

Selection of meiobenthic prey by juvenile spot (Pisces): an experimental study*

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ABSTRACT: Meiofauna are known to be important components of the diet of many juvenile fish, but whether these fish actively select certain taxa has yet to be fully determined. Harpacticoid copepods account for 70 % of the visible prey items in juvenile spot *Leiostomus xanthurus* collected from North Inlet Estuary, South Carolina, USA. The sediment fauna in North Inlet, however, is numerically composed of 70 % nematodes and only 17 % copepods. Controlled feeding experiments were conducted to determine if spot select copepods in preference to nematodes and whether prey motility is a factor in the selection. Spot were allowed to feed for 1 h in aquaria containing azoic sediment seeded with live (i.e. motile) and freshly-killed (i.e. immobile) copepods and live and freshly-killed nematodes. Spot selected live copepods over all other prey types. Greater copepod motility compared to nematodes is probably the primary factor in copepod selection by spot.

INTRODUCTION

Meiofauna, once thought to be a trophic dead end (McIntyre & Murison 1973), are now known to be an important component in the diets of fish (Hodson et al. 1981, Coull & Palmer 1984, Fitzhugh & Fleeger 1985). Harpacticoid copepods, in particular, have been found as the dominant prey item in many juvenile fish diets (Roelofs 1954, Stickney et al. 1975, Sheridan 1979, Sibert 1979). Comparisons of the number of harpacticoids found in fish guts with numbers present in the feeding habitats have led several authors to conclude that harpacticoids are actively selected over other meiofauna (Feller & Kaczynski 1975, Alheit & Scheibel 1982, Carle & Hastings 1982, Sogard 1984, Gee 1987). It has even been suggested that some juvenile fish undergo an 'obligatory harpacticoid feeding period' (de Morais & Bodiou 1984).

Spot *Leiostomus xanthurus* Lacepede enter south-eastern USA estuaries as planktivores and metamorphose into benthos-feeding juveniles between 15 and

30 mm standard length (Currin et al. 1984). At this stage they preferentially feed on meiofauna in muddy substrates (Smith & Coull 1987). Chestnut (1983) conducted visual gut content analyses of juvenile spot collected from the North Inlet Estuary, South Carolina, USA, and found a numerical dominance of harpacticoid copepods (40 to 80 % of total prey). The sediment fauna in North Inlet, however, is numerically composed of ca 70 % nematodes and only 17 % copepods (Coull 1985). Palmer (1988) found that when disturbance and drift were accounted for, spot predation on copepods was significant, but predation on nematodes was negligible. Thus, much indirect evidence suggests that juvenile spot selectively feed on copepods.

Juvenile spot feed by taking bites of sediment 2 to 3 mm deep (Roelofs 1954, Billheimer & Coull 1988); therefore only surface-dwelling meiofauna should be eaten. Epibenthic copepods flit through the surface floc of muddy sediments, while most nematodes wriggle amongst the sediment grains. The surface motility of copepods should make them more susceptible to predation than a burrowing nematode and thus explain copepod selection in the field. A field caging study investigating the effect of spot predation on meiofauna in muddy substrates on the North Inlet Estuary concluded that only certain species of epibenthic copepods were significantly reduced under high predation

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pressure (Ellis & Coull in press). These authors interpreted the species specific reduction in copepods as selection of the most readily available prey by spot (i.e. those most active on the sediment surface).

There have been many laboratory studies of predator selectivity for adult fish feeding on macrofauna (Vinyard 1980, Magnhagen & Weiderholm 1982, Magnhagen 1985, Main 1985), but none for juvenile fish feeding on meiobenthos. The present study was designed to test the hypotheses that juvenile spot (1) selectively feed on copepods in preference to nematodes, and (2) select motile prey in preference to non-motile prey.

MATERIALS AND METHODS

Aquarium design. Experiments were conducted in polyvinyl chloride (PVC) cylinders (15 cm dia. \times 20 cm high) to eliminate corner effects which could be present in rectangular tanks. These aquaria had 2 rectangular openings (10 cm \times 2.5 cm) centered opposite each other in the wall to allow water circulation when placed in running seawater tables. The openings were covered by a 63 μ m mesh to retain organisms.

Field sampling. Meiofauna and spot for the feeding experiments were collected from the North Inlet Estuary near Georgetown, South Carolina (33°21' N, 79°11' W). Sediments containing copepods and nematodes were scraped from the top 2 cm of intertidal mud flats, sieved through a 500 μ m sieve to remove macrofauna, and collected on a 125 μ m sieve, thus reducing sediment volume. The sediments remaining on the 125 μ m sieve were layered in plastic pans to 2 cm depth and covered by 4 cm of water. Copepods were extracted from the sediment by phototaxis to a focused fiber optic light stationed over 1 or 2 corners of the pan. Copepods moving towards the light source were removed, sediment-free, with a pipette. Nematodes were extracted following Couch (1988). Briefly, this method entailed layering muddy sediments over sand in a funnel and allowing the nematodes to burrow away from the mud through the sand and into sediment-free collection vessels. Spot were collected by seining intertidal creeks at low tide. Juveniles were scooped from the net in small plastic containers and transferred to buckets full of water to minimize shock.

Laboratory procedure. In June 1987, spot were allowed to feed in aquaria containing a 1 cm layer of azoic sediment and quantities of live and freshly-killed copepods and live and freshly-killed nematodes. The sediment for the experiment was processed following Chandler (1986). Sediment passing through a 125 μ m sieve was washed to remove lighter organics and was then heated to kill infauna. The heated sediment was reconstituted with seawater to its original consistency

and refrigerated until needed. Prior to the beginning of each experiment either live or dead prey items were stained with Rose Bengal. This was done in order to distinguish between originally live and dead prey in the preserved samples at the end of the experiment. To detect selection for color alone, treatments containing reciprocal staining patterns were established as follows:

- (1) Stained dead copepods and dead nematodes (live copepods and live nematodes unstained);
- (2) Stained live copepods and dead nematodes (dead copepods and live nematodes unstained);
- (3) Stained dead copepods and live nematodes (live copepods and dead nematodes unstained);
- (4) Stained live copepods and live nematodes (dead copepods and dead nematodes unstained).

To conduct the experiment 8 aquaria were placed side by side in a running seawater table. To obtain equal numbers of stained and unstained copepods, and stained and unstained nematodes, copepods and nematodes previously extracted and sorted were split into 32 equal portions with a Folsom plankton splitter. Sixteen of the 32 splits for nematodes and 16 of the 32 splits for copepods were used in the experiment; the other 16 were preserved in formalin and later counted for estimates of initial density. Stained prey types were produced by placing organisms in Rose Bengal for 30 min. To obtain stained dead organisms, live prey types were stained and then heat-killed. Copepod and nematode splits were placed in aquaria under the above treatment combinations so that each treatment occupied 2 aquaria. Two juvenile spot (starved for 24 h) were placed in 1 of the 2 aquaria under each treatment combination. The additional aquaria, without fish, served as controls. The fish were allowed to feed for 1 h and were then removed and frozen to stop digestion. All the sediment in both the experimental and control aquaria was flushed from the aquaria, preserved with 10 % formalin and passed through a 125 μ m sieve. Material remaining on the sieve was stored and later sorted and counted. The entire experiment was replicated 4 times during June 1987.

Standard length (SL) of each fish was measured to the nearest mm. The entire gut of each fish was removed and separated into a fore and hindgut portion at the pyloric caecum. Stained and unstained copepods and nematodes from both portions of the gut and from the sediment samples were enumerated.

Statistical analyses. Fish gut contents data. The counts of live and dead copepods and live and dead nematodes from the guts were divided by the initial abundance of each prey type (determined from plankton split counts) to estimate proportions of available prey ingested. The proportions were log-transformed to stabilize variance so that gut proportions could be com-

pared as ratios rather than as simple differences between treatments and controls.

For each of the response variables, and initial ANOVA model was constructed as a randomized block design with an aquarium effect nested within blocks.

$$Y_{ijk} = u + \text{TRT}_i + \text{EXPT}_j + \text{AQUA}_{ij} + E_{ijk},$$

where Y_{ijk} = log-transformed proportion of prey type (live copepods, dead copepods, etc.) in the k th fish ($k = 1, 2$) in the j th experimental replicate ($j = 1, 2, 3, 4$) of the i th staining treatment ($i = 1, 2, 3, 4$); u = overall mean; TRT_i = the fixed effect of stain treatment i ; EXPT_j = a block effect due to experimental replicate j ; AQUA_{ij} = a random nested effect for the aquarium within experimental replicate; E_{ijk} = represents variability between fish within an aquarium, $k = 1, 2$.

The 4 responses from the same fish cannot be considered independent. Thus, multivariate analysis of variance methods (MANOVA; Chatfield & Collins 1980, Ch. 8) were used to test hypotheses across all 4 prey types and also to provide comparisons between types.

The hypothesis of no stain-treatment effect was tested separately for each prey type by ANOVA and simultaneously across all 4 prey types by MANOVA. No significant differences were found (Table 1). Conse-

Table 1. Results of ANOVAs on gut content data showing stain-treatment effects and experiment (block) effects for the log-proportion of the 4 prey types ingested. * Significant at $\alpha = 0.05$

Prey type	Source	df	F	P
Live copepods	Treatment	3.9	0.27	0.8478
	Experiment	3.9	3.84	0.0506*
Dead copepods	Treatment	3.9	0.40	0.7557
	Experiment	3.9	2.86	0.0965
Live nematodes	Treatment	3.9	0.57	0.6468
	Experiment	3.9	1.21	0.3604
Dead nematodes	Treatment	3.9	0.21	0.8843
	Experiment	3.9	1.37	0.3124

quently, the insignificant stain-treatment effect was removed from the ANOVA models. The models became pure random-effects nested ANOVA models, with aquarium nested in experimental replicate (Sokal & Rohlf 1981, Ch. 10). Appropriate comparisons between proportions of available prey ingested were performed by methods equivalent to univariate ANOVA on selected differences. A Studentized t -test was used to determine whether the mean difference of the proportions compared was significantly different from zero.

Prey remaining in aquaria. The prey retained stain in the frozen fish guts and thus in the gut content analysis we could distinguish stained and unstained

prey. However, Rose Bengal leached from stained organisms when the sediment samples were placed in formalin. Thus it was impossible in some cases to differentiate between stained and unstained and thus live and dead prey types in the fixed sediment samples. Consequently staining treatment designations could not be used in the analyses and no live to dead prey comparisons made. The data were reduced to counts of total copepods and total nematodes remaining in sediments from fish and no fish aquaria. The counts of copepods and nematodes were again divided by the initial abundance of each prey type to yield proportions.

A 2-factor ANOVA design was used to estimate the proportion of copepods and nematodes removed. The feeding effect of the fish (the proportion of available prey removed from the sediments by the fish) under this model was the difference between the log-proportion of prey left in the aquaria without fish (F_1) and the log-proportion of prey left in the aquaria with fish (F_2) or $\text{Fish}_1 - \text{Fish}_2$. An ANOVA on the difference between copepod and nematode feeding effects was used to compare the proportion of nematodes removed by the fish to the proportion of copepods removed by the fish. The 95 % level of significance was used in all analyses. All statistical analyses were performed using Statistical Analysis System (SAS 1985) software.

RESULTS

Almost all fish were observed feeding during the experiments and no fish mortality occurred. Whether the fish fed continuously over the 1 h trial is unknown since feeding activity suspended sediments which prevented observation after the first few minutes. The number of live copepods added to each aquarium equaled the number of dead copepods and the number of live nematodes added equaled the number of dead nematodes in each experiment. The same 3 copepod species were dominant in all experiments. *Nannopus palustris* Brady, an epibenthic copepod, was the dominant copepod in all experiments and comprised 50 % of the individuals. *Stenhelix (D.) bifidia* Coull, an infaunal burrower, was second at 38 % and *Enhydrosoma propinquum* (Brady), also an infaunal burrower, was the third most abundant copepod (10 %).

Fish gut contents data

Fish used in the experiments were 28 to 42 mm (SL). All guts examined contained prey. Prey were found almost exclusively in the foregut and exhibited little digestion. The number of prey items in the guts ranged

Table 2. Results of comparisons between log-proportions of available prey ingested⁺, based on counts of prey in spot guts. Estimates equal the ratio of the log-proportion of prey type 'a' ingested to the log-proportion prey type 'b' ingested. Estimates and confidence intervals represent detransformed values. L: lower bound of the 95 % confidence interval; U: upper bound. The *t*-value (from Studentized *t*-test) and *p*-value are on log-transformed data

Comparison	a/b	Estimate (95 % CI)		<i>t</i>	<i>p</i>
		L	U		
(1) a Live copepods vs b Dead copepods	1.50	1.17	1.93	5.22	0.0136*
(2) a Live nematodes vs b Dead nematodes	0.78	0.49	1.24	-1.74	0.1808
(3) a Live copepods vs b Live nematodes	3.21	2.42	7.84	4.14	0.0255*
(4) a Dead copopods vs b Dead nematodes	1.65	1.05	2.60	3.53	0.0387*

⁺ Log-proportion of available prey ingested = \log_{10} (mean no. prey in guts/mean no. available in aquaria)
* Significant at $\alpha = 0.05$

from 28 to 1971 ($\bar{x} = 340$). A simple linear regression of fish length on number of prey ingested was not significant ($p = 0.899$). The effect of experimental replicate (or block) was significant for live copepods only (Table 1). All 4 prey types were present in the fish guts. Live copepods were ingested 1.5× more than dead copepods ($p = 0.014$) and 2.2× more than live nematodes ($p = 0.026$); 1.65× more dead copepods were ingested than dead nematodes ($p = 0.039$, Table 2). There was no statistically significant difference between ingestion of live and dead nematodes ($p = 0.181$, Table 2; Fig. 1).

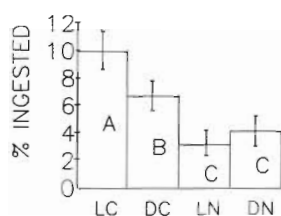


Fig. 1. Proportion of available prey ingested from the gut contents analysis. LC: live copepods; DC: dead copepods; LN: live nematodes; DN: dead nematodes. Bars with a similar letter were not significantly different at $\alpha = 0.05$ level

Aquarium counts

Compared with initial abundance, there were decreased numbers of organisms in both the no-fish (control) and the fish treatment aquaria. Decreases observed in the no-fish aquaria are thought to be due to loss during sediment removal from the aquaria and later sieve loss. Since sediments in both fish and no-fish aquaria were treated similarly, the loss through sediment handling is assumed to be equal. There was no

significant 'handling' effect among experimental replicates (blocks) in any case. Both copepods and nematodes were significantly reduced in aquaria with fish ($p = 0.0008$ and $p = 0.014$ respectively), but there was no significant difference between the number of copepods removed vs the number of nematodes removed overall ($p = 0.512$, Fig. 2).

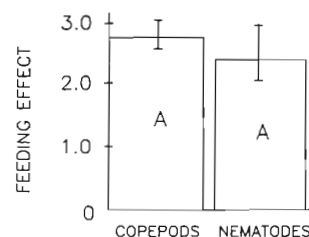


Fig. 2. Feeding effect of fish on copepods and nematodes from the sediment analysis. Feeding effect = \log_{10} [(mean no. of prey in the no-fish aquaria)/(mean no. of prey in the fish aquaria)]. Bars with a similar letter were not significantly different at $\alpha = 0.05$ level

DISCUSSION

The rationale behind looking at both removal of organisms from the sediment and concurrently prey numbers in the fish guts was to obtain alternative estimates of the predation effect. The unexpected loss of stain in the sediment samples caused the sediment data to be of no value in addressing the question of live vs dead removal, but did allow comparison of total copepod to total nematode removal (Fig. 2).

Results from the gut content analyses support what has been found in field and laboratory studies, i.e. given a choice between copepods and nematodes, spot selectively feed on copepods. Perhaps more importantly, spot selected live copepods over all other prey

types suggesting that prey motility may be an important factor in prey selection by spot. Recently, several studies have cited motility of prey as a key factor in prey selection (Rimmer & Power 1978, Ringler 1979, Pastorok 1980, Carle & Hastings 1982, Main 1985). Motion may affect the availability of prey to a predator. Increased activity of prey increases visibility and thus vulnerability to a predator (Magnhagen & Weiderholm 1982). Zaret (1980) suggested that motion produced degrees of conspicuousness in prey types that caused the formation of a 'searching image' (defined as changes in feeding behavior related to visual cues) in the predator, i.e. predators may learn to recognize prey items based on prey motility.

In our study the increased selection of live copepods may be due to characteristic motion. The dominant copepod used in the experiments, *Nannopus palustris*, is an epibenthic species that is active in the surface floc, flitting about from place to place. Most nematodes, on the other hand, are burrowers and move amongst sediment grains. The differences in motility between the 2 taxa may explain the difference in selection in the lab and field. The flitting motion of live copepods on the sediment surface probably attracts foraging spot making them more vulnerable as spot prey than other less motile organisms.

The validity of gut content analyses has recently been questioned due to possible differences in digestibility of prey types (Hyslop 1980). Von Hofsten et al. (1983), for example, have shown that almost no visible nematode remains were found in fish guts after a period of 3 h, and that digestion occurred within 30 min. Copepods, on the other hand, possess a chitinous exoskeleton which resists digestion, and it is often present in fish guts after soft internal parts have been removed (Alheit & Scheibel 1982). As a result, visual gut content analysis of field fish populations might be biased towards organisms, such as copepods, more resistant to digestion. In the present experiment, by only allowing the fish to feed for 1 h and then immediately freezing them, little digestion was allowed to occur. Prey were still whole in the guts. Thus digestive bias was eliminated.

Prey availability or vulnerability is not just a function of mobility, but also of abundance, distribution, size, and pigmentation of prey (Moore & Moore 1976). With meiobenthos, availability to benthic feeding predators depends on the fauna's vertical distribution in the sediment. Juvenile spot feed in the upper 3 mm of sediment (Billheimer & Coull 1988); thus one prey type could dominate gut contents if it was more abundant at the sediment surface than even a few mm deeper. In the field, copepods are typically more abundant than nematodes in the upper few mm (Coull, Palmer & Myers unpubl.), and nematodes are known to migrate

down into the sediment in response to disturbance (Fitzhugh & Fleeger 1985, Palmer & Molloy 1986). If downward migration occurred in our experiments, nematodes in the surface mm might have been less abundant than copepods, but this should have only affected the availability of live nematodes. Dead nematodes were also under-represented in fish guts, and not statistically different in gut abundance compared to live nematodes. This precludes vertical-micro distribution as a major factor in prey selection.

Predators are often restricted in the size of prey they can ingest due to mouth gape and/or size of the buccal cavity (Ringler 1979). Juvenile spot of the size used in the present study (28 to 42 mm SL) feed almost exclusively on meiofauna (Chestnut 1983) because their mouth gape or buccal cavity size can only accommodate meiofaunal-sized prey. Copepods and nematodes used in our experiments were of the same relative size but, of course, very different in shape. The more spherical shape of copepods apparently enhances their size to spot, and, if spot choose the largest available prey as in other fishes (Ware 1973, Werner & Hall 1974, O'Brien et al. 1976, Vinyard & O'Brien 1976, Main 1985), even dead copepods should be selected over nematodes as we found.

Bright or contrasting pigmentation of prey can increase detectability by visually-cued predators (Zaret & Kerfoot 1975, Clements & Livingston 1984), and certainly Rose Bengal staining of prey for the experiments may have prompted differential color selection by spot. However, since there were no significant differences in predation on stained vs unstained prey (Table 1), it appears that spot did not cue on color for prey selection.

While we have assumed that copepods are selected at the time of sediment biting it is also possible that selection occurred in the bucco-pharyngeal filter after the sediment was ingested. The filter is composed of gill arches, gill rakers and pharyngeal plates; the rakers form a sieve that traps food but allows sediment to pass out through the operculum. Exactly how the rakers trap food is unclear, but Yetman (1979) reported that the lateral gill rakers on the first gill arch had furrows containing mucus whereas inner rakers were also coated with mucus but had no furrows. Once the prey comes in contact with the mucus and moves around, it is thought to become entangled and trapped. Most fine sediment particles would pass directly between the rakers while sediment that adheres to the mucus is removed by back-flushing water over the rakers. Thus, live motile prey would be selectively retained while dead prey, acting as passive particles, would pass between the rakers or would be back-flushed through the mouth. Selective retention of live prey could explain the dominance of live copepods in

the fish guts but does not explain the low numbers of live nematodes (Fig. 1). Thus, selection after the bite alone cannot account for copepod selection.

Although juvenile spot consumed both harpacticoid copepods and nematodes in our experiments, they selectively preyed upon copepods, and motility appears to be a primary factor in this selection. Motion affects copepod availability as prey in several ways: (1) motion increases visibility to foraging fish; (2) the epibenthic lifestyle of many copepods causes them to be present at the sediment-water interface where they would be more available as prey; and (3) motion may increase copepod contact and retention in the buccopharyngeal filter of the fish after sediment is ingested. Of course other factors such as olfactory cues, taste, water-borne vibrations, etc. may interact causing the selection of copepods over nematodes as prey, but they are yet to be investigated.

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