Foraging Behavior of a Freshwater Copepod: Frequency Changes in Looping Behavior at High and Low Prey Densities*

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Summary. The foraging behavior of *Mesocyclops edax* in artificial patches of high and low prey density was examined. In low density patches *Mesocyclops* swam in an irregular curvilinear path with little or no looping behavior. In high density patches *Mesocyclops* exhibited extensive horizontal and vertical looping behavior. Horizontal loops were performed in the normal hop and sink swimming mode, while vertical loops were associated with predator attacks on single prey items. Previous studies on terrestrial invertebrates revealed similar looping behaviors by predators and have suggested such looping behavior will increase the time a predator will spend in high versus low density prey patches. When food is patchily distributed and consumers are food-limited, the adaptive significance of remaining in a high density food patch may be substantial.

Introduction

Patchiness is an important phenomenon in both terrestrial and aquatic ecosystems (Wiens 1976; Haury et al. 1978). In both types of ecosystems spatial heterogeneities in the biota may arise from a wide variety of physical, chemical, and biological interactions. In environments where food resources may be limiting, the existence of food in discrete patches places a selective pressure on consumers to exploit this heterogeneity in the most efficient manner by spending more time in patches of high prey density and less time in patches of low prey density (MacArthur and Pianka 1966; Pyke et al. 1977).

Efficient utilization of food patches is particularly critical in the pelagic of marine environments where the average food concentration may be so low that at times it appears inadequate to meet the respirational needs of certain consumers (Lasker 1966; Parsons and LeBrasseur 1970; Mullin and Brooks 1976). For certain calanoid copepods the proposed mechanism enabling efficient patch exploitation involves the ability of the copepods to continue to increase their ingestion rates even at food concentrations far above the average concentrations found in nature (Reeve and Walter 1977; Dagg and Grill 1980). The tendency of some marine zooplankton to move into regions of higher food concentration when placed in a gradient of food densities (Bainbridge 1953) may also offer a partial solution to the apparent paradox of zooplankton existing where their average food densities are so low.

Although extensive direct observations have been made on the foraging behavior of terrestrial vertebrates (Croze 1970 as cited by Curio 1976; Smith 1974; Smith and Sweatman 1974) and invertebrates (Fleschner 1950; Banks 1957; Sandness and McMurtry 1972), and aquatic vertebrates (Ivlev 1961; Beukema 1968; Rosenthal and Hempel 1970; Hunter and Thomas 1974; Thomas 1974) in response to patchy prey distributions, little attention has been given to the feeding behavior of zooplankton in patchy food environments. Dagg (1977) has demonstrated that different species of marine calanoids may vary in their capacity to survive in patchy distributions of food, and functional response data are available for many species of zooplankton at different food densities. However, few data exist on behavioral responses of zooplankton to heterogeneously distributed food resources.

In the present study I have examined the swimming behavior of a freshwater cyclopoid copepod in artificial prey patches of high and low density in an attempt to determine whether this predator has the ability to modify its foraging behavior in response to changes in prey density.

Methods

Adult female *Mesocyclops edax* (average body lengths 1.31–1.36 mm) were collected from Lake Mitchell, Norwich Vermont, and individually isolated in filtered lake water (Reeve Angel 934AH glass-fiber paper) the day before the start of the experiment. The experimental chamber was a large (18 cm diameter) round, flat-bottomed glass vessel filled to a depth of 3–4 cm with 750 or 1,000 ml of filtered lake water and various concentrations of prey representing high or low density patches. Two such vessels (one experimental, one control) were placed side by side in a glass-bottomed, 20 l aquarium tank surrounded by black cloth and illuminated by two 35 watt fluorescent light bulbs placed directly overhead at a distance of 1.5 m from the water surface. A single predator was gently pipetted into the center of one of the vessels. Within several seconds of being introduced the predator commenced swimming. Traces of the predator's horizontal swimming path were made with a felt-tipped pen on a transparent plastic sheet taped to the underside of the aquarium. Total time from the start of swimming to the end of the trial was recorded with a stopwatch and traces were marked at one minute intervals. A trial was terminated either when the copepod encountered the side of the vessel or after five minutes, whichever came first. Experiments were performed at room temperature (24–25 C) on three different dates, 12, 19, and 22 August, 1980. Between seven and ten predators were examined per treatment. On the latter two dates the *Mesocyclops* were killed and preserved in 10% formalin immediately following each trial and saved for later analysis of gut contents. All traces were analyzed with a cartographer's wheel and swimming speeds calculated from the data.

The prey organisms used included laboratory clones of *Paramecium*
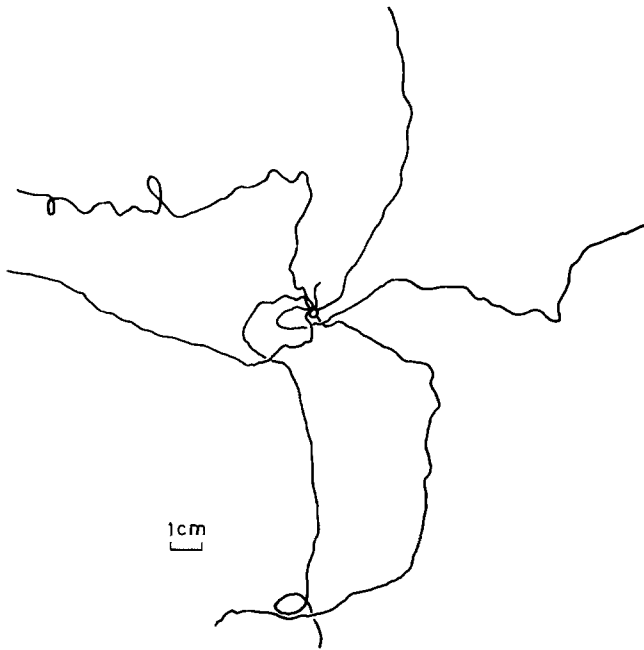

Fig. 1. Tracings of the horizontal swimming behavior of *Mesocyclops* in prey-treated and filtered lake water. Each line represents one predator
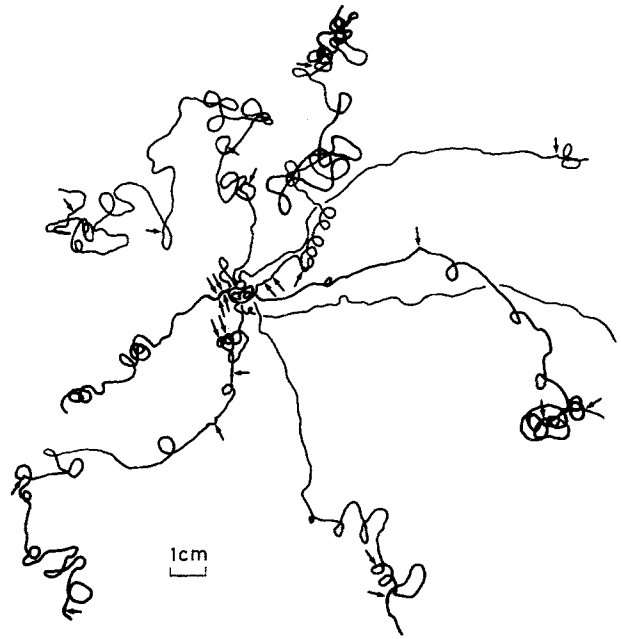
Fig. 2. Tracings of the horizontal swimming behavior of *Mesocyclops* in concentrated Lake Mitchell prey. Each line represents one predator. Each arrow indicates the location of one vertical loop by the predator

Table 1. Horizontal swimming behavior of *Mesocyclops* in the presence of different concentrations and types of prey. See methods for details of treatments

Treatment	Swim speed (cm/min)		Loops/min	
	$\bar{X}$	range	$\bar{X}$	max
treated, filtered water	9.13	0.2–25.8	0.13	0.67
few *Paramecium*	6.13	0.2–16.6	0.30	1.8
Brachionus and *Paramecium*	6.86	0.7–9.7	2.1	5.8
concentrated lake prey	7.92	2.1–10.7	2.3	4.4
concentrated lake prey plus *Brachionus*	8.68	6.6–12.9	2.1	3.9

aurelia and *Brachionus calyciflorus* (Gilbert 1975) and organisms collected the morning of the experiment from Lake Mitchell. "Prey-treated water" was glass fiber filtered lake water in which high concentrations (50 X average lake concentrations) of prey had been kept for a period of about 4 h. The "few *Paramecium* prey" treatment consisted of lake water in which high density cultures of *Paramecium* and *Brachionus* had been placed for about 4 h before being removed with 20 µm mesh Nitex. A small, undetermined percentage (roughly a few hundred per liter) of the *Paramecium* passed through the mesh and remained in this treated water. The *Brachionus* and *Paramecium* treatment had prey concentrations of 12,690 rotifers per liter plus 94,400 protozoans per liter. Both treatments with lake prey contained densities of prey 50 times the average prey density in Lake Mitchell at the time. This prey community consisted of *Peridinium* sp. (625,000/l), *Keratella cochlearis* (12,160/l), cyclopoid copepod nauplii (3,120/l), *Tropocyclops prasinus* copepodites (1,720/l), *Polyarthra* spp. (1,200/l), and *Asplanchna priodonta* (40/l). All larger prey (e.g. *Daphnia* spp., *Diaphanosoma leuchtenbergianum*, some *Asplanchna*) were removed from the lake prey treatments with a 202 µm mesh to minimize avoidance responses in the predator. *Brachionus calyciflorus* were added to one of the concentrated lake prey treatments to give an experimental concentration of 13,450 *Brachionus* per liter.

The above prey concentrations, although high for Lake Mitchell, are not believed to be excessive. In more eutrophic lakes where *Mesocyclops edax* are found, concentrations of a single rotifer species may exceed 30,000/l in high density patches (R.E. Magnien, unpublished data for *Kellicottia bostoniensis* in Star Lake, Norwich, Vermont). In addition, it is not unusual for zooplankton patch densities to vary by a factor of more than 50 fold during a single sampling period (Colebrook 1960; Dumont 1967; Patalas 1969).

Results

There was a pronounced difference in the horizontal swimming behavior of *Mesocyclops* in the treatments representing low density prey patches (few or no prey) versus those representing high density prey patches. In the low density treatments the *Mesocyclops* swam in an irregular path with varying degrees of curvature and infrequent looping behavior (Fig. 1, Table 1). In the high density treatments the swimming path was more tortuous with frequent looping and circling behavior (Fig. 2, Table 1). The frequency of horizontal looping behavior was more than an order of magnitude greater in the high prey density treatments (2.1–2.3 loops/min) than in the prey treated and filtered water (0.13 loops/min).

This horizontal looping behavior was performed in the normal hop and sink mode of swimming and is distinctly different from the rapid, tight, vertical looping behavior exhibited by *Mesocyclops* and other copepod predators during an attack or attempt to recapture a lost prey organism (Gilbert and Wiliamson 1978; Kerfoot 1978; Wiliamson 1980).

Figure 3 shows the tight vertical looping behavior of *Mesocyclops* during an attack on a prey. These vertical loops were generally smaller and more regular in shape and diameter than the horizontal loops exhibited by *Mesocyclops*. Although the vertical loops occassionally were executed in an oblique, or even horizontal plane, the orientation of the circular path of the loop always coincided with the dorso-ventral axis of the predator. Thus, a "vertical" loop performed in a horizontal plane was carried out with the predator on its side. Experimental design
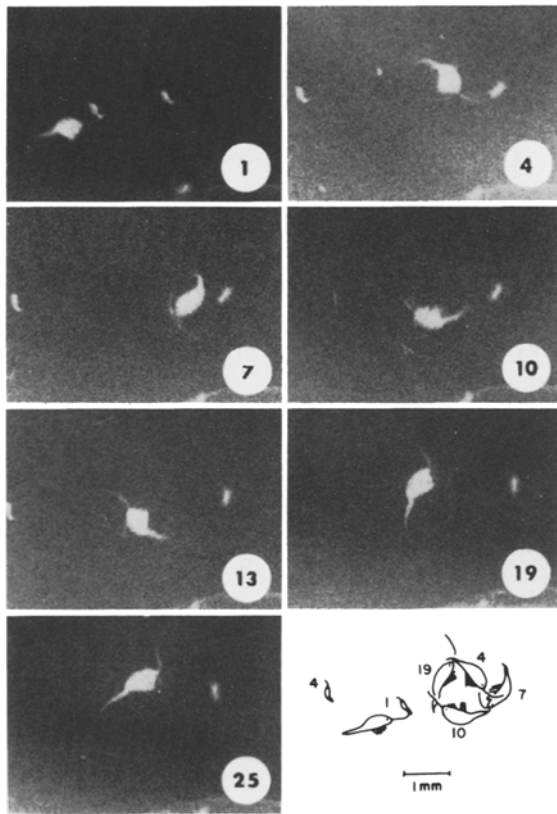
Fig. 3. Vertical looping behavior in *Mesocylops* during an unsuccessful attack on an adult female *Tropocyclops prasinus*. The sequence was taken from a 16 mm Ektachrome 7252 film shot at 32 frames per second with a Photosonics high-speed movie camera. Frame numbers are indicated for individual photographs as well as for the summary figure at lower right. White circles can be interpreted as fixed reference points. Note that the prey, which is near the tip of the predator's antenna in frame 1, successfully escapes to the far left in frame 4. The predator then responds with a vertical loop in an attempt to relocate the escaping prey. The entire attack and loop sequence takes about 0.75 s

precluded quantification of the vertical displacement of *Mesocyclops* during "horizontal" loops.

The location of vertical loops exhibited by *Mesocyclops* are marked with arrows in Fig. 2 to show their relative frequency and position with respect to the horizontal looping behavior. Vertical loops were scored as vertical loops, even when not performed in a strictly vertical plane. No vertical loops were exhibited by *Mesocyclops* in the prey treated and filtered water (Fig. 1).

Swimming speeds were extremely variable among the *Mesocyclops* within treatments and no significant differences between treatments were observed (Table 1). However, there was some evidence for an increase in the swimming speed of individual *Mesocyclops* during looping ($\bar{x} = 8.73$ cm/min) versus non-looping ($\bar{x} = 6.48$ cm/min) portions for their traces in the three high prey treatments (p = 0.0468, Kruskal-Wallis non-parametric rank test).

Gut content analyses revealed that control animals (in filtered water) had empty guts while experimental animals ingested mostly *Peridinium*, a few copepodites, and *Dinobryon* from the concentrated lake prey as well as *Brachionus* when presented. Up to 13 *Peridinium* and 1–3 *Brachionus* were ingested per predator within a 5 min trial. Although *Paramecium aurelia* are known to be ingested by *M. edax* (Williamson, unpublished) remains

of this protozoan were not distinguishable in the guts in the present experiments.

In the experiments performed on 19 August, the frequency of horizontal looping behavior in experimental animals placed in concentrated lake prey (0.48 loops/min) was similar to that for the control animals in filtered lake water (0.96 loops/min). Experimental prey concentrations on this date were similar for those previously given except that there were 500 *Bosmina* per liter, half as many *Peridinium* (315,000/l), and fewer *Keratella* (7,153/l). Details of these experiments are not reported in Table 1 because gut content analyses revealed that the predators in the high density prey treatments were not actively feeding. Out of five guts examined, two contained a single colony of *Dinobryon* and two contained a single *Peridinium* in them. Two of these five *Mesocyclops* did exhibit active horizontal looping behavior. Three out of four of the *Mesocyclops* which did not exhibit looping behavior in high prey densities in the experiments on 12 and 22 August had totally empty guts.

Discussion

Mesocyclops exhibits two distinct types of behavioral response to the presence of prey organisms. During an attack, or following the loss of a captured prey, *Mesocyclops* will often swim in one or a series of tight vertical loops which serve to maintain or increase the proximity of the predator with a single prey. In the presence of high densities of prey *Mesocyclops* swims in a series of horizontal circles and loops. This response is apparently stimulated by detection of one or more prey organisms, and may or may not require contact and/or ingestion of the response-eliciting prey.

The frequency of horizontal looping in *Mesocyclops* increased with increasing prey density. In a patchy food environment this behavior will serve to increase the probability that the predator will encounter subsequent prey by increasing the turning rate of the predator, and thus the time it spends, in high density prey patches (Pyke 1978).

Such specialized foraging behavior would tend to be most effective at increasing predator ingestion rates in situations where the availability of food in the environment is low (i.e. is limiting) and the difference in prey concentration between low and high density patches is large. In the above experiments predators were starved for one day to simulate a food-limited environment, and differences in prey concentration in low versus high density patches were maximized. The horizontal looping response of *Mesocyclops* may be less pronounced in nature under less extreme conditions.

Some of the *Mesocyclops* tested did not respond to high prey densities by exhibiting horizontal looping behavior. The predators tested on 19 August exhibited no significant difference in the frequency of horizontal looping in high versus low density prey patches. Similarly, a few *Mesocyclops* examined on the other two dates exhibited little or no horizontal looping in response to high prey densities (see Fig. 2). The low frequency of horizontal looping in these predators can be explained by the fact that they were not actively feeding – their guts were nearly or entirely empty, while *Mesocyclops* which did respond by looping contained several prey in their guts. However, we still must ask why these predators were not feeding. Handling of the predators prior to each trial, the limited amount of time available for each predator to respond (the predators usually hit the edge of the dish within a few minutes) and simple biological variability between individual predators may account for the lack of response in some of the predators. In the experiments

of 19 August the primary prey (*Peridinium*) was present at only one half the concentrations of the other lake prey trials; and *Bosmina,* a generally undesirable prey of *Mesocyclops* (Williamson 1980), was abundant on 19 August but absent during trials on the two other dates. This suggests the quality was well as the quantity of prey present may be important in eliciting the horizontal looping response in *Mesocyclops.* The importance of qualitative versus quantitative factors in regulating looping behavior in copepods provides a fertile area for future research.

The observations that *Mesocyclops* with empty or near empty guts generally did not exhibit either vertical or horizontal looping behavior, and that the frequency of vertical looping in the presence of prey increases with predator starvation (Williamson 1980), indicate that both looping responses are closely associated with foraging behavior and not just reactions to high particle densities. It is not clear from these data whether actual ingestion or just contact with the prey is needed to elicit the looping behavior. Nor is it known whether encounter with a single prey, or multiple prey are necessary to elicit horizontal looping in *Mesocyclops.* However, the low frequency of looping behavior in prey-treated water indicates physical encounters with prey, and not just allelochemicals, are necessary to stimulate looping in *Mesocyclops.*

Interestingly, while the horizontal looping behavior of *Mesocyclops* may serve to increase the ingestion rate of the predator, it will also tend to cause aggregation of the predators in areas where prey are most abundant. A number of theoretical and experimental models have supported the assertion that an increase in predator aggregation tends to increase the stability of predator-prey systems (Oaten 1977; Hassell 1978). Thus, while pelagic zooplankton prey are not afforded the structural refuges from predators made available to terrestrial organisms by vegetational heterogeneity, they may recieve at least a partial refuge induced by their own patchy distributions.

Complex behavioral responses to environmental stimuli have previously been well documented in marine copepods. Several species of copepods are known to aggregate in high-density swarms on coral reefs (Emery 1968; Hamner and Carleton 1979), and males of several other species have been shown to exhibit altered swimming behavior in response to pheromones released by conspecific females (Parker 1901; Roff 1972; Katona 1973; Kittredge et al. 1974; Griffiths and Frost 1976). Although freshwater copepods may exhibit swarming behavior (Colebrook 1960; Hebert et al. 1980), and males have been observed to pursue females (Gerritsen 1980), there is no convincing evidence for their response to sex pheromones (Holmes 1909). However, further research in this area is needed.

The response of some male marine copepods to female sex pheromones is strikingly similar to the response of *Mesocyclops* females to high prey densities (compare Fig. 3 in Kittredge et al. (1974) to my Fig. 2). In both cases a small area often is searched intensively with occassional "doubling back" behavior and some progressions in the form of a "curtate cycloid". Kittredge et al. (1974) believe this circular progression in swimming permits a copepod to detect and follow a gradient in a chemical substance in the water. If this holds true, the similar swimming pattern observed in *Mesocyclops* may enable the predator to locate an injured prey by following a gradient in body fluids or other substances released through a wound.

Responses similar to the looping behavior reported here for *Mesocyclops* have been previously noted in other cyclopoid copepods by Fryer (1957), who referred to them as " hunting reactions" by Kerfoot (1978), who termed this "shuttle behavior", and by Li and Li (1979).

The adaptive significance of such looping behavior in reference to prey patchiness has been examined most intensely in experiments with terrestrial invertebrates. In most cases the systems examined have involved predators interacting with prey on two dimensional surfaces, thus essentially eliminating the third dimension and the likelihood of any vertical looping behavior in the predator. In spite of this, however, two apparently distinct types of looping behavior, analogous to the vertical and horizontal looping in *Mesocyclops,* have been observed. Many insect predators turn more frequently and confine their search to a smaller area at high prey densities than at low prey densities (Fleschner 1950; Banks 1957; Dixon 1959). This behavioral response is analogous to the horizontal looping of *Mesocyclops* at high prey densities and has been recognized by many authors as an adaptation of the predator to feeding on prey with patchy distributions (see Pyke et al. 1977 and Pyke 1978). Behavior analogous to the vertical looping of *Mesocyclops* is found in the predatory mite, *Amblyseius largoensis,* which became "excited" and searched the surrounding area in tight circles when a prey which it had killed was taken away (Sandness and McMurtry 1972). A similar reaction to lost prey was observed in the Dipteran larva *Syrphus balteatus* by Chandler (1969).

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