PREDATION BY JUVENILE FISH ON HYPERBENTHIC MEIOFAUNA : A REVIEW WITH DATA ON POST-LARVAL LEIOSTOMUS XANTHURUS

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PREDATION BY JUVENILE FISH ON HYPERBENTHIC MEIOFAUNA : A REVIEW WITH DATA ON POST-LARVAL *LEIOSTOMUS XANTHURUS*

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MEIOFAUNA
HYPERBENTHOS
FISH
PREDATION

ABSTRACT – In recent years, the significance of meiofauna, notably harpacticoid copepods, in the diet of many species of post-larval and juvenile fish has been increasingly recognized. In many cases, however, much uncertainty remains regarding the manner in which these meiofaunal prey are utilized. Often, ingested meiofauna differ from those present in the sediment at the level of major taxon, species or demographic composition. An investigation of the life-styles demonstrated by meiofauna can aid in understanding these patterns of apparent selectivity. Of particular importance may be the tendency of many meiofaunal organisms to emerge, actively or passively, from sediments during immersion. In a number of cases, ingested meiofauna bear closer resemblance to near-bottom water-column assemblages than to sediment-dwelling ones. An example is presented for post-larval spot (*Leiostomus xanthurus*) in coastal Louisiana. Copepod prey of four size classes of spot (16 mm, 16-26 mm, 26-30 mm, 30-35 mm standard length) were compared to assemblages collected by various methods. Collections included sediment cores, settlement traps that collect water-column animals settling to (or moving along) the sediment surface, emergence traps that sample organisms moving away from the sediment surface at heights of approximately 7 cm and phytal samples (plant surfaces). Principal components analysis demonstrated that, as spot grew in size, their prey changed from an assemblage most closely resembling that found in settlement traps to one closely resembling a sediment assemblage. Additional study is needed to better understand the dynamics of hyperbenthic meiofauna and the manner in which this prey resource is utilized by fish and other predators.

MÉIOFAUNE
HYPERBENTHOS
POISSONS
PRÉDATION

RÉSUMÉ – L'importance de la méiofaune, notamment des Copépodes Harpacticoïdes, dans le régime alimentaire de nombreuses espèces de Poissons juvéniles est de plus en plus reconnue. Cependant, il persiste la plupart du temps, beaucoup d'incertitude en ce qui concerne la manière dont ces proies méiobenthiques sont utilisées. La méiofaune ingérée diffère souvent de celle qui se trouve dans le sédiment aux niveaux des taxons majeurs, des espèces ou de la composition démographique. Des recherches à propos des modes de vies concernant la méiofaune peuvent permettre de comprendre ces types de sélection apparente. La tendance de nombreux organismes de la méiofaune à émerger des sédiments de façon active ou passive pendant l'émersion semble d'une importance particulière. Dans certains cas, la méiofaune ingérée montre une ressemblance plus grande avec la structure faunistique la colonne d'eau qu'avec celle du sédiment. Nous présentons l'exemple de stades post-larvaires *Leiostomus xanthurus* de la côte de Louisiane. Les Copépodes-proies de 4 classes de taille de *L. xanthurus* (16 mm, 16-26 mm, 26-30 mm, 30-35 mm de longueur) sont comparés aux communautés récoltées par diverses méthodes. Ces prélèvements comprennent des carottages, des pièges « d'installation » qui recueillent les organismes de la colonne d'eau qui se fixent ou nagent à la surface du sédiment, des pièges retenant ceux qui s'échappent du sédiment jusqu'à une hauteur de 7 cm et des récoltes des phytontes de surface. Une analyse en composante principale montre que, tandis que la taille de *L. xanthurus* croit, les proies passent de celles des pièges « d'installation » à celles des communautés intrasédimentaires. Une étude complémentaire permettra de mieux comprendre la nature de la méiofaune hyperbenthique et comment les ressources alimentaires dues aux proies sont utilisées par le Poisson et les autres prédateurs.

INTRODUCTION

Meiofauna have been recognized as a significant component of marine and estuarine ecosystems for over fifty years (Coull & Giere, 1988). Over 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 a trophic sink (McIntyre, 1969; McIntyre & Murison, 1973) responsible primarily for recycling of organic matter within sediments, meiofauna are now recognized as an important pathway of energy transfer to selected juvenile fish and other epibenthic predators (Gee, 1989; Coull, 1990).

Although researchers have gained much insight into fish predation on meiofauna, a number of questions remain unanswered. Several questions deal with the manner in which the predatory behavior of meiofaunal-feeding fishes interacts with the behavior of their prey. One critical need in fish trophic ecology is synoptic studies of feeding habits and prey availability (Miller & Dunn, 1980). Determining prey availability, however, 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 should affect their predator-prey relations in a number of ways, including the degree of selectivity, real or apparent, demonstrated by the predator and the specific meiofaunal assemblage utilized among the several distinct groups available.

The purpose of this review is to broadly address meiofaunal-fish behavioral interactions and to explore in detail one aspect of prey behavior. Emergence of meiofauna is just being recognized and is an important behavioral influence on predatory interactions between fishes and their prey. This review is structured to examine :
1) the manner in which meiofaunal prey are utilized by fish,
2) prey selectivity at the level of major taxa, species, and demographic group, and
3) the significance of the specific habitat utilized by the meiofaunal prey, with particular emphasis on emergent meiofauna.

The nature of emergence by meiofauna is discussed, and the behavior of meiofauna, regarding emergence, as well as the predator's response, forms the central theme of this review. In addition, the results of studies with post-larval spot (*Leiostomus xanthurus*) from coastal Louisiana are included to further illustrate the significance of these interactions.

HOW DO FISH FEED ON MEIOFAUNA

Now that the significance of meiofauna in the diets of juvenile fish 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 data from 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, however, a number of different feeding modes can be identified. Keenleyside (1979) identified feeding four categories in benthic-feeding carnivorous fishes :
1) picking at small prey,
2) picking up substrate and sorting prey,
3) disturbing substrate, then picking up prey, and,
4) grasping relatively large prey.

Meiofaunal-feeding fish likely demonstrate all of these modes of feeding. Certain grassbed fishes, such as the spotted dragonet (*Callionymus pauciradiatus*), are among those meiofaunal feeders that pick at small prey (Sogard, 1984). Several marine fishes, mostly in the families Gobiidae and Sciaenidae, feed by biting the sediment and sorting prey. Perhaps the most well-studied meiofaunal feeding fish is spot, *Leiostomus xanthurus*. At sizes > 30 mm SL, juvenile spot feed heavily on meiofauna by biting into soft sediments, manipulating the sediment within the 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). Spot continue to feed heavily on meiofauna to standard lengths > 100 mm (Stickney *et al.* 1975). At these sizes, their reliance on meiofauna is so strong that the composition of stomach contents may be used to identify the site of feeding (Feller *et al.*, 1990). Spot is somewhat unique, not only in its prolonged utilization of meiofaunal-sized prey but also its sediment-sieving mode of feeding (McCall & Fleeger, 1993). However, the Atlantic croaker (*Micropogonias undulatus*) feeds in a similar manner. In addition, there is evidence that some gobies take bites of sediment (Grossman, 1980; Carle & Hastings, 1982; Toepfer & Fleeger, 1994). Other studies have found that gobies prey on meiofauna (Hartney, 1989; Aarnio & Bonsdorff, 1993; Zander, 1990); however, the source of meiofaunal prey is uncertain in these studies.

While there is no documentation of fishes deliberately disturbing the substrate and preying

on suspended meiofauna, it is likely that benthic fish prey heavily on meiofauna from the near-bottom water, perhaps suspended by currents or present in the water column by active emergence. Juvenile salmon and flatfishes are perhaps best studied. Several species of salmon are known to feed on harpacticoid copepods (Sibert *et al.*, 1977; Sibert, 1979; Webb, 1991), and most evidence suggests that the source of their prey consists of emergent copepods from seagrass beds. Cordell (1986) found that harpacticoids common in the diet are also common in epibenthic sled samples and Webb (1991) found that harpacticoids in the diet of salmon are capable swimmers that are ingested by salmon swimming over grass beds. The group perhaps best known for preying on emerged meiofauna is the juvenile flatfish. Many species of flatfish feed using a lay-in-wait method and strike at prey above them (Stickney *et al.*, 1973). Juveniles of several flatfish feed heavily on harpacticoid species known to be active in the near-bottom water (McCall, 1992; Toepfer & Fleeger, 1994). Juvenile predation on meiofauna may begin soon after metamorphosis, at standard lengths (SL) < 10 mm (McCall, 1992). At such sizes, the meiofaunal prey, which are between 0.5 and 1.0 mm, constitute a relatively large prey item. Other species of fish may well feed in the near-bottom waters. Likely prospects include gobies, blennies and pipefish.

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

PREY 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 impact on the interaction.

Major taxon selectivity

The question of whether juvenile teleosts select one component of the meiofauna over another has

been extensively investigated, and has been discussed in detail in two 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 fish, even though they are typically outnumbered, by as much as two orders of magnitude, by nematodes in the sediments. At least three explanations have been suggested for this phenomenon.

1) Active selection of harpacticoids over nematodes may result from greater energetic content, high concentrations of essential fatty acids, or movement-related visibility differences (Coull, 1990).

2) Differential rates of digestion for nematodes and harpacticoids may lead to nematodes becoming rapidly indistinguishable in the digestive tract, resulting in prey counts which are biased toward harpacticoids (Scholz *et al.*, 1991).

3) Differential availability of harpacticoids and nematodes resulting from 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.

To this list, we may now add a fourth potential explanation. Harpacticoids commonly emerge into near-bottom waters, while nematodes are underrepresented in this habitat (Armonies, 1988; Walters & Bell, 1986). Sun & Fleeger (1994) report that harpacticoids colonize through the water column while nematodes colonize on the sediment surface. This difference in behavior is potentially important to fish that do not bite sediments, but nevertheless ingest large numbers of harpacticoids.

Species selectivity

Relatively few studies have attempted to determine the species composition of harpacticoids preyed upon by juvenile fish. Although Feller *et al.* (1990) found that harpacticoids may be used to trace feeding in different habitats, most studies have found that the assemblage of copepods ingested by fish does not closely correspond to that found in meiobenthos in the area in which the fish were collected (Alheit and Scheibel 1982, Tito 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 than fish feeding in sandy areas (Gee, 1987), perhaps reflecting the more surficial distribution of harpacticoids in muds. Species-specific selectivity of predators for one or several

harpacticoid species has been observed in a number of studies (Woodin, 1977; Gee, 1987). Many investigators, however, still do not make time-consuming species-level identifications. Several recent investigations (Keats *et al.,* 1993; Keats & Steele, 1993; Shaw & Jenkins, 1992; Sogard, 1992; Zander & Heymer, 1992) point out the importance of harpacticoids in the diet of various fishes, but because species-specific identifications were not made, it is not possible to determine the meiofaunal assemblage that served as prey.

Given the increasing number of studies that conclude that juvenile fish do not select meiofaunal prey in proportion to their sediment abundance, it should prove prudent to more closely examine the species of meiofauna that are ingested. Such studies are necessary to understand why a particular subset of the meiofaunal community is disproportionately significant in the feeding ecology of juvenile fish. This could be of particular importance 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, although 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.

McCall (1992) found that juvenile starry flounder ingested male *Microarthridion littorale* in proportions much higher than their representation in sediments and suggested that this phenomenon might be the result of an increased tendency of males to enter the water column. Hicks and Marshall (1985) found that the guts of deep-sea carnivorous bivalves contained almost exclusively male harpacticoids, and go on to suggest that selective predation on males might account for the typical dominance of female harpacticoids in the deep sea.

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 copepods in a manner which was influenced by predator hunting behavior and by differences in size and activity of the male and female prey.

MEIOFAUNAL LIFE-STYLES

Prey selection by fish feeding on meiofaunal organisms may be a function of the meiofaunal habitat as modified by prey behavior. Given the diverse nature of meiofaunal assemblages, quantitative studies characterizing these assemblages in a given area are necessary for an understanding of the feeding behavior of juvenile fish utilizing them. If emergent behavior of meiofauna is an important factor in predator-prey interactions, it is important that the pattern of this behavior be examined in greater detail.

Hicks and Coull (1983), in their review of harpacticoid copepod ecology describe a variety of modes of existence. Within the benthos, harpacticoids may be found living interstitially, epibenthically, or as infaunal burrowers, with the interstitial lifestyle limited primarily to sandy substrates and the burrowers found mainly in muddy sediments. Hicks and Coull also recognize phytal harpacticoids and a few species which are wholly planktonic. To their list should be added another mode of benthic existence, that of tube-dwelling as demonstrated by Chandler and Fleeger (1984) for *Pseudostenhelia wellsi*. In addition, it is now well-established that many harpacticoid species occupy a hyperbenthic or demersal habitat, emerging to spend some fraction of their life in the near-bottom waters within a few mm-cm of the sediment surface (Sibert, 1981).

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 juvenile fish interacts with habitat utilization of harpacticoid copepods to produce specific predator-prey relationships. A given assemblage of potential prey does not result solely from the behavior of the predatory fish, or from that of the meiofauna in the area, but rather from how these two behaviors interact to bring predator into contact with prey.

The significance of emergent meiofauna

Perhaps the least understood, albeit potentially important, assemblage of harpacticoids with regard to trophic interactions with juvenile fish is the emerged, sometimes called hyperbenthic or demersal, assemblage. Beyer (1958) introduced the term hyperbenthos in reference to plankton populations near the sediment-water interface, although we use this term to refer to meiofauna emerged into the near-bottom water. Sibert (1981) illustrates that the hyperbenthos is typically dominated by animals of two origins, downward moving planktonic species and upwardly mobile

surface-dwelling benthic species. The existence of a near-bottom meiofaunal assemblage has been documented in recent years, and it is now apparent that the traditional meiofauna, particularly harpacticoids, occur regularly in the water column (Jacoby & Greenwood, 1989; 1993, Metaxas & Scheibling, 1994). This may result from passive resuspension (Hagerman & Rieger, 1981; Palmer & Gust, 1985), active emergence (Armonies, 1988; Bell *et al.*, 1988; Walters & Bell, 1986; Alldredge & King, 1985; Armonies, 1989) or a combination of the two. The relative importance of the two mechanisms is related to the species under consideration and to the habitat (Palmer & Gust, 1985). Passive resuspension, like active emergence, involves behavioral aspects of harpacticoid ecology, since the habitat occupied by the organisms greatly influences their likelihood of being resuspended (Palmer, 1988b). There is much to learn about the hyperbenthos because sampling problems have slowed study.

For harpacticoid copepods, evidence suggests that interstitial species avoid suspension by moving deeper in the sediment during flow events (Foy & Thistle, 1991), however, mud-dwelling, epibenthic harpacticoids do not appear to avoid emergence through behavior (Palmer, 1984). Thus, the emergence, by whatever mechanism, of harpacticoids into the water column may provide some adaptive advantage with regard to reproduction (Hicks, 1988), feeding (Decho, 1986; Sibert, 1981) or avoidance of infaunal predators (Thayer, 1985). Emergence 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 which are in near-bottom waters. This is likely true of juvenile fish which utilize this habitat as well. If, in fact, much predatory behavior is focused on the near-bottom water, then it is reasonable to suppose that the most significant prey assemblage is the one which frequents this habitat. Unfortunately, this is perhaps 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 and Bell (1986) found that harpacticoid copepods numerically dominated the taxa which actively migrated in a subtidal creek 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. This difference may well be reflected in greatly different prey assemblages in juvenile fish than might be predicted based on a knowledge of the benthic meiofauna. McCall (1992) found that harpacticoids collected in settlement traps differed from those in adjacent sediments, and were more closely similar to those ingested by juvenile starry flounder.

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

EXPERIMENTAL RESULTS WITH POST-LARVAL SPOT

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. Additional evidence comes from studies conducted on post-larval and juvenile spot (*Leiostomus xanthurus*) in a Louisiana estuarine complex. Spot's heavy and prolonged utilization of meiofauna (especially harpacticoid copepods, nematodes and small polychaetes) and amphipods as a food source is well documented (Smith & Coull, 1987; Marinelli & Coull, 1987; Stickney *et al.*, 1975; Palmer, 1988a; Sheridan & Livingston, 1979; Livingston, 1988). Much less is known, however, about early life-history (< 25 mm SL) feeding habits and ontogenetic shifts leading to meiofaunal feeding. Here, we focus on the feeding behavior of early post-larval spot (10-35 mm SL).

A total of 131 juvenile spot (from 12-35 mm SL) were seine-collected in winter and early spring of 1991 in Bay Champagne near the Louisiana Universities Marine Consortium facility at Port Fourchon, Louisiana. An assortment of meiofaunal samples were taken in conjunction with fish collections throughout the spring of 1991, but one sampling date (February 23, 1991) is discussed in detail because a broad size range of spot were collected, and weather conditions allowed collection of a complete array of meiofaunal samples. Collections were conducted by the methods of McCall (1992) and included : 1) vertically sectioned cores 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 and extruded at 2-mm-thick intervals to a

depth of 1 cm, 2) emergence traps that specifically sample the near bottom assemblage, 3) settlement/bedform traps to sample organisms settling to or moving along the sediment surface and 4) phytal samples collected by clipping submerged algae, mangrove roots, etc., in the area. Meiofauna were identified to the major taxon level, and copepods were identified, where possible, to species and demographic status. Copepod (calanoid, cyclopoid and harpacticoid) prey of juvenile spot determined by gut content analysis of various size classes were compared to assemblages collected by 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).

The habitat information given here promotes understanding of the life style of copepods while it provides clues as to the mode of feeding by spot. Additional interpretation of meiofaunal life styles comes from Sun and Fleeger (1994) who sampled meiofauna colonizing sediment depressions along the Louisiana coast.

The sediment meiofaunal assemblage was numerically dominated by nematodes, with harpacticoid copepods the second most abundant taxon (Table I). Nematode densities were relatively high (*ca.* 330cm^{-3} in the upper 2 mm of sediment). Nematodes were most abundant in the surface sediments (0-2 mm depth), but remained abundant to depths of at least 1 cm, as is typical in muddy sediments (Hicks & Coull 1983). Densities of both adult harpacticoids and copepodites were 14.9cm^{-3} and 5.3cm^{-3}, respectively, in the 0-2 mm stratum, somewhat low for soft-sediment

Table I. – Summary of four vertically-sectioned meiofaunal samples collected on February 23 at Bay Champagne site. Data are presented as densities in number per cm^3 ± 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.

Stratum (mm depth)	Total Meio.	Nematodes	Adult Harp.	Harp. Copep.
0-2	362 ± 82	332 ± 78	14.9 ± 0.4	5.3 ± 2.0
2-4	129 ± 26	121 ± 26	4.5 ± 0.9	1.0 ± 0.5
4-6	143 ± 15	140 ± 16	2.1 ± 1.7	0
6-8	137 ± 15	128 ± 16	1.5 ± 0.8	1.3 ± 0.6
8-10	104 ± 14	95 ± 14	1.0 ± 0.6	0.5 ± 0.4

intertidal habitats of this type (Fleeger, 1980; 1985). The most abundant harpacticoids in sediment samples were *Paronychocamptus wilsoni*, adult *Coullana* sp. (referred to as *Scottolana canadensis* in previous work from Louisiana) and *Enhydrosoma* sp. All were concentrated in the upper 2-4 mm of the sediments, and densities dropped rapidly with depth (Fig. 1).

Settlement/bedform traps collected relatively low numbers of copepods (< 10 per trap). The majority of those collected, however, were cyclopoids and harpacticoids, suggesting an epibenthic/hyperbenthic life style (Fig. 2a). The most abundant harpacticoid was *Paronychocamptus wilsoni*; *Mesochra mexicana* and *Harpacticus* sp. were also found, but in lower numbers. Emergence traps contained cyclopoids and calanoids, but were dominated by harpacticoids, of which the majority were again *Paronychocamptus wilsoni* and *Coul-*
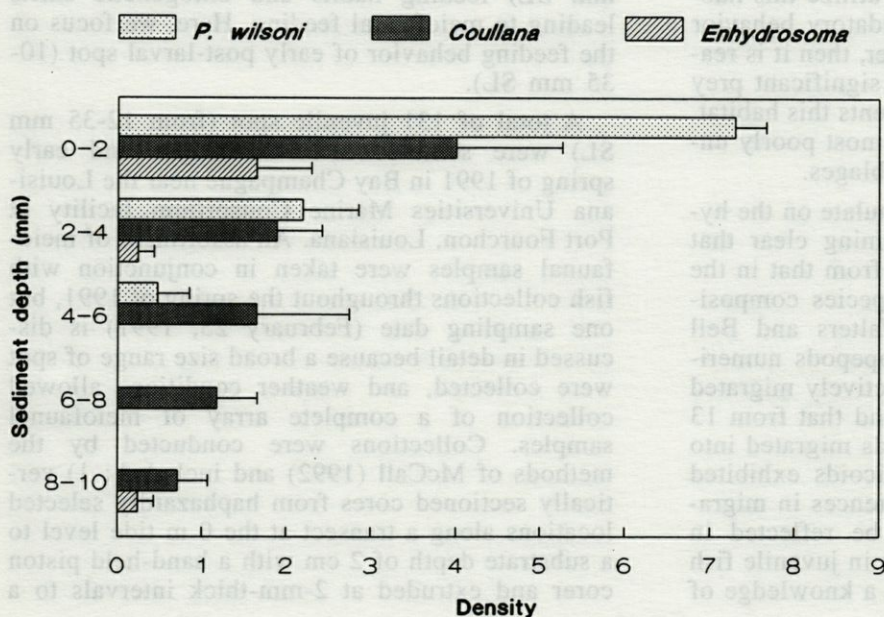

Fig. 1. – Vertical distribution of common harpacticoid species in sediment samples taken on February 23, 1991. Densities (no. cm^{-3} ± 1 SE) are given for each 2 mm thick sediment stratum. Each is based on four replicate samples.

a

Cyclopoid 29% Harpacticoid 71%

Oth 32%
Ho 9%
Mm 25%
Pw 34%

n=6

b

Cyclopoids 15% Harpacticoids 73% Calanoids 12%

Oth 27%
Co 15%
Pw 58.0%

n=7

c

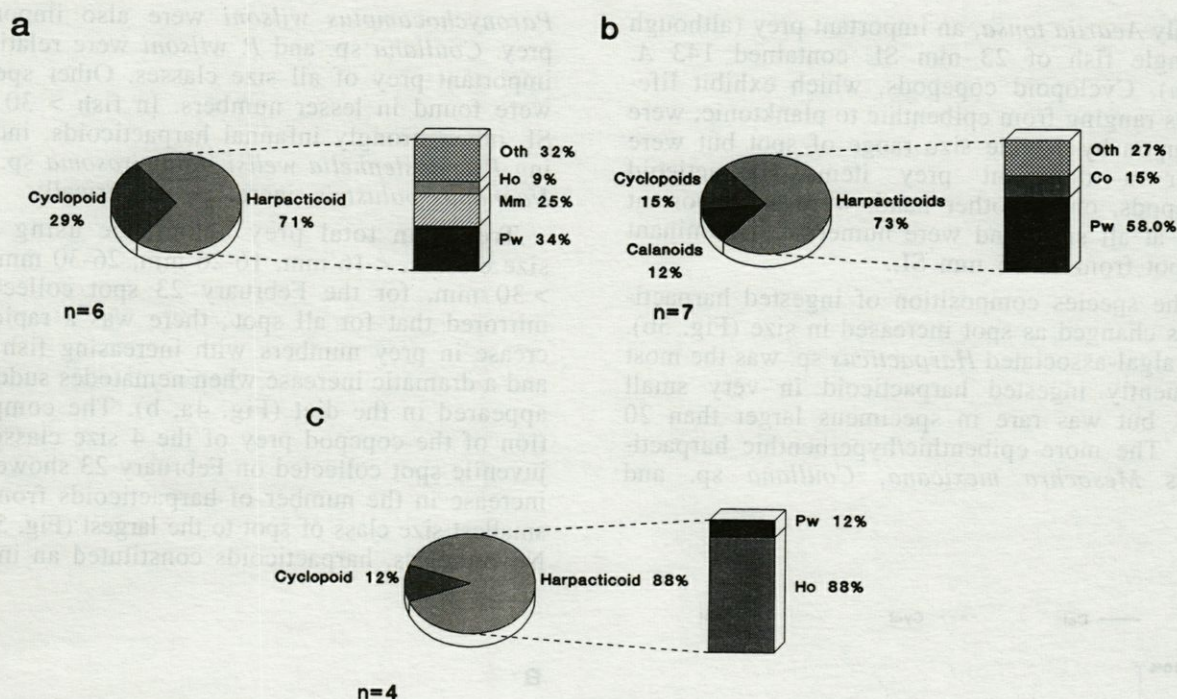Cyclopoid 12% Harpacticoid 88%

Pw 12%
Ho 88%

n=4

Fig. 2. – Composition of copepods collected in (a) settlement traps, (b) emergence traps and (c) algal samples on February 23, 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., Co = *Coullana* sp., Oth = other harpacticoids.

lana sp. (Fig. 2b). *P. wilsoni* was represented in emergence trap samples by all demographic groups, while over 90 % of *Coullana* in these traps were juvenile copepodites. Other harpacticoids collected in appreciable numbers included *Harpacticus* sp., *Zausodes arenicola* and *Pseudobradya* sp. *Pseudobradya*, however, was collected only in one trap. Harpacticoids dominated phytal samples (Fig. 2c). *Harpacticus* sp. were dominant, making up some 80 % of the phytal harpacticoids, although *Paronychocamptus wilsoni* was also present in substantial numbers. Nematodes were common in settlement traps, reflecting the fact that these traps collect not only organisms that are actively emergent, but also those that are resuspended from surface sediments. Nematodes were rare, however, in emergence traps.

Of the spot examined, 106 contained prey. Over all size classes studied, post-larval and juvenile spot diets were dominated numerically by copepods and nematodes (Table II). 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. This feeding shift was quite sudden and likely represents the initiation of sediment biting. At less than 25 mm SL, the strongly infaunal 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. Developing spot also underwent a change in the types of copepods consumed at the ordinal level (Fig. 3a). Only in the smallest fish examined (< 15 mm SL) were planktonic calanoid copepods,

Size Class	n	Mean # prey	% Nema.	% Cal.	% Cycl.	% Harp.	% Oth.
12-15	28	5.3 ± 1.0	0.0	49.0	14.1	17.4	18.8
15-18	20	7.4 ± 1.9	0.1	4.1	2.7	66.0	27.2
18-21	10	18.2 ± 8.4	0.0	8.2	1.6	75.3	14.8
21-25	9	45.4 ± 17.1	0.0	30.0	0.0	66.3	3.7
25-28	6	6.8 ± 3.0	73.5	0.0	0.0	11.8	23.5
28-32	17	80.8 ± 44.0	65.6	0.1	0.1	11.6	1.5
32-35	10	41.3 ± 11.5	35.2	0.1	1.8	53.5	9.2
35-40	6	19.8 ± 3.2	51.9	0.0	0.0	34.2	13.9

Table II. – 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.

mainly *Acartia tonsa*, an important prey (although a single 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. 3b). The algal-associated *Harpacticus* sp. was the most frequently ingested harpacticoid in very small spot, but was rare in specimens larger than 20 mm. The more epibenthic/hyperbenthic harpacticoids *Mesochra mexicana*, *Coullana* sp. and

Paronychocamptus wilsoni were also important prey. *Coullana* sp. and *P. wilsoni* were relatively important prey of all size classes. Other species were found in lesser numbers. In fish > 30 mm SL other strongly infaunal harpacticoids, including *Pseudostenhelia wellsi*, *Enhydrosoma* sp. and *Nannopus palustris*, increased numerically.

Trends in total prey abundance using four size classes, < 16 mm, 16-26 mm, 26-30 mm and > 30 mm, for the February 23 spot collections mirrored that for all spot; there was a rapid increase in prey numbers with increasing fish size and a dramatic increase when nematodes suddenly appeared in the diet (Fig. 4a, b). 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. 5a-d). Nevertheless, harpacticoids constituted an impor-
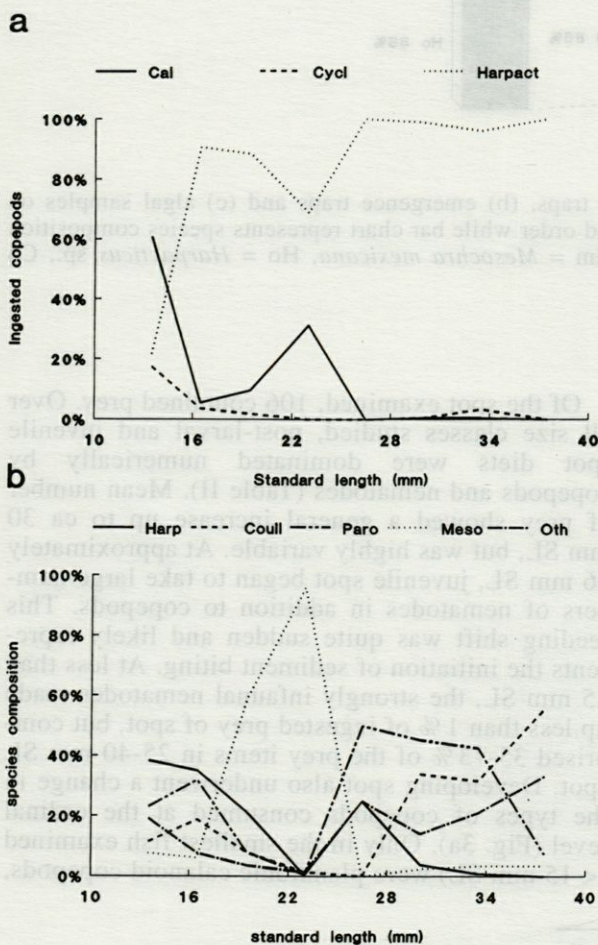
a

b

a

b

Fig. 3. – Copepod prey of 106 *Leiostomus xanthurus* in Bay Champagne, Louisiana in spring of 1991. (a) Percentage of copepod prey of various size classes represented by different orders of copepods. Cal = calanoids, Cyc = cyclopoids, Harpact = harpacticoids. (b) Percentage of ingested harpacticoids belonging to various species. Harp = *Harpacticus* sp., Coul = *Coullana* sp., Paro = *Paronychocamptus wilsoni*, Meso = *Mesochra mexicana*, Oth = other species of harpacticoids. Sample size within size class is indicated in Table II.
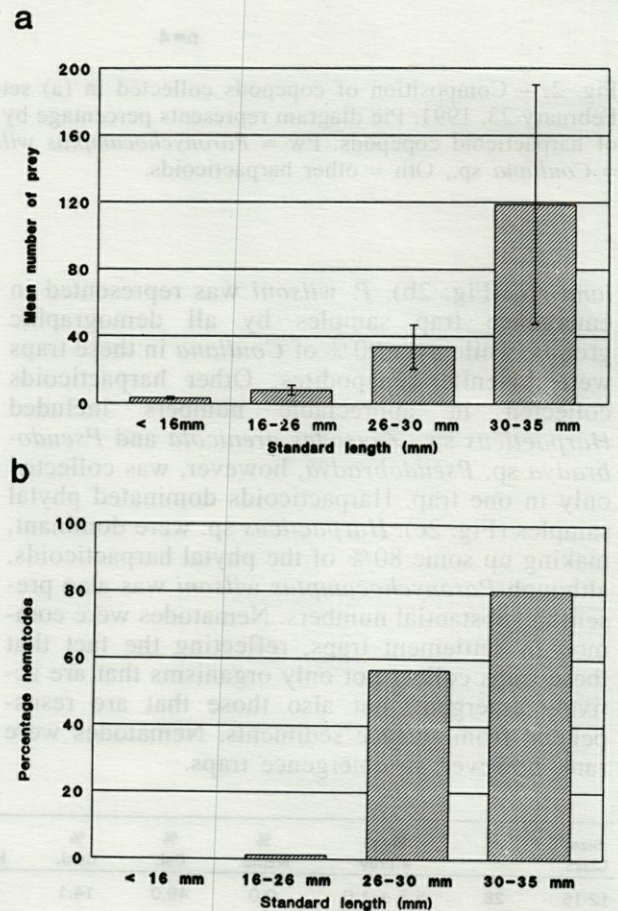
Fig. 4. – Prey contents of four size classes of spot collected on February 23, 1991. (a) Mean (and 1 SE) number of prey by size class. (b) Percentage of total prey (pooled) comprised by nematodes in each size class. Number of fish examined in each size class are as follows : < 16 mm – n=10, 16-26 mm – n=10, 26-30 mm – n=11, > 30 mm – n=11.
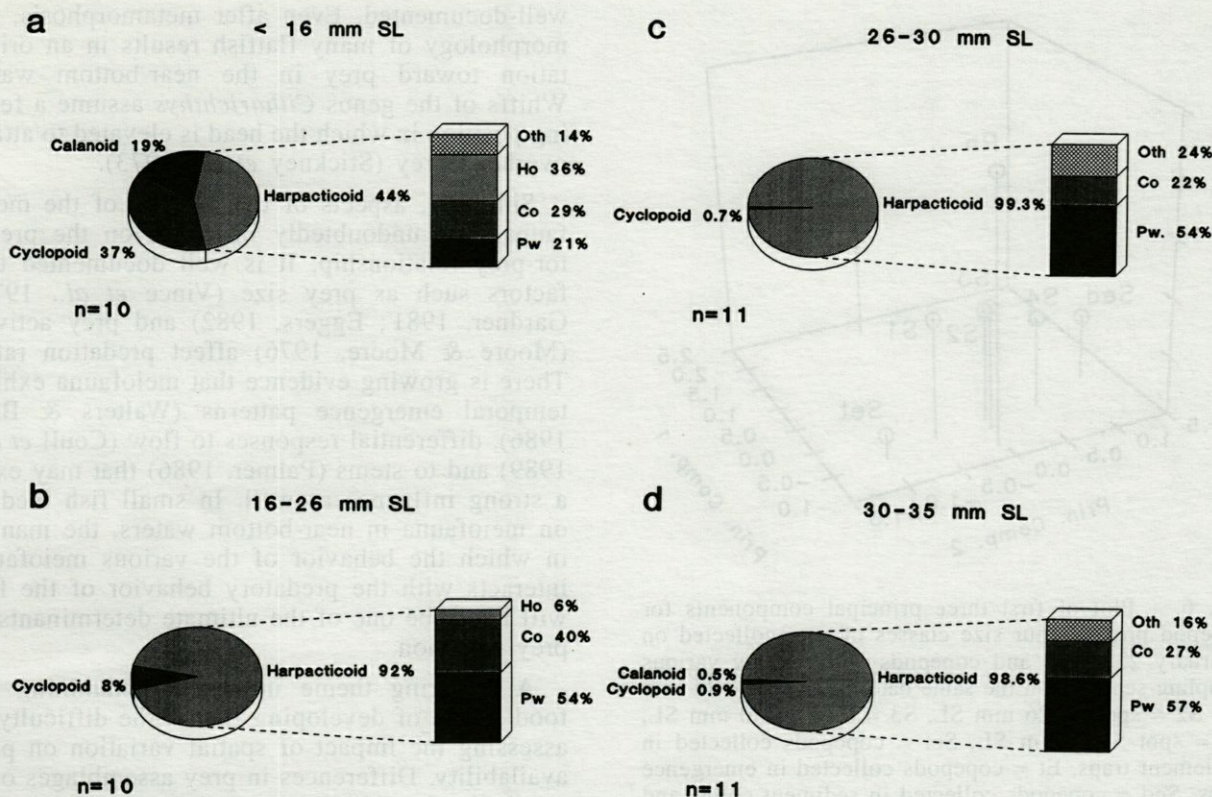
a

< 16 mm SL

Calanoid 19%

Harpacticoid 44%

Cyclopoid 37%

n=10

Oth 14%
Ho 36%
Co 29%
Pw 21%

c

26-30 mm SL

Cyclopoid 0.7%   Harpacticoid 99.3%

n=11

Oth 24%
Co 22%
Pw. 54%

b

16-26 mm SL

Cyclopoid 8%   Harpacticoid 92%

n=10

Ho 6%
Co 40%
Pw 54%

d

30-35 mm SL

Calanoid 0.5%
Cyclopoid 0.9%   Harpacticoid 98.6%

n=11

Oth 16%
Co 27%
Pw 57%

Fig. 5. – 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., Co = *Coullana* sp., Pw = *Paronychocamptus wilsoni*, Oth = other species of harpacticoids.

tant 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 *Coullana* sp. were found in all size classes of spot.

It should be noted that, although nematodes make up over 80 % of the prey of the largest size class of spot examined, they are still underrepresented in the diet relative to their sediment densities. In sediments, nematodes outnumber harpacticoid copepods by an order of magnitude or more, even in the uppermost 2 mm stratum. Thus, juvenile spot do ingest harpacticoids in 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 spot's bucco-pharyngeal filtering apparatus (Nelson & Coull, 1989). Another 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 gut contents towards harpacticoids.

A plot of the first 3 principal components yielded by PCA of the copepod-species-centered

data (Fig. 6) indicated that the prey assemblage of the smallest size class of spot did not closely resemble the sediment assemblage but grouped more closely with settlement-trap (near-bottom) assemblages. The prey ingested by intermediate size classes was less similar to the settlement-trap assemblage, moving closer to the sediment assemblage in principal component space. Prey of the largest spot examined were found to be most similar to the sediment copepods.

In summary, post-larval spot displayed a significant ontogenetic dietary shift from hyperbenthic/epiphytic species of copepods to sediment-dwelling meiofaunal prey. The diet of very early post-larval spot (< 16 mm) includes cyclopoid copepods, which inhabit a number of habitats, and planktonic copepods. The mouth of spot of this size moves from a somewhat terminal to a decidedly subterminal position (Yetman, 1979), and spot of this size probably shift from a diet of planktonic to hyperbenthic prey. Harpacticoid copepods that dominate the diet of these fish from 16-30 mm are ones known to exhibit epiphytic or hyperbenthic lifestyles, likely reflecting epibenthic feeding in these fish. The increased proportion of sediment-dwelling harpacticoids and the
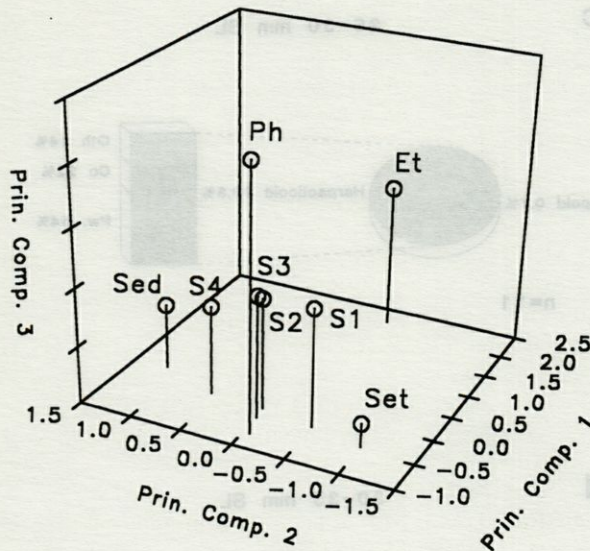
Fig. 6. – Plot of first three principal components for copepod prey of four size classes of spot collected on February 23, 1991 and copepods collected by various sampling schemes on the same date. S1 = spot < 16 mm SL, S2 = spot 16-26 mm SL, S3 = spot 26-30 mm SL, S4 = spot > 30 mm SL, Set = copepods collected in settlement traps, Et = copepods collected in emergence traps, Sed = copepods collected in sediment cores, and Ph = phytal copepods.

scarcity of calanoid and cyclopoids in the diet of larger spot (> 30 mm), coinciding with a dramatic increase in the number of nematodes in the diet, are certainly attributable to a shift in feeding location from the near-bottom water to the benthos.

FUTURE WORK

Many of the fish that rely heavily on a meiofaunal diet do so at a time when they are undergoing dramatic changes in both morphology and behavior. For example, the mouth of spot moves from a somewhat terminal to a decidedly subterminal position during its early post-larval development (Yetman, 1979). 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. This is probably the case in many predator-prey interactions between juvenile fish and meiofauna. Morphological changes probably exert a strong influence on the ability of fish to utilize various prey assemblages. The dramatic morphological changes undergone by developing flatfish are

well-documented. Even after metamorphosis, the morphology of many flatfish results in an orientation toward prey in the near-bottom water. Whiffs of the genus *Citharichthys* assume a feeding position in which the head is elevated to attack overhead prey (Stickney *et al.*, 1973).

Similarly, aspects of the biology of the meiofauna prey undoubtedly influence on the predator-prey relationship. It is well documented that factors such as prey size (Vince *et al.*, 1976; Gardner, 1981; Eggers, 1982) and prey activity (Moore & Moore, 1976) affect predation rates. There is growing evidence that meiofauna exhibit temporal emergence patterns (Walters & Bell, 1986), differential responses to flow (Coull *et al.*, 1989) and to stems (Palmer, 1986) that may exert a strong influence as well. 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.

A recurring theme in studies examining the food habits of developing fish is the difficulty in assessing the impact of spatial variation on prey availability. Differences in prey assemblages over relatively short distances can be a significant factor in determining the food of sediment-feeding fishes such as spot (Feller *et al.*, 1990). There is a need for studies employing broad-spatial sampling of fish and prey assemblages to address the relative role of ontogenetic shifts and spatial variation in dietary composition. Spatial variation of the hyperbenthos has been little studied, but it seems likely that broadly homogenous locations such as muddy salt-marsh bottoms might be little influenced by microhabitat differences, suggesting that apparent changes in diet associated with hyperbenthos are due to ontogeny rather than spatial variation.

There is a growing body of evidence that prey resources in the near-bottom water are critical to demersal juvenile fish. A variety of fish, including juvenile spot (this study), salmonids (Sibert, 1979; Cordell, 1986; Webb, 1991), starry flounder (McCall, 1992) and tonguefish (Toepfer & Fleeger, 1994), have been shown to rely heavily on such a prey assemblage. This study indicates that early 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. Researchers have made significant progress in determining the effect of such factors as flow. More studies investigating these and other effects as well as more effective ways of sampling the near-bottom meio-

fauna are needed to more fully understand the role of the hyperbenthos in the trophic ecology of fishes.

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