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Variation in Life-History Patterns of the Grass Shrimp *Palaemonetes pugio* in Two South Carolina Estuarine Systems *

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Abstract

A population of *Palaemonetes pugio* Holthuis 1949, inhabiting a fairly constant high salinity estuarine environment (North Inlet), exhibited more rapid growth, earlier first reproduction, a smaller clutch size, more fluctuating sex ratio, and shorter life span. A population in a less saline environment (Minim Creek) showed relatively slower growth, delayed first reproduction, larger clutch size, female-dominated sex ratio, and longer life span. Growth in both areas was rapid in summer and slower in winter, with the females growing much larger than the males. Summer generation females first reproduced at the age of 3.5 months in North Inlet and at 4.8 months in Minim Creek. Minim Creek females larger than 30-mm TL carried more eggs than North Inlet females of similar sizes. Life span in North Inlet was calculated to be 6–7 months for the summer generation and 9–10 months for the winter generation; in Minim Creek, the corresponding longevity estimates were 9–10 months and 12–13 months, respectively. Variations in life history patterns are hypothesized to be the results of numerous environmental factors acting differentially on the various life-stages of the organism. The results suggest that the reproductive flexibility of *P. pugio* enhances its ability to persist in a variety of environments.

Introduction

Analyses of the life history characteristics of organisms living in heterogeneous environments have shown diverse reproductive responses to temporal and spatial variations (Wilbur *et al.*, 1974; Giesel, 1976; Stearns, 1976, 1977). Each set of reproductive patterns presumably "corresponds to a local optimum that maximizes an individual's lifetime reproductive success in its particular environment" (Pianka, 1976). Present theory categorizes life history parameters into two basic paterns: (1) the combination of rapid development, early reproduction, numerous and small offspring, large reproductive effort and short life; and (2) the combination of slow development, delayed reproduction few and large offspring, small reproductive effort, and long life (Pianka, 1970; Schaffer, 1974; Stearns, 1976, 1977). In most cases, the predictions of these models are not consistent with much of the evidence (Stearns, 1977). Furthermore, most comparative studies have been done on inter-specific variations of life history patterns. Variability on this scale could be explained by differences in the biology of contrasted species. The relatively few field studies on intra-specific reproductive variations in barnacles (Barnes and Barnes, 1968), amphipods (Strong, 1972), salmon (Schaffer and Elson, 1975), mussels (Comely, 1978), nudibranchs (Todd, 1979), grapsid crabs (Jones, 1980), harpacticoid copepods (Palmer, 1980), littorinid snails (Roberts and Hughes, 1980), poeciliid fish (Stearns, 1980), and other species (Stearns 1976, 1977) have indicated significant variability in population and reproductive parameters among local populations. There is a need for carefully controlled experiments which will contrast different populations to elucidate life history patterns by examining intra-specific variations in reproductive traits (Stearns, 1976, 1980) and to determine whether or not such variations fit the accepted theories (Stearns, 1977).

The grass shrimp, *Palaemonetes pugio,* is a typical species in the heterogeneous estuarine ecosystems from Nova Scotia to Texas (Williams and Wigley, 1977). Ecological studies of this species (e.g. Wood, 1967; Welsh, 1975; Sikora, 1977; Provenzano *et al.*, 1978) have reported considerable variation in life history parameters, both within and between geographic populations. Such variation has been attributed to latitudinal or regional differences (Sastry and Vargo, 1977; Sikora, 1977).

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No simultaneous comparison of reproductive patterns among different local populations of *Palaemonetes pugio* has been conducted. Such a study could provide insight into the processes that shape life histories in heterogeneous environments and present evidence to test life history models in an estuarine organism seemingly well-adapted to a variety of habitats. The present study compared population and reproductive parameters of *P. pugio* populations from two different habitats within the same geographic area, including size-distributions, spawning patterns, ages of first reproduction, longevity, and growth trends.

Materials and Methods

Palaemonetes pugio Holthuis 1949 were collected from North Inlet and Minim Creek, Georgetown County, South Carolina, USA (Fig. 1). North Inlet is a well-mixed, high salinity estuary draining an extensive *Spartina alterniflora* salt-marsh (Kjerfve, 1978). Collections from North Inlet were taken around Oyster Landing in Crab Haul Creek (Lat. 33°21′N, Long. 79°11′W). Minim Creek is part of the North Santee River delta estuarine system characterized by wide salinity fluctuations due to heavy tidal and river run-off influence (Reis, 1977). Samples from Minim Creek were collected along the boat channel of Annandale Plantation (Lat. 33°12′N, Long. 79°18′W).

Samples were collected with a 3-mm mesh dip-net during low tide at approximately biweekly intervals from November 1978 to October 1979. To ensure representative sampling of the population, collections were taken along the banks to a depth of 1 m, around shell rubble and pilings, and under submerged vegetation. Because the primary aim of the study was not to determine abundance patterns, the samples were standardized by mixing the collected organisms in a large bucket and randomly subsampling with a 1-mm mesh dip-net enough individuals to fill a 150-ml specimen jar. During the spawning season, additional samples of gravid females were preserved for separate analysis of size distributions of ovigerous females. Samples were preserved in 10% buffered formalin. During each sampling, surface water temperature and salinity measurements were taken with a mercury thermometer and refractometer, respectively. Samples from both study areas were collected within two hours of each other.

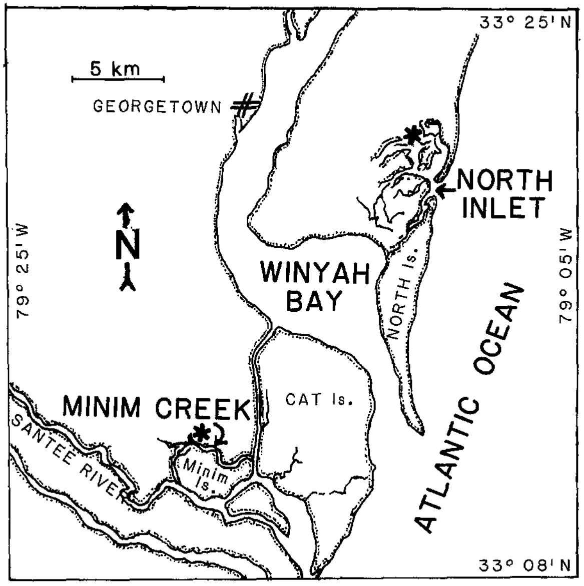

Fig. 1. Map of the study areas, showing the spatial relationship between North Inlet and Minim Creek, South Carolina, and the location of the sampling sites in each (*)

All *Palaemonetes pugio* in each specimen jar were identified according to the criteria of Holthuis (1952) and sexed following the methods of Meehean (1936) and P. A. Sandifer (personal communication). Maturity in males was determined by the presence of coagulated sperm on the gonopores after preservation (Meehean, 1936). All females with sizes equal to or greater than the smallest gravid female found were considered mature. Since mature female palaemonids may pass through a reproductively quiescent period during the spawning cycle (Pandian and Balasundaram, in press; personal observation), only gravid females were used in the analysis of spawning patterns. Total length (TL, the distance from the anterior end of the rostrum to the posterior edge of the telson) of each shrimp was measured to the nearest 0.5 mm under a dissecting microscope.

Eggs from each gravid female were stripped and counted. As females drop some advanced stage eggs upon contact with the preservative and hatching is not synchronous (personal observation), only females with pre-eyed eggs were included in the fecundity analysis.

The graphical method using probability paper for size-frequency analysis described by Harding (1949) and Cassie (1954) was used to obtain information on recruitment and growth patterns. Growth rates, in terms of daily length increments, were calculated by extrapolation from the growth curves determined by this method and averaged over the life span of the individuals in the cohorts.

Results

Physical Conditions

Water temperature curves in North Inlet and Minim Creek were nearly identical (Fig. 2A). Temperatures less than 10 °C occurred in January and February; temperatures greater than 30 °C occurred in July and August.

Salinity was significantly different between the two sites (Fig. 2B). North Inlet had a fairly constant high salinity regime; lower salinity readings (15–25‰ S) were measured only after continuous heavy rainfall during March and after Hurricane David in early September 1979. Minim Creek was subject to more variable salinity conditions, becoming practically freshwater in spring and seldom reaching a salinity of 20‰ S.

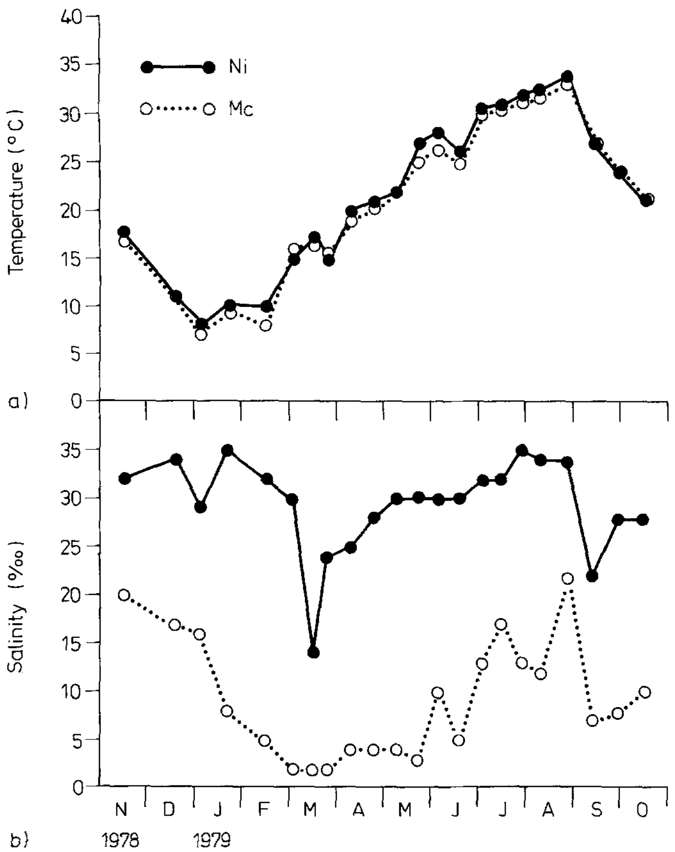

Fig. 2. Variations in temperature (A) and salinity (B) in North Inlet (NI) and Minim Creek (MC). Mean values (±SD) were 21.4 °C±8.1 C° and 29.8±4.8‰ S for NI, and 20.9 °C±8.0 C° and 10.2±6.9‰ S for MC

Population Structure

5 650 North Inlet and 4 889 Minim Creek grass shrimp were sexed and measured for the analysis of population structure. The size-frequency distributions of both populations were unimodal from mid-December to early March and became bimodal or polymodal afterwards as females grew larger than males and as new recruitment occurred (Figs. 3 and 4). The populations were distinctly bimodal by mid-March, as size differences between the sexes became more apparent.

The size distribution of North Inlet males was unimodal for all months, except in June and July when at least two modal groups occurred (Fig. 3). A similar pattern was noted for Minim Creek males (Fig. 4). Most of the overwintered males disappeared from the population by the end of July in Noth Inlet but were present in Minim Creek until late September.

The size structure of female shrimp was more complex. Unimodality in the female size-frequency histograms occurred only from mid-April to late May and in early August in North Inlet (Fig. 3), and from late May to mid-June and in mid-October in Minim Creek (Fig. 4). Most females of the overwintered generation disappeared in early August in North Inlet but persisted until late September in Minim Creek.

Two generations of recruits appeared in both populations during the year. In North Inlet, the first (summer) recruitment period started in early June, peaked in July–August and lasted until October. The second (winter) recruitment phase occurred from December to February with no clear peak. In Minim Creek, the new generation shrimp entered the population in mid-June and reached peak abundance in September and October. A second, smaller wave of recruitment lasted from December to mid-March, with a peak in January.

Juveniles apparently do not join the populations until some period after metamorphosis, since immediate postlarvae (6 to 7-mm TL) were not collected from either area. Except for a few times when individuals less than 13-mm TL were caught (one 8 mm and one 11 mm from North Inlet on August 26 and September 12, respectively, and a total of four shrimp between 11 and 13 mm from Minim Creek in July), the smallest shrimp taken during the times of recruitment were 13-mm TL. The collection of the 8–11 mm juveniles suggests that the absence of the small juveniles in the samples was not a function of the mesh size of the dip net.

The summer recruitment period in both areas was characterized by rapid growth of the new generation and progressive disappearance of larger, presumably older individuals. In June, the new recruits comprised discrete modal groups in two populations, but by late July they had grown to the size of the older generation. Summer recruits comprised 50% of the populations by the end of July in North Inlet and by early August in Minim Creek.

The overwintering populations consisted of varying proportions of summer-spawned, early fall-recruited shrimp and early fall-spawned, winter-recruited individuals. Winter-recruited shrimp accounted for 30–40% of the males by February to early March and completely replaced the older males by May in North Inlet and by June in Minim Creek. Winter-recruited females comprised 50–60% of the overwintering females in February to early March in both places.

Changes in population structures throughout the year were reflected in mean sizes of the shrimp in each sample (Fig. 5). Parallel trends in the increase and/or decrease of the average size of males and females were observed in the two populations. Mean size was smallest in fall when bigger individuals had presumably died, peaked in spring, and decreased in summer when the smaller recruits joined the population.

The average size of North Inlet males was significantly larger than that of Minim Creek in winter ($t=3.42$, $P < 0.001$), primarily due to the large percentage of winter recruits coming into the latter area (Figs. 3 and 4). In summer, Minim Creek males were significantly larger ($P < 0.001$) than North Inlet males as a result of the continued presence of large males (> 28-mm TL) in Minim Creek in July–August (Fig. 4). The pooled mean total length of North Inlet males ($\bar{x}=21.78$-mm TL ± 3.99 SD) was significantly smaller ($P < 0.001$) than that of Minim Creek males ($\bar{x}=22.34$-mm TL ± 4.20 SD).

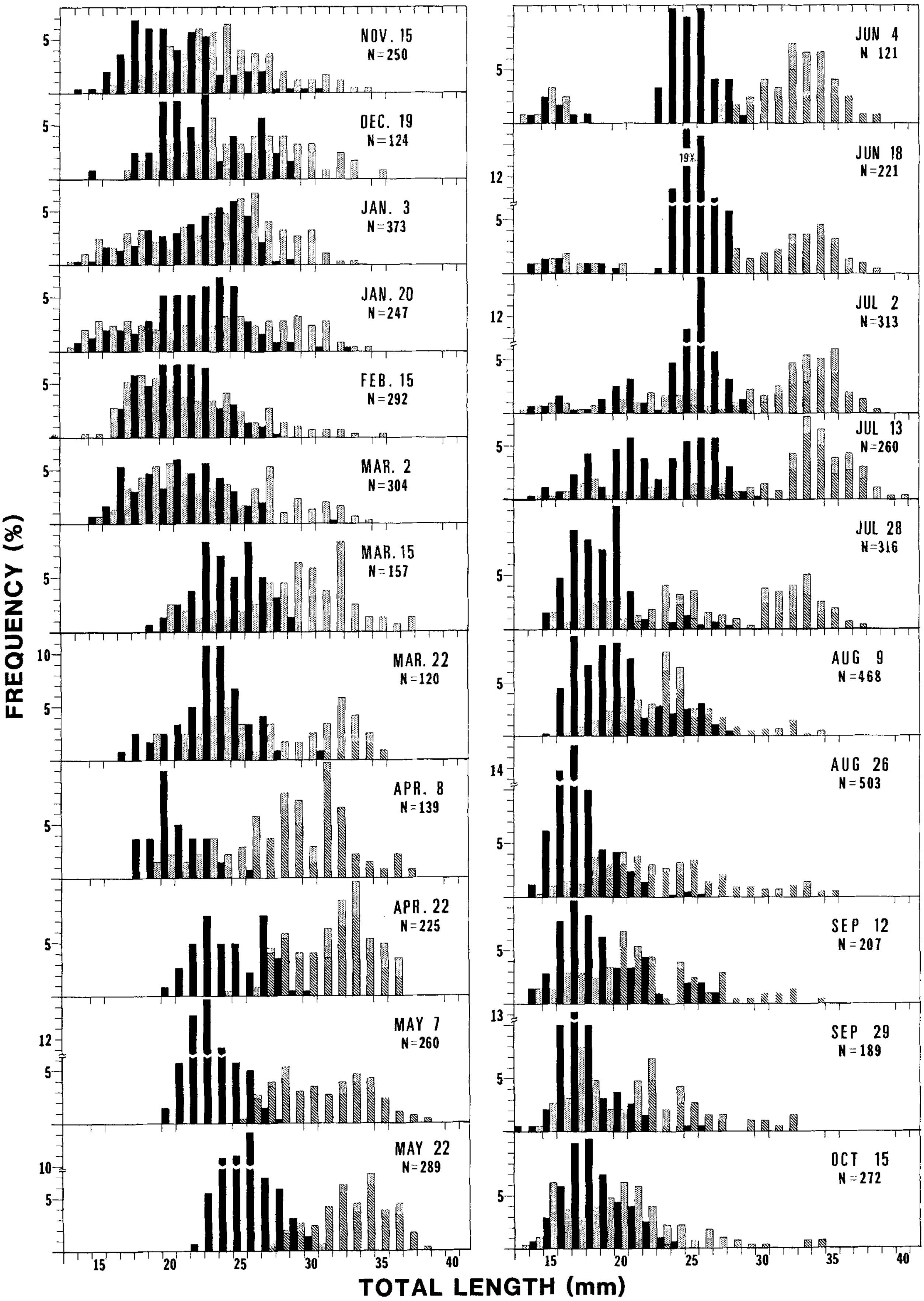

Fig. 3. *Palaemonetes pugio.* The size frequency distributions (as % of sample size *N*) of the North Inlet population from November 1978 to October 1979. Solid bars represent males; stippled bars, non-gravid females; and diagonal-lined bars, gravid females

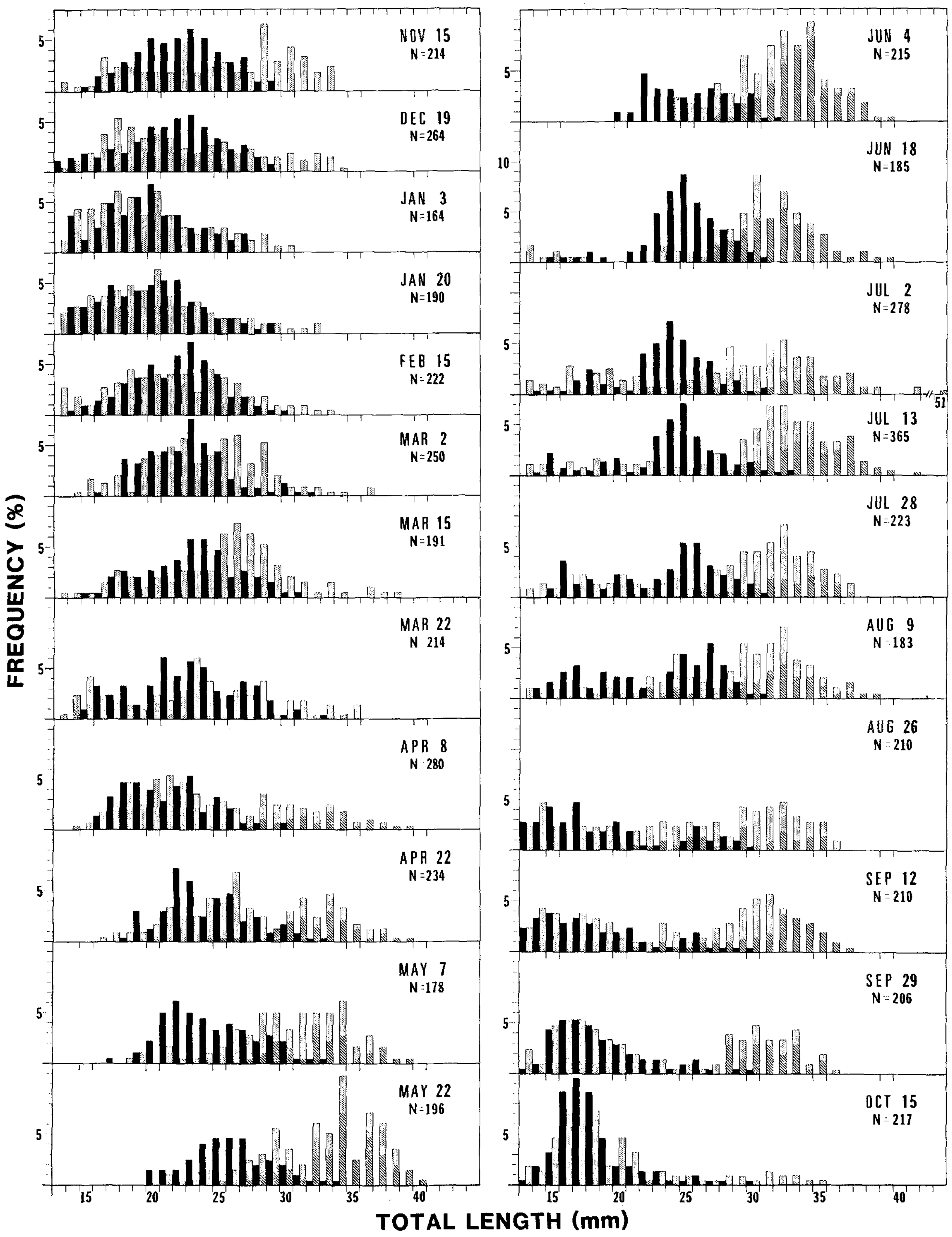

Fig. 4. *Palaemonetes pugio.* The size frequency distributions (as % of sample *N*) of the Minim Creek population from November 1978 to October 1979 (Bars as in Fig. 3)

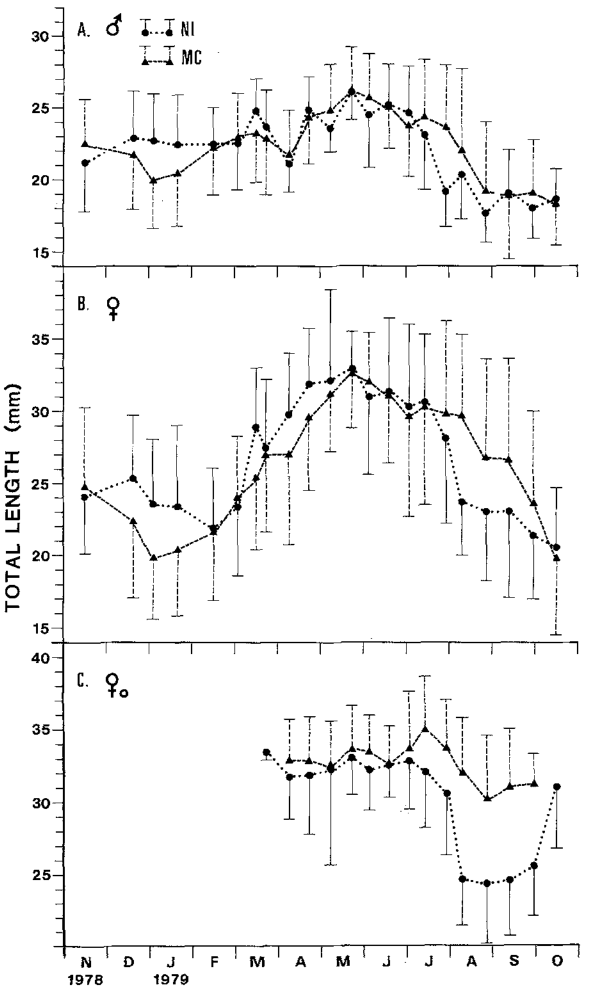

Fig. 5. *Palaemonetes pugio.* Mean total lengths and upper or lower values of 1 SD of shrimp collected in North Inlet (NI) and Minim Creek (MC). (A) males; (B) all females; (C) gravid females

Similarly, the mean size of North Inlet females ($\bar{x}=25.81$ mm ± 6.01) was significantly smaller ($P < 0.05$) than that of Minim Creek females ($\bar{x}=26.20$ mm ± 6.74). In winter and spring, the average size of North Inlet females was considerably larger than that of Minim Creek females, again due to the heavy winter recruitment in the latter area (Fig. 4). In summer and fall, this trend was reversed, with the Minim Creek values being significantly larger due to the persistence of larger females until October.

Females grew significantly larger ($P < 0.001$) than males in both populations (Fig. 5 A, B). North Inlet females averaged 7% larger than males in winter and up to 28% larger in summer. In Minim Creek, females were 5 and 22% larger than males in winter and summer, respectively.

Growth

Comparative information on the growth patterns of the two populations was obtained by following the progression of the February-March and June recruits (the last recruited group of the winter and the first of the summer generations, respectively) in the length-frequency histograms in Figs. 3 and 4. In both areas, growth was generally slower in winter than in summer (Fig. 6); rapid growth in summer allowed the shrimp to reach reproductive size by July–August. In North Inlet, no significant difference (Student's *t*-test, $P > 0.10$) was detected between the mean daily growth rates of summer and winter generation females (summer: $\bar{x}=0.143$ mm $d^{-1} \pm 0.111$; winter: $\bar{x}=0.090 \pm 0.067$). A similar pattern was found for the Minim Creek females (summer: $\bar{x}=0.133 \pm 0.109$; winter: $\bar{x}=0.089 \pm 0.041$). In both areas, overwintering females exhibit basically similar growth rates (Fig. 6 A).

On the other hand, both the winter and summer generations of Minim Creek males (winter: $\bar{x}=0.068 \pm 0.042$; summer: $\bar{x}=0.069 \pm 0.036$) showed consistently slower growth rates than their North Inlet counterparts (winter: $\bar{x}=0.086 \pm 0.041$; summer: $\bar{x}=0.087 \pm 0.060$) (Fig. 6 B). However, the mean daily increments were not significantly different, (Student's *t*-test, $P > 0.10$), either for the winter or summer generation.

The rapid turnover of generations coupled with the growth rates of each cohort indicate a life span of a year or less, depending on the season of recruitment. In North Inlet, the last cohort of the winter generation disappears

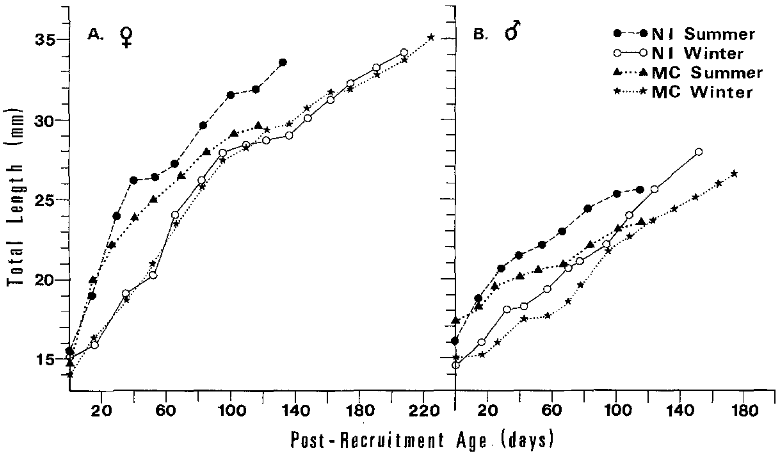

Fig. 6. *Palaemonetes pugio.* Growth patterns of (A) female and (B) male shrimp in North Inlet (NI) and Minim Creek (MC) as indicated by the progression of mean sizes of the last cohort recruited in winter and the first cohort joining the populations in summer

from the population by late August–early September, giving shrimp of this group a longevity of 9–10 months. The first cohort of the summer recruits, spawned in early spring, disappears by late October, a life span of about 6–7 months. In Minim Creek, life span was 9–10 months for the summer generation to 12–13 months for the winter recruits.

Sizes at Maturity

The smallest males with coagulated sperm outside of the gonopores were 15.0-mm TL in both populations. The smallest gravid females collected from North Inlet (NI) and Minim Creek (MC) measured 18.0- and 21.0-mm TL, respectively, both on August 26.

Analysis of the sizes of the smallest gravid females from each sample showed no significant difference between the minimum mean size of ovigerous females that had overwintered (NI: $\bar{x}=26.5 \pm 0.87$; MC: $\bar{x}=26.8 \pm 0.95$). For summer generation females, the difference between the minimum mean sizes of North Inlet gravid females ($\bar{x}=20.125 \pm 1.55$) and Minim Creek females ($\bar{x}=22.17 \pm 1.94$-mm TL) was significant ($t=2.1915$, $P < 0.05$).

Sex Ratio

The sex ratio of the grass shrimp showed temporal differences within and between the two populations (Fig. 7). In North Inlet, 51.96% of the 5 650 individuals sexed were males. This overall 1.08:1 ratio was significantly different from the expected 1:1 ratio ($\chi^2=8.72$, $P < 0.05$). Only 41.42% of the 4 889 shrimp sampled from Minim Creek were males; this 0.71:1 ratio was highly significantly different from 1:1 ($\chi^2=143.98$, $P < 0.001$).

The North Inlet population exhibited more temporal fluctuations in sex ratio, being male-biased in May, June and August, female-biased in April, and not significantly different from 1:1 (χ^2-test, $P > 0.10$) during all other months (Fig. 7). In Minim Creek, females outnumbered males by about 2 to 1 from April to September; the sex ratio did not differ significantly from 1:1 (χ^2-tests, $P > 0.10$) the rest of the year (Fig. 7). Between populations, the sex distributions were generally similar from October to April when sex ratios were usually even, but significantly different (χ^2-test, $P > 0.01$) from May to September. During the latter period, females comprised 60–70% of the Minim Creek population whereas females constituted 40–50% of the North Inlet population.

Spawning Patterns

In both areas, spawning started in late March and lasted until early fall. The reproductive peaks, determined by the incidence of ovigerous females, were quite different between the two populations (Fig. 8). Two spawning peaks were seen in the North Inlet population. The first occurred in April–May when almost 90% of all females were ovigerous. The second, smaller peak was observed in August–September when the females recruited in early summer spawned. In Minim Creek, a single spawning peak was noted in June, with continuous, low-level spawning from July to September (Fig. 8).

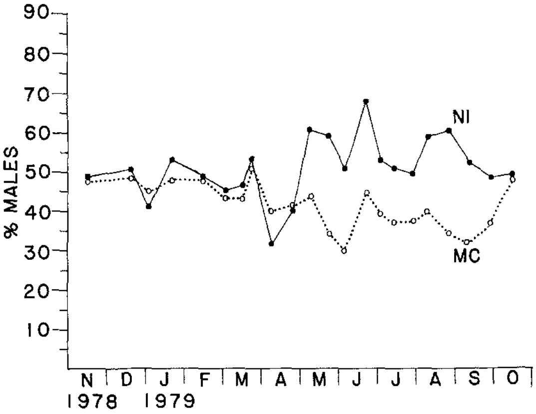

Fig. 7. *Palaemonetes pugio*. Temporal variations in the sex ratio of the shrimp in North Inlet (NI) and Minim Creek (MC)

Variation in reproductive cycles is indicated by the difference in the size-structure of gravid females (Figs. 3 and 4). Size-frequency distribution of ovigerous females were similar in the two populations from April to June, when the overwintered females spawned. By July, the

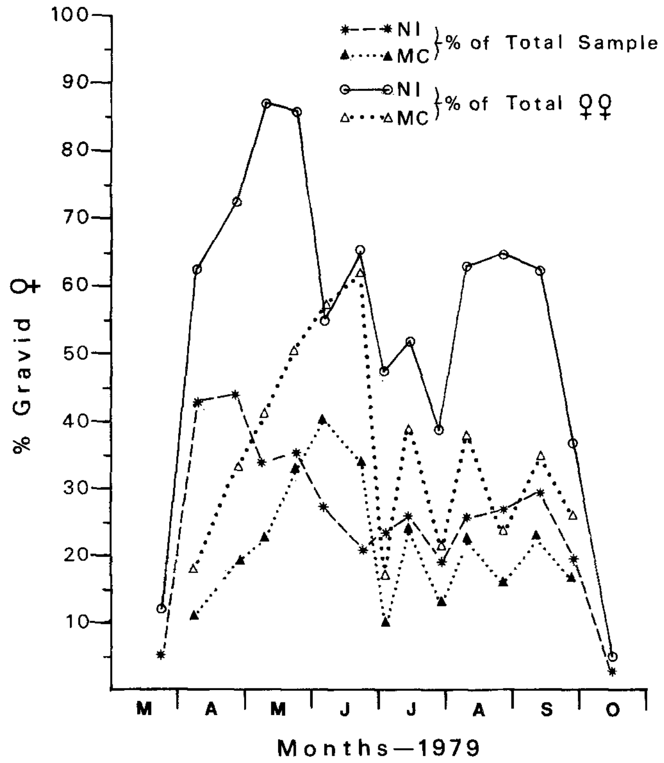

Fig. 8. *Palaemonetes pugio*. Spawning patterns of the shrimp populations in North Inlet (NI) and Minim Creek (MC) as indicated by the incidence of ovigerous females

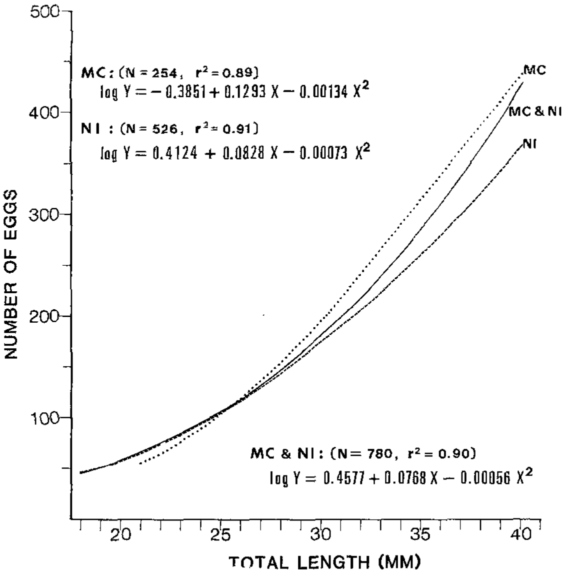

Fig. 9. *Palaemonetes pugio.* Clutch size (Y) versus body size (X) relationship in grass shrimp populations in North Inlet and Minim Creek

spring-spawned females in North Inlet became gravid, making the size-structure distinctly bimodal by the end of the month. The distribution curve became positively skewed by August as the larger females of the older generation disappeared from the population. By September, the spawners were all of the summer generation.

In Minim Creek, only a small percentage of the spring-spawned females were brooding in early August. By the end of August, 40% of the spawners were of the new generation, giving rise to distinct bimodality of the size-structure histogram at this time. The larger and older females continued to dominate the spawning segment of the population until the end of the spawning season in late September.

The disparity in the size-structure distributions was indicated by the differences in mean sizes of the gravid females at each sampling time (Fig. 5C). Mean sizes were generally not significantly different from April to early July. From mid-July until the end of the spawning season, the Minim Creek females were significantly larger ($P < 0.001$) than those from North Inlet for each sample. Overall statistics of the mean sizes showed that the North Inlet female sizes ($\bar{x} = 30.13 \pm 3.46$-mm TL) were more variable ($F = 7.12$, $P < 0.001$) and significantly smaller ($t = 2.60$, $P < 0.05$) than the Minim Creek values ($\bar{x} = 32.62 \pm 1.29$-mm TL).

Clutch Size

There was a difference between the two populations in the relationship between clutch size and body size. Although there was high variability in clutch size for a given female size, a trend of increasing brood size with increasing body size was evident in both populations.

Table 1. *Palaemonetes pugio.* Summary of life history patterns of grass shrimp populations in North Inlet (NI) and Minim Creek (MC), South Carolina

	North Inlet	Minim Creek	Remarks
Recruitment period	June to mid-February	Mid-June to mid-March	
Recruitment peaks	July – August	September – October; January	
Total replacement of parent generation	Mid-summer	Mid-fall	
Growth patterns	Slow in winter; rapid in summer	Slow in winter; rapid in summer	MC shrimp have slower growth rates than NI
Mean adult length	Maximum in spring	Maximum in spring	MC shrimp significantly larger than NI shrimp
Largest male collected	33.0-mm TL (Jan. 20)	34.0-mm TL (May 22)	
Largest female collected	40.0-mm TL (July 13)	51.0-mm TL (July 2)	
Lifespan: Summer recruits	6 – 7 months	9 – 10 months	
Winter recruits	9 – 10 months	12 – 13 months	
Sex ratio	More temporal fluctuations	Generally female-dominated	Significantly different
Overall sex ratio (M : F)	1.08 : 1	0.71 : 1	from 1 : 1
Size at maturity: Male	15-mm TL	15-mm TL	
Female	20.13 ± 1.55-mm TL	22.17 ± 1.94-mm TL	
Age at first reproduction			
(Summer generation female)	3.5 months	4.8 months	See text for explanation
Spawning period	Late March to mid-October	April to late September	
Spawning peaks	April – May; August – Sept.	June	
Composition of spawners	Overwintered females in spring; new-generation females in summer	Overwintered females in spring; overwintered ± new generation females in summer	
Mean size of spawners	30.13 ± 3.46-mm TL	32.62 ± 1.29-mm TL	
Clutch size	Smaller	Larger	

The relationship between egg number and body size was non-linear in both populations. The best fit (least squares method) in both cases was a quadratic equation on semi-log transformed egg count data. These regressions accounted for about 90% of the variation in both populations. To compare statistically the two regression equations, the data from both populations were pooled and similarly analyzed (Fig. 9). Analysis of covariance showed that the regression equations for the North Inlet and Minim Creek populations were significantly different ($P < 0.0001$). Minim Creek females larger than 30-mm TL generally carried more eggs than the North Inlet females of similar size.

Thus, there were basic similarities in the temporal patterns of population structure and reproductive dynamics, but distinct differences occurred in recruitment, growth and spawning trends, sex ratio and longevity (Table 1). The North Inlet population exhibited more rapid growth, earlier reproduction, fluctuating sex ratio, smaller clutch size and shorter life span.

Discussion

There are major differences in life history parameters of populations of *Palaemonetes pugio* from two habitats within the same geographic area (Table 1). There are also some general similarities as well as noticeable variation in population parameters of other populations of *P. pugio* throughout its geographic range. Polymodality, or at least bimodality, of seasonal size-frequency distributions occurs in grass shrimp populations in Narragansett Bay (Nixon and Oviatt, 1973; Welsh, 1975), and North Inlet (Sikora, 1977).

Spawning periods generally occur from early spring to early fall, coinciding with water temperatures of at least 18°–20 °C (Wood, 1967). The breeding season lasts from May to mid-September in Narragansett Bay, Rhode Island (Welsh, 1975; Sastry and Vargo, 1977), from April to mid-October in North Carolina (Broad, 1957; Knowlton and Williams, 1970), from March to October in South Carolina and Galveston Bay, Texas (Sikora, 1977; this study; Wood, 1967). Differences in reproductive period among the geographic populations are due primarily to differences in water temperature patterns in the areas. Recruitment periods differ in some locations as a result of the varied spawning times. Recruitment occurs from mid-July to October in Narragansett Bay (Welsh, 1975), from June to November in southern North Carolina (Knowlton and Williams, 1970), from June to February in North Inlet (Sikora, 1977; this study), and from June to March in Minim Creek (this study). The observation that immediate postlarvae do not join the population directly after metamorphosis has also been noted by Sikora (1977) who used a 1-mm mesh net for his sampling.

In all populations studied, growth to adult size is rapid during warmer months and slower during colder times (Wood, 1967; Knowlton and Williams, 1970; Nixon and Oviatt, 1973; Welsh, 1975). The growth rates calculated in this study agree with the values derived by Sikora (1977), who calculated the overall mean daily rates to be 0.085 and 0.106 mm d^{-1} for North Inlet males and females, respectively. Corresponding rates in the present study are 0.086 and 0.090 mm d^{-1}.

The slower growth in Minim Creek may be due to nutritional and physiological factors. Constantly fluctuating salinity and high siltation and turbidity due to river run off may cause Minim Creek to be deficient in nutritional items needed by the growing shrimp. *Palaemonetes varians* increased its metabolic rate in subnormal salinities (Lofts, 1956); this may hold true also for *P. pugio*. Lower survival and slower growth at reduced salinities (about 5‰ S) have also been reported for *P. pugio* by Thorp and Hoss (1975) and Floyd (1977).

The estimate of life span for the North Inlet shrimp agrees with that of Sikora (1977). Although both Wood (1967) and Welsh (1975) also reported longevity of about one year, Welsh noted that a small percentage of shrimp persists through a second winter. The life span of Minim Creek winter recruits may approximate this, but present evidence indicates that the shrimp in this area overwinter only once.

The difference in longevity in the two populations may be due to predation. There are more fish predatory on *Palaemonetes pugio* in North Inlet. Fish predators, especially *Bairdella chrysoura* (Darnell, 1958; personal observation) and *Fundulus* spp. (Nixon and Oviatt, 1973; Farr, 1977), become abundant in North Inlet in late spring and early summer (Cain and Dean 1976). The absence of large individual grass shrimp during summer, coupled with the growth rates that seem to be relatively constant as the individuals get larger, indicate that the population may be continuously cropped before individuals reach maximum size. The fish community in Minim Creek is predominantly composed of planktivores (Reis, 1977). Holthuis (1952) and Williams (1965) indicated that *P. pugio* has the potential to reach a size of 50-mm TL in females, as did Minim Creek shrimp. The fact that no such large individuals were collected from North Inlet supports the contention that predation affects longevity. Early reproduction in the North Inlet population may also contribute to the shorter life span since organisms that devote energy to reproduction at an early age are less likely to survive to later ages (Giesel, 1976; Stearns, 1976, 1977).

Reproductive Dynamics

Temporal variations in sex ratio in *Palaemonetes pugio* have been noted (Wood, 1967; Welsh, 1975; Sikora, 1977). Deviations from the expected 1 : 1 ratio may internally regulate the population size by affecting the reproductive potential of that population (Giesel, 1972). A female-biased sex ratio increases the reproductive potential (Wildish, 1977). The significant size dimorphism of the sexes of shrimp in both areas may not affect reproductive success of the males since a variety of mating behavioral patterns exists for shrimp of different sizes (Berg, 1979).

Fecundities differed markedly from those observed by Wood (1967) and from the contention of Sikora (1977) that clutch size could not be predicted from either female length or weight. Variation between clutch sizes of females of similar sizes in North Inlet and Minim Creek may be due to nutritional differences and/or differential allocation of energy (e.g. Cody, 1966). Anderson (1977) found that within the same grass shrimp population, energy allocation to reproduction temporally varies from 4 to 16% of the total caloric intake.

The two populations differed in the age of first reproduction. For the conditions prevailing in North Inlet and Minim Creek in April–May, egg development time is about 20 d (Little, 1968; personal observation). Larval development is completed in 40 d at 20 °C and 25‰ S and 65 d at 20 °C and 5‰ S (Floyd, 1977). Post-metamorphic growth to first oviposition is about 45 and 60 d for North Inlet and Minim Creek females, respectively. Thus, the ages of first reproduction are 3.5 months for North Inlet and 4.8 months for Minim Creek. Wood (1967) estimated growth to adult size in Galveston Bay shrimp as 2–3 months in summer, but it is not clear if his estimate was based from the onset of oviposition or from the time of metamorphosis or recruitment. P. A. Sandifer (personal communication) has raised *Palaemonetes pugio* from eggs to reproducing adults in as little as 3 months in simulated summer laboratory conditions.

Both slow growth and physiological stress could induce delayed reproduction in Minim Creek shrimp. In North Inlet, however, conditions seem optimal for rapid larval development and growth, and consequently, early reproduction. Another possible factor affecting early reproduction in North Inlet females may be interspecific competition from *Palaemonetes vulgaris*. Both species occur in North Inlet at about the same densities, but *P. vulgaris* is seldom collected in Minim Creek. The larvae and adults of both species have similar niche requirements. Thorp (1976) showed that *P. vulgaris* apparently displaces *P. pugio* from shell to mud stratum and contended that the shell substratum provides greater protection from predators than mud. If such displacement occurs in North Inlet, the additional vulnerability to predation could place an important selective pressure on earlier reproduction (Gadgil and Bossert, 1970). Coupled with the shorter life span, early reproduction on the part of the North Inlet females may then be adaptive.

Divergence in Life-History Patterns

Great variability in life history patterns exists between the two populations of *Palaemonetes pugio* studied. The differences may be due to several factors acting independently or jointly on various stages of the life cycle. The set of reproductive traits exhibited by the two populations fit some predictions of life history models. In the North Inlet population, there is rapid development, early reproduction and short life; in the Minim Creek population, there is slow development, delayed reproduction and long life. Both patterns may conform to the predictions of the stochastic model regarding the effects of age-specific mortality (Charnov and Schaffer, 1973), which predicts late maturity and its correlates in fluctuating environments when juvenile mortality is variable. Although it has not been demonstrated, juvenile mortality in Minim Creek may be highly variable since survival of the young stages is generally low in reduced salinity conditions (Floyd, 1977). The same model predicts earlier reproduction and the attendant traits when adult mortality fluctuates; this may be the case in North Inlet where predation on the adults could be an important factor.

Clutch size and type of environment do not meet generalizations of the models. Small clutches should be correlated with long-lived, delayed reproducers in fairly constant environments (Pianka, 1970). In the present study, smaller clutches are found in the short-lived, early reproducing North Inlet population. Although earlier maturity, shorter life and fast development are predicted for a physically harsh environment, Minim Creek is more physiologically stressful. Neither deterministic nor stochastic models fully account for the observed results, which supports Stearns' (1977, 1980) contention that generalizations from the models usually do not hold for intraspecific comparisons.

The apparent plasticity of reproductive patterns in *Palaemonetes pugio* is perhaps caused by a variety of factors not necessarily mutually exclusive. Giesel (1976) noted that the optimal pattern of reproductive traits depends on the interaction of physical and biotic aspects in the organism's environment. Whether or not the observed life history traits may be considered a life history tactic, i.e., "a set of coadapted traits designed by natural selection, to solve particular ecological problems" (Stearns, 1976) remains to be seen.

This study has provided a data base from which further work on intraspecific comparisons of reproductive patterns can be made. The results suggest that the ability of *Palaemonetes pugio* to persist in different environments arises from plasticity of life history adaptations under a variety of conditions. Perhaps the reproductive flexibility reported here and the developmental plasticity noted by Provenzano *et al.* (1978), and Sandifer and Smith (1979), are the basis of the success of *P. pugio* in estuarine habitats.

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