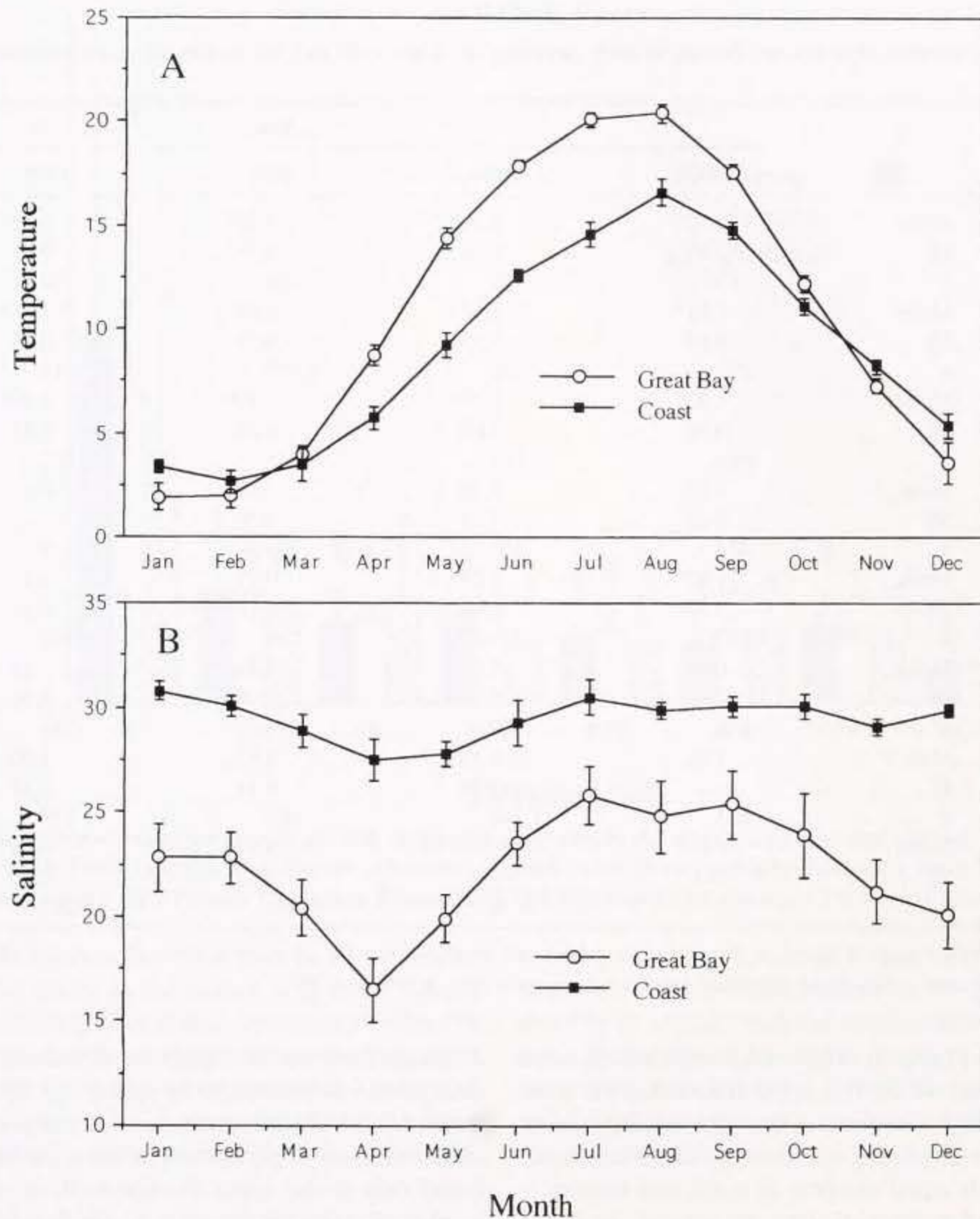
Figure 2. Mean (±SE) monthly temperatures (°C) and salinities (ppt) at the Great Bay and Coastal sites from 1989 to 1992.

The null hypothesis of equal numbers of males and females was, in all cases, tested using chi square analysis. Comparisons of sex ratio between sites, and between seasons within sites, were done using one-way analysis of variance (ANOVA) followed by Tukey's posterior test. Mann–Whitney U tests were used to compare the sizes of males and females at each site within each year. The alpha level for all statistics was 0.05.

RESULTS

Mean monthly temperature and salinity, from 1989 to 1992, at two of our sites is depicted in Fig. 2. In the upper estuary (Great Bay site, GB), mean monthly temperatures were 3–7°C warmer than the Coastal (CST) site from April through October (Fig. 2a). Mean salinity in Great Bay was highest in late summer (approx. 27 ppt), and lowest (approx. 16 ppt) in the spring when freshwater input was more abundant because of heavy rains and snowmelt. At the Coastal site, the salinity was relatively constant throughout the year (Fig. 2b). As expected, both temperatures and salinities at the sites that occur between Great Bay and the Coast are intermediate

to those depicted. Although complete temperature and salinity records are not available from the Isles of Shoals, the small amount of data available indicates this site is very similar to the Coastal site, located approximately 11 km away.

Observed mean sex ratios, from 1989 to 1992, at each of the sampling sites are given in Table 1. Although there was some interannual variation at each site, in each of the estuarine sites (Great Bay, Little Bay, Bellamy River), there were significantly more males than females in every year (p < .05). In the riverine sites (upper-, mid-, lower Piscataqua River) and at the Coast, the numbers of males and females were more nearly equal. However, even at these sites, there were significantly more males than females in some years (Upper Piscataqua River 1991; mid-Piscataqua River 1989, 1990; lower Piscataqua 1991; Coast 1990). As with the other sites, there are some interannual variation in sex ratio at the Isles of Shoals, but in each year for which data were available, there were significantly more females than males (p < .05).

When the data from all years and seasons were combined, sex ratio departed significantly from the expected 1:1 ratio in seven of

TABLE 1.

Mean number of males per female at each sampling site from 1989 to 1992 and in all years combined.

Site			Year			
		1989	1990	1991	1992	All Years
Great Bay	Mean	6.92*	5.32*	5.88*	3.03*	5.29*
	SE	2.65	0.86	3.28	0.53	0.82
	n	83	136	358	130	707
Little Bay	Mean	1.81*	1.86*	2.04*	1.68*	1.85*
	SE	0.15	0.12	0.39	0.14	0.07
	n	297	876	1,165	516	2,854
Bellamy R.	Mean	1.32*	1.32*	2.30*	1.56*	1.63*
	SE	0.16	0.01	0.37	0.37	0.63
	n	614	1,318	1,236	902	4,070
Upper Pisc. R.	Mean	1.27	1.29	1.39*	———	1.31*
	SE	0.21	0.19	0.20	———	0.04
	n	486	316	724	0	1,526
Middle Pisc. R.	Mean	1.42*	1.28*	0.95	0.93	1.14*
	SE	0.10	0.05	0.16	0.15	0.12
	n	1,197	1,210	489	342	3,238
Lower Pisc. R.	Mean	0.89	1.02	1.44*	1.11	1.12
	SE	0.16	0.06	0.08	0.02	0.12
	n	278	480	244	284	1,286
Coast	Mean	1.02	1.33*	1.22	1.00	1.18*
	SE	———	0.24	0.14	0.12	0.08
	n	253	1,248	463	777	2,488
Shoals	Mean	0.64*	———	0.52*	0.56*	0.57*
	SE	———	———	0.07	0.06	0.03
	n	222	0	1,893	1,201	3,316

Mean and standard error within years is based on three seasons. Mean and standard error for all years is from all years and all seasons combined. (n) = number examined; * denotes a significant departure from a 1:1 sex ratio (chi square, $p < .05$).

the eight sampling sites (Table 1). There were significantly more males than females in each of the five upper sites and at the coast ($p < .05$), and significantly more females than males at the Isles of Shoals ($p < .05$). In the remaining site (lower Piscataqua River) there were approximately equal numbers of males and females.

Using the aggregate data from all years and seasons, we found that the mean number of males per female in Great Bay (5.29) was significantly higher ($p < .001$) than every other site. Although there was a tendency for the number of males per female to decline as one moved toward the coast (Table 1), there was no significant difference in the mean sex ratio among these other sites ($p > .05$). This same tendency was also observed in each of the three upper estuarine sites. Although there was some interannual variation in each of these sites, in each year except 1991, sex ratio declined as one moved down the estuary from Great Bay to Little Bay to the Bellamy River. Unlike the three upper estuarine sites, there was no obvious clinical trend in sex ratio found in the riverine and coastal sites. The Shoals site, however, had the lowest mean sex ratio of all sites in each of the years for which we had data (Table 1).

In addition to the observed spatial differences in sex ratio, there were also some seasonal trends observed (Fig. 3). At the Great Bay site, there was a considerable amount of interannual variation within seasons. Although the mean number of males per female tended to be highest in the spring (6.37), and then to decline through the summer (5.45) and autumn (4.38), there were no significant differences ($p > .05$) between seasons. A similar, but less pronounced pattern was observed in Little Bay, but again, there were no significant differences between seasons ($p > .05$). Interestingly, at the Bellamy River site, the seasonal trend was reversed.

Although there was no significant difference between seasons, sex ratio tended to increase from spring (1.42), to summer (1.50), to autumn (1.84). Seasonal trends were much less pronounced at the other five sites. Significant seasonal differences in sex ratio were found only at the upper Piscataqua River site, where the mean number of males per female was significantly higher ($p < .001$) in the spring (1.71) than in either summer (1.10) or autumn (1.13), between which there was no significant difference ($p > .05$).

The mean size (CL) of male and female lobsters at each site and year is given in Table 2. In general, the mean size of males were significantly larger than that of females in the three upper estuarine locations. In the Piscataqua River sites, males and females were more similar in mean size. The only significant differences were found in the middle Piscataqua River, in 2 of the 4 years, and in the lower Piscataqua River, in 1 of the 4 years. In each of these instances, males were larger than females. At the coastal site, the mean size of males was larger than that of females in 1989; whereas the reverse was true in 1990. No difference in mean size was found in the remaining 2 years. Finally, at the Isles of Shoals site, where we had only 3 years of data, females were significantly larger than males in two of these (1989, 1992), but not in the other (1991).

Sex ratio varied with size class at certain sites (Table 3). The site where the change in ratio with size class was most pronounced was in Great Bay, which is the site farthest up the estuary. In the other estuarine sites (Little Bay and Bellamy River), males also tended to dominate the larger size classes, but not to the same extent as in Great Bay. In the riverine sites, there tended to be more males than females in many size classes, but the sex ratio was most
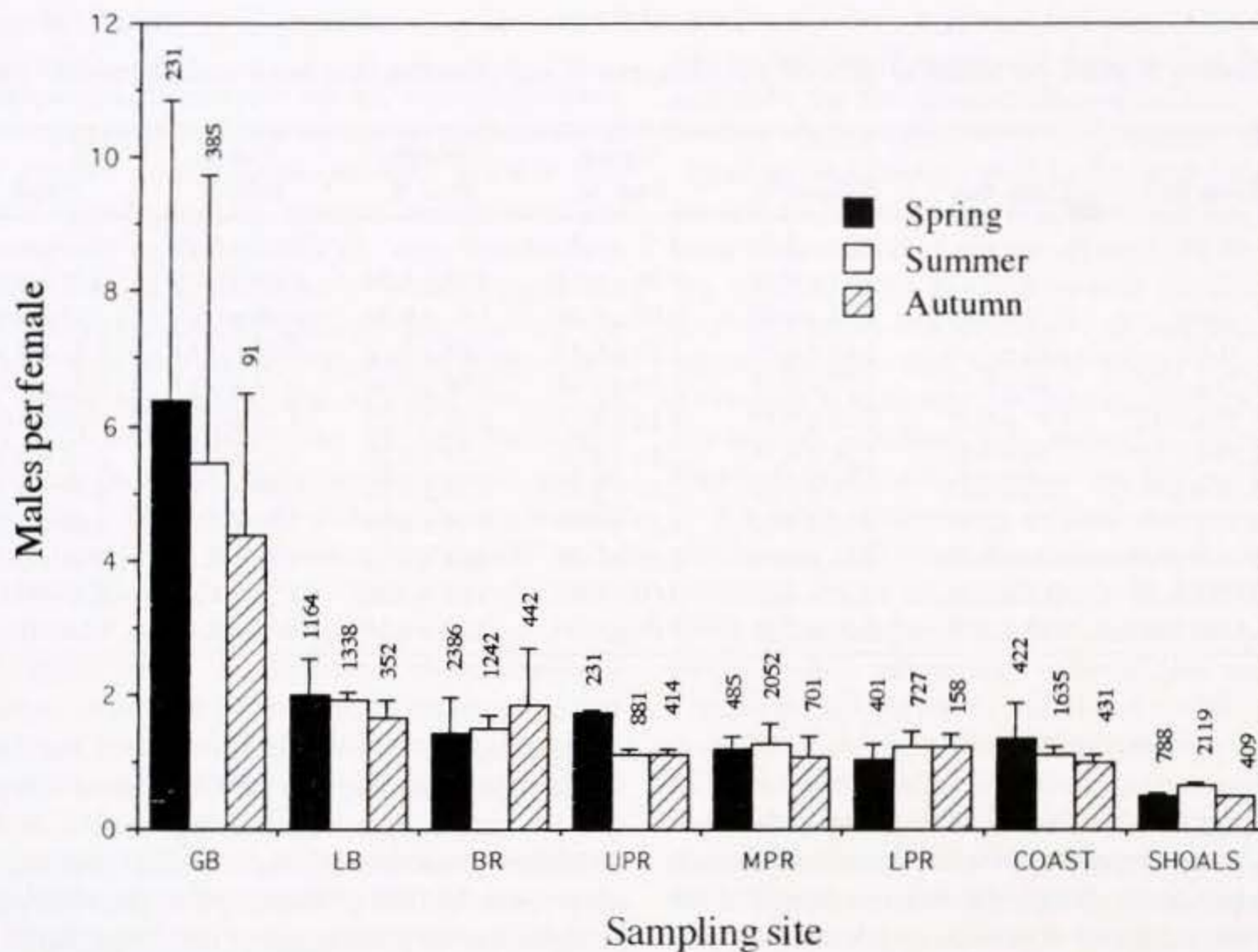
Figure 3. Mean (±SD) number of males per female at each of the sampling sites in the spring, summer, and autumn. Means are based on the 4 years included in the study (1989 to 1992). The number of lobster examined (*n*) is given vertically above each error bar. GB (Great Bay), LB (Little Bay), BR (Bellamy River), UPR (Upper Piscataqua River), MPR (Middle Piscataqua River), LPR (Lower Piscataqua River).

heavily skewed toward males in the largest (>85 mm CL) size classes. This was particularly true at the uppermost riverine site (upper Piscataqua), and, to a lesser extent, the middle Piscataqua site. At the coastal site, there was a less pronounced pattern of change in sex ratio with size class. There tended to be more males than females in the smaller size classes (<70 mm), about equal

numbers of males and females in the 71–90 mm size classes, and about twice as many males as females in the largest size class (>90 mm). At the Isles of Shoals site, however, there were consistently fewer males than females in all of the larger size classes (>65 mm), and the same number, or more, males than females in the smaller size classes.

TABLE 2.

Mean (and standard deviation) carapace length (mm) of male and female lobsters at each site in each year, and in all years combined.

Site	1989		1990		1991		1992		All Years	
	M	F	M	F	M	F	M	F	M	F
Great Bay	80.7*	71.2	81.3*	75.5	83.7*	78.7	77.7	76.7	82.3*	77.4
SD =	9.6	16.7	7.2	7.2	8.1	5.8	7.8	2.8	8.3	7.5
Little Bay	78.1*	74.9	75.3	73.5	81.7*	78.3	78.3*	76.0	80.0*	76.0
SD =	6.7	8.6	6.4	7.2	6.9	6.3	7.7	7.5	7.3	7.3
Bellamy River	73.6*	72.0	74.4*	72.0	80.4*	76.0	79.8*	76.8	76.6*	73.3
SD =	10.7	10.4	8.4	8.4	8.2	7.0	8.5	6.8	9.2	8.7
Upper Piscat. R.	51.7	53.7	53.0	50.9	75.1	74.8	No data	No data	57.6	57.2
SD =	14.7	14.2	13.3	13.4	9.5	6.5			16.2	15.6
M. Piscat. R.	72.2	71.7	74.9*	73.5	77.0*	75.3	78.1	70.4	73.9*	73.1
SD =	7.0	7.7	7.7	7.6	6.7	6.8	8.2	12.2	7.4	7.6
L. Piscat. R.	76.5*	74.3	65.3	63.9	72.2	70.3	78.0	80.9	70.0	68.5
SD =	8.8	10.8	12.4	12.3	11.9	13.2	7.7	8.6	12.4	12.9
Coast	77.7*	76.5	71.9*	74.4	75.5	75.2	75.1	67.5	74.1	74.9
SD =	5.5	5.1	13.2	11.8	9.7	10.4	3.9	16.4	11.3	10.6
Shoals	75.4*	80.1	No data	No data	79.6	80.1	80.1*	81.4	79.5*	80.6
SD =	5.8	11.9			7.5	7.6	8.4	8.7	7.8	8.3

* Between male and female lengths within a year and site indicates that the mean lengths of the two sexes are significantly different (Mann–Whitney U test, p < .05). Sample sizes are given in Table 1.

TABLE 3.

Mean (±SE) number of males per female in different size categories at each sampling size, based on data collected over 4 years.

Carapace Length (mm)	Great Bay	Little Bay	Bellamy R.	Upper Pisc. R.	Middle Pisc. R.	Lower Pisc. R.	Coast	Shoals
=<40	1.00	——	1.21 ± 0.49	1.52 ± 0.22	——	0.71 ± 0.20	0.93 ± 0.05	——
41–45	——	1.00	0.77 ± 0.19	1.29 ± 0.17	0.67 ± 0.29	0.55 ± 0.25	0.25 ± 0.17	——
46–50	——	0.75 ± 0.25	1.33 ± 0.47	0.90 ± 0.28	1.17 ± 0.96	0.68 ± 0.31	2.5 ± 0.90	1.5 ± 0.35
51–55	1.00	1.85 ± 1.06	1.14 ± 0.19	1.25 ± 0.43	1.45 ± 0.22	0.69 ± 0.19	1.31 ± 0.17	3.50 ± 1.77
56–60	1.33 ± 0.29	0.47 ± 0.22	1.27 ± 0.14	1.39 ± 0.23	0.96 ± 0.31	0.76 ± 0.15	1.23 ± 0.14	1.50 ± 0.35
61–65	1.75 ± 0.48	1.42 ± 0.27	1.16 ± 0.12	1.19 ± 0.17	0.99 ± 0.22	1.23 ± 0.20	1.65 ± 0.09	0.95 ± 0.19
66–70	2.38 ± 0.69	1.45 ± 0.15	1.34 ± 0.19	1.14 ± 0.26	1.21 ± 0.09	1.02 ± 0.18	1.35 ± 0.26	0.75 ± 0.16
71–75	3.00 ± 0.75	1.28 ± 0.15	0.79 ± 0.09	1.17 ± 0.23	1.14 ± 0.32	0.98 ± 0.25	0.97 ± 0.10	0.60 ± 0.02
76–80	3.42 ± 0.70	1.94 ± 0.20	1.38 ± 0.22	1.13 ± 0.06	1.16 ± 0.15	1.28 ± 0.09	1.08 ± 0.09	0.49 ± 0.01
81–85	12.82 ± 5.68	2.74 ± 0.28	2.53 ± 0.41	1.69 ± 0.17	1.11 ± 0.12	1.38 ± 0.18	0.98 ± 0.20	0.62 ± 0.03
86–90	9.05 ± 1.78	3.9 ± 0.34	5.12 ± 2.03	7.00 ± 0.00	3.05 ± 1.04	1.79 ± 1.21	0.93 ± 0.17	0.58 ± 0.04
>90	14.5 ± 5.48	6.43 ± 3.05	9.11 ± 2.41	3.00 ± 0.00	2.19 ± 1.28	0.80 ± 0.14	2.2 ± 1.08	0.55 ± 0.03

DISCUSSION

Results of this study indicate that this estuarine population of lobsters departs, in many ways, from the expected 1:1 sex ratio typical of coastal populations. Among the most consistent of our findings was the observed spatial difference in sex ratio. In each season of each year, the upper estuary had more males than females. This skewed ratio tended to decrease, in a clinal fashion, as one moved down the estuary toward the coast, where the sex ratio approximated the expected 1:1 ratio. Surprisingly, this clinal trend continued outside the estuary, so that at the Isles of Shoals, which is located about 11 km from the mouth of the estuary, there were consistently more females than males (Table 1).

Lobster populations with skewed sex ratios have been reported by others (Skud and Perkins 1969, Briggs and Mushacke 1979, Munro and Therriault 1983, Campbell and Pezzack 1985, Karnofsky et al. 1989, Estrella and McKiernan 1989), and several explanations have been put forth to explain the disparity between numbers of males and females. Fishery-related factors, including differential catchability of males and females (Miller 1990, and regulations that protect some (e.g., ovigerous, V-notched) females (Estrella and McKiernan 1989), can result in skewed sex ratios. Differential catchability of the sexes is an unlikely explanation for our results, because Becker (1994), who also worked in the Great Bay estuarine system, found sex ratios virtually identical to ours using SCUBA sampling. Furthermore, if males and females differed in their trapability, as suggested by Fogarty and Borden (1980), Miller (1990), and Campbell (1992), we would have expected skewed sex ratios in all of our study sites because the same types of traps, including identically sized escape vents, were used at all locations. It is possible, however, that the skewed ratio favoring females at the Isle of Shoals may have resulted from differences in mean size, and therefore, trapability, of the sexes. When data from the 2 years were combined, females were significantly larger than the males (Table 2). It has been suggested that female lobsters in some areas (Rhode Island) have a proportionately wider carapace width than similarly sized males (Fogarty and Borden 1980). This difference in body proportion between the sexes may not be geographically universal, however, because Krouse and Thomas (1975) found no significant differences in the carapace length–width ratios of males and females along the Maine coast. If females in our study area do have a proportionately wider carapace, they would not move as readily through escape vents, so it is possible that the larger mean size of the females at this site influenced sex ratio in the catch. It is also possible that regulatory protection of certain females may explain the sex ratio observed at the Isles of Shoals, where females outnumbered males. At this location, percentages of ovigerous and V-notched females (5–12%) are relatively high as compared to the estuary (<1%) (Howell, W. H. & W. H. Watson. Dept. of Zoology, Univ. of New Hampshire, Durham, NH 03824. Unpubl. data). Thus, both size and protective management may explain the preponderance of females at the Isles of Shoals, but it is also possible that this site simply has a distinctive physical habitat that has resulted in an aggregation of females such as that reported by Campbell (1990).

Ecological factors may also affect sex ratio. Skud and Perkins (1969) and Briggs and Mushacke (1979) found a segregation of the sexes by depth, while Karnofsky et al. (1989) suggested that intraspecific competition effected sex ratio. Our sampling locations were similar in depth (≈3–10 m), so it is highly unlikely that our observations resulted from segregation of the sexes by depth. It is also unlikely that intraspecific competition was a factor. Karnofsky et al. (1989) found that there were nearly twice as many males as females in a small, shallow cove in Buzzards Bay, MA, USA and that a disproportionately large proportion of the males were missing one or more claws. The authors suggested that the cove may function as a refuge for injured males, and that these individuals had been displaced to this shallow water site by aggressive, intraspecific competition for mating shelters. Moreover, they suggested that the relative paucity of females at their study site resulted from the preference of females for deeper areas where the dominant males held mating shelters. We have no information about where mating occurs in our study area, including the depth of mating shelters and whether or not the spatial distribution of females is affected by the distribution of dominant males. Thus, it is possible that the mechanism described by Karnofsky et al. (1989) may be applicable to this study, but it is doubtful, because we saw no indication that the proportion of males missing claws differed among sites (Howell and Watson).

The spatial and temporal trends of the data in this study indicate that sex ratio may be associated with seasonally changing gradients of salinity and/or temperature that are typical of northern estuaries. In particular, it is likely that male and female lobsters differ in their physiological and behavioral responses to salinity

and/or temperature and that these differences result in the sex ratio patterns we observed.

Water temperature affects many, if not all, aspects of lobster biology. In a laboratory study, Crossin et al. (1998) documented that lobsters are capable of sensing temperature, and that they behaviorally thermoregulate; seeking preferred temperatures and avoiding water that is either too warm or too cool. Results from related studies, also done in our laboratory, further suggest that males and females may respond differently to changing temperature. In one study, 75% of females, but only 50% of males, exited their shelters as shelter temperature was increased (Jury, S. H. Dept. of Zoology, Univ. of New Hampshire, Durham, NH 03824. Unpubl. data); whereas in another study, in which males and females were placed in a thermal gradient tank, males generally preferred warmer temperatures than females, particularly in the spring and fall, when ambient temperatures were seasonally lower (Jury, S. H. The effect of acclimation temperature and sex on the behavioral thermoregulation of the American lobster, *Homarus americanus*. In prep.). Although these data are preliminary, they suggest that males and females differ in their temperature preferences, and that spatial and temporal differences in temperature could thus affect sex ratio.

Although laboratory studies on temperature are relatively scarce, numerous field studies have documented that water temperature affects the temporal and spatial distribution of lobsters, and that males and females differ in their movements in response to seasonally changing temperatures (Munro and Therriault 1983, Roddick and Miller 1992, Lawton and Lavalli 1995, Estrella and Morrisey 1997). It has been suggested, for example, that seasonal onshore–offshore migrations are associated with temperature selection, and are adaptive for accelerating growth and egg development (Saila and Flowers 1968, Cooper and Uzmann 1971, Pezzack and Duggan 1986, Estrella and Morrissey 1997). This may also be true, on a geographically smaller scale, for seasonal migrations that occur within New England estuaries, including Great Bay (Watson et al. 1999). Differential migration of the sexes, associated with seasonal changes in water temperature, can also effect sex ratio. Roddick and Miller (1992) found, for example, that males and females arrived at, and departed from, a small embayment in Nova Scotia in different months, and these differences in seasonal movements resulted in skewed sex ratios. Adult females have also been reported to move to deeper water earlier in the autumn than males (Campbell and Stasko 1986, Robichaud and Campbell 1991), which results in temporal and spatial segregation of the sexes. Munro and Therriault (1983) found more males than females in estuarine locations in the Magdelaine Islands, and speculated that this resulted from differential migration of the sexes. Both sexes left the estuaries as temperatures cooled in the autumn, but males were more likely to return in the spring as temperature increased. A similar situation may exist in the Great Bay Estuary. In a study concurrent with this one, Watson et al. (1999) documented that lobsters tended to migrate up the Great Bay Estuary in the spring as temperatures increased, and down the estuary in the summer and autumn. Although Watson et al. saw no marked differences in the movements of males and females, their data were somewhat equivocal on this point, and they suggested that differential movement of the sexes was possible. Munro and Therriault (1983) suggested that the reason for males returning earlier than the females was to take advantage of the warmer temperatures of the estuarine sites for molting. Indeed, they found that all males <75 mm CL molted twice each year.

It has also been suggested that there are seasonal differences in the catchability of males and females, that these differences are caused by the two sexes molting at different times, and that differential catchability results in seasonally changing sex ratios (Tremblay and Eagles 1997). In the Great Bay Estuary, however, we saw no evidence that males and females molted at different times or in different locations (Howell and Watson unpubl. data). We conclude from this that there is no difference between the sexes in location and temperature of molting. Thus, although our skewed sex ratios may indeed be related to temperature-mediated differences in movement between the sexes, it seems unlikely that it is strongly correlated with molting, as suggested by Munro and Therriault (1983) and Tremblay and Eagles (1997).

A number of laboratory and field studies have documented that salinity can also effect the temporal and spatial distribution of lobsters. Lobsters are considered to be poor osmoregulators (Dall 1970), and several previous field studies have shown that lobsters use behavioral mechanisms to avoid low salinities (Munro and Therriault 1983, Reynolds and Casterlin 1985, Maynard 1991, Jury et al. 1995). In a recent laboratory investigation Jury et al. (1994a) measured hemolymph osmolarity, oxygen consumption, heart rate and ventilation rate of lobsters under salinity regimes similar to those found in the Great Bay Estuary under spring runoff conditions. They found that exposure to decreasing salinity (from 20 to 10 ppt) caused an increase in oxygen consumption, heart, and scaphognathite rate. At the lowest salinity (10 ppt), females required more energy than males to maintain the same hemolymph osmolarity. Females also recovered more slowly than males as salinities were subsequently increased. This study has been confirmed by Houchens (1996), and extended to show that female lobsters suffer significantly more mortality than males when held at 5–10 ppt. For this reason, upper estuarine locations where salinities are the lowest, particularly in the spring, probably represent a stressful and potentially lethal environment for females. In a second set of experiments, Jury et al. (1994b) measured the behavioral response of lobsters to reductions in salinity. When given a choice of salinity, females were more selective in their preference for higher salinity, and females found low salinities more aversive than did males. Results from these studies indicate that lobsters respond to changes in salinity, that male and female lobsters differ in their physiological and behavioral responses, so that males find low salinity less aversive and less stressful. It is likely that these differences partially explain the observed skewed sex ratios found in this study. In general, we found an inverse relationship between lobster sex ratio and salinity. Physiological and behavioral differences in the way each sex responds to salinity could also explain the seasonal trends in sex ratio that we observed. The number of males per female was highest in the spring in the upper estuary, when salinities were lowest, and then declined over summer as salinities increased. We believe that the observed reduction in sex ratio was caused by the arrival of more females as salinity increased in these areas.

Aside from the physiological and/or behavioral reasons already discussed, it is possible that the observed spatial pattern in sex ratio may also relate to the reproductive biology of lobsters. Because lobster embryos and larvae are quite vulnerable to low (<14 ppt) salinity (Scaratt and Raine 1967, Charmantier et al. 1998, Forward 1989), relatively low salinity environments, such as those in the upper estuary, may be suboptimal for reproduction. Unpublished data on the distribution of ovigerous females in this study support this view (Howell and Watson). We caught and examined 8,153

female lobsters as part of this study, and 168 of these (2.06%) were ovigerous. Of these 168, only 43 were caught in the estuarine and riverine sites, and the remaining 125 were from the Coast and Shoals. The low incidence of ovigerous females in the estuary is similar to the situation reported for blue crabs in the upper Chesapeake Bay by Hines et al. (1987), and it is likely that ovigerous females avoid the low salinity conditions of the estuary, because salinity is generally too low for larval survival. Note, however, that Munro and Therriault (1983) found a higher percentage of ovigerous females (13–16%) in estuaries than they did at the coast (7%). The difference between their study and ours may have resulted from the fact that our upper estuarine salinities are typically as low as 10–15 ppt in any given year; whereas the lowest reported by Munro and Therriault was 22 ppt.

We also found that sex ratio was more skewed in larger size classes (>80 mm CL) in all of our estuarine and riverine locations. Changes in American lobster sex ratio with size class have also been noted by Karnofsky et al. (1989). They found that females dominated the 50–59 mm CL size class, but that males were more numerous than females in size classes ≥60 mm CL. As a result, males were not only more common, they were also larger. We believe that the observed changes in sex ratio with size class are related to changes in mobility with size. Wahle and Steneck (1992) suggested that small lobsters (≤≈60 mm CL) are dependent on their shelters to avoid predation, but that this vulnerability is eventually outgrown, and lobsters ≥≈60 mm CL are able to move about more freely, because they are virtually immune to predation. Once this release has occurred, mobility generally increases as lobsters continue to increase in size (Campbell and Stasko 1986, Campbell 1989). The fact that both mobility and skewness in sex ratio increase with size class indicates that changes in sex ratio with size may result from differential movement of the sexes. When small, both sexes move little, and sex ratio is approximately 1:1. As size (and mobility) increase, males, which are more tolerant of low salinity than females, may travel further up the estuary, especially in the spring, resulting in the predominance of males in the larger

size classes in this location at this time. Studies are currently underway to determine if the aforementioned differences in the behavior of male and female lobsters exist, even in the smaller size classes, or if they manifest themselves only as they reach sexual maturity. If the latter situation is true, it supports the view that the strongest influence on female migratory behavior in the estuary is related to reproduction and the seeking of appropriate habitats for hatching of larvae. In the Great Bay Estuary, ovary dissections indicate that approximately 50% of females have reached sexual maturity of 80 mm CL (Howell and Watson unpl. data), and it is in size classes greater than this that we observe the most skewed sex ratios.

In summary, we believe that the skewed sex ratio patterns we observed in this study resulted from differential movement of the sexes; probably in response to salinity and temperature cues. Both sexes tend to move down the estuary in the summer and autumn. Males, which are more tolerant of low salinity and warmer temperatures, return to upper estuarine areas earlier than females in the spring, which accounts for the elevated sex ratio seen in these locations. Although some females move up the estuary as salinity rises, thereby making the sex ratio more nearly equal, more females than males remain in the lower estuary, because they are less tolerant of low salinity and warmer temperatures, and/or because it is a more favorable (higher salinity) location to release their larvae. The fact that sex ratio is most skewed among the largest size classes, which are also the most mobile, supports our contention that skewed sex ratio in our study site results from differential movement of the sexes.

ACKNOWLEDGMENTS

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SKEWED SEX RATIO IN AN ESTUARINE LOBSTER (HOMARUS AMERICANUS) POPULATION

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ABSTRACT A total of 19.485 lobsters were caught at eight sites in the estuarine and coastal waters of New Hampshire from 1989

to 1992. and their size and sex were determined. The sex ratio of lobsters caught farthest from the coast, in Great Bay. was heavily

skewed in favor in males. Sex ratios in other estuarine and river sites were also skewed toward males, and there was a tendency for

the number of males per female to decline as one moved down the estuary toward the coast, where the sex ratio was nearly 1:1. The

single offshore site was dominated by females, with about 0.6 males for each female. There were also seasonal trends in the sex ratios

in the upper estuarine sites, where the number of males per female tended to decline from summer through autumn. In general,

differences in the sex ratios between sites were those of primarily adult lobsters larger than 80 mm carapace length (CL). At all sites,

the sex ratio of lobsters smaller than this size was close to 1:1, whereas in the upper estuary the mean sex ratio of lobsters greater than

80 mm CL was more than 14:1. These data, in conjunction with seasonal variations of sex ratios, suggest that differential movements

of adult male and female lobsters is the primary cause of skewed sex ratios in the Great Bay Estuary.

INTRODUCTION

The American lobster. Homarus americanus (Milne-Edwards),
is broadly distributed in the western north Atlantic from Labrador
to North Carolina (Squires 1990). Within this range, the species
supports important commercial and recreational fisheries, particu-
larly in New England and the Canadian Maritime provinces. Be-
cause of their commercial importance, lobsters have received a
considerable amount of attention from the scientific community
(see reviews by Cobb and Phillips 1980a, Cobbs and Phillips
1980b, Factor 1995). Not surprisingly, most of these studies have
focused on coastal and off-shore populations where lobsters are
most abundant.

Although lobsters are considered to be stenohaline, and gener-
ally limited to marine (>25 ppt salinity) habitats (Dall 1970), there
are smaller exploited populations found in estuarine habitats
(Thomas 1968, Thomas and White 1969, Munro and Therriault
1983. Reynolds and Casterlin 1985. Vetrovs 1990). The physi-
ological ecology and population structure of these lobsters is
poorly understood. In recent years, we have been studying one
such population located in the Great Bay Estuary of New Hamp-
shire, USA (Jury et al. 1994a, Jury 1994b, Jury et al. 1995. Crossin
et al. 1998, Watson et al. 1999). This system, located in the south-
eastern portion of the state, is characterized by extensive mudflats
separated by deep (10-20 m) channels, strong tidal mixing and

flushing, and marked seasonal changes in temperature and salinity. Monthly mean temperatures can vary from 0-18°C at the coast, and from 0-25°C in the upper estuary (Loder et al. 1983). The system receives freshwater from seven rivers that drain an area of approximately 2400 km 2 . Salinities in the upper estuary may drop to 10-15 ppt in the spring, as freshets associated with snow and ice melt, and heavy rains enter the system. At the coastal terminus, average salinities are much more stable, typically ranging from 30-33 ppt (Loder et al. 1983).

Among the data we have gathered is information on sex ratio by location, season, and size class. The sex ratio of many geographically separate American lobster populations has been reported. Although most coastal lobsters populations that have been examined approximate the expected 1 : 1 ratio (Cooper 1970, Stewart 1972. Krouse 1973. Cooper et al. 1975, Pecci et al. 1978), there are several instances where skewed ratios have been observed. These include reports of populations with more males than females (Briggs and Mushacke 1979, Munro and Therriault 1983, Karnofsky et al. 1989). as well as reports of populations with more females than males (Skud and Perkins 1969, Estrella and McKiernan 1989). Explanations for these skewed sex ratios have included differential catchability (Krouse and Thomas 1975. Fogarty and Borden 1980, Miller 1990, Tremblay and Eagles 1997). segregation of the sexes by depth (Skud and Perkins 1969. Briggs and Mushacke 1979). differences in migratory behavior (Munro and Therriault 1983). physiological and behavioral differences be-

tween the sexes (Jury et al. 1994a, Jury et al. 1994b), and fisheries regulations that protect some females (Estrella and McKiernan 1989). In this paper, we report consistent spatial differences in lobster sex ratio within a New England estuary, and differences in sex ratio between size classes of lobsters found in upper estuarine areas.

MATERIALS AND METHODS

The Great Bay estuarine system lies in the southeastern corner of New Hampshire. USA. It receives freshwater from seven rivers, which mixes with saltwater entering from the western Gulf of Maine. Lobsters were sampled at eight sites in the estuarine and coastal waters from 1989 to 1992 (Fig. 1). These spanned a distance (by water) of approximately 37 km, ranging from Great Bay proper, which is about 26 km inland, to the Isles of Shoals, which lie 1 1 km offshore. The eight sites fall into three broader spatial categories, which we have arbitrarily designated as "estuarine" (Great Bay. Little Bay, Bellamy River), "riverine" (upper, mid-, and lower Piscataqua River), and "coastal" (Coast, Isles of Shoals). Along this line of sites, physical and chemical characteristics vary from those of a typical New England estuary (greatly fluctuating temperature and salinity, strong tidal mixing, soft substrate) to those of a typical New England coast (relatively stable temperature and salinity, less tidal current, and harder substrates of cobble and rock).

Howell et al.

Maine

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Figure 1. Location of the study sites within the estuarine and coastal waters of New Hampshire. GB (Great Bay). LB (Little Bay), BR (Bellamy

River), UPR (Upper Piscataqua River), MPR (Middle Piscataqua River), LPR (Lower Piscataqua River). CST (Coast), SHL (Shoals).

All lobsters were caught in traps baited with herring and tended

two to three times per week. Most were caught in our own traps as

part of a larger study on estuarine lobsters, but many were caught

by commercial lobstermen with whom we fished, and a small

number were caught by the New Hampshire Department of Fish

and Game. All traps from which we collected data were made of

vinyl-coated wire, equipped with one or two escape vents (1 7/8"

H x 6" W). and had either a single (research traps) or double parlor (commercial traps). Although winter sampling was limited because of upper estuarine ice cover and general lack of commercial fishing activity, we were able to sample all sites adequately during the spring (April-June), summer (July-September), and autumn (October-December) in most years. All lobsters had their carapace

length (CL) and abdomen width measured to the nearest millimeter, all were molt-staged using external shell criteria and/or pleopods (Aiken 1973. Aiken 1980), and all were sexed by examining the first pair of pleopods (Templeman 1944). Most were also tagged, before release, with numbered modified sphyrion tags (Scarratt 1970). because in another part of the study, we were examinine movement and growth (Watson et al. in press).

At each study site, except the Shoals, both temperature and salinity (YSI Meter Model 33) were measured at the surface each time our traps were hauled. In 1991. data were collected from surface and bottom waters. There was always <2°C and 2 ppt difference between surface and bottom values because of extensive vertical mixing (Loder et al. 1983).

Lobster Sex Ratio

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Figure 2. Mean <±SE) monthly temperatures (°C) and salinities (ppt) at the Great Bay and Coastal sites from 1989 to 1992.

The null hypothesis of equal numbers of males and females was, in all cases, tested using chi square analysis. Comparisons of sex ratio between sites, and between seasons within sites, were done using one-way analysis of variance (ANOVA) followed by Tukey's posterior test. Mann-Whitney U tests were used to compare the sizes of males and females at each site within each year. The alpha level for all statistics was 0.05.

RESULTS

Mean monthly temperature and salinity, from 1989 to 1992, at two of our sites is depicted in Fig. 2. In the upper estuary (Great Bay site, GB), mean monthly temperatures were 3-7°C warmer than the Coastal (CST) site from April through October (Fig. 2a). Mean salinity in Great Bay was highest in late summer (approx. 27 ppt), and lowest (approx. 16 ppt) in the spring when freshwater input was more abundant because of heavy rains and snowmelt. At the Coastal site, the salinity was relatively constant throughout the

year (Fig. 2b). As expected, both temperatures and salinities at the sites that occur between Great Bay and the Coast are intermediate to those depicted. Although complete temperature and salinity records are not available from the Isles of Shoals, the small amount of data available indicates this site is very similar to the Coastal site, located approximately 1 1 km away.

Observed mean sex ratios, from 1989 to 1992. at each of the sampling sites are given in Table I . Although there was some interannual variation at each site, in each of the estuarine sites (Great Bay. Little Bay, Bellamy River), there were significantly more males than females in every year ($p < .05$). In the riverine sites (upper-, mid-, lower Piscataqua River) and at the Coast, the numbers of males and females were more nearly equal. However, even at these sites, there were significantly more males than fe-males in some years (Upper Piscataqua River 1991: mid-Piscataqua River 1989. 1990; lower Piscataqua 1991; Coast 1990). As with the other sites, there are some interannual variation in sex ratio at the Isles of Shoals, but in each year for which data were available, there were significantly more females than males ($p < .05$).

When the data from all years and seasons were combined, sex ratio departed significantly from the expected 1:1 ratio in seven of

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TABLE 1.

Mean number of males per female at each sampling site from 1989 to 1992 and in all years combined.

Mean and standard error within years is based on three seasons. Mean and standard error for all years is from all years and all seasons combined. (n)

= number examined: * denotes a significant departure from a 1:1 sex ratio (chi square, $p < .05$).

the eight sampling sites (Table 1). There were significantly more

males than females in each of the five upper sites and at the coast

($p < .05$). and significantly more females than males at the Isles of

Shoals ($p < .051$. In the remaining site (lower Piscataqua River)

there were approximately equal numbers of males and females.

Using the aggregate data from all years and seasons, we found

that the mean number of males per female in Great Bay (5.29) was

significantly higher ($p < .001$) than every other site. Although there

was a tendency for the number of males per female to decline as

one moved toward the coast (Table 1). there was no significant

difference in the mean sex ratio among these other sites ($p > .05$).

This same tendency was also observed in each of the three upper

estuarine sites. Although there was some interannual variation in

each of these sites, in each year except 1991. sex ratio declined as

one moved down the estuary from Great Bay to Little Bay to the

Bellamy River. Unlike the three upper estuarine sites, there was no

obvious clinical trend in sex ratio found in the riverine and coastal sites. The Shoals site, however, had the lowest mean sex ratio of all sites in each of the years for which we had data (Table 1).

In addition to the observed spatial differences in sex ratio, there were also some seasonal trends observed (Fig. 3). At the Great Bay site, there was a considerable amount of interannual variation within seasons. Although the mean number of males per female tended to be highest in the spring (6.37), and then to decline through the summer (5.45) and autumn (4.38). there were no significant differences (p > .05) between seasons. A similar, but less pronounced pattern was observed in Little Bay, but again, there were no significant differences between seasons (p > .05). Interestingly, at the Bellamy River site, the seasonal trend was reversed.

Although there was no significant difference between seasons, sex ratio tended to increase from spring (1.42), to summer (1.50). to autumn (1.84). Seasonal trends were much less pronounced at the other five sites. Significant seasonal differences in sex ratio were found only at the upper Piscataqua River site, where the mean number of males per female was significantly higher (p < .001) in the spring (1.71) than in either summer (1.10) or autumn (1.13). between which there was no significant difference (p > .05).

The mean size (CL) of male and female lobsters at each site and year is given in Table 2. In general, the mean size of males were significantly larger than that of females in the three upper estuarine locations. In the Piscataqua River sites, males and females were more similar in mean size. The only significant differences were

found in the middle Piscataqua River, in 2 of the 4 years, and in the lower Piscataqua River, in 1 of the 4 years. In each of these instances, males were larger than females. At the coastal site, the mean size of males was larger than that of females in 1989: whereas the reverse was true in 1990. No difference in mean size was found in the remaining 2 years. Finally, at the Isles of Shoals site, where we had only 3 years of data, females were significantly larger than males in two of these (1989. 1992), but not in the other (1991).

Sex ratio varied with size class at certain sites (Table 3). The site where the change in ratio with size class was most pronounced was in Great Bay, which is the site farthest up the estuary. In the other estuarine sites (Little Bay and Bellamy River), males also tended to dominate the larger size classes, but not to the same extent as in Great Bay. In the riverine sites, there tended to be more males than females in manv size classes, but the sex ratio was most

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Sampling site

Figure 3. Mean (±SD) number of males per female at each of the sampling sites in the spring, summer, and autumn. Means are based on the

4 years included in the study (1989 to 1992). The number of lobster examined (h) is given vertically above each error bar. GB (Great Bay), LB

(Little Bay). BR (Bellamy River), UPR (Upper Piscataqua River), MPR (Middle Piscataqua River), LPR (Lower Piscataqua River).

heavily skewed toward males in the largest (>85 mm CL) size

classes. This was particularly true at the uppermost riverine site

(upper Piscataqua), and, to a lesser extent, the middle Piscataqua

site. At the coastal site, there was a less pronounced pattern of

change in sex ratio with size class. There tended to be more males

than females in the smaller size classes (<70 mm), about equal

numbers of males and females in the 71-90 mm size classes, and

about twice as many males as females in the largest size class (>90

mm). At the Isles of Shoals site, however, there were consistently

fewer males than females in all of the larger size classes (>65 mm),

and the same number, or more, males than females in the smaller

size classes.

TABLE 2.

Mean (and standard deviation) carapace length (mm) of male and female lobsters at each site in each year, and in all years combined.

* Between male and female lengths within a year and site indicates that the mean lengths of the two sexes are significantly different (Mann-Whime> U

test, p < .05). Sample sizes are given in Table 1.

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TABLE 3.

Mean (±SE| number of males per female in different size categories at each sampling size, based on data collected over 4 years.

DISCUSSION

Results of this study indicate that this estuarine population of

lobsters departs, in many ways, from the expected 1:1 sex ratio

typical of coastal populations. Among the most consistent of our

findings was the observed spatial difference in sex ratio. In each

season of each year, the upper estuary had more males than fe-

males. This skewed ratio tended to decrease, in a clinal fashion, as

one moved down the estuary toward the coast, where the sex ratio

approximated the expected 1:1 ratio. Surprisingly, this clinal trend

continued outside the estuary, so that at the Isles of Shoals, which

is located about 1 1 km from the mouth of the estuary, there were

consistently more females than males (Table 1).

Lobster populations with skewed sex ratios have been reported by others (Skud and Perkins 1969. Briggs and Mushacke 1979. Munro and Therriault 1983, Campbell and Pezzack 1985, Kamofsky et al. 1989. Estrella and McKiernan 1989), and several explanations have been put forth to explain the disparity between numbers of males and females. Fishery-related factors, including differential catchability of males and females (Miller 1990), and regulations that protect some (e.g., ovigerous, V-notched) females (Estrella and McKiernan 1989), can result in skewed sex ratios. Differential catchability of the sexes is an unlikely explanation for our results, because Becker (1994), who also worked in the Great Bay estuarine system, found sex ratios virtually identical to ours using SCUBA sampling. Furthermore, if males and females differed in their trapability, as suggested by Fogarty and Borden (1980), Miller (1990). and Campbell (1992). we would have expected skewed sex ratios in all of our study sites because the same types of traps, including identically sized escape vents, were used at all locations. It is possible, however, that the skewed ratio favoring females at the Isle of Shoals may have resulted from differences in mean size, and therefore, trapability. of the sexes. When data from the 2 years were combined, females were significantly larger than the males (Table 2). It has been suggested that female lobsters in some areas (Rhode Island) have a proportionately wider carapace width than similarly sized males (Fogarty and Borden 1980). This difference in body proportion between the sexes may not be geographically universal, however, because

Krouse and Thomas (1975) found no significant differences in the carapace length-width ratios of males and females along the Maine coast. If females in our study area do have a proportionately

wider carapace, they would not move as readily through escape vents, so it is possible that the larger mean size of the females at this site influenced sex ratio in the catch. It is also possible that regulatory protection of certain females may explain the sex ratio observed at the Isles of Shoals, where females outnumbered males. At this location, percentages of ovigerous and V-notched females (5-12%) are relatively high as compared to the estuary (<\%) (Howell. W. H. & W. H. Watson. Dept. of Zoology. Univ. of New Hampshire. Durham. NH 03824. Unpubl. data). Thus, both size and protective management may explain the preponderance of females at the Isles of Shoals, but it is also possible that this site simply has a distinctive physical habitat that has resulted in an aggregation of females such as that reported by Campbell (1990).

Ecological factors may also affect sex ratio. Skud and Perkins (1969) and Briggs and Mushacke (1979) found a segregation of the sexes by depth, while Karnofsky et al. (1989) suggested that intraspecific competition effected sex ratio. Our sampling locations were similar in depth (=3-10 m), so it is highly unlikely that our observations resulted from segregation of the sexes by depth. It is also unlikely that intraspecific competition was a factor. Karnofsky et al. (1989) found that there were nearly twice as many males as females in a small, shallow cove in Buzzards Bay, MA, USA and that a disproportionately large proportion of the males were missing one or more claws. The authors suggested that the cove may

function as a refuge for injured males, and that these individuals had been displaced to this shallow water site by aggressive, intraspecific competition for mating shelters. Moreover, they suggested that the relative paucity of females at their study site resulted from the preference of females for deeper areas where the dominant males held mating shelters. We have no information about where mating occurs in our study area, including the depth of mating shelters and whether or not the spatial distribution of females is affected by the distribution of dominant males. Thus, it is possible that the mechanism described by Karnofsky et al. (1989) may be applicable to this study, but it is doubtful, because we saw no indication that the proportion of males missing claws differed among sites (Howell and Watson).

The spatial and temporal trends of the data in this study indicate that sex ratio may be associated with seasonally changing gradients of salinity and/or temperature that are typical of northern estuaries. In particular, it is likely that male and female lobsters differ in their physiological and behavioral responses to salinity

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and/or temperature and that these differences result in the sex ratio patterns we observed.

Water temperature affects many, if not all, aspects of lobster biology. In a laboratory study, Crossin et al. (1998) documented that lobsters are capable of sensing temperature, and that they behaviorally thermoregulate: seeking preferred temperatures and avoiding water that is either too warm or too cool. Results from related studies, also done in our laboratory, further suggest that males and females may respond differently to changing temperature. In one study. 75% of females, but only 50% of males, exited their shelters as shelter temperature was increased (Jury. S. H. Dept. of Zoology. Univ. of New Hampshire, Durham, NH 03824. Unpubl. data); whereas in another study, in which males and females were placed in a thermal gradient tank, males generally preferred wanner temperatures than females, particularly in the spring and fall, when ambient temperatures were seasonally lower (Jury. S. H. The effect of acclimation temperature and sex on the behavioral thermoregulation of the American lobster. Homarus americanus. In prep.). Although these data are preliminary, they suggest that males and females differ in their temperature preferences, and that spatial and temporal differences in temperature could thus affect sex ratio.

Although laboratory studies on temperature are relatively scarce, numerous field studies have documented that water temperature affects the temporal and spatial distribution of lobsters, and that males and females differ in their movements in response to seasonally changing temperatures (Munro and Therriault 1983. Roddick and Miller 1992, Lawton and Lavalli 1995. Estrella and

Morrisey 1997). It has been suggested, for example, that seasonal onshore -offshore migrations are associated with temperature selection, and are adaptive for accelerating growth and egg development (Saila and Flowers 1968. Cooper and Uzmann 1971, Pezzack and Duggan 1986. Estrella and Morrissey 1997). This may also be true, on a geographically smaller scale, for seasonal migrations that occur within New England estuaries, including Great Bay (Watson et al. 1999). Differential migration of the sexes, associated with seasonal changes in water temperature, can also effect sex ratio. Roddick and Miller (1992) found, for example, that males and females arrived at. and departed from, a small embayment in Nova Scotia in different months, and these differences in seasonal movements resulted in skewed sex ratios. Adult females have also been reported to move to deeper water earlier in the autumn than males (Campbell and Stasko 1986. Robichaud and Campbell 1991). which results in temporal and spatial segregation of the sexes. Munro and Therriault (1983) found more males than females in estuarine locations in the Magdelaine Islands, and speculated that this resulted from differential migration of the sexes. Both sexes left the estuaries as temperatures cooled in the autumn, but males were more likely to return in the spring as temperature increased. A similar situation may exist in the Great Bay Estuary. In a study concurrent with this one, Watson et al. (1999) documented that lobsters tended to migrate up the Great Bay Estuary in the spring as temperatures increased, and down the estuary in the summer and autumn. Although Watson et al. saw no marked differences in the movements of males and females, their data were somewhat equivocal on this point, and they suggested that differential movement of the sexes was possible. Munro and Therriault

(1983) suggested that the reason for males returning earlier than the females was to take advantage of the wanner temperatures of the estuarine sites for molting. Indeed, they found that all males <75 mm CL molted twice each year.

It has also been suggested that there are seasonal differences in the catchability of males and females, that these differences are caused by the two sexes molting at different times, and that differential catchability results in seasonally changing sex ratios (Tremblay and Eagles 1997). In the Great Bay Estuary, however, we saw no evidence that males and females molted at different times or in different locations (Howell and Watson unpubl. data). We conclude from this that there is no difference between the sexes in location and temperature of molting. Thus, although our skewed sex ratios may indeed be related to temperature-mediated differences in movement between the sexes, it seems unlikely that it is strongly correlated with molting, as suggested by Munro and Therriault (1983) and Tremblay and Eagles (1997).

A number of laboratory and field studies have documented that salinity can also effect the temporal and spatial distribution of lobsters. Lobsters are considered to be poor osmoregulators (Dall 1970). and several previous field studies have shown that lobsters use behavioral mechanisms to avoid low salinities (Munro and Therriault 1983. Reynolds and Casterlin 1985. Maynard 1991. Jury et al. 1995). In a recent laboratory investigation Jury et al. (1994a) measured hemolymph osmolarity. oxygen consumption, heart rate and ventilation rate of lobsters under salinity regimes similar to

those found in the Great Bay Estuary under spring runoff conditions. They found that exposure to decreasing salinity (from 20 to 10 ppt) caused an increase in oxygen consumption, heart, and scaphognathite rate. At the lowest salinity (10 ppt). females required more energy than males to maintain the same hemolymph osmolarity. Females also recovered more slowly than males as salinities were subsequently increased. This study has been confirmed by Houchens (1996). and extended to show that female lobsters suffer significantly more mortality than males when held at 5-10 ppt. For this reason, upper estuarine locations where salinities are the lowest, particularly in the spring, probably represent a stressful and potentially lethal environment for females. In a second set of experiments. Jury et al. (1994b) measured the behavioral response of lobsters to reductions in salinity. When given a choice of salinity, females were more selective in their preference for higher salinity, and females found low salinities more aversive than did males. Results from these studies indicate that lobsters respond to changes in salinity, that male and female lobsters differ in their physiological and behavioral responses, so that males find low salinity less aversive and less stressful. It is likely that these differences partially explain the observed skewed sex ratios found in this study. In general, we found an inverse relationship between lobster sex ratio and salinity. Physiological and behavioral differences in the way each sex responds to salinity could also explain the seasonal trends in sex ratio that we observed. The number of males per female was highest in the spring in the upper estuary, when salinities were lowest, and then declined over summer as salinities increased. We believe that the observed reduction in sex ratio was caused by the arrival of more

females as salinity increased in these areas.

Aside from the physiological and/or behavioral reasons already discussed, it is possible that the observed spatial pattern in sex ratio may also relate to the reproductive biology of lobsters. Because lobster embryos and larvae are quite vulnerable to low (<14 ppt) salinity (Scaratt and Raine 1967, Charmantier et al. 1998. Forward 1989). relatively low salinity environments, such as those in the upper estuary, may be suboptimal for reproduction. Unpublished data on the distribution of ovigerous females in this study support this view (Howell and Watson). We cauaht and examined 8.153

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female lobsters as part of this study, and 168 of these (2.06%) were ovigerous. Of these 168. only 43 were caught in the estuarine and riverine sites, and the remaining 125 were from the Coast and Shoals. The low incidence of ovigerous females in the estuary is similar to the situation reported for blue crabs in the upper Chesapeake Bay by Hines et al. (1487). and it is likely that ovigerous females avoid the low salinity conditions of the estuary, because salinity is generally too low for larval survival. Note, however, that Munro and Therriault (1983) found a higher percentage of ovigerous females (13-16%) in estuaries than they did at the coast (7%).

The difference between their study and ours may have resulted from the fact that our upper estuarine salinities are typically as low as 10-15 ppt in any given year; whereas the lowest reported by Munro and Therriault was 22 ppt.

We also found that sex ratio was more skewed in larger size classes (>80 mm CL) in all of our estuarine and riverine locations. Changes in American lobster sex ratio with size class have also been noted by Karnofsky et al. (1989). They found that females dominated the 50-59 mm CL size class, but that males were more numerous than females in size classes >60 mm CL. As a result, males were not only more common, they were also larger. We believe that the observed changes in sex ratio with size class are related to changes in mobility with size. Wahle and Steneck (1992) suggested that small lobsters (<=60 mm CL) are dependent on their shelters to avoid predation. but that this vulnerability is eventually outgrown, and lobsters >=60 mm CL are able to move about more freely, because they are virtually immune to predation. Once this release has occurred, mobility generally increases as lobsters continue to increase in size (Campbell and Stasko 1986, Campbell 1989). The fact that both mobility and skewness in sex ratio increase with size class indicates that changes in sex ratio with size may result from differential movement of the sexes. When small, both sexes move little, and sex ratio is approximately 1:1. As size (and mobility) increase, males, which are more tolerant of low salinity than females, may travel further up the estuary, especially in the spring, resulting in the predominance of males in the larger

size classes in this location at this time. Studies are currently underway to determine if the aforementioned differences in the behavior of male and female lobsters exist, even in the smaller size classes, or if they manifest themselves only as they reach sexual maturity. If the latter situation is true, it supports the view that the strongest influence on female migratory behavior in the estuary is related to reproduction and the seeking of appropriate habitats for hatching of larvae. In the Great Bay Estuary, ovary dissections indicate that approximately 50% of females have reached sexual maturity of 80 mm CL (Howell and Watson unpl. data), and it is in size classes greater than this that we observe the most skewed sex ratios.

In summary, we believe that the skewed sex ratio patterns we observed in this study resulted from differential movement of the sexes: probably in response to salinity and temperature cues. Both sexes tend to move down the estuary in the summer and autumn. Males, which are more tolerant of low salinity and warmer tem-peratures, return to upper estuarine areas earlier than females in the spring, which accounts for the elevated sex ratio seen in these locations. Although some females move up the estuary as salinity rises, thereby making the sex ratio more nearly equal, more fe-males than males remain in the lower estuary, because they are less tolerant of low salinity and warmer temperatures, and/or because it is a more favorable (higher salinity) location to release their larvae. The fact that sex ratio is most skewed among the largest size classes, which are also the most mobile, supports our contention that skewed sex ratio in our study site results from differential movement of the sexes.

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