Size-Specific Effects of Density on the Growth, Fecundity and Mortality of the Fish *Fundulus heteroclitus* in an Intertidal Salt Marsh

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ABSTRACT: Three size classes of *Fundulus heteroclitus* (L.) (small, 40–50 mm total length; medium, 50–69 mm TL; large, $\geq$ 70 mm TL) were maintained on an intertidal salt marsh in separate enclosures (10 m²) for 10 months at 3 densities (1, 2 and 4 ind. m⁻²). During the final 6 weeks of the experiment (March–April 1979) the effects of density on individual growth as well as mortality and fecundity of the enclosed populations were assessed. Although fish density and growth were inversely related in all size classes, the growth rate of small *F. heteroclitus* remained positive even after 6 weeks at the highest experimental density. Medium size fish grew when enclosed at densities of 1 and 2 ind. m⁻² but not at 4 ind. m⁻². The growth of large fish was positive only in cages containing 1 ind. m⁻². Over the range of experimental treatments, fecundity of medium size *F. heteroclitus* exhibited the strongest negative response to high density. However, the gonadosomatic index for large fish was lower than for either of the other size classes at all experimental densities, suggesting that fecundity of large individuals may be severely impaired even below the lowest density (1 ind. m⁻²) used in the experiment. Density and fish losses (mortality + escape) were directly related only in the small and large fish size classes. After 6 weeks at a density of 4 m⁻², 77 % of the small fish and 60 % of the large fish were lost compared to only 32 % of the medium size individuals. Escape accounted for an estimated 13.2 % of all losses and was independent of density. Total losses reflected a density-dependent trend in small and large fish mortality.

INTRODUCTION

Early field investigations of competitive interactions (e. g. Andrewartha and Birch, 1954; MacArthur, 1958) were largely observational. Recently there has been a proliferation of rigorous field experimentation demonstrating the role of interspecific competitive interactions in determining the local abundance and distribution of organisms (Connell, 1961; Dayton, 1971; Wilbur, 1972; Menge, 1976; Hairston, 1980). Although intraspecific competition was the focus of many classical laboratory experiments (e. g. Nicholson, 1933; Gause, 1934; Park, 1954), it has not been studied under experimental field conditions as intensively as has interspecific competition. Eisenberg (1966) found that food additions dramatically increased the fecundity of enclosed populations of the snail *Lymnaea elodes*. Stiven and Hunter (1976) showed that the growth rate of caged *Littorina irrorata* (marsh periwinkle) was reduced at high densities in a salt marsh habitat. In

another intertidal snail study, Underwood (1976) found that different age classes of *Nerita atramentosa* exhibited alternative responses to density. At high density, juvenile and adult growth rates decreased; only adult mortality increased. These experiments and others conducted in aquatic habitats (Frank, 1965; Behrens, 1971; Stiven and Kuenzler, 1979) used either gastropod or bivalve molluscs. Vertebrates are usually unsuitable for use in controlled experiments in the field because their high motility dictates cage sizes of impractical proportions. Although there have been some studies with fish, few have dealt with size (age)-specific effects of density. Beverton and Holt (1957) implied that of all the density-dependent responses studied in fish populations, the relationship between density and growth was the best known. Backiel and LeCren (1978) cited numerous examples of increases in fish growth rates in response to decreased density under field conditions. Weatherley (1972) stated that because of individual growth plasticity in fish, general relationships

between growth and density could be misleading or unrealistic, and work in this area should consider differential effects due to fish size. Most controlled experiments dealing with fish growth have been performed on young age classes, presumably because of their normally rapid growth rate and the short time interval required to produce results. Edwards et al. (1970) altered the densities of both young plaice and the bivalve mollusc *Tellina* (the siphons of *Tellina tenuis* were eaten by the fish) in large outdoor, flow-through seawater tanks and found that fish at high density relative to their food supply showed reduced growth.

Recent studies of the production dynamics of the common mummichog *Fundulus heteroclitus* (L.) have suggested that this abundant cyprinodontid fish has an important role in energy transfers within the salt marsh (Valiela et al., 1977; Meredith and Lotrich, 1979) Although mummichog production estimates in these studies were presented on a per m^2 basis, there were no direct measurements of the marsh area required to produce the observed fish growth rates.

The present work was part of an investigation to test the effects of *Fundulus heteroclitus* size and density on the benthic infaunal community of a North Carolina salt marsh (Kneib, 1980). Kneib (1980) showed that infaunal densities were affected more by fish size than fish density. In the statistical analysis of those data, the effects of *F. heteroclitus* density alone were obscured because small and large mummichogs had opposite effects on the densities of most small benthic invertebrates. However, the effect of fish size on invertebrate abundance patterns was intensified at certain fish densities. High infaunal numbers occurred in response to increasing the density of large *F. heteroclitus*. The lowest infaunal densities occurred when only small mummichogs were present or when all fish were excluded. Predation by the grass shrimp *Palaemonetes pugio* Holthuis, was presumed to be the reason for these results because the shrimp are known to reduce infaunal densities (Bell and Coull, 1978) and there was evidence indicating that only large *F. heteroclitus* could control shrimp densities in the experimental enclosures. Regardless of the exact mechanism, changes in size-specific mummichog densities altered the abundance of potential prey species. It follows that competition should act through the altered prey densities to affect parameters that control predator *(F. heteroclitus)* population dynamics.

Mummichogs follow the rising tide onto the salt marsh where they feed on a variety of benthic and epibenthic invertebrates (Butner and Brattström, 1960; Schmelz, 1964; Kneib and Stiven, 1978; Weisberg et al., 1981). The fish are frequently stranded by the ebbing tide in shallow pools and water-filled depressions on the marsh surface, where they are exposed to rigorous physical conditions. *Fundulus heteroclitus* is remarkably well adapted for survival in a wide range of temperature and salinity regimes and under oxygen deficient conditions which could result from being stranded at high densities in shallow marsh pools (Lewis, 1970; Griffith, 1974; Mitton and Koehn, 1976; Targett, 1978, 1979) These characteristics make mummichogs excellent subjects for field experiments in the intertidal salt marsh where the fish can be maintained in cages containing artificial pools simulating a physical environment to which they are well adapted and normally encounter.

The purpose of the present investigation was to assess the size-specific effects of density on individual growth, fecundity and mortality in enclosed field populations of *Fundulus heteroclitus*.

MATERIALS AND METHODS

Study Area

The experiments were conducted in the intertidal zone of Tar Landing Marsh located on Bogue Banks at 34° 42′ N, 76° 42′ W in the vicinity of Beaufort, North Carolina, USA. The site was within the boundaries of Fort Macon State Park which provided protection from human disturbance. The dominant vegetation in the study area is the cord grass *Spartina alterniflora*. There is little freshwater input to the marsh and salinity remains around 30–36 ppt. Tidal range at the study site is ~ 85 cm. A detailed description of the area has been reported elsewhere (Kneib and Stiven, 1978).

Experimental Enclosures and Treatments

All experiments were conducted in cages constructed of fiberglas screening (~ 1.5 mm mesh) and measuring 3.16 m square (10 m^2) × 1 m high. The 27 cages were arranged in 3 equal rows parallel to the tide line. Enclosures were contiguous within a row The bottom edges of the enclosures were buried 15–20 cm in the marsh sediment and the sides were stapled to (1.5 m × 5 cm × 5 cm) treated wooden posts. Two pits (50 × 50 × 50 cm) dug at the low end of each cage retained water and provided a low tide refuge for the experimental fish.

Experimental enclosures received either small (40–50 mm TL), medium (50–69 mm TL) or large (≥ 70 mm TL) *Fundulus heteroclitus* at densities of 10, 20 or 40 individuals per cage (1, 2 or 4 ind. m^{-2}, respectively). There were 3 replicates of each treatment combination. Since sexual differences in growth and mortality occur in *F. heteroclitus* (Kneib and Stiven, 1978),

equal numbers of males and females were added to each enclosure. Half of the fish in each cage were marked by the subcutaneous injection of Liquitex® acrylic paint, a technique previously used on mummichogs by Lotrich and Meredith (1974). Four colors (cadmium red medium, cobalt blue, permanent green light and cadmium yellow light) and 2 injection locations (dorsal and ventral caudal peduncle) yielded a sufficient number of distinct combinations to individually mark half of the fish in any cage. The marks were easily distinguishable after at least 3 months and as previously reported by Lotrich and Meredith (1974) produced very low marking mortality which in the present investigation allowed a high percentage recovery (usually 80–100 % in low density cages).

Fish infrequently crossed cage partitions. However, a marked fish from one treatment cage was occasionally recaptured in an adjacent cage, sometimes resulting in an enclosure with 2 identically marked fish. The stray was invariably identified by its sex or size and returned to the appropriate treatment.

Enclosures were monitored periodically to assure maintenance of the treatment levels. Fish were removed from the enclosures by placing minnow traps in each enclosure pit for 30 min at low tide. Each trap was baited with a freshly collected mussel *(Geukensia*

demissa), the shell of which was cracked slightly to attract fish into the trap but to prevent them from feeding on the bait. All fish removed from the cages were measured (total length, TL), counted and returned to the pits. *Fundulus heteroclitus* of appropriate size were added when necessary, to compensate for losses due to mortality and/or escape. Although the fish densities were maintained for 10 months from the initiation of the experiment in June 1978, a full complement of marked fish was not maintained until March 1979, at which time monitoring occurred in a sequence as follows: (1) In mid-March 1979, fish were removed from all cages and freshly captured *F. heteroclitus* were measured, marked and added in the appropriate size-density combinations. (2) After 2 weeks, the enclosures were sampled, the fish measured and losses compensated with additions of both marked and unmarked fish. (3) Three weeks later (mid-April 1979), the enclosures were again sampled, but all losses, whether from marked or unmarked experimental populations, were replaced by fresh unmarked *F. heteroclitus*. (4) At the end of April 1979, all fish were removed from the enclosures and preserved in 10 % seawater formalin.

Growth Determinations

Density effects on growth were determined by 2 methods. The 6 week incremental increase in length (TL, mm) achieved by individual marked fish was compared in an ANOVA with fish density and size as main effects. Fish size was included as a factor because growth in *Fundulus heteroclitus* as in other fish, slows with age (Beverton and Holt, 1957; Kneib, 1976).

A second approach compared mean dry weights of marked fish from each experimental density in an analysis of covariance. The analysis included fish that had been marked both 4 and 6 weeks before the termination of the experiment. After the gut contents were removed, experimental fish were dried at 60 °C for 1 week to obtain a relatively stable dry weight. Gonads were dried and weighed separately but added to the body weight to yield the total weight used in all calculations. The sexes were treated separately because length-weight relationships in *Fundulus heteroclitus* differ by sex (Kneib and Stiven, 1978). A logarithmic transformation was applied to the length and weight data to linearize the relationship.
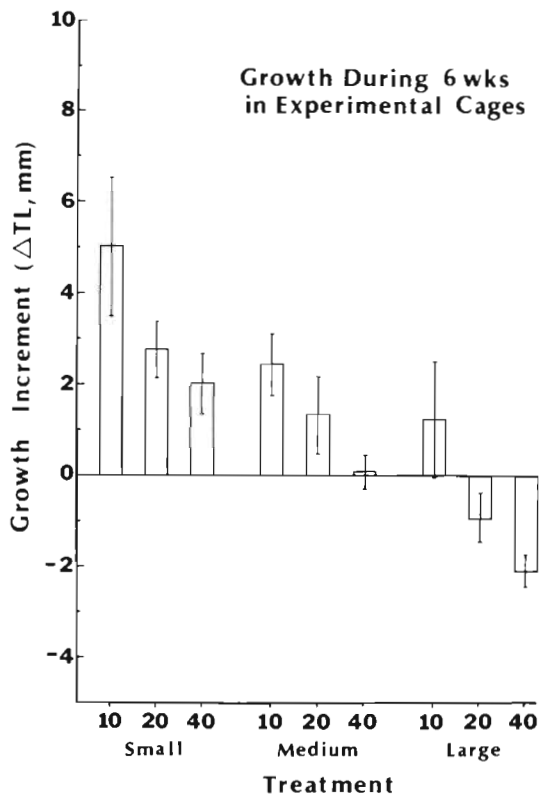
Fecundity Determinations

It was not possible to evaluate fecundity directly by counting the number of eggs produced per female

Fig. 1 *Fundulus heteroclitus*. Mean change in total length (mm) ± 2 SE of marked individuals after 6 weeks at each combination of fish size and density

mummichog at each density because multiple spawnings were possible. However, 2 indirect assessments of fecundity relative to fish density were made for each fish size class. The first compared the proportion of females carrying ripe oocytes (defined in Kneib and Stiven, 1978) at the end of the experiment. Density effects were compared separately for each fish size class in three 2×3 contingency tables from which chi-square values were calculated. In the second approach, an ANOVA was performed on dry gonad weight as a percent of total dry body weight (gonadosomatic index, GSI). Because the data were expressed as proportions, an arcsin $\sqrt{\times}$ transformation was applied prior to statistical analysis. All marked fish subjected to the experimental treatments for 4–6 weeks were included.

Mortality

The proportions of marked fish missing from each treatment (after 2 and 6 weeks) were analyzed in contingency tables using chi-square to assess the relative importance of density on the losses of fish in each size class. Some losses were due to escape, complicating the direct estimate of density dependent mortality. However, escape losses were estimable from the number of marked fish that were assigned to a particular cage but were recaptured in an adjacent cage. Although most enclosures shared 2 sides, those on the ends of rows shared only 1. Assuming that escape was equally likely through any of the 4 sides of a cage, the number of actual escapes from an enclosure was the same as the number of fish recaptured from the enclosures adjoining on both sides or $1.5 \times$ the recovered fish for enclosure occupying terminal positions in a row.

RESULTS

Growth

Both fish size and fish density were factors determining incremental growth as measured by change in total length (Fig. 1). An ANOVA indicated that statistical differences in growth due to fish size (F, $P < 0.001$) and fish density (F, $P < 0.001$) were highly significant. There was no significant size x density interaction (F, $P > 0.05$). Note that the mean change in length was negative for large fish held at densities of 20 and 40 fish per cage.

The mean weight for a fish of a given length was also affected by density. This evaluation was conducted as an analysis of covariance on fish weight with fish length and fish density as covariates. The first step in the analysis was to compare the slopes of the weight on

Table 1 *Fundulus heteroclitus*. Results from analysis of covariance showing calculated mean dry weights (mg), adjusted for length, at each experimental fish density. Table values: antilog, of means from transformed (ln $\times$) data

Sex	Fish density (ind. cage^{-1})		
	10	20	40
Males	851.7	849.1	798.9
Females	856.1	814.9	756.4

Table 2. *Fundulus heteroclitus*. Numbers of marked females with and without ripe oocytes after 6 weeks at 3 density treatments. Chi-square values testing for the effect of density on the proportions of ripe females in each size class are shown

Fish size class	Fish density (ind. cage^{-1})		
	10	20	40
Small			
ripe	7	3	6
not ripe	3	6	8
		$\chi^2 = 2.85$ ns	
Medium			
ripe	4	9	4
not ripe	1	8	13
		$\chi^2 = 6.49$ ·	
Large			
ripe	2	3	4
not ripe	4	12	15
		$\chi^2 = 0.38$ ns	

· $P < 0.05$; ns $P > 0.05$

length regression lines for fish held at each of the 3 densities. This was done by performing an ANOVA on the weight data with length and density as the independent variables. The interaction term, length $\times$ density, was then used as a test for differences in slopes. There was no statistical evidence for any differences (F, $P > 0.05$) in the slopes among density groups for either sex.

Having satisfied the equality of slopes assumption, the mean dry weights adjusted for length were calculated for both sexes at each experimental density (Table 1). The effect of density on mean weight was statistically significant in both males (F, $P < 0.01$) and females (F, $P < 0.001$). However, increased density had a greater effect on the weight of females.

Fecundity

Effects of the 3 fish densities on the proportion of marked female mummichogs carrying ripe oocytes were compared in contingency tables for each fish size class (Table 2). There was no statistical evidence that
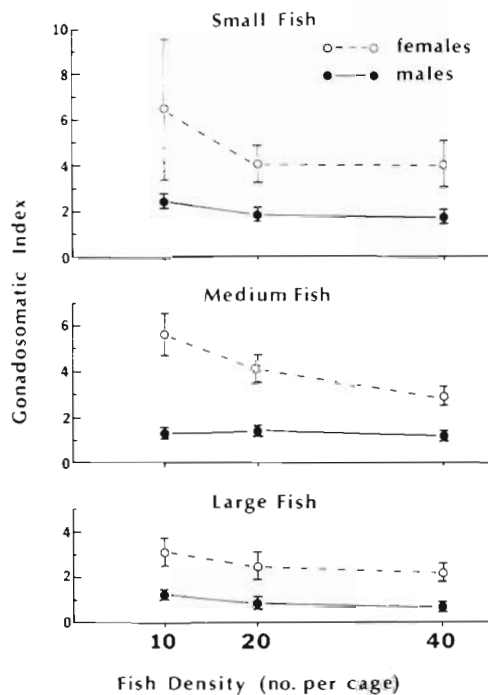
Fig. 2. *Fundulus heteroclitus*. Effect of density on gonadosomatic index of males and females. Results are presented for each fish size class separately. Points are mean GSI ± 2 SE

density affected the percentage of either small or large fish carrying ripe ova, but the proportion of ripe females in the medium size class decreased significantly with density

Density also affected gonadosomatic index (GSI) (Fig. 2). A 2-factor ANOVA indicated a significant density effect on the GSI of both medium (F, P < 0.001) and large (F, P < 0.05) fish However, there were no significant differences in the GSI of small fish due to density (F, P > 0.05). Of course, sex was a highly significant factor (F, P < 0.001) affecting the GSI of all fish size classes. There was a significant density × sex interaction (F, P < 0.05) only in medium size fish, reflecting the proportionally greater effect of density on female GSI in this size class (Fig. 2). The highest variance was associated with mean GSI values of small fish. Although large fish of both sexes responded to increased density by decreasing GSI, the response was relatively small (Fig. 2).

Mortality

The proportions of marked fish lost from each density treatment after 2 and 6 weeks were compared with separate chi-square tests for each fish size class. Losses (Fig. 3) were significantly density dependent for small fish at both 2 and 6 weeks (χ^2, P < 0.001).
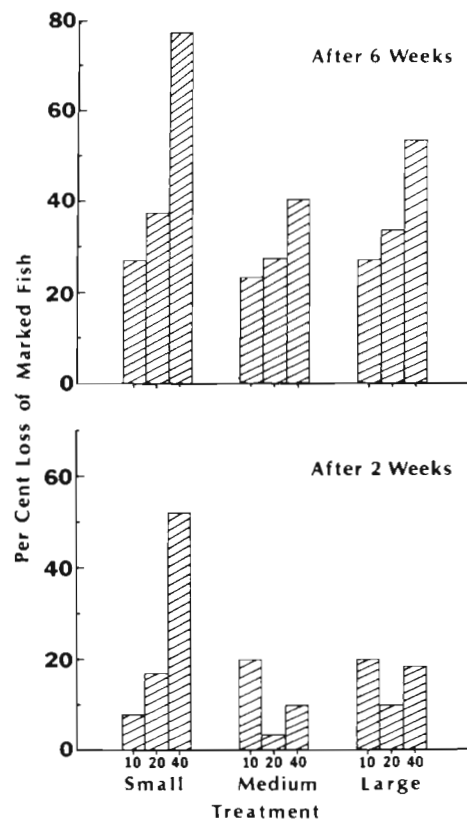

Fig. 3. *Fundulus heteroclitus*. Percent of marked individuals lost from experimental enclosures after 2 and 6 weeks at the indicated treatment combinations of fish size and density. Half of the fish in each density treatment were marked and each treatment was replicated 3 times. Therefore, density treatments of 10, 20 and 40 individuals per cage were represented by 15, 30 and 60 marked individuals, respectively

There was no detectable pattern in the losses of medium (χ^2, P = 0.154) or large (χ^2, P = 0.723) fish at 2 weeks, but at 6 weeks there was a significant trend in the losses of large fish with increasing density (χ^2, P = 0.047). There continued to be no statistical evi-

Table 3. *Fundulus heteroclitus*. Estimates of escape losses from each of the experimental treatments. Table values: numbers of marked fish estimated to have escaped. Values in parentheses: percentages of total losses of marked fish attributable to escape

| Fish density | Fish size class | | | Total |
(ind. cage^{-1})	Small	Medium	Large	
10	1	–	–	1
	(25.0)			(7.1)
20	3	–	5	8
	(25.0)		(50.0)	(26.7)
40	12	5	–	17
	(14.6)	(19.2)		(11.1)
Total	16	5	5	26
	(16.3)	(12.8)	(8.3)	(13.2)

dence for a similar tendency in medium fish (χ^2, P = 0.452).

Estimates of the number of marked fish that escaped from the cages (Table 3) indicated that escape losses made a relatively insignificant contribution to the trend in total losses (13.2 % of all losses during this study were estimated to have escaped.) Therefore, the density-dependent trends in total losses (Fig. 3) can be assumed to reflect density-dependent trends in mortality.

DISCUSSION

Density-Dependent Growth

Growth, as measured by change in length, was shown to be inversely related to density in *Fundulus heteroclitus*. Although absolute changes in length were greatest for the smallest fish, all size classes showed growth reductions with density. Large fish at densities of 20 and 40 per cage exhibited negative absolute growth, resulting in losses of up to 4 mm TL per fish in a 6 week period. It is not likely that these results were due to size-specific measurement error because the number of fish exhibiting negative growth, as well as the magnitude of the length changes, increased with fish density regardless of fish size. After 6 weeks the percentages of large fish exhibiting negative changes in length were: 27.3, 50.0 and 100.0 at densities of 10, 20 and 40 fish per cage, respectively. Similarly, the percentages were 0, 13.6, 33.3 for medium fish and 0, 0, 7.1 for small fish. Fin damage, which could cause inaccurate measurements of total length, was not a problem even at high density Length losses are known to occur in other fish species but being limited by the vertebral column are usually ignored as a response measurement in favor of weight changes which are of greater magnitude (Ursin, 1979). In the present study, analyses of differences in mean dry weight verified the length increment findings that reductions in growth due to increased densities affected each size class in the same manner A comparison of the mean dry weights (adjusted for length) showed a significant inverse relationship between weight and density. Again, confirming the growth in length results.

The causes of growth inhibition at high density may be quite varied and species-dependent. The possibilities range from growth-inhibiting chemicals (e. g Pfuderer et al., 1974) to behavior (Magnuson, 1962) and the effects of resource overutilization (Weatherley, 1972). Edwards et al. (1970) conducted experiments with 0-group plaice in large tanks. Manipulating densities of both the fish and their food supply *(Tellina*

tenuis), the investigators found that food limitation and not crowding was responsible for the observed decreased growth rate at high fish densities. This is probably the case in the present study of mummichog responses to density. All *Fundulus heteroclitus* size classes responded to increased density with decreased growth. Samples of benthic invertebrates from each enclosure combined with fish gut content analysis suggested that *F. heteroclitus* at high density (4 ind. m^{-2}) reduced the size of particular prey populations (Kneib, 1980). The prey species most affected was dependent on the fish size treatment (Kneib and Stiven, in preparation). Perhaps due to habitat complexity (Vince et al., 1976), large *F. heteroclitus* could not feed heavily on the small invertebrate species that were preferred by small fish. In enclosures containing only small fish, the densities of small invertebrates were reduced, probably due to predation by small *F. heteroclitus* and the presence of grass shrimp *Palaemonetes pugio* (Bell and Coull, 1978). Small fish were unable to prey effectively on the large grass shrimp. However, gut content analyses indicated that the shrimp were a preferred food of large *F heteroclitus* in experimental enclosures. Thus, large fish probably controlled the density of grass shrimp, allowing the rapid increase of small infaunal invertebrates which could have been utilized by small *F. heteroclitus*. Each fish size class was subjected to 3 constant density levels of the same size fish, and no experiments were conducted with mixed size classes. However, the available data suggest that the presence of large *F. heteroclitus* may benefit small mummichogs perhaps through the control of decapod competitors.

The Effect of Density on Fecundity

The 2 approaches used in the present study to detect density-related changes in size-specific fecundity of *Fundulus heteroclitus* produced similar results. There was an inverse relationship between density and the proportion of medium-size females containing ripe oocytes. The same relationship held for the gonadosomatic index (GSI) Small fish did not show statistically significant differences in fecundity measures due to density However, an effect may have been masked by the high variability expected from young fish entering their first reproductive episode (Fig. 2). The effect of age on fecundity in fishes is, in general, viewed as an uncertain and inconsistent relationship (Bagenal, 1978; Wootton, 1979). There is some observational evidence that age of maturation may be delayed under low food conditions (McFadden et al., 1965). However, de Vlaming (1971) found that starvation had no effect on the initiation of the reproductive

cycle in an estuarine goby *(Gillichthys mirabilis)*, but could cause gonad regression. Although age is not considered a reliable determinant of fecundity, some measure of fish size is generally accepted as related to the number of ova produced. However, normal environmental variability distorts the relationship (Nikolskii, 1969). Although the largest fish produce the greatest number of eggs, their contribution to total population fecundity is often small because the population usually comprises relatively few large individuals (Weatherley, 1972). Egg quality (i. e. fat and protein content) is usually highest in the medium size fish that make up most of the reproductive population (Nikolskii, 1969). Medium size *F. heteroclitus* were shown to contribute most to population fecundity in the Tar Landing area (Kneib and Stiven, 1978). The fecundity of this size class was also most affected by density in the present study. Large fish also showed an inverse relationship between density and fecundity (Fig. 2), but it was not as strong as in the medium size class. In fact, the mean GSI of large fish was smaller than for either of the other size classes. Mummichogs are multiple spawners (Foster, 1967) and as Wootton (1979) pointed out, GSI may be a misleading index of potential annual fecundity in fish that spawn more than once in a season. Although collections for the present study were made in the spring when most of the population experiences a reproductive peak, larger mummichogs may spawn later in the season, perhaps explaining their lower GSI. However, large fish grew only slightly at the lowest experimental density (1 ind. m^{-2}) and therefore, a more likely explanation is that they may not have had sufficient energy reserves to invest in reproduction.

Several other studies have shown an inverse relationship between fish density and fecundity. Bagenal (1978) cites several examples from both field observations and controlled experiments. As with the relationship between fish growth and density, there have been several hypotheses advanced concerning density-related mechanisms causing reductions in fecundity Warren (1973) presented evidence for a chemical factor that operated in crowded laboratory conditions. However, in field situations it is generally agreed that food limitation affects fish size which in turn affects fecundity (Nikolskii, 1962). Wootton (1979) considered food availability as the most important environmental determinant of fish fecundity. This opinion is supported by several field observational studies (McFadden et al., 1965; Wydoski and Cooper, 1966; Leggett and Power, 1969) and laboratory experiments (Scott, 1962; Hester, 1964; de Vlaming, 1971; Wootton, 1977). The manner in which reduced fecundity occurs in the absence of adequate food resources may vary with fish species. The guppy *Lebistes reticulatus* responded to

decreased food by reducing the number but not the size of young (Hester, 1964) Brown trout *Salmo trutta* from infertile streams were shown by McFadden et al (1965) to produce fewer eggs than trout of the same size from fertile streams. Scott (1962) showed that the number of atretic ova increased in starved rainbow trout *Salmo gairdneri*.

Mummichogs in the Tar Landing marsh have been shown to contain an often large but highly variable number of degenerating ova (Kneib, 1976), perhaps reflecting individual variation in condition due to nutritional state. In multiple spawners, like *Fundulus heteroclitus*, the number of spawnings as well as total egg production may decrease with reduced food supply (Wootton, 1977). However, there are no reliable estimates of the number of times *F. heteroclitus* may spawn in a single season.

In nature, density effects may also occur at the egg stage just after spawning. Mummichogs are known to eat their own eggs (Chidester, 1916; Schmelz, 1964; Able and Castagna, 1975) and probably newly hatched fry. At high density, the effects of decreased food resources would probably result in an even higher rate of cannibalism, especially if protective refuges for eggs (Able and Castagna, 1975) and/or fry (Taylor et al., 1977) were limited.

Regardless of the actual mechanism, reduced reproductive success in *Fundulus heteroclitus* at high density would have important consequences for the population size structure, since the effects of a single weak year class would be reflected in the population for several years. Changes in the survival or fecundity of the medium size class of *F. heteroclitus* would be expected to produce the most dramatic effects on the future population structure.

Density-Dependent Mortality

Although the reproductive success (or failure) of one generation may affect the intensity of intraspecific competition in the next generation, mortality has an immediate influence on current competitive interactions. In the present investigation, losses of small and large *Fundulus heteroclitus* were significantly higher in cages maintained at 4 ind. m^{-2} than at lower densities. Although escape losses accounted for 13.2 % of the total losses, there was no relationship between density and escapes. Therefore, the density-dependent trends observed in total losses (Fig. 3) reflect the effect of mortality. The effect of escape losses was only to amplify the density-dependent mortality trend. Losses at densities of 10 and 20 individuals per cage were not significantly different within or among size classes,

falling in the range of 25–35 % after 6 weeks. In the same time period, the highest density (40 per cage) resulted in losses of up to 77 %. The lowest losses (24–32 %) were suffered by medium size fish. This agrees with field estimates of *F. heteroclitus* mortality trends (Valiela et al., 1977; Kneib and Stiven, 1978).

In general, there is a two-sided literature dealing with the effects of density on mortality in fishes. For every example suggesting density-dependent mortality, there is another that shows either no evidence of increased mortality with density or an inverse relationship (Backiel and LeCren, 1978). Beverton and Holt (1957) suggested that there was little evidence for density-dependent mortality in natural populations of adult fish. Nikolskii (1969) also contended that densities high enough to affect a critical resource like food supply may result in mortality of very young fish. Older fish would be affected only indirectly. That is, a decreased food supply may cause fish to seek food more actively, making them more susceptible to predation. Nikolskii also suggested that fish in a poor nutritional state may more easily succumb to disease and parasites. Adult fish are more likely to respond to decreased food supply not by dying but by losing weight. The growth and mortality responses of large mummichogs supported this hypothesis early in the present experiment, but continued high density resulted in a significant increase in mortality (60 % at 4 ind. m^{-2} compared to 29.4 % at 1 ind. m^{-2}) after 6 weeks.

Although distinct density-dependent mortality occurred in the present investigation, it may not be a strong influence in natural situations for 2 reasons. First, only the highest experimental density (4 ind. m^{-2}) produced significantly increased mortality. It is unlikely that mummichogs would attain sustained marsh densities this high and may normally respond to high density by emigrating Therefore, the observed mortality may be a caging effect (*sensu* Krebs et al., 1973). Second, the food supply in the enclosures was diminished by maintaining the density-size class treatments in them for ten months prior to the mortality measurements. In a sense, the cages were preconditioned against the survival of each size class. Small crustaceans (the primary food of small fish) attained high densities in large fish cages while larger crustaceans (taken primarily by large fish) were abundant in small fish enclosures (Kneib, 1980). Algae and fouling organisms, a potential food source for the enclosed fish and a common problem in subtidal caging experiments, did not grow on the cage walls in the present study. The lack of fouling organisms may be related to the position of the experiment in the mid to high intertidal zone and grazing by the abundant marsh periwinkle *Littorina irrorata*.

Considering the combined effects of density on growth, fecundity and mortality, medium-size fish responded least to density and seemed most tolerant of crowded conditions. Small fish survived and grew at densities of 1 and 2 per m^2 of marsh surface, but experienced heavy mortality losses at higher densities. Large fish required at least 1 m^2 of marsh to maintain a positive growth rate. At higher densities, large mummichogs responded first by exhibiting negative growth followed, at the highest experimental density (4 m^{-2}), by high mortality over an extended period (6 weeks). The density tolerance of medium size fish may be related to an ability to utilize a wider range of prey sizes than either of the other fish size classes. Under the experimental conditions, medium fish may not have experienced the same effective food shortages as the other 2 fish sizes.

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