Size-dependent interactions in salt marsh fish
(Fundulus heteroclitus Linnaeus) and shrimp
(Palaemonetes pugio Holthuis)

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Abstract

Competition and predation are major biotic interactions that influence the structure of aquatic communities. The relative importance of each type of interaction is usually a function of the relative size of the organisms involved. This study used field experiments to assess potential size-dependent interactions among small juvenile killifish (Fundulus heteroclitus) and grass shrimp (Palaemonetes pugio) and larger adult killifish. Density, species combinations, and predation risk were manipulated within field enclosures on an intertidal salt marsh on Sapelo Island, Georgia. Intraspécific and interspecific competitive effects between small juveniles (larval killifish and postlarval grass shrimp) were examined in the absence and presence of predators (larger adult killifish) to determine interactions and modifications of interactions due to predators. In the absence of predators both negative intraspecific and interspecific effects occurred in the form of reduced growth of juvenile grass shrimp. Survival of juvenile shrimp was the same in the presence or absence of juvenile killifish. However, when larger adult killifish were present, the interspecific competitive effect of reduced growth in juvenile grass shrimp was not significantly different from controls. Growth and survival of juvenile fish were unaffected by increased density of conspecific juveniles and the presence of juvenile grass shrimp and adult fish predators. These results provide field evidence for interspecific competitive interactions between juveniles of two of the most abundant species of nekton utilizing salt marsh habitat along the eastern coast of North America. However, when larger adult killifish predators were present these interspecific competitive effects among similar sized juvenile killifish and grass shrimp disappeared. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: Fish; Fundulus heteroclitus; Shrimp; Palaemonetes pugio; Competition; Predation; Size; Interactions; Intertidal marsh

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1. Introduction

Most aquatic communities are typically composed of species that exhibit substantial change in size during ontogeny (Neill, 1988). Large differences in size can cause organisms to exhibit marked shifts in both habitat and resource utilization, and can produce communities where different life stages (e.g. juveniles and adults) interact with different competitors and predators (Werner and Gilliam, 1984; Osenberg et al., 1992). Since size is a major factor determining whether an interaction between two organisms is competitive or predatory, our understanding of size-dependent interactions in aquatic communities should enhance our understanding of how these communities are structured.

Classical categorization of interactions between species in size-structured populations at one stage or size is oversimplistic (Wilbur, 1988). For instance, even when considering a simple two-species system, such a community may consist of similarly sized individuals that compete at one stage or size, with predation also occurring among individuals of sufficiently different size. Thus, simultaneously occurring size-dependent competitive and predatory interactions may influence the structure of aquatic communities where smaller juveniles and larger adults share habitat.

While predation has an obvious negative effect on individuals that are consumed, predation or the risk of predation may produce more subtle effects by altering the behavior of prey organisms through predator avoidance or escape activities (Helfman, 1986). Altered spatial distributions of prey in response to predation risk can change foraging patterns and potentially increase interspecific competitive interactions between individuals seeking refuge (e.g. Werner et al., 1983; Mittelbach, 1984; Werner and Gilliam, 1984; Werner, 1986; Mittelbach and Chesson, 1987; Werner and Hall, 1988). Such predator induced behavioral responses may also increase intraspecific effects within particular size classes susceptible to predation (Werner and Hall, 1988).

It has become clear that direct interactions such as predation and competition can interact in complex ways that are not always predictable (Wootton, 1993, 1994). This is particularly true when only pair-wise interactions between species are examined in the absence of a major predator. It has been well established that predators can alter interactions between prey species and affect the community structure in aquatic and marine food webs (Sih et al., 1985; Kneib, 1991; Wootton, 1993, 1994).

This work was conducted to determine the nature of size-dependent interactions between larval killifish (*Fundulus heteroclitus* Linnaeus), postlarval grass shrimp (*Palaemonetes pugio* Holthuis), and adult killifish. In salt marshes in the eastern United States, killifish and grass shrimp are among the most abundant natant macrofaunal residents (Kneib and Stiven, 1978). Populations of these species are markedly size-structured and exhibit distinct ontogenetic shifts in diet and habitat-use (Kneib, 1987a, 1987b) (Fig. 1). Along the southeastern coast of the United States, larval killifish and postlarval grass shrimp utilize shallow pools of water on the vegetated marsh surface during low tide periods while larger adults are found in adjacent tidal creeks (Kneib, 1984; Kneib and Stiven, 1982). As juveniles grow in size they eventually begin to move with receding tides to subtidal habitats in adjacent marsh channels.

The large range in size and size-dependent patterns of habitat and food resource-use allow for a diverse array of potential interspecific interactions among individuals in these
Fig. 1. Size-dependent trophic relationships and habitat utilization of fish (Fundulus heteroclitus) and shrimp (Palaemonetes pugio). Direction of arrows represents flow of energy from prey to predator and thickness of arrows indicates the relative strengths of the interactions.

species. Small postlarval grass shrimp and larval killifish are potential competitors in refuge habitats on the intertidal marsh (Kneib, 1984). Larger adult killifish prey on juveniles of both species, although there is some evidence of an apparent preference for smaller conspecifics (Kneib, 1987b) (Fig. 1). It has been suggested that juveniles utilize the vegetated intertidal marsh as a refuge to reduce the risk of predation from larger adult fish which they would encounter in adjacent creek channels at low tide (Kneib, 1987a).

Laboratory studies demonstrated asymmetrical competitive interactions among juveniles in laboratory microcosms (Cross and Stiven, 1997). Juvenile grass shrimp exhibited reduced growth in the presence of juvenile killifish while juvenile killifish exhibited no changes in growth or survival in the presence of juvenile grass shrimp. The results of the laboratory experiments prompted the design of the field studies described here that addressed the following questions: (1) do juvenile killifish and grass shrimp (hereafter referred to as fish and shrimp) exhibit intra- and interspecific competition in the field, and (2) does the presence of a major predator (adult fish) modify interspecific competitive interactions among juveniles? It was predicted that if juvenile fish were competitively superior to juvenile shrimp in the field, as was demonstrated in the laboratory, then the apparent preference of adult fish for conspecific juveniles could lead to reduced competitive effects in juvenile shrimp.

2. Materials and methods

2.1. Study site

Field experiments were conducted in salt marshes bordering the upper reaches of the
Duplin River Estuary in the Sapelo Island National Estuarine Research Reserve on Sapelo Island, GA, USA (81°17’W, 31°27’N). The site was typically inundated twice a day by unequal tides with a mean tidal range of 2.1 m (Kneib and Wagner, 1994) and the dominant macrophyte was *Spartina alterniflora*. Most of the laboratory work conducted in the preparation of the field studies was done at the University of Georgia Marine Institute facilities on Sapelo Island, Georgia. Sorting and counting of meiofauna was done at the University of North Carolina at Chapel Hill.

2.2. Field enclosures

Density, species combination, and predation risk were manipulated in enclosures constructed in a salt marsh bordering the Duplin River Estuary. Nine sets of three contiguous enclosures (27 total) were arranged in two rows nearly parallel to an adjacent tidal creek at an elevation of approximately 184 cm above mean low water.

Each square enclosure (1.1 m on a side) was framed with untreated pine lumber (5 × 5 × 150 cm) that served as an attachment site for the walls. Walls were 0.5-mm mesh polypropylene fabric and were attached to the frame with thin wood slats held in place with stainless steel wood screws. Enclosure walls extended 1.2 m above the marsh surface and 10 cm of the bottom edge of each wall was inserted below the marsh surface.

Four embedded 100-mm diameter petri dishes served as low tide refuges for juvenile organisms in each enclosure and were arranged as shown in Fig. 2. These artificial refuges simulated shallow pools of water on the intertidal marsh that are utilized by

Fig. 2. Diagram of the inside of an enclosure showing the arrangement of artificial refuges.
juvenile fish and shrimp at low tide (Kneib, 1993). The petri dishes were held in place by 102-mm diameter PVC collars that were sunk into the marsh substrate. Enclosures were then visually inspected for naturally occurring pools of water remaining at low tide, and if present, were filled with sterile sand to insure the use of artificial refuges by juvenile fish and shrimp.

One larger predator refuge was placed near the center of each enclosure to provide a deeper water habitat to accommodate larger adult fish on the intertidal marsh at low tide (Fig. 2). Predator refuges were made from 15.24-cm diameter × 15-cm long PVC pipe sections. Glass petri dishes (150-mm diameter) were attached to the bottoms with silicon aquarium sealant. It became apparent early in the initial experimental run that during low tide, the water in the predator refuges was becoming too hot during the day for the larger adult fish to survive. Sun shades were made from wall fabric and were suspended over the predator refuges to reduce direct solar radiation. The shades prevented excessive heating of the water in the predator refuges and eliminated further mortality of predators during subsequent experimental runs.

Fish and shrimp trapped inside enclosures during the construction were removed prior to the initiation of experiments. Other potential macrofaunal predators (e.g. Eurytium) of juvenile fish and shrimp were also removed from the enclosures. Enclosures were visually inspected every few days for fouling or growth of organisms on wall surfaces. None was observed on enclosure walls above the surface of the sediments and no noticeable collections of organic matter or sediments accumulated around the periphery of the enclosures.

2.3. Experimental organisms

Fish eggs were obtained from adult fish caught in minnow traps in nearby tidal creeks. Adults were maintained in 76-l aquaria supplied with flowing estuarine water. Spawning boards constructed by cutting grooves in pieces of untreated pine (Kneib and Parker, 1991) were placed into aquaria for use by fish as spawning sites. Spawning boards were checked daily for the presence of eggs during natural spawning periods. Eggs were removed from boards, arranged in a single layer on damp paper towels in petri dishes, and rinsed daily with estuarine water throughout the incubation period (12–14 d). Fully developed larvae were stimulated to hatch by immersion in estuarine water (DiMichele and Taylor, 1980).

Postlarval shrimp were collected at low tide in 20 × 20-cm glass pans placed in the marsh (Kneib, 1987a) and also from the adjacent areas of the marsh with a fine mesh net when the marsh surface was partially covered with water. Captured juvenile shrimp were immediately transported to the laboratory in plastic buckets and used in experiments within 24 h.

Adult fish (predators) were collected in minnow traps placed in tidal creeks before each experimental run. Two adult fish (65–80 mm total length) were placed in each enclosure receiving the predation treatment. Enclosures were examined for predator survival every two days during the initial experimental run and dead predators were replaced. After the first experimental run there was no mortality of predators during the course of subsequent experimental runs.
Standard lengths of larval fish (SL, the distance from the anterior margin of snout to posterior margin of notochord) were measured to the nearest 0.1 mm at 6 × magnification using a stereomicroscope fitted with an ocular micrometer. The initial size range was 5.5–7.0 mm for larval fish.

Juvenile shrimp were measured for total length (TL, the distance from anterior tip of rostrum to posterior edge of telson) (Alon and Stancyk, 1982). A chamber was constructed from Lucite © and paraffin that allowed delicate manipulation and positioning of shrimp during measurements (Cross and Stiven, 1997). Consistent levels of water in the chamber permitted more uniform body positioning along the anterior–posterior body axis, thus allowing more precise length measurements. Initial lengths were determined for 10 randomly chosen juveniles from each treatment group. The size range for juvenile shrimp used in the experiments was 6–11 mm.

To facilitate measurement of initial lengths, young fishes and shrimp were immobilized by immersing petri dishes containing estuarine water and the subjects in an ice water bath for approximately 5 min. Immobilized animals were measured to the nearest 0.1 mm at 6 × magnification using a stereomicroscope fitted with an ocular micrometer. After measurements were obtained, chilled fish and shrimp were allowed to recover for approximately 15 min in petri dishes containing water at ambient temperature before being placed into plastic bags for transport to the field site.

Linear regression models of length and dry mass (measured on extra juvenile shrimp and fish not used in the field experiments) were used to estimate initial dry mass for experimental organisms (Table 1).

### 2.4. Field experiments

A total of four experimental runs were conducted June 17–June 26, July 14–July 23, July 31–August 9, and August 23–September 1, 1993. The 12 experimental fish and shrimp treatments (Table 2) were randomly assigned to 24 of the 27 enclosures each time an experiment was conducted providing two replicates for each treatment in the first three experimental runs. Two of the remaining three enclosures were used as meiofauna cage controls in the first experimental run. The fourth and final experimental run was conducted to provide three replicates for effects of fish on shrimp treatments. Treatments designed to assess competitive effects of shrimp on fish were eliminated to provide an extra replicate for detecting competitive effects of fish on shrimp, thereby

<table>
<thead>
<tr>
<th>Regression</th>
<th>Intercept</th>
<th>slope</th>
<th>$R^2$</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
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<tr>
<td>Shrimp</td>
<td>−0.0253</td>
<td>0.3098</td>
<td>0.88</td>
<td>661.7</td>
<td>0.0001</td>
</tr>
<tr>
<td>Fish</td>
<td>−0.8866</td>
<td>0.4401</td>
<td>0.96</td>
<td>750.7</td>
<td>0.0001</td>
</tr>
</tbody>
</table>

* $n$=87 for shrimp and 33 for fish.
increasing the statistical power for detecting these particular effects. This was done since no significant shrimp on fish effects had been identified from previous experiments (Cross and Stiven, 1997) or from earlier experimental runs in this study. Replicates from the four experimental runs were combined to increase the statistical power of the analyses. The beginning of each experimental run coincided with the same approximate phase of the tidal cycle (usually 2–3 days after spring tides). This phase of the tidal cycle is when larval fish and juvenile shrimp naturally appear on the marsh surface in large numbers (Kneib, 1986a,b, 1987b).

Organisms were introduced into their appropriate enclosures just as the incoming tide was flooding the field site. Predators were introduced into appropriate enclosures ten minutes after juveniles were released to allow the juveniles time to disperse.

At the end of each experimental run (8 d), all surviving organisms were removed from enclosures at low tide and counted. Dry mass of all surviving juvenile fish and shrimp was determined if five or fewer remained, or five were randomly selected if there were more than five surviving individuals.

2.5. Experimental design and analysis

Density, species combination, and predation risk were manipulated in field enclosures to determine whether competition between juvenile fish and shrimp occurred in enclosures placed in marsh habitat and whether the presence of large adult fish predators modified competitive effects between juveniles (Table 2). Effects on each species were analyzed separately using a Model I ANOVA factorial design with all factors considered fixed. Specific a priori hypotheses were used to assess both intraspecific and interspecific competitive effects on growth and survival among juveniles and effects of predators on interspecific competitive effects between juveniles.

Comparing low and high densities of each species alone both in the absence and presence of adult fish predators assessed intraspecific effects between juveniles. After testing for an interaction between density and predation an a priori comparison was
performed to detect intraspecific effects by contrasting the control density treatments (30 individuals) for each species with the high density treatments (90 individuals) without predators.

For the determination of interspecific effects among juveniles and the modification of these effects, an initial density of 30 juvenile individuals for each species in the absence of competitors and predators served as a control. The controls were compared against the performance of competitor treatments (presence of juveniles of the other species) and predator treatments (presence of adult fish). Thus, four treatments were used to assess effects of interspecific competition and predation for each species (target species): (1) 30 juvenile individuals of the target species alone (control), (2) 30 juvenile individuals of the target species and predators (control + predator), (3) 30 juvenile individuals of the target species and 60 juvenile individuals of the other species (competitor treatment), and (4) 30 juvenile individuals of the target species and 60 juvenile individuals of the other species and predators (competitor + predator treatment). Interspecific competitive effects among juveniles of each species were determined with an a priori contrast comparing the control density (30 individuals) of the target species alone with the interspecific competitor treatment consisting of 60 individuals of the competitor and 30 individuals of the target species (both treatments without predators present). The 2:1 ratio of density was used in the competitor treatments since this ratio produced interspecific effects for juvenile shrimp in the presence of juvenile fish in laboratory microcosm experiments (Cross and Stiven, 1997).

Potential modification of interspecific effects due to the presence of predators was determined by comparing interspecific competitive effects between juveniles in the presence and absence of predators. Two additional a priori contrasts were examined (using effects of juvenile fish on juvenile shrimp as an example): (1) control (30 shrimp alone) vs. competitor treatment with predators (60 fish, 30 shrimp, and adult predators), and (2) competitor treatment (60 fish and 30 shrimp) vs. competitor treatment with predators (60 fish, 30 shrimp, and adult predators). It was predicted that adult fish predators could reduce competitive effects of juvenile fish on juvenile shrimp, if they existed, because of the apparent selective predation on conspecific juveniles. If an interspecific effect was present in the absence of predators, but absent when predators were present, this would provide evidence that the presence of predators modified competition between juveniles.

Response variables used in the analyses of competitive effects were mean daily instantaneous growth rate and survivorship. Since young grow exponentially in size, the instantaneous growth rate \( G \) was calculated from \( S_i = S_0 e^{Gi} \) as \( G = \frac{\ln(S_t) - \ln(S_i)}{t} \), where \( S_i = \text{size (dry mass) at beginning of experiment (i)} \) and at the end of the experiment \( t \) (8 d). All analyses were performed using instantaneous growth rates \( G \) but figures show raw data in mm d\(^{-1}\) for clarification of actual growth.

All growth and survival data were analyzed for normality using the Kolmogorov-Smirnov test of goodness of fit at a rejection level of \( P<0.05 \). Variance homogeneity was determined using Levene's test for the homogeneity of variances among treatments (Snedecor and Cochran, 1982). Growth data were normal and variances were homogeneous between treatments. Survivorship data were arcsine transformed to achieve normality. All probability levels for type I error rates for a priori contrasts (when
contrasts were used) were corrected using the Bonferroni correction of type I error rates. Statistical analyses were conducted using Statistical Analysis System (SAS, 1993) and power analyses were determined with SigmaStat Statistical Software (SigmaStat Version 2.0, SigmaStat, 1997).

2.6. Benthic food resources

To determine if juvenile shrimp and fish were capable of reducing food resources in their artificial aquatic refuges, benthic meiofauna samples were obtained from two randomly chosen petri dishes within the high density fish and shrimp treatment enclosures during the first experimental run. Two initial subsamples of benthic meiofauna were obtained three days prior to the initiation of the first experimental run and after three days into the run. Two of the remaining enclosures without fish and shrimp were used as controls. The two subsamples obtained from each enclosure were averaged providing two replicates for each treatment. Samples were collected just prior to the flooding tide by randomly choosing two petri dishes and pouring the contents through a 1.0-mm mesh sieve into sealable plastic bags. The sieve allowed juvenile fish and shrimp to be separated from the sediments and returned to the petri dishes for the continuation of the experiment. Plastic bags containing sediments were sealed and then placed into a cooler for transport to the laboratory.

Samples were rinsed with tap water through a 0.5-mm mesh sieve onto a 63-μm mesh sieve to retain meiofauna. After rinsing for approximately one minute the contents retained on the 63-μm sieve were rinsed with filtered estuarine water into labeled glass bottles. Bottled samples were then stained with a solution of 10% buffered formalin and rose bengal and stored until they could be analyzed.

Meiofauna were visually sorted from sediments and enumerated under a stereomicroscope at 25× magnification. Organisms were enumerated to taxonomic groups (copepods-including nauplii, ostracods, and nematodes) and stored in buffered formalin in microcentrifuge tubes.

Effects of juvenile fish and shrimp on numbers of meiofauna for each taxonomic group were determined by ANOVA using time (initial and final) and density (control and high density fish or shrimp treatments) as main factors. A significant interaction between the two factors was used as an indication of a change in abundance due to the presence of juvenile fish or shrimp.

3. Results

3.1. Direct competitive effects

Juvenile shrimp exhibited intraspecific effects of reduced growth in the high density treatments compared to controls (Fig. 3, P<0.05). However, no differences in growth were seen when predators were present (Fig. 3). Reduced growth was also observed for juvenile shrimp when interspecific competitor treatments for shrimp were compared to controls for shrimp (Fig. 4, Table 3). However, when controls for juvenile shrimp were
Fig. 3. Mean growth in length (mm day$^{-1}$) of juvenile shrimp. Error bars are ±S.E. (*$P<0.05$ for comparisons of treatments with low density control).

Fig. 4. Mean growth in dry mass (g day$^{-1}$) of juvenile shrimp. Error bars are ±S.E. (**$P<0.01$ for comparisons of treatments with low density control).

Table 3
Results of Anova for mean growth in dry weight of juvenile shrimp$^*$

<table>
<thead>
<tr>
<th>Source of variation</th>
<th>MS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Competitor</td>
<td>0.0341</td>
<td>16.0</td>
<td>0.004</td>
</tr>
<tr>
<td>Predation</td>
<td>0.0004</td>
<td>0.16</td>
<td>0.689</td>
</tr>
<tr>
<td>Competitor × Predation</td>
<td>0.0039</td>
<td>1.82</td>
<td>0.189</td>
</tr>
<tr>
<td>0/30 vs. 60/30$^b$</td>
<td>0.3133</td>
<td>14.73</td>
<td>0.002</td>
</tr>
<tr>
<td>0/30 vs. 60/30 + $P^c$</td>
<td>0.0134</td>
<td>6.32</td>
<td>0.055</td>
</tr>
<tr>
<td>60/30 vs. 60/30 + $P^d$</td>
<td>0.0036</td>
<td>7.70</td>
<td>0.611</td>
</tr>
</tbody>
</table>

$^a$ Control (0 fish and 30 shrimp) vs. 60 fish and 30 shrimp.
$^b$ Control vs. 60 fish and 30 shrimp with predators.
$^c$ Treatment with 60 fish and 30 shrimp vs. 60 fish and 30 shrimp with predators.
$^d$ Significant $P$-values are in bold and $P$-values for a priori contrasts are adjusted using the Bonferroni correction for multiple contrasts. Number of replicates per treatment was 9. All treatment df=1 and error df=27.
compared with the competitor + predator treatment for juvenile shrimp (60 fish and 30 shrimp and predators), there was no difference in growth of shrimp (Fig. 4). In addition, there was no significant difference in growth between the competitor treatment with and without predators (Table 3). The a priori contrasts also revealed no differences in survival between treatments for juvenile shrimp (Fig. 5).

Growth of juvenile fish did not differ between fish in the high density treatments and the controls (Fig. 6). In addition, controls for juvenile fish showed no differences in growth of juvenile fish compared with the other treatments to assess interspecific effects of shrimp on fish (Fig. 6). Juvenile fish did not exhibit reduced survival in the presence of juvenile shrimp in these experiments. Also, the presence of adult predators had no effect on the survival of juvenile fish in the enclosures (Fig. 7).

There were no statistically significant reductions in final numbers of copepods, ostracods, nematodes, and copepod nauplii relative to controls for the fish or shrimp treatments (Fig. 8–11).

Fig. 5. Mean proportion of juvenile shrimp surviving in the enclosures. Error bars are ±S.E.

Fig. 6. Mean growth in length (mm day⁻¹) of juvenile fish. Error bars are ±S.E.
Fig. 7. Mean proportion of juvenile fish surviving in the enclosures. Error bars are ±S.E.

Fig. 8. Mean numbers of copepods per petri dish at beginning and end of experiment. Error bars are ±S.E.

Fig. 9. Mean numbers of ostracods per petri dish at beginning and end of experiment. Error bars are ±S.E.
4. Discussion

4.1. Competitive effects

Both intraspecific and interspecific competitive effects were observed in juvenile shrimp in this study when predators were not present. Interspecific competitive effects among juvenile fish and shrimp were asymmetrical with fish being the dominant competitor. Juvenile shrimp exhibited reduced growth when juvenile fish were present. Juvenile fish exhibited no negative effects on growth or survival in both the presence and absence of juvenile shrimp. The asymmetry of the interspecific competitive interaction among juveniles was also evident in previous experiments conducted in laboratory microcosms where growth of juvenile shrimp was reduced in the presence of juvenile fish (Cross and Stiven, 1997). Asymmetrical interactions are more commonly observed in studies of interspecific competition while symmetrical interactions are rare (Lawton and Hassell, 1981; Connell, 1983; Schoener, 1983; Underwood, 1986).
While negative interspecific effects on juvenile shrimp growth were detected in these experiments, survival of juvenile shrimp was unaffected by the presence of juvenile fish. However, demonstration of a significant effect on juvenile shrimp survival would have been statistically difficult due to two control replicates for juvenile shrimp that exhibited total mortality in the second experimental run. Potential causes for total mortality of shrimp in these two controls are unknown, and paradoxically, it was during this same experimental run that the higher density treatments exhibited the highest survival of shrimp for all of the replicates in the other experimental runs. The observed total mortality of shrimp in the treatments least likely to show such effects (controls) produced a high level of variability and reduced the differences between controls and other treatments. When survival data were analyzed using time (experimental run) as a block effect, this experimental run was the only one significantly different from the other runs. Interspecific effects of juvenile fish on juvenile shrimp survival were not found in previous experiments conducted in laboratory microcosms (Cross and Stiven, 1997). In general, interspecific effects on survival of organisms in marine soft sediment systems have rarely been demonstrated while effects on growth are much more commonly detected (Wilson, 1990; Olafsson et al., 1994).

It is usually assumed that competition will be most intense between taxonomically similar species (usually congeneric) (Hutchinson and MacArthur, 1959). Consequently, most studies of interspecific competition have examined effects between congeneric organisms or closely related species (Connell, 1983; Schoener, 1983; Goldberg and Scheiner, 1993; but see Brown et al., 1979; Carpenter, 1979; Williams, 1981; Hay and Taylor, 1985). The two species in this study are taxonomically distant, one being a vertebrate and the other a crustacean. However, the size range of juveniles overlaps during the period in which both species utilize the vegetated intertidal marsh, presumably as a refuge from predators found in subtidal habitats (Kneib, 1987a). Similar size and predation risk may lead to the utilization of common refuge habitat during the larval stage of fish and postlarval stage of shrimp. The sharing of habitat and food resources is probably largely responsible for producing potential competitive effects in these taxonomically disparate species. Size can impose constraints in food resource utilization, which in this case includes the benthic meiofauna. Young grass shrimp (Broad, 1957; Alon, 1987) and killifish (Kneib, 1986b) consume small crustaceans (e.g. copepods and ostracods), and overlap in food resource utilization may be an important factor producing competitive effects among juveniles.

Reductions in meiofauna in artificial refuges were not demonstrated in this study. However, impacts of predators on meiofauna are difficult to detect in the field due to the great spatial and temporal variability in density that occurs over relatively small scales (Bell, 1980). The significant time required to process benthic meiofauna samples limits most studies to a few replicates. Low replication can preclude the detection of effects of consumers on meiofauna unless effects are very strong. The lack of statistically significant effects of fish and shrimp on food resources in this study should be viewed cautiously, since the statistical power was low (Table 4).

While there is some accumulating evidence that food limitation impacts invertebrate organisms in soft sediment marine systems (e.g. see review by Olafsson et al., 1994), few experimental studies have demonstrated strong interspecific competition for food in
Table 4
Power of statistical analyses for detecting a significant reduction in meiofauna using $\alpha = 0.05$

<table>
<thead>
<tr>
<th>Meiofauna Taxa</th>
<th>Predator</th>
<th>Power</th>
</tr>
</thead>
<tbody>
<tr>
<td>Copepods</td>
<td>Shrimp</td>
<td>0.05</td>
</tr>
<tr>
<td>Ostracods</td>
<td>Shrimp</td>
<td>0.05</td>
</tr>
<tr>
<td>Nematodes</td>
<td>Shrimp</td>
<td>0.05</td>
</tr>
<tr>
<td>Nauplii</td>
<td>Shrimp</td>
<td>0.07</td>
</tr>
<tr>
<td>Copepods</td>
<td>Fish</td>
<td>0.05</td>
</tr>
<tr>
<td>Ostracods</td>
<td>Fish</td>
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</tr>
<tr>
<td>Nematodes</td>
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<td>0.06</td>
</tr>
<tr>
<td>Nauplii</td>
<td>Fish</td>
<td>0.34</td>
</tr>
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</table>

marine soft sediment systems (Peterson, 1982; Kneib, 1991). Most studies of food limitation in soft sediment systems have focused on adult organisms (Olafsson et al., 1994) and there is very limited information supporting food limitation for natant macrofaunal organisms in salt marsh systems (e.g. Weisberg and Lotrich, 1982; Kneib, 1993).

An absolute reduction in food resources is not the only necessary condition for competitive effects to be related to food resource limitation. Observed interspecific effects could be due to behavioral mechanisms such as interference between juveniles. Even if the absolute abundance of meiofauna food resources was not reduced, the availability of food resources for juvenile shrimp may have been reduced due to a reduction in feeding time or an increase in assimilated energy allocated to escape or avoidance activities in juvenile shrimp. Such behavioral influences could lead to reduced growth in the subordinate competitor. Statistically insignificant reductions in food resources combined with behaviorally modified food availability or energy allocation could be a potential cause of interspecific effects observed in juvenile shrimp. Resource deprivation experiments demonstrated that young fish and shrimp are susceptible to mortality from lack of food within the time frame of these experiments (Cross and Stiven, 1997). Recently hatched larval fish exhibit an initial resistance to starvation, perhaps due to residual energy reserves in yolk (Cross and Stiven, 1997). This may impart an early competitive advantage to larval fish over postlarval shrimp. When larval fish and postlarval shrimp initially encounter each other under natural circumstances on the intertidal marsh, the shrimp postlarvae would have just settled from the planktonic stage at least several weeks from the egg stage. It is possible that natural conditions may be more severe for juvenile fish and shrimp with regard to food resources than those found within the experimental enclosures. In order to accommodate the larger fish predators in the enclosures at low tide, the artificial predator refuges were necessarily slightly deeper than many naturally occurring intertidal depressions found on the marsh. The greater volume and depth of water in the predator refuges could have lessened the severity of physical stresses from high temperature and low dissolved oxygen levels for juveniles that chose to use the deeper predator refuges. A larger volume of water and bottom surface area in predator refuges may have provided more meiobenthic food resources for juveniles and may also have lessened the impact of juveniles on meiofauna in the shallow artificial refuges from which meiofauna samples were collected. It was
observed that juvenile shrimp would sometimes use predator refuges, even if predators were present, but juvenile fish were rarely found in the deeper predator refuges, whether predators were present or not (Cross, personal observations). This differential use of the predator refuges would seem to benefit juvenile shrimp more than fish and impart any competitive advantage due to increased availability of food resources to shrimp.

Careful thought should be given to sampling schemes in studies of effects of consumers on meiofauna in intertidal systems. The timing of sampling should take into account the relevant time scales over which both consumers and meiofauna interact. Timing of sampling in an intertidal system should coincide with the time period in which the impact of predation on meiofauna would be most detectable. In these experiments benthic meiofauna samples were obtained from enclosures just before inundation by the next high tide. This sampling scheme allowed meiofauna to be exposed to predation by juvenile fish and shrimp in the refuges for the greatest amount of time before tidal inundation could replenish or redistribute meiofauna from surrounding sediments into the artificial refuges. The effects of high variability in the meiofauna make the consideration of these factors imperative, if real effects are to be detected statistically.

Demonstrations of interspecific competitive effects have not been very frequent in marine soft sediment systems (Peterson, 1979). The demonstration of competition in these systems has been hampered by the nature of the substrates and animals inhabiting such environments (Dayton, 1984; Peterson, 1979; although see Peterson, 1977, 1982; Peterson and Andre, 1980; Peterson and Black, 1987). Substrates are generally loose and easily transported, and many organisms inhabiting such systems are burrowers and can increase the porosity and erodability of sediments (Rhoads, 1974). These factors in combination make it difficult to manipulate organisms without altering the structure of this unstable environment (Virmstein, 1977, 1980; Dayton, 1984). However, the use of enclosures in vegetated intertidal soft substrates does not produce noticeable “cage effects” often seen in unvegetated intertidal systems or subtidal systems (Bell, 1980; Kneib and Stiven, 1982). Above ground vegetation reduces hydrologic flow rates to a large degree and this, in combination with below-ground root structure adds to the stability of sediments and helps reduce sediment transport. Hence, the use of certain types of enclosures in intertidal marshes does not appear to alter hydrodynamics due to the existing naturally reduced dynamics of the water column and sediments.

4.2. Effects of predators on interspecific competition

The prediction that predation or predation risk from adult fish could indirectly affect the outcome of interspecific competition between juveniles was developed from a demonstration of direct interspecific effects between juveniles in laboratory microcosms (Cross and Stiven, 1997) and a knowledge of size-dependent trophic interactions in these species. Adult fish attain the largest size and occupy a higher trophic level than adult shrimp. Adult fish can consume both juvenile and adult shrimp (depending on relative size), but seem to prefer conspecific juveniles (Kneib, 1987b). Size structure is a very important element of this system not only because size dictates habitat and resource-use, but it also determines the trophic relationship between the species. Small
juveniles share refuge habitat on the vegetated intertidal during low tides while larger adults move with the tides onto and off the marsh, spending low tide periods in adjacent subtidal creek habitat. This system seems to have the potential for changing competitive and trophic interactions that are dependent on the relative size of interacting individuals. These size-dependent interactions are also time-dependent at the scale of tidal cycles, since small and large individuals are effectively separated during low tides, and small juveniles are confined to microhabitats during low tides when the competitive potential among juveniles would likely be more intense.

The effect of a predator on interactions between two or more competing prey species has been defined as a type of indirect interaction. There has been a confusing proliferation of definitions that vary in their semantics (Kneib, 1991), but most definitions consider indirect interactions as involving at least three interacting species (Miller and Kerfoot, 1987; Kneib, 1991). The system in this study consists of only two interacting species, but the effect of predators (adult fish) on smaller juvenile shrimp resembles an indirect effect generally thought of as occurring in assemblages of three or more species. This pseudo-indirect effect emerges in this system consisting of two species as a result of changing size-dependent interactions between juveniles and adults of both species. The large differences in size, in combination with the selective predation on juvenile conspecifics by the predator, leads to a situation analogous to that of a true indirect effect. In this system, the substantial size-dependent differences in habitat and food resource-use, and the apparent tendency for adult fish to consume conspecifics, produce a situation where the larger individuals of the fish could be considered as a third “ecological species” (sensu Polis, 1984).

Examples of interactions involving predators modifying competitive interactions among prey in marine intertidal systems predominate from studies conducted in rocky intertidal systems, such as the classic studies of Paine (1966, 1969, 1984) and others (Lubchenko, 1978; Lubchenko and Menge, 1978; Garrity and Levings, 1981; Underwood et al., 1983; Dungan, 1986, 1987; Sterner, 1986; Wootton, 1993, 1994). Very few studies of these interactions have been conducted in vegetated intertidal soft substrate systems (Kneib, 1991).

One plausible explanation of how predators could reduce interspecific competition for a subordinate competitor that is also a less-preferred prey, is a reduction in the abundance of the dominant competitor. The effect of these interactions is to provide more resources for the less-preferred prey (Vanni, 1987). There were no statistically significant reductions in the number of juvenile fish surviving in the predator treatments. However, it should be noted that the power of detecting a difference in survival of juvenile fish between the competitor treatments with and without predators (the greatest difference observed) is only 0.36 (at $\alpha = 0.05$). The statistical detection of differences in survival is difficult with the high variability found in these field experiments.

However, a reduction in the number of juvenile fish as a result of predation is not the only mechanism that could explain why juvenile shrimp are released from competitive effects. Predators can have consequences on prey populations and communities that extend beyond the obvious lethal effect of reducing prey numbers (Peckarsky et al., 1993). Sublethal effects on prey growth and fecundity can result from altered behavior of prey organisms, generally due to predator avoidance (Fraser and Huntingford, 1986;
Formanowicz and Brodie, 1988). Predator avoidance by prey may alter microhabitat-use or feeding behavior such that feeding efficiency of prey organisms is reduced (Werner and Hall, 1988; Peckarsky et al., 1993). Thus, nonlethal effects of predators can potentially indirectly influence interactions between species through changes in behavior.

A potential explanation for the modification of interspecific effects not related to absolute food limitation is through the occurrence of agonistic behavior between juveniles. The dominant competitor in this system may interfere with the feeding efficiency of juvenile shrimp or may increase energetic demands on juvenile shrimp as a result of increased escape or avoidance activities. The predators could alter these potential behavioral interactions by selectively pursuing the dominant competitor among the smaller juveniles. Studies of resource partitioning through microhabitat utilization and differences in feeding behavior are areas that could provide useful information on behavioral mechanisms that produce or ameliorate potential interspecific competitive effects in these species. Experiments examining microhabitat utilization and modification through predation are currently being explored as possible factors that influence interactions among juveniles. Elaborating the behavioral factors that affect these size-dependent interactions will enhance our understanding of the population and community level responses in this system.

5. Conclusions

Competition may be an important interaction between juvenile fish and shrimp when they share refuge habitat on the vegetated intertidal salt marsh. Experiments conducted in enclosures on the vegetated intertidal revealed that juvenile shrimp exhibited reduced growth in the presence of juvenile fish, but effects of juvenile fish on juvenile shrimp survival were not detected. The interspecific competitive interaction appeared to be asymmetrical with no detectable competitive effects of juvenile shrimp on juvenile fish. Although competition for food resources is a likely mechanism for interspecific competitive effects, we were not able to demonstrate reductions in this study, but this may be due to the low power of the statistical design. The interspecific competitive effect between juvenile fish and shrimp was modified by the presence of adult fish predators. Direct interspecific effects of reduced growth in juvenile shrimp did not occur when adult fish predators were present in enclosures.

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References


