Behavioral Influences on Predator-Prey Interactions Between Juvenile Teleosts and Meiofauna.

John Nathan Mccall

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Behavioral influences on predator-prey interactions between juvenile teleosts and meiofauna

McCall, John Nathan, Ph.D.
The Louisiana State University and Agricultural and Mechanical Col., 1992
BEHAVIORAL INFLUENCES ON PREDATOR-PREY INTERACTIONS BETWEEN JUVENILE TELEOSTS AND MEIOFAUNA

A Dissertation

Submitted to the Graduate Faculty of the Louisiana State University and Agricultural and Mechanical College in partial fulfillment of the requirements for the degree of Doctor of Philosophy

in

Department of Zoology and Physiology

by

John Nathan McCall

B.S., The University of West Florida, 1974
December 1992
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ABSTRACT

Predator-prey relationships between post-larval and juvenile teleosts are greatly influenced by the manner in which feeding behavior of fish interacts with the behavior of meiofaunal prey. Juvenile starry flounder (*Platichthys stellatus* Pallas) in a southeastern Alaskan bay fed disproportionately on the harpacticoid copepod *Microarthridion littorale* (Poppe), particularly on males. This apparent selectivity was not due to differing vertical distribution of harpacticoid species or to feeding in other locations. Comparison of ingested prey to harpacticoid assemblages collected by various techniques (including near-bottom collections) suggested that the prey selection shown by starry flounder may be the result of emergent behavior of its harpacticoid prey. Species-level prey identifications indicated that harpacticoid density at the site was not limited by flounder predation. Post-larval and juvenile spot (*Leiostomus xanthurus* Lacépède) from the northern Gulf of Mexico showed ontogenetic changes in prey selection. Post-larval spot preyed on a copepod assemblage most closely resembling that collected in settlement/bedform traps, suggesting that they also utilized prey in the near-bottom waters. At larger sizes, the diet of juvenile spot was more similar to sediment-dwelling assemblages. This switch coincided with a dramatic increase in the number of nematodes in the diet.
In laboratory experiments, juvenile spot demonstrated an ability to recognize and selectively feed in meiofaunal aggregations similar to those formed by meiofauna in the field. This utilization was manifested in a greater proportion of feeding strikes allocated to high density treatments and an increased processing time of feeding strikes taken in such areas. Stomach contents of spot contained a significantly higher proportion of harpacticoid copepods than did the sediments on which they fed. The ability of juvenile spot to recognize and selectively utilize aggregations may be a means of increasing feeding efficiency, perhaps prolonging the period when juveniles subsist on a diet of meiofaunal-sized prey. A greater understanding of meiofaunal behavior, particularly that of hyperbenthic meiofauna, is necessary to more clearly understand the nature of predator-prey interactions between fish and meiofauna.
CHAPTER 1

PREDATOR-PREY INTERACTIONS BETWEEN JUVENILE TELEOSTS AND MEIOFAUNA
INTRODUCTION

Meiofauna have been recognized as a significant component of marine and estuarine ecosystems for over fifty years (Coull & Giere 1988). In the last twenty years, however, our view of their place in the trophic dynamics of marine and estuarine food webs has changed dramatically. Once considered to be something of a trophic sink (McIntyre 1969, McIntyre & Murison 1973), meiofauna are now recognized as a significant pathway of energy transfer to juvenile fish and other epibenthic predators (Gee 1989).

Much recent research has focused on the role of meiofauna, particularly harpacticoid copepods, as food for juvenile fishes. This work has been reviewed by Gee (1989) and Coull (1990). The consensus now is that meiofaunal prey, primarily harpacticoids, are important prey in the diet of a variety of fish, including flatfish, gobies, salmonids, certain juvenile sciaenids and assorted others. In most cases, meiofaunal predation is limited to fish of standard lengths less than 30-60 mm standard length (length from the tip of the upper jaw to the posterior end of the hypural bone), although a small number of larger fishes utilize this resource.

Although researchers have gained significant insight in many areas related to fish predation on meiofauna, a number of questions remain unanswered. Several of these deal with the manner in which the predatory behavior of
meiofaunal-feeding fishes interacts with the behavior of their prey. Miller & Dunn (1980) identified synoptic studies of fish feeding habits and prey availability as one area of critical need in studies of fish trophic ecology. Determining prey availability is not as straight-forward as measuring prey densities. Many components of prey preference, including encounter rates and capture success, are under the influence of both prey and predator behavior (Sih & Moore 1990). Interactions between juvenile fish behavior and the behavior of their meiofaunal prey could be expected to influence their predator-prey relations in a number of ways, including the degree of selectivity, real or apparent, demonstrated by the predator, the specific meiofaunal assemblage utilized among the several distinct groups available, and the degree to which predators are able to recognize and take advantage of meiofaunal patchiness.

**SELECTIVITY**

The degree to which meiofaunal-feeding fish select one prey type over another and the causal factors underlying such selection are the subject of ongoing debate. Fish and meiofauna present an excellent opportunity for the investigation of selective feeding, since large numbers of individuals can be collected and processed to allow for proper statistical analysis of selection.
Selectivity can be considered at three levels: major taxon, species and demographic group. Each level of selectivity carries with it specific questions about the manner in which behavioral mechanisms of both predator and prey affect the interaction.

**Major taxon selectivity:**

The question of whether juvenile fishes select one component of the meiofauna over another has been extensively investigated, and has been discussed in detail in recent reviews (Gee 1989, Coull 1990). This question typically focuses on two meiobenthic groups, harpacticoid copepods and nematodes. In general, harpacticoids are the most common meiofaunal prey of juvenile fishes, even though nematodes typically outnumber them by as much as two orders of magnitude in the sediments. At least three explanations have been suggested for this phenomenon:

1) active selection of harpacticoids over nematodes by the fish, due perhaps to greater energetic content, high concentrations of essential fatty acids, or movement-related visibility differences (Coull 1990),

2) differential rates of digestion for harpacticoids and nematodes, with nematodes becoming rapidly indistinguishable in the digestive tract while harpacticoids do not, resulting in prey counts biased toward harpacticoids (Scholz et al. 1991) and,

3) differential availability of harpacticoids and
nematodes, owing primarily to their differing vertical
distribution within the sediment (Gee 1989). Nematodes are
typically distributed to a much greater depth in the
sediment than harpacticoids, particularly in the muddy
sediments in which fish predation on meiofauna is most
significant. Many studies of meiofaunal feeding in fish
report data only on prey major taxon with the underlying
assumption that all harpacticoid copepods are sediment-
dwelling.

Species selectivity:

Relatively few studies have attempted to determine the
species composition of harpacticoids preyed upon by
juvenile fish. Those which have have often found that the
assemblage of copepods ingested by the fish does not
closely correspond to that found in meiobenthos in the area
in which the fish were collected (Alheit & Scheibel 1982,
de Morais & Bodiou 1984, Gee 1987). This tendency seems to
be substrate-related, with fish feeding in areas with muddy
substrates preying on an assemblage more closely resembling
that collected in sediment samples (Gee 1987). This likely
reflects the more surficial distribution of harpacticoids
in these areas. In addition, harpacticoids frequent near-
bottom waters where nematodes are underrepresented (Walters

Species-specific selectivity of predators for one or
several harpacticoid species has been observed in a number
of studies (Gee 1987). Many investigators, however, still choose not to invest the time necessary to make time-consuming species-level identifications.

Given the increasing awareness that fish feeding on meiofauna do not select prey proportional to their abundance in the sediments, it might be prudent to more closely examine the species of meiofauna that are ingested. This is necessary if we are to understand why a particular subset of the meiofaunal community is disproportionately significant in the feeding ecology of juvenile fish. Species-level prey identification could be particularly important in assessing the energetic value of meiofauna to juvenile fish, and could influence estimates of the value of a given habitat to developing juveniles.

Demographic group selectivity:

The question of whether one demographic group might be more heavily preyed upon than others has remained largely unaddressed. There are size, behavioral and morphological differences among males, females and copepodites of harpacticoid copepods that might well be expected to contribute to such differential predation.

Hicks & Marshall (1985) found that the guts of deep-sea carnivorous bivalves contained almost exclusively male harpacticoids, and suggest that bioluminescence or chemical cues might play a role. Selective predation on female calanoid copepods in freshwater ponds has been related to
greater visibility of females, particularly those carrying eggs (Hairston et al. 1983). Furthermore, Maly (1970) found that predation could alter the adult sex ratios of calanoid copepod prey in a manner which was influenced by predator hunting behavior and by differences in size and activity of the male and female prey.

MODES OF UTILIZATION OF MEIOFAUNAL PREY

Now that the significance of harpacticoid copepods, and meiofauna in general, in the diet of juvenile fishes can no longer be questioned, we must begin to address more sophisticated questions about the ways in which meiofaunal predators interact with their prey. This requires a consideration of the manner in which the predatory behavior of the meiofaunal feeder interacts with the morphology and behavior of the potential prey.

Hyatt (1979) examined a variety of aquatic ecosystems and found that in most cases, carnivores feeding on benthic invertebrates made up the greatest percentage of fish species. Within this broad class a number of different feeding modes can be identified (Keenleyside 1979):

1) picking at small prey,
2) disturbing substrate, then picking up prey,
3) picking up substrate and sorting prey, and
4) grasping relatively large prey.

Meiofaunal-feeding fish likely demonstrate all of these
modes of feeding. Among those meiofaunal feeders that pick at small prey, the most notable are the juvenile flatfishes (de Morais & Bodiou 1984, Gee 1987). This mode of predation is also utilized by some grassbed fishes such as the spotted dragonet, *Callionymus pauciradiatus* (Sogard 1984). While there is no documentation of fishes deliberately disturbing the substrate and preying on suspended meiofauna, it is likely that fish prey heavily on animals suspended in the water column by hydrodynamic forces. Perhaps the most well-studied meiofaunal-feeding fish is spot, *Leiostomus xanthurus*, which feeds by biting into soft sediments, manipulating the sediment within its mouth, extracting the contained organisms with gill rakers and pharyngeal teeth, and then expelling the sediment through the gill openings and the mouth (Billheimer & Coull 1988).

In short, meiofaunal-feeding fish rely on the full gamut of feeding strategies available to benthic carnivores, and the particular strategy utilized by a given species or size class will doubtless influence the manner in which it interacts with meiofaunal prey.

**The importance of meiofaunal habitat utilization**

Hicks & Coull (1983), in their review of harpacticoid ecology, describe a variety of modes of existence. Within the benthos, harpacticoids may be found living interstitially, epibenthically, or as burrowers, with the
interstitial lifestyle limited primarily to sandy substrates and the burrowers found mainly in muddy sediments. Hicks and Coull also recognize phyal harpacticoids and a few species that are wholly planktonic. To their list should be added tube-dwelling as demonstrated by Chandler & Fleeger (1984). In addition, it is now well-established that many harpacticoid species occupy a hyperbenthic or demersal habitat, spending all or part of their time in the near-bottom waters within a few centimeters of the sediment surface.

Given the diversity of feeding strategies utilized by predatory fishes and the wide range of microhabitats occupied by harpacticoid copepods, it is appropriate to consider the manner in which the feeding behavior of predators interacts with microhabitat utilization of harpacticoid copepods to produce specific predator-prey relationships. The available pool of prey for a meiofaunal-feeding fish is the result of a variety of interacting factors, both biological and physico-chemical. Of particular significance is the manner in which the behavior of the predatory fish and that of the meiofauna in the area interact to bring predator into contact with prey. The significance of hyperbenthic meiofauna

Perhaps the least understood albeit potentially important assemblage of harpacticoids with regard to trophic interactions with juvenile fish is the hyperbenthic
or demersal assemblage. Beyer (1958) introduced the term hyperbenthos in reference to plankton populations just above the sediment-water interface. The hyperbenthos consists of a mixture of assemblages with animals of at least two origins, downward moving planktonic species and upwardly mobile surface-dwelling benthic species. There is also the possibility that some species are permanent residents of the near-bottom waters. Hydrodynamic forces that act to concentrate hyperbenthic organisms near the sediment-water interface might also lead to high hyperbenthic concentrations of detritus, phytoplankton or benthic algae in the near-bottom water (Sibert 1981). Therefore, it might be energetically advantageous to remain in the hyperbenthos. Although this habitat presents serious methodological problems in sampling, the existence of a near-bottom meiofaunal assemblage has been documented in recent years. It is now apparent that sediment-dwelling meiofauna, particularly harpacticoids, occur regularly in the water column, due either to passive resuspension (Hagerman & Rieger 1981, Palmer & Gust 1985), active migration (Alldredge & King 1985, Walters & Bell 1986, Armonies 1988; 1989, Bell et al. 1988) or a combination of the two (Fleeger et al. 1983). The relative importance of the two mechanisms is related to the species under consideration and to type of substrate (Palmer & Gust 1985). Passive resuspension, like active migration,
involves the behavior of harpacticoids, since the habitat occupied by the organisms greatly influences their likelihood of being resuspended (Palmer 1988b). Active emergence appears to be under the influence of diurnal or tidal cues (Sibert 1981, Walters 1988, Armonies 1988) while passive occurrence in the near-bottom water may be due to hydrodynamic erosion or disturbance (Palmer 1988b).

The emergence, by whatever mechanism, of harpacticoids into the water column may provide some adaptive advantage with regard to reproduction (Hicks 1988), feeding (Sibert 1981, Decho 1986) or avoidance of infaunal predators (Ambrose 1984). It almost certainly, however, increases their susceptibility to predation by small fish feeding near the sediment surface. Very few species of fish actually bite into sediments in search of prey (spot is a notable exception). Most adult demersal predatory fish feed on individual prey near the sediment-water interface (Ringler 1979). Juvenile fish that utilize this habitat are less well-studied, but may also rely on a similar prey assemblage. If, in fact, much predatory behavior occurs in the near-bottom water, then it is reasonable to suppose that the most significant prey assemblage is the hyperbenthos. Unfortunately, this is the most poorly understood of all meiofaunal assemblages.

As information begins to accumulate on the hyperbenthic meiofauna, it is becoming clear that this
fauna is often quite different from that in the sediments, both with regard to species composition and demographic status. Walters & Bell (1986) found that harpacticoid copepods numerically dominated the taxa that actively migrated in a subtidal seagrass bed. They found that from 13 to 67% of all benthic harpacticoids migrated into the water column. Adult harpacticoids exhibited both diel and sampling-date differences in migration. These differences may well be reflected in greatly different prey assemblages in juvenile fishes than might be predicted based on a knowledge of the benthic meiofauna.

Bell et al. (1988) found that the adult sex ratios of abundant copepods collected in the water column differed significantly from conspecifics on the substratum. Males are typically much more abundant in the water column than on seagrass blades or in sediments. This observation is in keeping with the hypothesis that active emergent behavior is linked to a precopulatory association between adult males and juvenile females (Hicks 1988). The potential impact of this differential utilization of the near-bottom habitat and its associated greater potential risk of predation has remained largely unexamined.

THE INFLUENCE OF MEIOFAUNAL PATCHINESS

Another factor that could exert a great effect on fish feeding but has received little attention is the patchiness
of prey distributions. Prey organisms in general are often aggregated in the environment. This is particularly true of meiofauna and, in fact, is a well-documented aspect of meiofaunal ecology (Hicks & Coull 1983). This patchiness can be observed at a variety of spatial scales, ranging from microscale (cm$^2$) through mesoscale (m$^2$-km$^2$) and interhabitat levels.

Meiofaunal patchiness may be related to a number of biotic or abiotic factors. Those that have been examined include food resources (Decho & Fleeger 1988, Lee et al. 1977, Hicks 1984), hydrodynamics, disturbance (Hogue 1982, Hogue & Miller 1981) and social behavior (Heip 1975). Clearly, many of the suggested causes may be interrelated. Regardless of the cause, the effect is that large-scale differences in meiofaunal density may exist over relatively short distances.

Findlay (1981) found harpacticoid aggregation to be under the influence of dispersion patterns of the dominant species, with patch sizes ranging from 0.3 cm$^2$ to 32 cm$^2$. In addition, smaller patches were sometimes aggregated into larger patches.

The level of patchiness may vary from species to species. On the interhabitat level, Coull et al. (1979) found that some species of harpacticoids exhibited distinct zonation across a gradient from a subtidal creek bottom to high intertidal marsh, while other species were present
across the entire gradient. Most investigations of meiofaunal patchiness are carried out only once. Therefore, it is unclear how long-lived meiofaunal patches are and whether the scale of patchiness is constant over time (Sun & Fleeger 1991).

Meiofaunal patchiness could be of great significance to fishes feeding on them. Ivlev (1961) showed that fish achieved greater feeding success when food was aggregated than when food was distributed uniformly. If a feeding fish is able to distinguish prey patches and feed selectively in areas of higher prey density, it should enjoy greater feeding efficiency and possibly higher fitness. This could be particularly important if the average concentrations of prey are potentially limiting (Miller & Dunn 1980). Meiofaunal-feeding fish may well be limited by average prey concentrations, given the fact that meiofaunal biomasses typically are about 1 g m$^{-2}$ and are much lower than that of macrofauna (Coull 1988). Through natural selection, a high premium should be placed on the ability of meiofaunal predators to locate areas of higher prey density. This question has not been investigated. The ability to locate prey aggregations would be most significant in relatively large, active fish subsisting on a diet of meiofauna, such as juvenile spot.
CHAPTER 2

SOURCE OF HARPACTICOID COPEPODS IN THE DIET OF JUVENILE STARRY FLOUNDER
Dear Dr. McCall,

'Source of harpacticoid copepods in the diet of juvenile ...'
MEPS article M 145, to be published in one of the forthcoming issues of Marine Ecology Progress Series', Your Fax of August 21, 1992

Permission is granted by Inter-Research for the material stated to be used for the purpose described, provided the original source of publication is correctly stated.

Sincerely,

Inter-Research

August 24, 1992
INTRODUCTION

A large body of research has recently highlighted the importance of meiofauna in the diet of a wide variety of juvenile fishes. Gee (1989) and Coull (1990) reviewed literature for meiofauna in general and for harpacticoid copepods, respectively. Although there was a time when the significance of meiofauna as food for juvenile fish was widely debated (see McIntyre 1969), it is now well established that in a number of groups, including flatfish, gobies and selected salmonids, meiofauna play a critical role in the survival and growth of juvenile fish. Many questions remain, however, concerning the modes of utilization of such prey.

While meiofauna consists of a diverse assemblage of organisms, nematodes and harpacticoid copepods are normally numerically dominant (Coull 1988). Nematodes are usually much more abundant than harpacticoid copepods, particularly in muddy substrates where they may comprise as much as 97% of all meiofauna (e.g. Fleeger et al. 1989). This numerical dominance of nematodes, however, is seldom reflected in the diet of meiobenthic predators. Generally, harpacticoid copepods are selectively ingested over all other taxa. This topic is still a matter of some debate (see discussions in Gee 1989 and Coull 1990), but it is apparent that harpacticoid copepods are important food items, often to the complete exclusion of other prey types.
Species-specific-selective feeding on harpacticoids has been indicated in a few studies. Sibert (1979) found that *Harpacticus uniremis* was consumed by salmon fry in British Columbia in greater proportions than its abundance in the sediments would predict. This is likely due in part to the fact that *H. uniremis* is largely epiphytic, found predominately on seagrasses. Hicks (1984) found that juvenile flatfish feeding on intertidal sandflats in New Zealand fed exclusively on the harpacticoid *Parastenhelia megarostrum*. This species was dominant in the sediments, but was by no means the only copepod present. Fish and crustacean predators feeding in a sandy habitat in England were highly selective for a particular species of harpacticoid, *Asellopsis intermedia*, apparently resulting primarily from their surficial distribution in the sediment (Gee 1987). Most locales contain a variety of harpacticoid species, which may differ greatly in size, morphology, behavior and microhabitat utilization (Hicks & Coull 1983). Given an assortment of potential harpacticoid prey species, it is likely that predator selectivity will prove to be common. Some researchers have taken advantage of this fact to gain insight into feeding behavior of juvenile fish (Feller et al. 1990), but misleading conclusions can result from major taxon level identifications.

A multi-year investigation of feeding in juvenile starry flounder (*Platichthys stellatus* Pallas) in a
southeast Alaskan bay has shown intensive predation on harpacticoid copepods in the intertidal zone (McGregor 1991). This flounder is highly selective for a particular species of harpacticoid, *Microarthridion littorale* (Poppe). Furthermore, juvenile starry flounder prey much more heavily on male *M. littorale* than on other demographic groups.

Several hypotheses can be advanced to explain the high degree of selection for *Microarthridion littorale* in general and males in particular exhibited by juvenile *Platichthys stellatus*. These explanations fall into 2 general categories: those which invoke true selection of prey by the action of the predator and those in which apparent selection is due to an inaccurate assessment of the available prey (the researcher samples in a different fashion from the fish). The purpose of this work is to further characterize the feeding of *P. stellatus* and the nature of the harpacticoid community with the specific goal of determining the source the prey and the factors leading to the apparent high selectivity for particular prey types.

**METHODS**

**Long-term studies:**

Juvenile (10 to 25 mm standard length) *Platichthys stellatus* were collected approximately every 2 wk from March of 1987 through July of 1988. The collection site
was a beach in Auke Bay, ca. 30 km north of Juneau, Alaska. Auke Bay is a small, relatively shallow bay (70% less than 60 m in depth), with a predominately muddy substrate. Fish were collected in a sheltered cove adjacent to an intertidal mudflat ca. 60 m wide. The beach is characterized by a transition from a *Mytilus trossulus* zone in the high intertidal, through a barnacle-*Fucus* zone, to the mudflat which begins just above the mean low water level. There are patches of the seagrass *Zostera marina* in the area.

Fish were collected with a 17 x 2 m beach seine with 6 mm stretch mesh at low tide, usually between the 0 m and -1 m levels on the beach, in water less than 1 m in depth. The 0 m tide level is defined as the mean lower-low water mark. Collections were made in the morning, corresponding to summertime low tides in the region. Flounder were preserved in 10% buffered formalin. Stomachs were dissected and prey items enumerated and identified to major taxon.

Meiofauna collections were obtained in association with seining and consisted of 4 replicate cores taken with hand-held piston corer constructed from a 50 cm³ syringe. The upper 5 cm of sediment and any overlying water were retained. Samples were passed through 500 µm and 63 µm sieves. Organisms retained on the 63 µm sieve were extracted using sucrose flotation, stored in 5% formalin,
stained with rose bengal and identified to major taxon under a stereomicroscope.

These samples, along with flatfish stomach contents, were subsequently transported to our laboratory at Louisiana State University. There, harpacticoid copepods were identified, where possible, to species and demographic group (adult male, adult female, gravid female and copepodite).

**Short-term studies:**

An intensive investigation was carried out during July of 1989. During a 2 wk period, approximately 150 juvenile flatfish were collected by seining on 4 occasions, in a similar fashion to the collections during the long-term study.

In addition, an effort was made to more completely describe the harpacticoid community on the beach. This investigation included several components:

1) Two series of vertically-sectioned samples from the 0 m tide level. These were taken on July 7 and 20, 1989. The first collection included 4 replicate samples from randomly chosen locations on the 0 m transect (as in the long-term study), each of which was separated into 6 vertical sections, five 2 mm thick sections ranging from the surface of the sediment to a depth of 1 cm, and a section from 1 to 2 cm. The core-extruding device was based on that described by Fuller & Butman (1988). The
July 20 collection consisted of 6 replicate samples from the same transect, each of which was sectioned into 2 mm thick strata to a depth of 1 cm. These samples were part of a larger effort described below. All samples were preserved in 5% buffered formalin containing rose bengal. The samples were sorted to major taxon and the harpacticoid copepods were identified to species and demographic status when possible.

2) On July 20, samples were also collected from other tide levels on the beach. The tide levels sampled included +3, +2, +1 and -1 m, in addition to the 0 m collection described above. An attempt was made to sample at -3 m from shipboard, but was unsuccessful due to the rocky nature of the substrate. The samples collected at this time were part of a larger effort to describe changes in the meiofaunal community from high in the intertidal to depths of 50 m in Auke Bay (Fleeger et al. unpubl.). All samples were processed as described above.

In addition, semi-quantitative meiofaunal collections were made from nearby seagrass beds and algal habitats to determine the nature of the harpacticoid community inhabiting that area. In these areas, the epiphytic harpacticoid communities were sampled by taking clippings from the vegetation, which were fixed and stained as for benthic samples.
It is now well documented that harpacticoid copepods are common in near-bottom waters overlying many sediments (Palmer 1988a), entering the water column by either passive or active means. The result could be differential prey availability. Eight replicate emergence traps and eight settlement traps were set in place at the 0 m transect on July 21, 1989, to determine if certain species are more inclined than others to leave the sediments upon immersion. Emergence traps were of the dimensions described by Walters & Bell (1986). The traps were not, however, placed flush with the sediment but rather some 1 cm above the sediment surface. This allows free movement of water at the sediment-water interface and enables organisms which did not emerge from the sediment immediately beneath the trap to enter. The inverted funnel design requires organisms to reach a height of some 6 to 7 cm above the sediment surface to enter the trap. The emergence traps were placed at random locations along the transect at low tide and allowed to remain in place for 24 h. On collection, the contents were fixed with 10% formalin, stained with rose bengal. Samples were then analyzed in a manner similar to sediment meiofaunal samples.

Settlement traps were similar to those of Fegley (1988), which sample animals settling to the sediment surface. They consisted of test tubes (1.2 cm i.d. x 12.2 cm long) buried flush with the sediment and filled with
filtered seawater. The surrounding sediment was replaced to a depth of 5 cm by azoic sediment to avoid the sloughing of animals into the trap. The dimensions of the traps were chosen to minimize hydrodynamic effects that could sweep trapped animals out of the tube. This is a significant consideration in the design of settlement traps, particularly with animals such as harpacticoid copepods that are strongly influenced by the hydrodynamic regime. The traps utilized had an aspect ratio (ratio of trap length to opening diameter) of 10. Lau (1979) demonstrated that cylindrical traps with this aspect ratio would retain trapped particles up to trap Reynolds numbers of 20 000. Fegley calculated that for traps of these dimensions, a current speed of 140 cm s⁻¹ at the trap opening was required for resuspension of trapped particles. These traps were placed in position at random locations on the transect at low tide and were left in position for 24 h. They were then collected, and the contents fixed, stained and analyzed as described above.

Sigma-Scan™ image analysis software was employed to determine average lengths of the most common species of harpacticoid copepods. A stereomicroscope equipped with camera lucida and digitizing pad was employed to measure of harpacticoids. Statistical analyses were performed with Statistical Analysis System software (SAS 1990).
RESULTS

The diet of juvenile *Platichthys stellatus* less than 30 mm standard length is dominated by harpacticoid copepods, which comprise 89% of its prey. *P. stellatus* settle out of the water column in late June or early July and juveniles are present on the beach throughout the summer, although in late summer or early fall they have reached sizes (>35 mm SL) at which meiofauna become insignificant to their diet.

This site also supports very high densities of harpacticoid copepods. Mean densities of adults in May 1987 were $2.6 \times 10^6$ m$^{-2}$, among the highest harpacticoid densities observed worldwide. The sediment assemblage was dominated by 3 species, *Halectinosoma* sp., *Amphiascoides dimorphus* Lang and *Microarthridion littorale*, although some 10 to 12 other species were present in lesser numbers. Harpacticoid densities underwent dramatic variations seasonally, with extremely high densities in the late spring decreasing through the summer and fall. This work focuses on the summer months when flatfish predators were abundant.

Summer collections reveal that *Halectinosoma* sp. was the most abundant species, followed by *Amphiascoides dimorphus*. *Microarthridion littorale* was the third most abundant species, not approaching the densities of the 2 more abundant species (Table 2.1). Typically 30 to 40% of
Table 2.1. Density (number per 10 cm² ± 1 standard error), percentage of adults that were male, and ratio of copepodites to adults for the three most abundant species of sediment-dwelling harpacticoid copepods during summer of 1987 (includes one sample from 1988). All collections consisted of four replicate cores on the 0 m transect with the exception of the 6/16 and 8/23 collections, which consisted of three replicate samples.

<table>
<thead>
<tr>
<th>Date</th>
<th>Halectinosoma sp.</th>
<th>A. dimorphus</th>
<th>M. littorale</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>density</td>
<td>density</td>
<td>density</td>
</tr>
<tr>
<td></td>
<td>percent male</td>
<td>percent male</td>
<td>percent male</td>
</tr>
<tr>
<td></td>
<td>copep./adult</td>
<td>copep./adult</td>
<td>copep./adult</td>
</tr>
<tr>
<td>6/16/87</td>
<td>637.4 ± 45.5</td>
<td>97.7 ± 15.7</td>
<td>37.7 ± 7.0</td>
</tr>
<tr>
<td></td>
<td>42.7</td>
<td>28.2</td>
<td>38.3</td>
</tr>
<tr>
<td></td>
<td>0.32</td>
<td>0.14</td>
<td>1.85</td>
</tr>
<tr>
<td>7/10/87</td>
<td>196.9 ± 39.1</td>
<td>75.8 ± 22.4</td>
<td>60.8 ± 15.5</td>
</tr>
<tr>
<td></td>
<td>23.0</td>
<td>18.0</td>
<td>40.3</td>
</tr>
<tr>
<td></td>
<td>0.01</td>
<td>0.01</td>
<td>0.83</td>
</tr>
<tr>
<td>7/27/87</td>
<td>394.2 ± 55.9</td>
<td>147.4 ± 24.0</td>
<td>81.5 ± 9.0</td>
</tr>
<tr>
<td></td>
<td>15.4</td>
<td>14.1</td>
<td>28.9</td>
</tr>
<tr>
<td></td>
<td>0.01</td>
<td>0.00</td>
<td>0.70</td>
</tr>
<tr>
<td>8/10/87</td>
<td>427.2 ± 173.6</td>
<td>140.3 ± 35.2</td>
<td>38.2 ± 14.8</td>
</tr>
<tr>
<td></td>
<td>7.3</td>
<td>14.4</td>
<td>38.3</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>0.01</td>
<td>0.69</td>
</tr>
<tr>
<td>8/23/87</td>
<td>219.8 ± 70.6</td>
<td>103.0 ± 5.9</td>
<td>59.7 ± 28.9</td>
</tr>
<tr>
<td></td>
<td>8.9</td>
<td>9.2</td>
<td>29.5</td>
</tr>
<tr>
<td></td>
<td>0.01</td>
<td>0.01</td>
<td>0.47</td>
</tr>
<tr>
<td>9/8/87</td>
<td>179.0 ± 53.4</td>
<td>42.9 ± 7.2</td>
<td>29.7 ± 6.6</td>
</tr>
<tr>
<td></td>
<td>6.1</td>
<td>11.0</td>
<td>46.0</td>
</tr>
<tr>
<td></td>
<td>0.06</td>
<td>0.00</td>
<td>0.27</td>
</tr>
<tr>
<td>7/1/88</td>
<td>446.0 ± 132.5</td>
<td>156.4 ± 56.0</td>
<td>30.6 ± 12.9</td>
</tr>
<tr>
<td></td>
<td>16.1</td>
<td>11.0</td>
<td>43.1</td>
</tr>
<tr>
<td></td>
<td>0.02</td>
<td>0.00</td>
<td>0.27</td>
</tr>
</tbody>
</table>
adult *M. littorale* were male, a higher proportion than that shown by the two more abundant species. *M. littorale* also showed the highest ratio of copepodites to adults during the summer, with copepodite densities approaching or exceeding 50% of adult densities in most months. Copepodites of other species were relatively rare in summer after a peak in late spring.

Stomach content analyses of 120 *Platichthys stellatus* less than 25 mm standard length reveal that *Microarthridion littorale* dominates their diet (Table 2.2). In fact, *M. littorale* comprised greater than 76% of the copepods in the stomach contents. In addition, a sexual bias was evident. Male *M. littorale* were taken as prey in greater numbers than females or copepodites. On average, 73% of ingested *M. littorale* were male. A comparison of starry flounder stomach contents to sediment meiofauna samples on 2 representative sampling dates indicates that *M. littorale* made up a much higher proportion of the harpacticoids ingested by juvenile *P. stellatus* than in the sediment assemblage (Fig. 2.1). Furthermore, male *M. littorale* were proportionately much more abundant in *P. stellatus* gut contents than in sediment samples (Fig. 1.1). The most abundant sediment harpacticoid species, *Halectinosoma* sp. and *Amphiascoides dimorphus*, were rare in *P. stellatus* stomachs. The second most abundant genus of harpacticoid taken as prey was *Tisbe*, a genus that has been noted for
Table 2.2. Stomach contents of juvenile (<25 mm SL) Platichthys stellatus collected on ten sampling dates in 1987-1989, with number of fish examined (n), mean number of harpacticoid copepods per fish, percentage of harpacticoids that were Microarthridion littorale, percentage of M. littorale which were male and ratio of M. littorale copepodites to adults.

<table>
<thead>
<tr>
<th>Date</th>
<th>n</th>
<th>Mean no. harpact.</th>
<th>% M.littorale</th>
<th>% Male</th>
<th>Copepodite to Adult ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>7/27/87</td>
<td>16</td>
<td>44.8</td>
<td>84.7</td>
<td>74.0</td>
<td>0.37</td>
</tr>
<tr>
<td>8/11/87</td>
<td>8</td>
<td>8.4</td>
<td>62.7</td>
<td>71.0</td>
<td>0.35</td>
</tr>
<tr>
<td>8/23/87</td>
<td>5</td>
<td>4.0</td>
<td>50.0</td>
<td>77.8</td>
<td>0.11</td>
</tr>
<tr>
<td>9/8/87</td>
<td>2</td>
<td>4.0</td>
<td>37.5</td>
<td>66.7</td>
<td>0.00</td>
</tr>
<tr>
<td>6/14/88</td>
<td>2</td>
<td>3.5</td>
<td>71.4</td>
<td>100.0</td>
<td>0.00</td>
</tr>
<tr>
<td>7/1/88</td>
<td>19</td>
<td>15.6</td>
<td>79.5</td>
<td>68.9</td>
<td>0.33</td>
</tr>
<tr>
<td>7/7/89</td>
<td>15</td>
<td>19.6</td>
<td>81.3</td>
<td>66.9</td>
<td>0.15</td>
</tr>
<tr>
<td>7/17/89</td>
<td>19</td>
<td>28.2</td>
<td>87.2</td>
<td>83.2</td>
<td>0.41</td>
</tr>
<tr>
<td>7/19/89</td>
<td>20</td>
<td>14.0</td>
<td>71.4</td>
<td>73.3</td>
<td>0.33</td>
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<tr>
<td>7/21/89</td>
<td>14</td>
<td>26.2</td>
<td>74.3</td>
<td>69.1</td>
<td>0.28</td>
</tr>
</tbody>
</table>
Fig. 2.1. Comparison of sediment harpacticoid assemblage with that found in stomachs of juvenile Platichthys stellatus on 2 sampling dates. (a) Sediment assemblage on July 27, 1987. Species composition is represented in pie diagram, with demographic breakdown of Microarthridion littorale depicted in bar graph. (b) Sediment assemblage on July 1, 1988. (c) Harpacticoids in guts of P. stellatus collected on July 27, 1988. (d) Harpacticoids in P. stellatus guts on July 1, 1988.
its epibenthic lifestyle in other locales (Walters & Bell 1986).

Average lengths of harpacticoid species at the site were determined by image analysis (Table 2.3). While Microarthridion littorale were significantly larger than the other abundant sediment-dwelling species, males were not significantly larger than females. Furthermore, males in the stomach contents of Platicthys stellatus were not significantly larger than male or female M. littorale in the sediment. In fact, evidence indicated that ingested M. littorale were smaller than those in the sediment.

Core samples taken in a perpendicular transect on the beach from the +3 to the -1 m tide level did not reveal a location where Microarthridion littorale was more abundant than at the area of fish collection. Densities of M. littorale were highest at the -1 m and 0 m transects, with lower densities at +1 m (Fig. 2.2). Transects at +2 and +3 m revealed negligible densities of M. littorale.

Semi-quantitative samples taken from fronds of Fucus were dominated by Harpacticus sp., a preferred prey of juvenile salmonids (Sibert 1979) while Microarthridion littorale was rare in these samples. Harpacticoids were also present in samples taken from clipped leaves of Zostera marina. The samples contained species found in sediment samples, notably Amphiascoides dimorphus, in addition to Harpacticus sp. M. littorale was rare.
Table 2.3. Means and standard errors for lengths (mm) of adult male and female *Microarthridion littorale*, *M. littorale* copepodites, and adult females of *Amphiascoides dimorphus* and *Halectinosoma* sp. Male *A. dimorphus* and *Halectinosoma* were rare and were not included in the analysis. Groups found to differ significantly (p < 0.05) in length by Duncan's multiple range test are indicated by different letters.

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean</th>
<th>S.E.</th>
<th>Group</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. littorale</em> ♂</td>
<td>0.653</td>
<td>.0159</td>
<td>A</td>
</tr>
<tr>
<td><em>M. littorale</em> ♀</td>
<td>0.631</td>
<td>.0167</td>
<td>A</td>
</tr>
<tr>
<td><em>A. dimorphus</em> ♀</td>
<td>0.552</td>
<td>.0128</td>
<td>B</td>
</tr>
<tr>
<td><em>Halectinosoma</em> sp. ♀</td>
<td>0.569</td>
<td>.0077</td>
<td>B</td>
</tr>
<tr>
<td><em>M. littorale</em> cop.</td>
<td>0.387</td>
<td>.0263</td>
<td>C</td>
</tr>
</tbody>
</table>
Fig. 2.2. Microarthridion littorale. Density (no. cm$^3$) and vertical distribution on July 19, 1989 at (a) -1 m tide level, (b) 0 m tide level, and (c) +1 m tide level. Means and 1 SE are indicated.
A series of vertically sectioned cores taken in July 1989 indicated that densities of all common species of harpacticoids decreased rapidly with depth (Fig. 2.3a). Vertical distribution of adult *Microarthridion littorale* was compared to that of other adult harpacticoids by 2-sample Kolmogorov-Smirnov tests for 0 m collections on July 7 and 20, 1987, and -1 m collections on July 20, 1987. The July 20 collection at 0 m indicated a significantly more surficial distribution for *M. littorale* than for other adult harpacticoids ($D_{0.05} = 0.162$, $D_{max} = 0.373$). However, *M. littorale* made up only 16% of the harpacticoid assemblage in the surface sediments in this collection. Test results for the other 2 collections indicated that *M. littorale* distributions were not significantly different from that of other adult harpacticoids. Similarly, densities of all demographic groups (males, female and copepodites) of *M. littorale* were highest at the surface and decreased rapidly with depth (Fig. 2.3b). Two-sample Kolmogorov-Smirnov tests were utilized to compare distributions of adult male and female *M. littorale*. In no case were the distributions found to be significantly different. Similarly sectioned cores at the 1, 2 and 3 m tidal levels also showed no concentration of *M. littorale* in surface sediments. Vertical distribution of *M. littorale* was similar over all tide levels at which they were collected (Fig. 2.2).
Fig. 2.3. Densities and vertical distributions of harpacticoid copepods on 0 m transect on July 7, 1989. Density is expressed as no. cm$^3$. Mean and 1 SE are indicated. (a) Vertical distribution of 3 most abundant species. Hal = Halectinosoma sp., Amph = Amphiascoides dimorphus, Micr = Microarthridion littorale. (b) Vertical distribution of demographic groups of Microarthridion littorale.
Two sampling approaches, emergence traps and settlement traps, were employed to measure the tendencies of harpacticoids to leave the sediment during immersion (Fig. 2.4a and 2.4b). Harpacticoids made up some 70% of the copepods in emergence trap collections, with the remaining 30% approximately equally split between cyclopoids and calanoids. The most abundant harpacticoids in emergence trap collections were of the genus *Tisbe*, a genus frequently found in hyperbenthic collections (Walters & Bell 1986). Approximately 60% of the copepods collected in settlement traps were harpacticoids, with most of the remainder being cyclopoids. Calanoids were rare in settlement trap collections. Copepods must swim some 7 cm above the sediment surface to enter emergence traps. Settlement traps, on the other hand, are effective collectors of the near-bottom fauna (Fegley 1988) and settlement trap harpacticoid assemblages resembled that ingested by *Platichthys stellatus* with *Microarthridion littorale* making up some 40% of the harpacticoids collected in these traps (76% in stomach contents).

Table 2.4 presents similarity values of the harpacticoid assemblages collected in the entire sediment cores, the upper 2 mm of the sediment, settlement traps, emergence traps and those found in guts of *Platichthys stellatus*. At the species level, sediment collections
Fig. 2.4. Harpacticoid copepods collected in (a) emergence traps and (b) settlement traps on July 21, 1989. Pie diagram represents species composition; bar graph depicts the demographic composition of Microarthridion littorale.
Table 2.4. Percent similarities of harpacticoid copepod assemblages represented in different collections. FLATFISH PREY = copepods identified in *Platichthys stellatus* gut contents, UPPER SED = copepods in upper 2 mm of sediment cores, ENTIRE SED = copepods in entire upper 1 cm of sediment cores, EMERGE = copepods collected in emergence traps, and SETTLE = copepods collected in settlement traps.

<table>
<thead>
<tr>
<th></th>
<th>FLATFISH PREY</th>
<th>UPPER SED</th>
<th>ENTIRE SED</th>
<th>EMERGE</th>
<th>SETTLE</th>
</tr>
</thead>
<tbody>
<tr>
<td>FLATFISH PREY</td>
<td>*</td>
<td>25.4</td>
<td>31.3</td>
<td>35.1</td>
<td>66.2</td>
</tr>
<tr>
<td>UPPER SED</td>
<td></td>
<td>*</td>
<td>92.1</td>
<td>56.9</td>
<td>55.2</td>
</tr>
<tr>
<td>ENTIRE SED</td>
<td></td>
<td></td>
<td>*</td>
<td>59.4</td>
<td>61.0</td>
</tr>
<tr>
<td>EMERGE</td>
<td></td>
<td></td>
<td></td>
<td>*</td>
<td>62.6</td>
</tr>
<tr>
<td>SETTLE</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>*</td>
</tr>
</tbody>
</table>
(both the entire 1 cm core and the upper 2 mm) and emergence traps showed <40% similarity to *P. stellatus* prey. The greatest similarity to flounder diets (66.2%) occurred in the settlement trap collections, implying that the visually feeding *P. stellatus* were ingesting harpacticoids in the near-bottom waters.

**DISCUSSION**

Juvenile *Platichthys stellatus* prey almost exclusively on harpacticoid copepods and their diet is dominated by male *Microarthridion littorale*. This harpacticoid is not dominant in the sediments, nor can selection by explained by prey size differences. Harpacticoids in the gut contents of juvenile *P. stellatus* do not closely resemble those in the sediments or in emergence traps, but do closely resemble those in settlement traps (Table 2.4). Thus, it seems likely that *P. stellatus* feeds heavily on harpacticoids from near-bottom water.

Selective feeding in many fish species has been explained by prey-size selection. Such selection can be for larger (Brooks & Dodson 1965, Werner & Hall 1974) or smaller (Schmitt & Holbrook 1984, Bence & Murdoch 1986) prey types. *Microarthridion littorale* is significantly larger than other abundant sediment harpacticoids. Male *M. littorale*, however, do not differ significantly in length from females. In fact, the male is more slender and likely
represents a smaller energetic gain. It does not appear that prey size provides a complete explanation for the feeding selection demonstrated by *Platicthys stellatus*.

Alternatively, *Platicthys stellatus* may feed at a site other than the site of fish collection. This is a common criticism of studies attempting to compare fish food habits to that available in the environment (Gee 1987). Flatfish have been shown to use tidal migration as a feeding strategy (Wolff et al. 1981), moving onto tidal flats at high tide and returning to adjacent channels with the falling tide. Feller et al. (1990), working with the sciaenid *Leiostomus xanthurus*, found that the species composition of the harpacticoids in the diet can be used to identify the location in which the fish feed.

I could find no area in which *Microarthridion littorale* was more abundant than at the site of fish collection. Furthermore, I found no tide level where the *M. littorale* population was dominated by males. *M. littorale* were not present at extensively sampled subtidal stations (18-25 m) near my study site from 1985 to 1989 (Fleeger & Shirley 1990). My inability to sample at -2 and -3 m depths is troublesome, but not overly so. All fish collections were made at low tide. Tidal ranges in the bay are from 5 to 7 m, resulting in an extremely strong tidal current. It is highly unlikely that the fish fed at lower tidal levels than that at which they were collected, since
the juvenile flatfish would have had to work their way up to the point of collection against a very strong outflowing tide. In addition, there is no indication that adjacent algal and seagrass beds are heavily utilized as feeding areas. The selectivity of *Platichthys stellatus* cannot be explained solely as resulting from feeding in another locale.

A third potential explanation of the observed selection is that harpacticoids may differ in vertical distribution within the sediment, with the more surficial species more easily preyed upon than deeper interstitial or burrowing animals. This pattern has been observed by Gee (1987) who showed that an epibenthic harpacticoid was selectively preyed upon by juvenile flatfish. Furthermore, Fleeger (1979) observed consistently high mortality rates in *Microarthridion littorale* and hypothesized that its surficial nature might lead to greater susceptibility to predation. My study indicates that *M. littorale* does not differ significantly in vertical distribution from other abundant harpacticoids. It appears that differing vertical distributions cannot be invoked as an explanation for the selection of male *M. littorale* as prey.

A fourth factor that might explain selection relates to the behavior of harpacticoid copepods. For example, species (or sexes) that emerge from the sediments probably increase their susceptibility to predation (Palmer 1988b),
particularly by visual predators preying on small prey organisms.

There has recently been increasing recognition of a hyperbenthic (or near-bottom) meiofaunal assemblage, containing elements of 2 origins: downward-moving planktonic species and upward-moving benthic species (Sibert 1981, Fleeger et al. 1983). Walters & Bell (1986) found that large numbers of harpacticoid copepods (19 of 36 species) migrated from the sediment into the water column in a Florida seagrass bed. Sibert (1981) analyzed pump samples collected 30 cm and 5 cm above the sediment surface in British Columbia. He found that the "plankton" density was always greater at 5 cm than at 30 cm, and that these samples were dominated by copepod nauplii and harpacticoid copepods. Sibert also pointed out the potential significance of the hyperbenthos as food for demersal predators, and discussed a sample of chum salmon fry collected at his study site. Salmon fry stomach contents revealed that approximately 60% of their prey were Microarthridion littorale, and, while M. littorale was among the more abundant harpacticoids, it did not constitute a majority of the available prey. It is possible that juvenile salmon may also exploit emergent M. littorale in the near-bottom waters. In addition, preliminary work on postlarval spot (Leiostomus xanthurus) suggests a reliance on hyperbenthic prey before shifting to
an infaunal meiofaunal assemblage (McCall unpubl.). Given that many juvenile fish feed in the near-bottom waters, more study is warranted on the dietary role played by the ubiquitous hyperbenthic meiofauna.

Settlement trap data indicated that *Microarthridion littorale* may indeed be more abundant in the near-bottom water than their sediment density would indicate. Demographic evidence, however, was contradictory. The hyperbenthic *M. littorale* assemblage did not appear to be dominated by males, as might be predicted from the feeding habits of juvenile *Platichthys stellatus*. While species-specific predation on harpacticoid copepods has been observed in a number of circumstances, sex-specific predation is less well-documented. Maly (1970), investigating predation on calanoid copepods of the genus *Diaptomus*, found differential predation on males and females due to an interaction between the hunting behavior of the predator and the size and activity of male and female copepods. He also found that the adult sex ratios of the prey could be altered by sex-biased predation. Hicks & Marshall (1985) found that certain deep-sea carnivorous bivalves feed almost exclusively on male harpacticoids, and went on to speculate that this could play a role in biasing sex ratios in the deep sea toward females. They further suggested that bioluminescence may be a factor leading to this selection. In Alaska,
behavioral differences between the harpacticoid sexes, particularly swimming behavior associated with copulation, may play a role in the sexual bias shown in flatfish feeding. As in most harpacticoids, male *M. littorale* engage in a precopulatory association with juvenile females (copepodites) in which the male grasps the copepodite with a specially adapted antennule. Hicks (1988) discusses the link between swimming behavior and precopulatory associations between mature males and late-stage female copepodites, and suggests that these associations must normally take place in the water column. Emergent behavior could lead to greater susceptibility to predation not only through increased availability, but also through greater visibility due to movement.

If, in fact, males and copepodites of *Microarthridion littorale* emerge from the sediments and are disproportionately abundant in the near-bottom waters while searching for partners, then males, which are significantly larger than copepodites, might well be more readily preyed upon by epibenthic predators such as *Platichthys stellatus*. The greater size of male *M. littorale* might also explain why they are taken in greater numbers than the cyclopoid copepods which are also abundant in the near-bottom water and have an approximate size range of 0.38 to 0.45 mm. The observed feeding pattern of the juvenile fish thus might be the result of a combination of behaviors, the emergent
behavior of the copepods and the feeding behavior of the fish.

Many researchers examining feeding in meiofaunal predators have been content to identify prey to major taxon (Sogard 1984, St. John et al. 1989). In this case, species-specific identification aided greatly in the identification of the source of copepods in the diet of juvenile Platichthys stellatus as different assemblages are found in the sediment, the hyperbenthos and on vegetation. A simple comparison illustrates that major taxon identifications can be misleading in other ways. Densities of the harpacticoid assemblage at the Auke Bay site compared to the number of juvenile flatfish collected in seine samples (an admittedly crude indicator of flatfish density) showed a sharp decline in the density of adult harpacticoids coincident with the arrival of juvenile flatfish (Fig. 2.5a). Harpacticoid numbers remained low during the summer and fall when the flatfish are present on the beach. It would be tempting to conclude that flatfish predation exerts a controlling influence on harpacticoid abundance, and in fact relationships of this type have been cited as evidence of predator control of prey populations (Heip & Smol 1975). However, if flatfish numbers are compared to the density of their primary prey, Microarthridion littorale (Fig. 5b), the apparent relationship between predator abundance and prey density
Fig. 2.5. Comparison of (a) total adult harpacticoid densities at Auke Bay site to number of juvenile flatfish captured over the period from March 1987 to Jan 1988 and (b) densities of adult Microarthridion littorale to flatfish captured over the same period.
becomes much more ambiguous. *M. littorale* densities, while showing a decline coincident with the arrival of the flatfish, increased shortly thereafter. This illustrates well the dangers inherent in correlational approaches to predation impact assessments, and the value of species-level identification of prey items. While there are certainly instances where the time-intensive process of species identification of harpacticoid prey may not yield valuable information (Coull 1990), there are cases where species identification and even information on demographic status can be of great interest. These results are also in agreement with the finding of Hicks (1984) and Gee (1987) who concluded that fish predation did not limit harpacticoid densities.
CHAPTER 3

HYPERBENTHIC AND MEIOBENTHIC PREY IN THE DIET OF POST-LARVAL LEIOSTOMUS XANTHURUS
INTRODUCTION

Much research on predator-prey interactions between fish and meiofauna has focused on a relatively few species of teleost fishes. Notable among these is spot (*Leiostomus xanthurus*), a member of the Family Sciaenidae. As an estuarine-dependent juvenile, spot is among the most abundant fishes in estuaries of the western Atlantic and northern Gulf of Mexico during spring and early summer. Meiofaunal feeding in spot has been extensively investigated on the lower Atlantic coast, where relatively large tidal amplitudes are common (Kjelson & Johnson 1976, Sheridan 1979, Kobylinski & Sheridan 1979, Hodson et al. 1981, Currin et al. 1984, Smith & Coull 1987, Ellis & Coull 1989, Nelson & Coull 1989, Archambault & Feller 1991). The feeding ecology of spot has been less well-studied on the microtidal upper Gulf coast (McCall et al. unpubl.).

Spot is unique in its prolonged reliance on meiofaunal prey (Stickney et al. 1975). McCall et al. (unpubl.) studied spot from 12-60 mm standard length in Louisiana. They found that spot fed on harpacticoids throughout this size range, and that changes occurred in the species composition of the ingested harpacticoids with ontogeny. Nematodes also served as prey, but they were abundant in gut contents only in the larger size ranges of spot. Much is known about sediment-biting in spot > 25 mm (Billheimer & Coull 1988), however the feeding habits of smaller spot
have not been well characterized. In this study, we ascertained the origin of the harpacticoid prey of post-larval (< 25 mm) spot and explored the ontogeny of the onset of sediment-feeding.

Harpacticoid copepods, and meiofauna in general, live in a variety of assemblages within a geographic area such as a bay or salt marsh. Although many prey species are widespread, a foraging fish may come in contact with different species groups dependent on its feeding strategy (Feller et al. 1990). Within the sediments, harpacticoids show a variety of modes of existence including epibenthic, burrowing, tube-dwelling (Chandler & Fleeger 1984) and interstitial (Coull 1988). Furthermore, meiofauna are not restricted to an infaunal existence. Phytal assemblages are associated with seagrasses or algae (Hicks & Coull 1983). A poorly understood group is the hyperbenthic or demersal meiofauna (Sibert 1981, Fleeger et al. 1983, Walters & Bell 1986, Armonies 1989). This assemblage is found in the near-bottom water, within a few centimeters of the sediment surface, and is inadequately sampled by traditional coring and net-towing techniques. Hyperbenthic meiofauna probably include elements of both emergent (active or passive) meiofauna and a resident assemblage of non-sediment-dwelling harpacticoid and cyclopoid copepods.

McCall (1992) showed that an approach that relates different potential prey assemblages to diet can be useful
in more fully understanding the feeding behavior of a meiofaunal-feeding flatfish. This approach is adopted here in examining the source of prey of post-larval and juvenile spot.

METHODS

Juvenile spot were collected in winter and early spring of 1991 in Bay Champagne near the Louisiana Universities Marine Consortium facility at Port Fourchon, Louisiana. Bay Champagne is a small, shallow bay, separated from the open Gulf by a narrow sand beach. Juvenile spot appear in the bay in late January or early February, and are in residence throughout the spring. They frequent the bay margins and marsh edges, where they are among the most abundant teleosts the bay during these months (Baltz et al. 1992).

Juvenile spot were collected by seining along the margins of the bay on 3 occasions at approximately 2 wk intervals from February 23 through March 22. Collections were made with a variety of small-mesh seines at high tide in the intertidal zone in two primary locations: adjacent to small black mangroves (*Avicennia germinans*) along the western edge of the bay and adjacent to stands of *Spartina alterniflora* on the bays eastern margin. Two sites were utilized because inclement weather conditions occasionally made sampling impossible in one site.
Upon collection, fish were preserved immediately in 10% formalin. In the laboratory, the digestive tract was dissected under a stereomicroscope and prey identified. For fish less than 25 mm SL, the entire digestive tract was examined. In larger fish, only the portion anterior to the pyloric caecum was examined to lessen any bias that might result from differential digestion rates. In the case of copepods, identification was typically possible not only to the species level, but also to demographic group.

An assortment of meiofaunal samples were taken in conjunction with fish collections in an attempt to characterize the various assemblages. These collections included:

1) Vertically sectioned cores - cores were taken from haphazardly selected locations along a transect at the 0 m tide level to a substrate depth of 2 cm with a hand-held piston corer constructed from a 50 cm³ syringe. A core-extruding device similar to that described by Fuller & Butman (1988) was then used to section the core into 2-mm-thick strata to a depth of 1 cm. The 1-2 cm section was retained intact. Core sections were preserved in 10% buffered formalin with rose bengal stain. Four replicate cores were taken on each sampling date.

2) Emergence traps: Traps, similar to those used by Walters & Bell (1986), were used to sample emergent fauna. These traps require organisms to reach levels of some 6-7
cm above the sediment surface to enter the trap. Trap mouths were placed 1 cm above the sediment surface to allow for free water movement.

3) Settlement/bedform traps: Settlement traps similar to those described by Fegley (1988) were used to sample organisms settling to or moving along the sediment surface. Nine settlement traps were placed along the 0 m transect at haphazardly chosen locations. These traps consisted of test tubes (1.2 cm i.d. x 12.2 cm long) that were buried flush with the sediment surface and surrounded by a ring of azoic sediment. These trap dimensions produce an aspect ratio of 10, which was shown by Lau (1979) to retain trapped particles up to Reynolds' numbers of 20 000, requiring a current speed of approximately 140 cm s\(^{-1}\) at the trap opening to resuspend trapped particles (Fegley 1988). The traps were filled with filtered seawater and left in place through one tidal cycle (24 hours).

4) Phytal samples: Phytal meiofauna were sampled by clipping samples of submerged algae, mangrove roots, etc., in the area. Phytal samples were placed in plastic bags while still submerged to minimize the loss of phytal fauna.

All meiofaunal samples were preserved in 10% buffered formalin with Rose Bengal stain. Meiofauna were identified to the major taxon level, and copepods were identified, where possible, to species and demographic status.
Copepod (calanoid, cyclopoid and harpacticoids) prey of juvenile spot of various size classes were compared to assemblages collected by the various sampling techniques. Comparisons were conducted using principal components analysis of the correlation matrix of the species-centered mean abundances of copepod species in the various assemblages (Ludwig & Reynolds 1988). Eight assemblages were compared for collections from February 23, 1991, including four types of collections (sediment cores, emergence traps, settlement traps and phytal samples) and four size-classes of spot (see below). Abundances of 14 copepod species were included for this analysis (8 x 14 data matrix). A similar analysis for samples collected on March 9, 1991, included the same 4 types of collections outlined above. For this analysis, only 1 size class of juvenile spot was available. Again, 14 copepod species were included in the analysis (5 x 14 data matrix).

RESULTS

Stomach-content analyses were performed on 122 juvenile spot (12-35 mm SL), of which 106 contained prey. Their diets were dominated numerically by copepods and nematodes (Table 3.1). Mean number of prey showed a general increase up to ca 30 mm SL, but was highly variable. At approximately 26 mm SL, juvenile spot began to take large numbers of nematodes in addition to copepods.
Table 3.1. Summary of spot feeding data. Results are presented by size class (mm SL). Indicated are size classes, number of fish containing prey examined in each size class (n), mean and one standard error of number of prey within size classes, and percentage of prey of each size class made up of nematodes, calanoid copepods, cyclopoid copepods, harpacticoid copepods and other prey. Fish with empty stomachs are excluded.

<table>
<thead>
<tr>
<th>Size Class</th>
<th>n</th>
<th># prey</th>
<th>Mean ± SE</th>
<th>Nema. %</th>
<th>Cal. %</th>
<th>Cycl. %</th>
<th>Harp. %</th>
<th>Oth. %</th>
</tr>
</thead>
<tbody>
<tr>
<td>12-15</td>
<td>28</td>
<td>5.3 ± 1.0</td>
<td>0.0</td>
<td>49.0</td>
<td>14.1</td>
<td>17.4</td>
<td>18.8</td>
<td></td>
</tr>
<tr>
<td>15-18</td>
<td>20</td>
<td>7.4 ± 1.9</td>
<td>0.1</td>
<td>4.1</td>
<td>2.7</td>
<td>66.0</td>
<td>27.2</td>
<td></td>
</tr>
<tr>
<td>18-21</td>
<td>10</td>
<td>18.2 ± 8.4</td>
<td>0.0</td>
<td>8.2</td>
<td>1.6</td>
<td>75.3</td>
<td>14.8</td>
<td></td>
</tr>
<tr>
<td>21-25</td>
<td>9</td>
<td>45.4 ± 17.1</td>
<td>0.0</td>
<td>30.0</td>
<td>0.0</td>
<td>66.3</td>
<td>3.7</td>
<td></td>
</tr>
<tr>
<td>25-28</td>
<td>6</td>
<td>6.8 ± 3.0</td>
<td>73.5</td>
<td>0.0</td>
<td>0.0</td>
<td>11.8</td>
<td>23.5</td>
<td></td>
</tr>
<tr>
<td>28-32</td>
<td>17</td>
<td>80.8 ± 44.0</td>
<td>65.6</td>
<td>0.1</td>
<td>0.1</td>
<td>11.6</td>
<td>1.5</td>
<td></td>
</tr>
<tr>
<td>32-35</td>
<td>10</td>
<td>41.3 ± 11.5</td>
<td>35.2</td>
<td>0.1</td>
<td>1.8</td>
<td>53.5</td>
<td>9.2</td>
<td></td>
</tr>
<tr>
<td>35-40</td>
<td>6</td>
<td>19.8 ± 3.2</td>
<td>51.9</td>
<td>0.0</td>
<td>0.0</td>
<td>34.2</td>
<td>13.9</td>
<td></td>
</tr>
</tbody>
</table>
This feeding shift was quite sudden. At less than 25 mm SL, nematodes made up less than 1% of ingested prey of spot, but comprised 35-73% of the prey items in 25-40 mm SL spot. Prior work has indicated that it is at approximately this size that juvenile spot begin feeding directly on the benthos by biting into the sediment (McCall et al. unpubl.).

Developing spot also underwent a change in the types of copepods consumed at the ordinal level (Fig. 3.1a). Only in the smallest fish examined (< 15 mm SL) were planktonic calanoid copepods, mainly *Acartia tonsa*, an important prey (although one fish of 23 mm SL contained 143 *A. tonsa*). Cyclopoid copepods, which exhibit lifestyles ranging from epibenthic to planktonic, were fed upon by a wide size range of spot but were never a dominant prey item. Harpacticoid copepods, on the other hand, were an important prey at all sizes and were numerically dominant in spot from 15-25 mm SL.

The species composition of ingested harpacticoids changed as spot increased in size (Fig. 3.1b). *Harpacticus* sp. was the most frequently ingested harpacticoid in very small spot, but were rare in fish larger than 20 mm. The harpacticoids *Mesochra mexicana*, *Scottolana canadensis* and *Paronychcamptus wilsoni* were also important prey. *M. mexicana* was by far the dominant prey in fish of a narrow size range (20-22 mm), likely resulting from a sampling
Fig. 3.1. Copepod prey of Leiostomus xanthurus. (a) Percentage of copepod prey of various size classes represented by different orders of copepods. Cal = calanoids, Cycl = cyclopoids, Harpact = harpacticoids. (b) Percentage of ingested harpacticoids belonging to various species. Harp = Harpacticus sp., Scot = Scottolana canadensis, Paro = Paronychocamptus wilsoni, Meso = Mesochra mexicana, Oth = other species of harpacticoids.
bias (see below). *S. canadensis* and *P. wilsoni* were relatively important prey of all size classes. Other species were found in lesser numbers. In fish > 30 mm SL other harpacticoids, including *Pseudostenhelia wellsii*, *Enhydrosoma* sp. and *Nannopus palustris*, began to increase in importance.

To determine the assemblage utilized as prey, complete batteries of meiofaunal samples were collected on 2 dates, February 23 on the western margin of the bay and March 9, 1991, on the eastern margin, some 2 km distant. The change in sampling location was necessitated by water conditions associated with a frontal system. Both collections were in areas of muddy substrate. On each date, juvenile *Leiostomus xanthurus* were also collected. Spot collected on February 23 spanned a broad size range, allowing comparison of feeding habits of different size classes. However, on March 9, the size range of collected spot was narrower, and conclusions were limited to larger size classes. Juvenile spot were also collected on March 22; unfortunately, weather conditions prevented the collection of concurrent meiofaunal samples.

The sediment meiofaunal assemblage on February 23 was numerically dominated by nematodes, with harpacticoid copepods the second most abundant taxon (Table 3.2). Nematode densities were relatively high (ca. 330·cm$^{-3}$ in the upper 2 mm of sediment). Nematodes were most abundant
Table 3.2. Summary of vertically-sectioned meiofaunal samples collected on February 23 at Bay Champagne East site and March 9 at Bay Champagne West site. Data are presented as densities in number per cm$^3 \pm 1$ standard error for each 2 mm thick sediment stratum for total meiofauna and for major components. Total Meio. = total meiofauna, Adult Harp. = adult harpacticoid copepods, Harp. Copep. = harpacticoid copepodites.

February 23

<table>
<thead>
<tr>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>0-2</td>
<td>362 ± 82</td>
<td>332 ± 78</td>
<td>14.9 ± 0.4</td>
<td>5.3 ± 2.0</td>
</tr>
<tr>
<td>2-4</td>
<td>129 ± 26</td>
<td>121 ± 26</td>
<td>4.5 ± 0.9</td>
<td>1.0 ± 0.5</td>
</tr>
<tr>
<td>4-6</td>
<td>143 ± 15</td>
<td>140 ± 16</td>
<td>2.1 ± 1.7</td>
<td>0</td>
</tr>
<tr>
<td>6-8</td>
<td>137 ± 15</td>
<td>128 ± 16</td>
<td>1.5 ± 0.8</td>
<td>1.3 ± 0.6</td>
</tr>
<tr>
<td>8-10</td>
<td>104 ± 14</td>
<td>95 ± 14</td>
<td>1.0 ± 0.6</td>
<td>0.5 ± 0.4</td>
</tr>
</tbody>
</table>

March 9

<table>
<thead>
<tr>
<th>Stratum (mm depth)</th>
<th>Total Meio.</th>
<th>Nematodes</th>
<th>Adult Harp.</th>
<th>Harp. Copepide</th>
</tr>
</thead>
<tbody>
<tr>
<td>0-2</td>
<td>421 ± 116</td>
<td>363 ± 112</td>
<td>17.2 ± 2.7</td>
<td>8.5 ± 2.2</td>
</tr>
<tr>
<td>2-4</td>
<td>302 ± 47</td>
<td>276 ± 48</td>
<td>6.1 ± 1.4</td>
<td>3.6 ± 1.7</td>
</tr>
<tr>
<td>4-6</td>
<td>170 ± 32</td>
<td>161 ± 32</td>
<td>4.2 ± 1.6</td>
<td>0.2 ± 0.2</td>
</tr>
<tr>
<td>6-8</td>
<td>223 ± 32</td>
<td>217 ± 31</td>
<td>1.2 ± 0.5</td>
<td>0</td>
</tr>
<tr>
<td>8-10</td>
<td>195 ± 16</td>
<td>192 ± 16</td>
<td>0.2 ± 0.2</td>
<td>0.2 ± 0.2</td>
</tr>
</tbody>
</table>
in the surface sediments (0-2 mm depth) on both sampling
dates, but remained high to depths of at least 1 cm, as is
typical in muddy sediments (Hicks & Coull 1983). Densities
of both adult harpacticoids and copepodites were 14.9 cm$^3$
and 5.3 cm$^3$, respectively, in the 0-2 mm stratum. These
densities are somewhat low for soft-sediment intertidal
habitats of this type (Fleeger 1980; 1985).

The most abundant harpacticoids in sediment samples
collected on February 23 were Paronychocamptus wilsoni,
Scottolana canadensis and Enhydrosoma sp. All were
concentrated in the upper 2-4 mm of the sediments, and
densities dropped rapidly with depth (Fig 3.2a).

Settlement/bedform trap samples on February 23
collected large numbers of small nematodes (Table 3.3).
This is indicative of the fact that these traps sample not
only fauna that are actively emergent, but also those that
are resuspended from surface sediments. The site was
exposed to substantial wave action in late February,
resulting in a large suspended sediment load. The number
of copepods collected was low (< 10 per trap). The
majority of those collected were harpacticoids, the
remainder cyclopoids (Fig. 3.3a). The most abundant
harpacticoid was Paronychocamptus wilsoni; Mesochra
mexicana and Harpacticus sp. were also found, but in lower
numbers. February 23 emergence traps contained cyclopoids
and calanoids, but were dominated by harpacticoids, of
Fig. 3.2. Vertical distribution of common harpacticoid species in sediment samples taken on (a) February 23, 1991, and (b) March 9, 1991. Densities (no. cm³ ± 1 SE) are given for each 2 mm thick sediment stratum.
Table 3.3. Mean and standard error of major taxa collected in settlement traps (Settle) and emergence traps (Emerge) and percent composition of phytal samples for February 23 and March 9, 1991. Nema = nematodes, Cal = calanoids, Cyc = cyclopoids, Harp = harparcticoids.

<table>
<thead>
<tr>
<th></th>
<th>Nema</th>
<th>Cal</th>
<th>Cyc</th>
<th>Harp</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Settle</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2/23</td>
<td>66.6 ± 0.7</td>
<td>0</td>
<td>2.5 ± 0.6</td>
<td>7.2 ± 1.8</td>
</tr>
<tr>
<td>3/9</td>
<td>22.8 ± 7.8</td>
<td>0</td>
<td>5.0 ± 1.5</td>
<td>17.1 ± 6.5</td>
</tr>
<tr>
<td><strong>Emerge</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2/23</td>
<td>2.4 ± 0.7</td>
<td>7.0 ± 2.0</td>
<td>5.4 ± 1.4</td>
<td>33.6 ± 12.9</td>
</tr>
<tr>
<td>3/9</td>
<td>2.0 ± 0.8</td>
<td>90.1 ± 30.9</td>
<td>26.0 ± 4.9</td>
<td>17.6 ± 4.0</td>
</tr>
<tr>
<td><strong>Phytal</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2/23</td>
<td>1.0%</td>
<td>0.5%</td>
<td>12.3%</td>
<td>81.3%</td>
</tr>
<tr>
<td>3/9</td>
<td>0.3%</td>
<td>0</td>
<td>12.0%</td>
<td>85.6%</td>
</tr>
</tbody>
</table>
Fig. 3.3. Composition of copepods collected in settlement traps on (a) February 23, 1991 and (b) March 9, 1991. Pie diagram represents percentage by copepod order while bar chart represents species composition of harpacticoid copepods. Pw = Paronychocamptus wilsoni, Mm = Mesochra mexicana, Ho = Harpacticus sp., Oth = other harpacticoids.
which the majority were *Paronychocamptus wilsoni* and *Scottolana canadensis* (Fig. 3.4a). *P. wilsoni* was represented in emergence trap samples by all demographic groups, while over 90% of *S. canadensis* in these traps were copepodites. Other harpacticoids collected in appreciable numbers included *Harpacticus* sp., *Zausodes arenicola* and *Pseudobradya* sp. *Pseudobradya*, however, was collected only in one trap. Nematodes were rare in emergence traps (Table 3.3). Harpacticoids dominated phytal samples on both dates. *Harpacticus* sp. were dominant, making up some 80% of the phytal harpacticoids, although *Paronychocamptus wilsoni* was also present in substantial numbers.

Juvenile spot were divided into 4 size classes, <16 mm, 16-26 mm, 26-30 mm and >30 mm, to provide relatively equal numbers in size classes and to include two size classes below and two above 26 mm SL, the size at which nematodes began to dominate the diet. Only for the February 23 collection were juvenile spot of all 4 size classes collected in suitable numbers to permit comparison of prey composition to copepods collected by various sampling techniques.

The trends in total prey abundance for the February 23 spot collections mirrored that for all spot; a rapid increase in prey numbers with increasing fish size and a dramatic increase when nematodes suddenly appeared in the diet (Fig 3.5).
Fig. 3.4. Composition of copepods collected in emergence traps on (a) February 23, 1991 and (b) March 9, 1991. Pie diagram represents percentage by copepod order while bar chart represents species composition of harpacticoid copepods. Pw = Paronychocamptus wilsoni, Sc = Scottolana canadensis, Oth = other harpacticoids.
Fig. 3.5. Prey contents of four size classes of spot collected on February 23, 1991. (a) Mean (and 1 SE) number of prey by size class. (b) Percentage of total prey (pooled) comprised by nematodes in each size class.
The composition of the copepod prey of the 4 size classes of juvenile spot collected on February 23 showed an increase in the number of harpacticoids from the smallest size class of spot to the largest (Fig. 3.6). Nevertheless, harpacticoids constituted an important prey resource in even the smallest fish. There was a decline in the importance of the epiphytic or hyperbenthic Harpacticus sp. as the fish grew larger. The widespread Paronychocamptus wilsoni and Scottolana canadensis were found in all size classes.

In the principal components analysis of copepod-species-centered data, the first principal component accounted for approximately 42% of the variation in the data. Inspection of the associated eigenvector indicated that the first component associated positive loadings with copepod species found primarily in the water column and negative loadings with species restricted to the sediments. The second component, less interpretable, accounted for an additional 21% of the variation in the data.

A plot of the first 2 principal components (Fig. 3.7) indicated that the prey assemblage of the smallest size classes of spot did not closely resemble the sediment assemblage but rather grouped more closely with settlement-trap (near-bottom) and phytal assemblages. Prey assemblages of larger spot were more similar to sediment copepod assemblages.
Fig. 3.6. Composition of copepod prey in stomach contents of spot of four size classes collected on February 23, 1991. (a) Spot < 16 mm SL, (b) spot 16-26 mm SL, (c) spot 26-30 mm SL and (d) spot > 30 mm SL. Pie diagram represents percentage by copepod order while bar chart depicts species composition of harpacticoid copepods. Ho = Harpacticus sp., Sc = Scottolana canadensis, Pw = Paronymchocamptus wilsoni, Oth = other species of harpacticoids.
Fig. 3.7. Plot of first three principal components for copepod prey of four size classes of spot collected on February 23, 1991 and copepods collected by various sampling schemes on the same date. $S_1 =$ spot $< 16$ mm SL, $S_2 =$ spot 16-26 mm SL, $S_3 =$ spot 26-30 mm SL, $S_4 =$ spot $> 30$ mm SL, $Set =$ copepods collected in settlement traps, $Et =$ copepods collected in emergence traps, $Sed =$ copepods collected in sediment cores, and $Ph =$ phytal copepods.
Sampling on March 9, designed to provide a second dataset for comparison of ingested copepods to those collected by different techniques, was flawed by the narrow size range of the collected spot (only 5 fish < 30 mm SL were collected). For this reason, we were unable to make wide-ranging conclusions about ontogenetic changes in predation based on these data. Nonetheless, these samples do provide a convenient test for larger spot with samples collected at a different site and comprising a slightly different fauna.

March 9 sediment cores were also dominated by nematodes, which showed slightly higher densities than in February 23 samples (Table 3.3). Since another sampling site was utilized for these samples, it cannot be determined whether this represents differences between sampling sites or dates. Harpacticoids were again the second most abundant taxon and, like the February samples, harpacticoid densities were relatively low. The 3 dominant sediment species in thes samples were *Paronychocamptus wilsoni*, *Cletocamptus deitersi* and *Enhydrosoma* sp. (Fig. 3.2b). As with February 23 samples, most of the harpacticoids were concentrated in the upper 2-4 mm of the sediment, although *C. deitersi* was found in moderate densities in the 4-6 mm stratum. Although *Scottolana canadensis*, the second most abundant species collected in cores on February 23, was absent from the March 9 samples,
differences may be between sites rather than sampling dates. All demographic groups were present in sediment harpacticoid samples, although, for all species other than *P. wilsoni*, females outnumbered males.

Settlement-trap samples from March 9 were dominated by harpacticoids, although large numbers of nematodes were also collected. *Mesochra mexicana*, *Paronychocamptus wilsoni* and *Harpacticus* sp. were the most abundant harpacticoid species (Fig. 3.3b). *M. mexicana* was notably patchy, and was absent from 4 traps but the most abundant harpacticoid in 3 others. *M. mexicana* in settlement traps were dominated by males, which made up over 90% of those collected.

The calanoid *Acartia tonsa* dominated March 9 emergence-trap samples. Harpacticoids made up only 13% of the collected copepods (Fig. 3.4b). Of the harpacticoids collected, *Scottolana canadensis* was the most abundant species, followed by *Paronychocamptus wilsoni*. Smaller numbers of *Mesochra mexicana* and *Harpacticus* sp. were collected. As in the February 23 emergence traps, collected *S. canadensis* were primarily copepodites.

Juvenile spot collected on March 9 did not encompass a broad enough size range to allow investigation of ontogenetic changes in prey composition. Nonetheless, fish of the size classes that were available showed much the same pattern as those from February samples, with larger
size classes of spot relying heavily on harpacticoid copepods.

Juvenile spot were also collected on March 22. However, high water levels associated with a cold front prevented the sampling of the intertidal meiofaunal assemblages.

Principal components analysis of the March 9 assemblages yielded ambiguous results (Fig. 3.8). The first 2 principal components seemed to account for similar types of variation to that seen in the analysis of February 23 data (water-column vs. sediment), except that the axes were reversed. The prey assemblage taken by juvenile spot did not group closely with the sediment copepod assemblage, and in fact was quite different from any assemblage.

DISCUSSION

Juvenile spot (15-40 mm SL) showed distinct ontogenetic changes in the composition of their meiofaunal prey, and these changes were attributable to changes in feeding behavior. Early post-larval spot preyed on a copepod assemblage comprised of demersal calanoids, cyclopoids and hyperbenthic harpacticoids that most closely resembled collections made with settlement traps. At larger sizes, spot ingested copepods, primarily harpacticoids, that were more similar to sediment assemblages. This is indicative of a shift from a
Fig. 3.8. Plot of first three principal components for copepod prey of largest size class of spot collected on March 9, 1991 and copepods collected by various sampling schemes on the same date. $S4 = \text{spot} > 30 \text{ mm SL}$, $Set = \text{copepods collected in settlement traps}$, $Et = \text{copepods collected in emergence traps}$, $Sed = \text{copepods collected in sediment cores}$, and $Ph = \text{phytal copepods}$. 
planktonic or hyperbenthic feeding mode to a benthic one in which juvenile spot bite into the sediment and winnow out contained organisms of sufficient size. Simultaneously, a dramatic increase in the contribution of nematodes to the diet of spot occurred around 25–28 mm SL. In spot < 25 mm SL, nematodes comprised less than 1% of the diet. In those between 25–28 mm SL, over 70% of the ingested prey were nematodes.

Results of principal components analyses must be interpreted with caution, given the low number of copepods collected by some techniques and the lack of consistency between February and March samples. The determination of the source of the copepod prey of juvenile spot is further complicated by the widespread (across-assemblage) occurrence of two abundant species. *Scottolana canadensis* and *Paronychocamptus wilsoni* were found in each type of meiofaunal collection, indicating that they frequent sediments, the near-bottom water and the water column. There is some indication that there may be demographic group differences in utilization by these species. For example, *S. canadensis* collected in emergence traps were almost entirely copepodites. A preliminary attempt to investigate the various species assemblages at the level of demographic group, however, resulted in essentially the same conclusions as species level analyses.
The high frequency of *Mesochra mexicana* found in the stomach contents of 1 size class of juvenile spot (19-25 mm) is particularly interesting. Because most of these fish were collected at a single site on a single sampling date (March 22), generalization of the results is difficult. Weather conditions prevented the collection of meiofaunal samples on this date. However, settlement-trap samples collected in the same site on March 9 contained high abundances of *M. mexicana*. Furthermore, a large percentage of the *M. mexicana* ingested by spot on March 22 were male (> 75%). Settlement traps on March 9 also collected a high percentage of male *M. mexicana* (> 90%). It seems likely that spot were feeding on a near-bottom harpacticoid assemblage dominated by male *M. mexicana*. There is evidence that male harpacticoid copepods of many species are more prone to emergent behavior than their female counterparts. Bell et al. (1988) found that male harpacticoids of many species were found in greater proportions in the water column than in the sediment. Starry flounder prey heavily on male *Microarthridion littorale*, perhaps due to greater emergence (McCall, 1992).

The dissimilarity of prey of larger juvenile spot (>25 mm SL) collected on March 9 to the sediment assemblage collected on that date is troublesome, but is likely due to the fact that fish were feeding on an infaunal assemblage lower in the intertidal zone than the site at which samples
were collected. Stomach contents contained substantial numbers of *Scottolana canadensis* and *Pseudostenhelia wellsi*, 2 species that are commonly collected in sediment samples but were not present in samples at this site. The characterization of the feeding of spot is further complicated by the likelihood that spot do not restrict their feeding to a particular prey assemblage, but rather feed opportunistically on any available prey of suitable size. Spot in other locales are highly opportunistic (Currin et al. 1984).

The change in prey utilization by juvenile spot from a near-bottom or hyperbenthic assemblage to a sediment-dwelling one likely results from ontogenetic changes in mouth morphology and behavior in combination with behavioral aspects of meiofaunal ecology and temporal changes in assemblage structure. The selection of prey by predators influenced by a number of factors, including hunger (Beukema 1968), prey size (Vince et al. 1976, Gardner 1981, Eggers 1982), prey activity (Moore & Moore 1976) and others. Unfortunately, the role played by predator and prey behaviors has gone relatively unexplored. In small fish feeding on meiofauna in near-bottom waters, the manner in which the behavior of the various meiofauna interacts with the predatory behavior of the fish will likely be one of the ultimate determinants of prey selection.
Feeding by spot in Louisiana differs from that observed on the western Atlantic coast. In Atlantic estuaries, spot utilize the regular semi-diurnal tides to move into extensive, food-rich high intertidal habitats, and the species of harpacticoids ingested typically reflect tidal-zonation patterns (Feller et al. 1990). Spot in northern Gulf of Mexico estuaries face a much less predictable tidal regime. Gulf tides are diurnal rather than semi-diurnal and are microtidal, often overshadowed by changes in water level associated with weather fronts. It seems unlikely that spot in coastal Louisiana would develop feeding patterns tightly tied to tidal conditions. Instead, the relatively constant water levels with which they are confronted would encourage the maximal utilization of the various meiofaunal assemblages available to them.

There has been considerable debate over the degree, if any, to which sediment-feeding spot select one meiofaunal taxon over another. It has been suggested that harpacticoids are selectively ingested over nematodes, based on the results of food habit studies that have found disproportionately high numbers of harpacticoids in the guts of juvenile spot. A number of explanations have been suggested, including differing availability (Gee 1989), differential digestion rates (Scholz et al. 1991) and actual active selection for harpacticoids (Nelson & Coull 1989).
In this study, larger spot were found to prey heavily on both nematodes and harpacticoids. Nematodes, in fact, made up some 80% of total prey items in spot of the largest size class. In the sediments nematodes outnumber harpacticoids by an order of magnitude or more, even in the uppermost 2 mm stratum. Thus, it appears that juvenile spot do ingest harpacticoids in proportionately greater numbers than would be predicted by their sediment abundance. This could be attributable to active selection or to mechanical selection for the more complexly shaped harpacticoids within the bucco-pharyngeal filtering apparatus (Nelson & Coull 1989). An alternative possibility is that the larger spot, in addition to feeding on sediment-dwelling nematodes and harpacticoids, also ingest harpacticoids in the near-bottom waters, thus biasing their stomach contents towards harpacticoids.

These results add to the growing body of evidence that prey resources in the near-bottom water are critical to demersal juvenile fish. A variety of fish, including salmonids (Sibert 1979), starry flounder (McCall 1992) and tonguefish (Toepfer 1992), have been shown to rely heavily on such a prey assemblage. This study indicates that post-larval spot rely on prey that more closely resemble hyperbenthic assemblages than sediment-dwelling ones. Certainly, additional unstudied fish species also use hyperbenthic assemblages. Previous work (e.g. Sogard 1984)
has reported harpacticoids only to major taxon, making it difficult to determine the overall importance of the hyperbenthos. More studies on hyperbenthic meiofauna and more effective ways of sampling this important ecological assemblage are needed to more fully understand the role of the hyperbenthos in the trophic ecology of fishes.
CHAPTER 4

RECOGNITION AND UTILIZATION OF PREY AGGREGATIONS BY JUVENILE SPOT (LEIOSTOMUS XANTHURUS)
INTRODUCTION

The significance of meiofauna in the diet of many post-larval and juvenile fishes has been the subject of intensive study in recent years (see reviews by Gee 1989 and Coull 1990). Meiofauna, particularly harpacticoid copepods, are now recognized as a very important component of the diet of a number of small (<30 mm) benthic-feeding fishes. The behaviors of meiofaunal-feeding fishes and their prey doubtless exert significant influences on these predator-prey relationships, but little is known about the manner in which these behaviors interact. For example, meiofauna are highly variable spatially, typically aggregated at the cm² level (Phillips & Fleeger 1985, Fleeger & Decho 1987, Decho & Fleeger 1988). There is high local variation in densities of estuarine meiofauna in Louisiana (Fleeger 1985). Findlay (1981) found that nematodes were patchy at the 5 cm² scale and that harpacticoid copepods were patchy at scales ranging from 0.5 cm² to 32 cm². Meso-scale (m-km) variation also occurs (Coull et al. 1979, Hogue 1980, Phillips & Fleeger 1985). Patchiness is a consistent phenomenon in prey distribution patterns, and must be significant to predators that rely on this food source. However, no studies have examined the effect of small-scale faunal patchiness on fish behavior.

The extent to which young fishes can distinguish and exploit patches of prey may have an important impact on
their growth and survival, especially when food is limiting (Miller & Dunn 1980). The ability to locate prey patches could be especially significant to fishes feeding on meiofauna which, because of their small size, must be consumed in large numbers to be energetically rewarding.

One fish, the spot (*Leiostomus xanthurus*), is unique in its heavy and prolonged reliance on meiofauna as a food source. Meiofauna have been shown to be an important dietary component in spot as large as 100 mm standard length (SL) (Stickney et al. 1975, Sheridan 1979). Spot in Louisiana rely heavily on meiofauna, primarily nematodes and harpacticoids, at sizes up to at least 60 mm SL (McCall et al. unpubl.). Considerable experimental work has been done on the relationship between spot and its meiofaunal prey (Chao & Musick 1977, Smith & Coull 1987, Ellis & Coull 1989, Nelson & Coull 1989, Archambault & Feller 1991, Scholz et al. 1991). At sizes > 30 mm SL, spot feed by taking mouthfuls of sediment and manipulating it within the buccal cavity, sieving prey organisms with gill rakers and pharyngeal teeth (Billheimer & Coull 1988). The uningested sediment is expelled through the gill openings and the mouth.

In this paper we report the results of 2 experiments designed to test the ability of juvenile spot to locate and utilize meiofaunal aggregations. We examined 2 questions concerning patch utilization by juvenile spot: 1) Do spot
forage disproportionately in high-density aggregations and, 2) Do they exhibit increased processing time of strikes taken from aggregations? In addition, we examined whether juvenile spot prey selectively on one component of the meiofauna.

METHODS

Juvenile spot, 39-58 mm SL, were collected by seining in the shallow subtidal zone of Bay Champagne, near Port Fourchon, Louisiana, in the spring of 1989 and 1990. The fish were held in the laboratory in 40 l aquaria containing artificial seawater (25%) for approximately 7 days, and were periodically allowed to feed on meiofauna-containing sediments from the collection site. Weak or abnormal individuals were excluded from experiments.

Meiofauna were collected by scraping the upper centimeter of sediment from an intertidal mudflat near Port Fourchon, Louisiana. The sediment was rinsed through 250 and 125 μm sieves and the portion retained on the sieves was placed in seawater and returned to our laboratory in Baton Rouge. Meiofauna were extracted by sucrose flotation (Heip et al. 1974) and the resulting concentrated collection of meiofauna was retained for choice experiments.

Azoic sediment was prepared through the method of Chandler (1986), which creates a well-sorted sediment with
a flocculent surface layer similar to the natural sediment. Azoic sediment was added to plastic petri dishes (100 x 15 mm) to a depth of approximately 1 cm. Artificial seawater (25%) was added, and the mixture was stirred and allowed to settle. After approximately 2 h, the overlying water was aspirated off to remove any unsettled clay particles. Artificial seawater was added and the trays were placed under refrigeration until use.

Eight sediment trays were placed in 20 l aquaria in 2 rows of 4 (Fig. 4.1). Care was taken to minimize loss of sediment. Trays were left undisturbed for 30 min to allow the sediment to resettle before meiofauna was added (see below).

Living meiofauna were used to prepare sediment trays with different prey densities. Concentrated meiofauna was aliquoted into progressively more dilute subsamples using a sample-splitter (Jensen 1982). Aliquots were produced to create approximate densities in trays of:

1) Control = 0 meiofauna.
2) Low = 0.25X (where X approximates a standard field density)
3) Intermediate = 1X
4) High = 4X

In each year, eight randomly selected low-density aliquots of meiofauna were fixed with 10% buffered formalin and stained with rose bengal for the estimation of actual
Fig. 4.1. Location of sediment trays used in choice experiments. Densities were randomized within each row for each replicate.
densities. Randomly selected intermediate and high density aliquots were also counted to provide a check on the effectiveness of the sample-splitter. The basic aliquot corresponded to a low-density treatment. Four basic aliquots corresponded to an intermediate density, while 16 comprised high density treatments.

Because aliquots of meiofauna also contained detritus, azoic detritus was added to sediment trays to equalize detrital amounts. The detritus was created by removing detrital material collected in the pre-sieving of the meiofaunal collections. This material was then dried, washed thoroughly and fractionated in a blender to achieve a consistency approximating natural detritus. Detritus was added to each density treatment as follows:

1) 10 ml detritus added to control
2) 7 ml added to intermediate
3) 3 ml added to low density
4) no addition to high density

To control for any influence of sucrose from extractions, azoic detrital supplements were soaked in a sucrose solution for 5 min and washed prior to their inclusion in sediment trays.

Meiofauna and detritus were added to sediment trays by pouring the aliquots slowly through plastic tubes that extended above the water-air interface but were pressed down onto the sediment trays. Each density treatment
appeared twice (once in each row) in each aquarium. Placement of density treatments within rows was random. Tubes were left in place for 15 min minutes to allow meiofauna to enter sediments. Some meiofauna were observed in the tubes after this time, but the number of swimming meiofauna observed was a small percentage of the total addition. After the settlement period, tubes were removed from the aquaria.

Spot, starved for 24 h, were placed in the aquaria and allowed to feed for a maximum of 30 min, timed from the first feeding activity. Aquaria were enclosed on three sides and lighted from above. One side was left open to allow videotaping for later analysis. If an individual fish did not begin feeding within 20 min, the trial was aborted.

After the feeding trial, all fish were sacrificed for stomach content analysis and preserved in 10% formalin. At a later date, the entire digestive tract was removed and its contents identified. Taxon composition of the stomach contents was then compared to meiofaunal aliquots to determine the degree of selectivity in the feeding of spot.

Videotapes from the two experiments were viewed and the number of feeding strikes in the various trays recorded. A feeding strike was defined as an effort by the fish to take sediment into its buccal cavity followed by a period of manipulation and, finally, the expulsion of the
sediment. Analysis of videotapes at slow motion allowed precise determination of the location of the feeding strike and the processing time. On numerous occasions, fish were observed to take a number of small bites from a tray before manipulating it. This was treated as 1 feeding strike. Fish occasionally struck at the aquaria bottoms outside of feeding trays, but only feeding strikes in sediment trays were considered.

The location and sequence of feeding strikes were recorded. Two fish (of 10 total) in the 1989 experiment and three (of 16) in 1990 did not feed and were excluded from the experiment. On several occasions, feeding activity was so vigorous that water cloudiness prevented the observation of feeding behavior. For these replicates, only those feeding strikes up to this point are included in the analysis.

Three questions were addressed in the analysis of the experiments:

1) Do spot feed disproportionately in trays with higher densities of meiofauna?

Analysis of selection in feeding experiments of this type can be problematical due to the lack of independence of the feeding choices (Peterson & Renaud 1989). Furthermore, in experiments in which an animal is observed over a period of time and its habitat or feeding choices recorded, there is a lack of independence between
observations (Swihart & Slade 1985), i.e. the location (or choice) of the animal at time \( t+1 \) is dependent on its location at time \( t \). In these experiments, although individual feeding strikes are not independent, the relatively long period over which fish were observed (30 min) coupled with the small total area available to them assured that all feeding areas were equally accessible and that the relative proportions of feeding strikes was a reasonably unbiased indicator of feeding area preference. The question of patch selection was addressed in a highly conservative manner, treating each fish as a single observation and examining the percentage of strikes in various prey densities as compositional data, applying multivariate analysis of variance (MANOVA) to analyze the vector of log-transformed ratios of percentages (Aitchison 1982, 1984).

A nonparametric analysis was also employed to explore patch selection by spot. We utilized a \( \chi^2 \) goodness-of-fit test to compare the distribution of first strikes for each fish to that predicted by a random-feeding model (i.e. equal probability of first strike in any of the 4 density treatments). For this analysis, the results from the 2 years were combined. We performed a similar analysis on the distribution of the area of highest frequency of strikes, again combining the results from 1989 and 1990.
To determine whether juvenile spot showed a change in their patch utilization over time, relative density values were assigned to strikes in areas of different densities. A relative value of 0 was assigned to strikes in control areas, 0.25 for low density areas, 1 for intermediate areas and a value of 4 for strikes taken from high density areas. These values reflect the relative densities of meiofauna assigned to each density treatment. The mean relative density was then calculated, for all fish, for the first ten feeding strikes (1-10), the next ten (11-20), etc., up to feeding strikes 121-130. This allowed an examination of the pattern of patch choice demonstrated by feeding fish as they gained experience.

Finally, the probability of repeat strikes as a function of density was examined to ascertain if recent feeding success influenced the tendency of a fish to make repetitive feeding strikes in an area. To eliminate the effect of lengthy runs in one area, we observed only those strikes that were not themselves repeat strikes, and determined the probability that they were followed by a strike in the same area.

In addition to questions regarding the choice of feeding patches, the manner in which feeding strikes were processed was examined and related to the prey density of the feeding area. This allowed the investigation of a separate but related question:
2) Are all feeding strikes processed equally, or is processing time related to prey density?

Observations made during the 1989 experiment led to the evaluation of an additional question in 1990. We noted that fish seemed to process strikes from some areas for much longer periods of time than others, suggesting that fish might sense when a strike had been relatively successful and invest more time in extracting prey. In the 1990 experiment, observations were made on the processing time of strikes with the goal of testing the null hypothesis that all feeding strikes are processed equally. This was tested using analysis of variance of the processing time of randomly selected strikes (since processing time followed a log-normal distribution, analysis was done on the log of processing time), with preplanned contrasts designed to compare specific levels.

3) Do spot prey selectively on components of the meiofauna?

Stomach contents of the juvenile spot were compared to the meiofaunal aliquots to assess the degree of prey selection. We tested the null hypothesis that ingested prey proportions did not differ from proportions in the meiofaunal aliquots using MANOVA of the log-ratio transformed proportions.
RESULTS

Density estimates of meiofauna added to feeding patches (sediment trays) were compared to representative field densities of sediments of the type in which spot feed in the field (Table 4.1). Our experimental meiofaunal densities appear to effectively bracket typical field densities. In each experiment, meiofauna was dominated by nematodes and harpacticoids, which together made up over 98% of total meiofauna. Nematodes comprised 91% of all meiofauna in 1989 and 80% in 1990. Because of the numerical and taxonomic variability between the 2 years, results were analyzed separately unless otherwise noted.

Patch choice: Juvenile spot took substantially more feeding strikes in the highest-density treatments than in other areas (Fig. 4.2). The mean number of strikes increased with the density of meiofauna. Spot took an average of approximately 120 feeding strikes in the 1989 experiment, of which almost 40% were in highest density aggregations, and approximately the same number of strikes in 1990, with some 45% from high density areas.

An initial MANOVA indicated that the vector of log-ratio-transformed proportions did not differ significantly between years ($F = 0.5343, P > F = 0.6650$), so the results of the 2 years were combined for analysis of treatment effects. MANOVA indicated that the log-ratio-transformed proportions of feeding strikes differed among treatments
Table 4.1. Densities (number per 10 cm²) of meiofaunal treatments in the two experiments (n = 8). Actual counts were done on low density treatments; mean of other treatments are estimated from them. Standard error of low-density treatments are presented. Included are representative field densities from the literature. Inter = intermediate density treatment, Nema = nematodes, Harp = harpacticoid copepods.

<table>
<thead>
<tr>
<th>Treatment - Year</th>
<th>Total</th>
<th>Nema</th>
<th>Harp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low - 1990</td>
<td>138 ± 10.7</td>
<td>110 ± 8.5</td>
<td>27 ± 2.3</td>
</tr>
<tr>
<td>Low - 1989</td>
<td>212 ± 12.6</td>
<td>192 ± 11.9</td>
<td>17 ± 1.4</td>
</tr>
<tr>
<td>Inter - 1990</td>
<td>552</td>
<td>440</td>
<td>108</td>
</tr>
<tr>
<td>Inter - 1989</td>
<td>848</td>
<td>768</td>
<td>68</td>
</tr>
<tr>
<td>High - 1990</td>
<td>2208</td>
<td>1760</td>
<td>432</td>
</tr>
<tr>
<td>High - 1989</td>
<td>3392</td>
<td>3072</td>
<td>272</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Source</th>
<th>Total</th>
<th>Nema</th>
<th>Harp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fleeger (1985) Louisiana intertidal marsh</td>
<td>590</td>
<td>490</td>
<td>80</td>
</tr>
<tr>
<td>Coull (1985) South Carolina intertidal mud</td>
<td>1247</td>
<td>856</td>
<td>102</td>
</tr>
<tr>
<td>Phillips and Fleeger (1985) Louisiana intertidal mudflat</td>
<td>1900</td>
<td>1700</td>
<td>200</td>
</tr>
<tr>
<td>Fleeger (1985) Louisiana subtidal mud</td>
<td>2310</td>
<td>2250</td>
<td>50</td>
</tr>
</tbody>
</table>
Fig. 4.2. Mean and one standard error of number of feeding strikes in thirty minutes taken from areas of different meiofaunal densities for (a) 8 fish in 1989 and (b) 13 fish in 1990.
Univariate tests and simultaneous $T^2$ 95% confidence intervals showed that $ln$(high/control) and $ln$(intermediate/control) differed significantly from 0, while $ln$(low/control) did not, indicating that high and intermediate density areas received significantly more feeding strikes than would be predicted from a random feeding model. Highest density treatments received a significantly higher proportion of feeding strikes (Table 4.2).

Analysis of feeding patch utilization by goodness-of-fit tests revealed that the initial feeding strikes did not differ significantly from random (Table 4.3), but the distribution of the highest frequency of strikes did (Table 4.4). In fact, of the 21 fish utilized in the 2 experiments, 16 took the greatest number of feeding strikes in high density areas.

**Change in feeding pattern over time:**

Fish increasingly concentrated their feeding in areas of higher meiofaunal density over the course of a trial. Mean relative concentration of the feeding area increased over time, although the pattern was erratic (Fig. 4.3). Feeding early in the experiment did not differ substantially from that predicted under a random feeding model. Late in the experiments, however, most fish focussed their feeding activity on high density areas.
Table 4.2. Mean and standard error of log-ratios of proportions of strikes taken in areas of different meiofaunal density. Results of univariate t-tests for equality to 0 are also indicated. MANOVA results for test of the null hypothesis of no difference between treatments are also given.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mean</th>
<th>S.E.</th>
<th>t</th>
<th>P &gt; t</th>
</tr>
</thead>
<tbody>
<tr>
<td>ln (high/contr)</td>
<td>1.145</td>
<td>0.221</td>
<td>5.176</td>
<td>0.0001</td>
</tr>
<tr>
<td>ln (inter/contr)</td>
<td>0.625</td>
<td>0.178</td>
<td>3.512</td>
<td>0.0022</td>
</tr>
<tr>
<td>ln (low/contr)</td>
<td>0.276</td>
<td>0.228</td>
<td>1.210</td>
<td>0.2404</td>
</tr>
</tbody>
</table>

MANOVA results: $F = 22.182$, $P > F = 0.0001$
Table 4.3. Distribution of first strikes. The number of fish taking their initial feeding strike in areas of each prey density are presented by year, and for the total of the two years. Expected numbers are given parenthetically for total.

<table>
<thead>
<tr>
<th></th>
<th>1989</th>
<th>1990</th>
<th>Total</th>
<th>(\chi^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Low</td>
<td>3</td>
<td>3</td>
<td>6</td>
<td>0.165</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(5.25)</td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>2</td>
<td>4</td>
<td>6</td>
<td>0.165</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(5.25)</td>
<td></td>
</tr>
<tr>
<td>Intermed</td>
<td>1</td>
<td>2</td>
<td>3</td>
<td>1.136</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(5.25)</td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>2</td>
<td>4</td>
<td>6</td>
<td>0.102</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(5.25)</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>8</td>
<td>13</td>
<td>21</td>
<td>1.592</td>
</tr>
</tbody>
</table>

Degrees of freedom = 3

\(P = 0.661\)

Table 4.4. Distribution of highest frequency of strikes. Number of fish taking the greatest number of strikes in areas of each prey density are presented by year, and for the total of the two years. Expected numbers are presented parenthetically for total.

<table>
<thead>
<tr>
<th></th>
<th>1989</th>
<th>1990</th>
<th>Total</th>
<th>(\chi^2)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>3.440</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(5.25)</td>
<td></td>
</tr>
<tr>
<td>Low</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>5.250</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(5.25)</td>
<td></td>
</tr>
<tr>
<td>Intermed</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td>0.298</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(5.25)</td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>6</td>
<td>10</td>
<td>16</td>
<td>22.012</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>(5.25)</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>8</td>
<td>13</td>
<td>21</td>
<td>31.000</td>
</tr>
</tbody>
</table>

Degrees of freedom = 3

\(P < 0.001\)
Fig. 4.3. Mean relative density of feeding area for intervals of 10 feeding strikes (1-10, 11-20, ..., 131-140) for 21 fish combined over both experiments. Error bars represent one standard error.
Observation of the feeding fish indicated that the recognition of areas containing high densities of prey occurred only after a successful feeding strike was made. Fish did not move immediately to high density prey patches. Feeding strikes appeared random until high density areas were located, after which most effort was usually focused on those areas. Spot did not feed exclusively in areas of high concentration, even after those areas have been located. Individuals sampled surrounding areas, even while focussing their of feeding effort in high density areas.

Effect of prior feeding on patch choice:

There was also a relationship between the feeding activity following a strike and the prey density of the patch from which the strike was taken. The probability of repeat strikes was higher in high density trays than in those containing lower concentrations of meiofauna (Table 4.5). This tendency was more pronounced in the 1989 experiments than in 1990, perhaps due to the higher absolute prey densities utilized in 1989.

Processing time:

Fish spent a greater time processing strikes from high density food areas. Processing times were determined for 630 feeding strikes made by 9 fish during the 1990 experiment. The mean processing time for feeding strikes taken in high density feeding areas was 6.27 sec, that from intermediate densities 2.37 sec, while processing times for
Table 4.5. Probability of repeat strikes in an area as a function of the meiofaunal density of the area. Results are presented for eight fish in 1989, thirteen fish in 1990 and for the combined total of the two experiments. Number of strikes evaluated for each is presented parenthetically.

<table>
<thead>
<tr>
<th></th>
<th>1989</th>
<th>1990</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control</td>
<td>0.18 (120)</td>
<td>0.48 (127)</td>
<td>0.33 (247)</td>
</tr>
<tr>
<td>Low</td>
<td>0.17 (151)</td>
<td>0.36 (168)</td>
<td>0.27 (319)</td>
</tr>
<tr>
<td>Intermediate</td>
<td>0.29 (173)</td>
<td>0.52 (165)</td>
<td>0.40 (338)</td>
</tr>
<tr>
<td>High</td>
<td>0.36 (217)</td>
<td>0.58 (244)</td>
<td>0.48 (461)</td>
</tr>
</tbody>
</table>
strikes from low and control densities were about 1.25 sec. Comparison of processing times through analysis of variance using a randomized block design indicated that there was a highly significant effect of prey density on the log of processing time ($F = 25.79$, $P > F = 0.0001$). The significant interaction between fish and density (Table 4.6) was investigated, and involved primarily processing times in control and low densities. Duncan's multiple range test indicated that processing times for high density areas were significantly longer than those for all other densities, and those for strikes in intermediate densities are significantly higher than for low and control densities. Processing times did not differ significantly between control and low density treatments.

**Selectivity:**

Comparison of ingested prey to meiofaunal additions indicates that the two assemblages were relatively similar (Fig. 4.4). Meiofaunal aliquots used in the 1989 experiment were comprised of approximately 91% nematodes and 8% harpacticoids, while juvenile spot ingested the 2 prey in proportions of 85% and 14%, respectively. In 1990, the additions were comprised of 80% nematodes and 20% harpacticoids, while the fish consumed 77% nematodes and 23% harpacticoids. Stomach content analyses show that, in all fish, nematodes were the most abundant prey (Table 4.7). However, MANOVA comparisons of ingested meiofaunal
Table 4.6. ANOVA results for analysis of processing time of spot feeding strikes. Also presented are geometric means (and 95% confidence intervals) of processing time for feeding strikes from different densities. Means differing significantly by Duncan’s multiple range test are indicated by having different letters.

<table>
<thead>
<tr>
<th>Effect</th>
<th>df</th>
<th>MS</th>
<th>F</th>
<th>P &gt; F</th>
</tr>
</thead>
<tbody>
<tr>
<td>Density</td>
<td>3</td>
<td>52.64</td>
<td>27.75</td>
<td>0.0001</td>
</tr>
<tr>
<td>Fish</td>
<td>8</td>
<td>7.31</td>
<td>3.85</td>
<td>0.0001</td>
</tr>
<tr>
<td>Fish*Dens</td>
<td>27</td>
<td>1.90</td>
<td>4.05</td>
<td>0.0001</td>
</tr>
<tr>
<td>Error</td>
<td>591</td>
<td>0.4685</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Geometric Mean</th>
<th>95% C.I.</th>
</tr>
</thead>
<tbody>
<tr>
<td>High</td>
<td>4.97</td>
<td>4.56 - 5.42</td>
</tr>
<tr>
<td>Inter</td>
<td>1.64</td>
<td>1.44 - 1.87</td>
</tr>
<tr>
<td>Low</td>
<td>0.95</td>
<td>0.82 - 1.10</td>
</tr>
<tr>
<td>Control</td>
<td>0.94</td>
<td>0.81 - 1.11</td>
</tr>
</tbody>
</table>
Fig. 4.4. Comparison of taxa of ingested prey to that present in sediment additions in (a) 1989 and (b) 1990. Nema = nematodes, Harp = harpacticoid copepods.
Table 4.7. Summary of stomach contents of eight fish in the 1989 experiment. Nema = nematodes, Harp = harpacticoid copepods.

<table>
<thead>
<tr>
<th>Standard length</th>
<th>Nema (%)</th>
<th>Harp (%)</th>
<th>Other (%)</th>
<th>Total (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>40</td>
<td>128 (92.1)</td>
<td>8 (5.8)</td>
<td>3 (2.1)</td>
<td>139</td>
</tr>
<tr>
<td>42</td>
<td>189 (87.9)</td>
<td>24 (11.2)</td>
<td>2 (0.9)</td>
<td>215</td>
</tr>
<tr>
<td>41</td>
<td>139 (76.8)</td>
<td>41 (22.7)</td>
<td>1 (0.5)</td>
<td>181</td>
</tr>
<tr>
<td>43</td>
<td>48 (71.6)</td>
<td>19 (28.4)</td>
<td>0</td>
<td>67</td>
</tr>
<tr>
<td>53</td>
<td>148 (89.7)</td>
<td>17 (10.3)</td>
<td>0</td>
<td>165</td>
</tr>
<tr>
<td>40</td>
<td>437 (83.6)</td>
<td>85 (16.3)</td>
<td>1 (0.1)</td>
<td>523</td>
</tr>
<tr>
<td>41</td>
<td>151 (88.8)</td>
<td>19 (11.2)</td>
<td>0</td>
<td>170</td>
</tr>
<tr>
<td>58</td>
<td>64 (84.2)</td>
<td>7 (9.2)</td>
<td>5 (6.6)</td>
<td>76</td>
</tr>
<tr>
<td>TOTALS</td>
<td>1304 (84.9)</td>
<td>220 (14.3)</td>
<td>12 (0.8)</td>
<td>1536</td>
</tr>
</tbody>
</table>
Table 4.7 (cont.). Summary of stomach contents of thirteen fish in the 1990 experiment.

<table>
<thead>
<tr>
<th>Standard length</th>
<th>Nematodes (%)</th>
<th>Harp (%)</th>
<th>Other (%)</th>
<th>Total (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>40</td>
<td>53 (85.5)</td>
<td>9 (14.5)</td>
<td>0</td>
<td>62</td>
</tr>
<tr>
<td>45</td>
<td>92 (82.9)</td>
<td>19 (17.1)</td>
<td>0</td>
<td>111</td>
</tr>
<tr>
<td>40</td>
<td>72 (81.8)</td>
<td>16 (18.2)</td>
<td>0</td>
<td>88</td>
</tr>
<tr>
<td>39</td>
<td>291 (85.6)</td>
<td>48 (14.1)</td>
<td>1 (0.3)</td>
<td>340</td>
</tr>
<tr>
<td>44</td>
<td>300 (84.0)</td>
<td>54 (15.1)</td>
<td>3 (0.9)</td>
<td>357</td>
</tr>
<tr>
<td>40</td>
<td>172 (76.8)</td>
<td>50 (22.3)</td>
<td>2 (0.9)</td>
<td>224</td>
</tr>
<tr>
<td>38</td>
<td>42 (65.6)</td>
<td>21 (32.8)</td>
<td>1 (1.6)</td>
<td>64</td>
</tr>
<tr>
<td>37</td>
<td>96 (67.1)</td>
<td>47 (32.9)</td>
<td>0</td>
<td>143</td>
</tr>
<tr>
<td>36</td>
<td>139 (67.8)</td>
<td>66 (32.2)</td>
<td>0</td>
<td>205</td>
</tr>
<tr>
<td>48</td>
<td>213 (72.7)</td>
<td>80 (27.3)</td>
<td>0</td>
<td>293</td>
</tr>
<tr>
<td>37</td>
<td>31 (83.8)</td>
<td>6 (16.2)</td>
<td>0</td>
<td>37</td>
</tr>
<tr>
<td>44</td>
<td>232 (72.5)</td>
<td>87 (27.2)</td>
<td>1 (0.3)</td>
<td>320</td>
</tr>
<tr>
<td>39</td>
<td>308 (72.3)</td>
<td>116 (27.2)</td>
<td>2 (0.5)</td>
<td>426</td>
</tr>
<tr>
<td>TOTALS</td>
<td>2041 (76.4)</td>
<td>619 (23.2)</td>
<td>10 (0.4)</td>
<td>2670</td>
</tr>
</tbody>
</table>
proportions to those in the meiofaunal additions indicated that the proportions were significantly different ($F = 3.375, P > F = 0.047$). Univariate tests indicated that $\ln(\text{percentage nematodes/percentage harpacticoids})$ differed significantly between stomach contents and sediments, with stomachs containing a higher percentage of harpacticoids.

**DISCUSSION**

Juvenile spot are capable of effectively recognizing and utilizing high density patches of their meiofaunal prey. This ability was expressed in an increased probability of feeding in high density areas, a tendency to increasingly utilize high density areas over time and a greater tendency to strike repetitively in high density aggregations. Location of profitable feeding areas was apparently accomplished by first randomly sampling the sediments, then concentrating in areas of highest prey abundance. Even after locating high-density feeding areas, however, spot continued to sample surrounding sediments. Optimal foraging theory predicts that a predator must periodically sample to make optimum use of a patchy environment (Townsend & Winfield 1985). The environment is constantly changing, and the forager must sample to keep its perception from becoming obsolete.

Furthermore, juvenile spot processed feeding strikes in a manner dependent on the prey density of the area from
which the strike was taken. Strikes taken from control or low density areas were quickly expelled, while relatively more profitable strikes were manipulated within the buccal cavity for a much longer time, presumably allowing more efficient removal of meiofauna. This is in keeping with the idea that the fish senses when it has made a highly successful feeding strike. There may be a tradeoff between the value of increased processing time of a successful strike and that of taking more strikes in a profitable area. The manner in which the fish balances the relative benefits of the two behaviors remains to be investigated.

Juvenile spot are heavily reliant on meiofauna at relatively large sizes, beyond the size at which most other fishes shift to larger prey organisms. Prolonged utilization of meiofauna implies that spot is able to delay the point in development at which a diet of small prey no longer meets metabolic and growth requirements. This could be accomplished in several fashions:

1) If spot had lower energetic requirements than other, similarly-sized fishes, a meiofaunal diet might be adequate. Spot is an active fish and shows oxygen consumption rates similar to those of the Atlantic croaker (*Micropogonias undulatus*) and the pinfish (*Lagodon rhomboides*) (Kjelson & Johnson 1976, Moser & Gerry 1989).

2) It has been suggested that harpacticoid copepods may be assimilated more efficiently than other prey types (Volk et
al. 1984). Insufficient research has been done to provide rigorous answers, and it is questionable that this factor alone enables spot to persist on a meiofaunal diet.  

3) Relatively continuous feeding on meiofauna, as opposed to periodic feeding bouts by fish feeding on larger prey, could increase the daily ration of meiofauna and allow spot to subsist on this diet at larger sizes (Archambault & Feller 1991).  

4) Our work suggests that efficient utilization of time spent feeding may also contribute to prolonged utilization of meiofauna by spot. By concentrating feeding in areas which are higher in prey density, the fish can increase energy gained per unit time spent foraging. As a result, meiofaunal feeding would be more profitable than might be indicated by the average density of prey in the habitat as a whole.  

In addition, spot's apparently more thorough processing of strikes from high density areas may provide an additional means of most effectively utilizing the time spent foraging. A trade-off may well exist between processing time and search time. Juvenile spot must balance the potential gains of greater processing time with that of taking more feeding strikes within a given time period.  

Spot in the field are group foragers, typically feeding in large schools (Weinstein 1983). It is likely
that this further heightens the efficiency of feeding, since it has been demonstrated that fish foraging in groups are better able to locate prey patches (Pitcher et al. 1982).

The ability of juvenile spot to feed disproportionately in areas of higher meiofaunal density may be significant to meiofaunal patch dynamics as well. Although the existence of patchiness in meiofaunal distribution is well documented, the longevity of such patches is relatively unknown (Sun & Fleeger 1991). It is possible that large schools of a predator such as spot, able to recognize and feed selectively on dense aggregations of meiofauna, could greatly impact patch longevity. Such feeding may also impact disturbance-mediated dispersal (Palmer 1988b). While most researchers have concluded that meiofaunal communities are not greatly affected by fish predation (Alheit & Scheibel 1982, de Morais & Bodioiu 1984, Gee 1987), large schools of a relatively large predator such as spot which are able to identify and exploit high density prey aggregations could certainly have a significant, albeit seasonal, effect on spatial variability of the meiofaunal community.

There has been considerable attention devoted recently to the apparently selective nature of spot predation on the meiobenthos. Coull and coworkers have argued that spot feed selectively on harpacticoid copepods over nematodes
(Coull 1990). Scholz et al. (1991) suggests that the apparent selection for harpacticoids may result from more rapid digestion of nematodes, resulting in a bias toward harpacticoid copepods in stomach content analyses. Gee (1989) argues that the apparent selection may result in many cases from differential availability of prey resulting from microhabitat considerations (i.e. nematodes are typically found deeper in the sediment than harpacticoids).

Although the experimental situation utilized here is admittedly artificial, it does have some advantages with regard to the evaluation of feeding selectivity. The counting of replicate samples of meiofaunal aliquots provides information on the exact composition of the prey assemblage. Fish were allowed to feed for only 30 min and preserved immediately thereafter, greatly reducing the potential for bias from differential prey digestion rates. A video record of each feeding incident was available. Finally, the method of addition and the relatively shallow sediment layer should result in essentially equal availabilities of prey types which might otherwise segregate vertically in deeper substrates. This work provided evidence of slight but significant selective predation on harpacticoids over other meiofaunal components. We could not determine, however, whether this selection resulted from active selection on the part of the fish, mechanical selection within the buccopharyngeal
apparatus or was the result of differential availability within the sediments. Differential digestive rates for nematodes and harpacticoids, as suggested by Scholz et al. (1991), cannot explain the difference found in our study.

Juvenile spot in the field encounter small- and meso-scale variability in meiofaunal densities. Great variation in prey density and species composition is found within and between intertidal and subtidal habitats, and meiofauna in saltmarsh estuaries show high variation in densities at the cm² level. The ability of spot to recognize this variability and take advantage of it to increase their feeding efficiency is potentially a highly significant adaptation to the utilization of estuarine habitats as nursery grounds.
CHAPTER 5

SUMMARY AND CONCLUSIONS
The significance of meiofauna, particularly harpacticoid copepods, in the trophic ecology of post-larval and juvenile teleosts is no longer in question. It is apparent that many species of fish rely heavily, often exclusively on this prey resource for a short, but critical period of their existence.

There has been, however, a tendency to treat meiofaunal prey as passive particles to be gathered by foraging fish. Investigators have sampled meiofauna in sediment cores, examined fish stomach contents, and assumed that in the intersection of the two lay all that was to be known about predator-prey interactions. My research shows that this is not the case. Meiofauna exhibit a wide range of behaviors and occupy a variety of microhabitats. Predator-prey interactions between fish and meiofauna are subject to the same complexities as those involving larger organisms. The interaction of the predators feeding strategy and the activity patterns of its meiofaunal prey are quite significant in determining prey choice.

In Chapter 2, I found that juvenile starry flounder fed disproportionately on the harpacticoid copepod *Microarthridion littorale*, particularly on males of this species. *M. littorale* was not significantly more surficial in distribution than other, more abundant harpacticoids. Neither was it significantly larger. Collections from emergence and settlement traps suggested that the selective
predation shown by starry flounder may be related to emergent behavior on the part of the harpacticoid prey, with heavy predation on animals entering the water column, either actively or by erosion.

Similarly, post-larval spot fed on a copepod assemblage that most nearly resembled that collected in settlement traps suggesting that they, too, relied heavily on hyperbenthic or demersal meiofauna (Chapter 3). At larger sizes, spot shifted to predation on a sediment assemblage, coinciding with the onset of a sediment-biting mode of feeding at standard lengths around 25 mm.

It is probable that the lack of agreement many researchers have found between the species of meiofauna ingested by juvenile fish and the commonly sampled sediment-dwelling meiofauna is due to the fact that many fish do not, in fact, feed on meiofauna in the sediment but, rather, on meiofauna in the near-bottom waters. This assemblage may or may not bear close resemblance to that in the sediment. There may well be considerable overlap, as was found in Bay Champagne, Louisiana, where the harpacticoids Paronychocamptus wilsoni and Scottolana canadensis span a wide range of microhabitats. On the other hand, there may be striking differences, either at the major taxon, species or demographic level.

Another manner in which predator and prey behaviors may interact is in the formation (by meiofauna) and the
recognition (by predators of meiofauna) of aggregations. Juvenile spot showed a pronounced ability to recognize and selectively utilize high density aggregations of meiofauna (Chapter 4). These aggregations, which may be the result of passive or active processes, are an important and widespread element of meiofaunal ecology. The fact that juvenile teleosts can take advantage of this dispersion pattern may be very significant, not only in the trophic ecology of the fish but also in the patch dynamics of meiofauna.

Juvenile spot also processed feeding strikes in a manner dependent on the density of the meiofaunal patch from which the strike was taken. This represents an additional means by which the fish can increase its energy gain while foraging and provides insight into the means by which spot is able to subsist on a meiofaunal diet at relatively large sizes.

Meiofauna are an important prey for many species of juvenile fish. It is now time to take the logical next step and begin to more fully investigate the manner in which this significant prey resource is utilized.
REFERENCES


VITA

John Nathan McCall was born in Century, Florida on July 24, 1952. He attended Jay High School in Jay, FL, and graduated in 1970. He attended Pensacola Junior College in Pensacola, Florida from 1970 until 1972, when he graduated with an A.A. degree. He then attended the University of West Florida, also in Pensacola, and received a B.S. in Biology in 1974.

In 1975, Mr. McCall joined the faculty of Jay High School, where he remained until 1987, teaching biology, chemistry and earth science. From 1982-1987, John was the chairperson of the Science Department. He served as the head boys track coach from 1982-1987, the head cross country coach from 1984-1987 and was an assistant basketball coach from 1978-1987.

In 1978, he married Karen Diamond, also of Jay, Florida. Their first child, Jessica, was born in 1982. A second daughter, Molly, was born in 1985.

In 1987, Mr. McCall was admitted to the Ph.D. program in Zoology at Louisiana State University in Baton Rouge, Louisiana. He was also admitted to a Master’s degree program in Experimental Statistics in 1989. He will receive the Master of Applied Statistics degree in Experimental Statistics in August of 1992, and is a candidate for the Ph.D. degree in Zoology.
DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: John Nathan McCall

Major Field: Zoology

Title of Dissertation: BEHAVIORAL INFLUENCES ON PREDATOR-PREY INTERACTIONS BETWEEN JUVENILE TELEOSTS AND MEIOFAUNA

Approved:

[Signatures]

Major Professor and Chairman

Dean of the Graduate School

EXAMINING COMMITTEE:

[Signatures]

Date of Examination: July 28, 1992