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The influence of visibility and escape ability on sex-specific susceptibility to fish predation in *Eudiaptomus gracilis* (Copepoda, Crustacea)

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Abstract

The susceptibility to fish predation in males, ovigerous, and non-ovigerous females of the freshwater copepod *Eudiaptomus gracilis* is investigated in the laboratory by direct observation of the predation sequence of zebrafish, and by studying mortality when confronted with zebrafish or roach. Ovigerous females had the highest encounter rate indicating that the highly visible egg-clutch is a major determinant of their susceptibility. Males were least successful in escaping, the main reason being their inability or disinclination to react fast enough when attacked. This difference in escape reaction may have evolved because of sex-specific requirements in mate encounter and mate location.

Ovigerous females and males had higher mortality than non-ovigerous females in all experiments while ovigerous mortality was higher than male mortality only in the zebrafish experiments. Neither experiment showed any difference in male and overall female mortality but as a consequence of the abrupt change in susceptibility between the ovigerous and non-ovigerous condition, it follows that sex-specific mortality rates may be dependent on the reproductive condition within diaptomid populations. A consequence of the sex-specific difference in escape ability is that the sex-specific mortality may be influenced by variation in the attack efficiency within and among predator populations.

Introduction

The selective prey choice of planktivorous fish may depend on small-scaled and continuous variation in morphology and behaviour within their zooplankton prey populations (Zaret, 1980a; O'Brien, 1987) indicating that prey susceptibility also may be influenced by the distinct character of prey sex. Males and females of diaptomid copepods exhibit several sex-specific morphological, behavioural, and life history traits, that might influence their susceptibility to fish predation – some that falls on one sex, some that falls on the other. The traits in question may affect the encounter rate with the predator or the ability to escape from the predator when once encountered.

The few studies on sex-specific fish predation on diaptomid copepods have focused on differences between the sexes in encounter rates without considering the problem of potential differences in escape performance. Male diaptomids have been reported to be more active and fastswimming than females and this may result in a higher encounter rate with predators (Maly, 1970). Usually, however, fish swim much faster than diaptomids and hence differences in swimming speed will probably not influence the sex-specific encounter rate with fish, but since planktivorous fish may select moving objects (Zaret, 1980b; Wright & O'Brien, 1984), male may be more frequently attacked when once encountered. Females, on the other hand, are usually larger than males and carry the eggs in an easily detectable egg sac. They may for these reasons be more visible and located at a greater distance than males, by visually dependent predators (Hairston *et al.*, 1983).

Planktonic copepods in general perform strong escape reactions in response to mechanical disturbances in the water, as when a predator is approaching or attacking (Confer & Blades, 1975; Drenner *et al.*, 1978; Gerritsen, 1978). The escape ability may potentially differ between sexes because of differences in size, and it may be affected by drag from the egg sac. Also the motivation to escape may differ because of sex-specific interests in detecting potential mates.

What will be the sum of this? In this paper I investigate if males and females of the calanoid copepod *Eudiaptomus gracilis* differ in susceptibility to fish predation, by taking into account both sex-specific encounter rates and escape behaviours. Since the egg sac *a priori* seems to be a critical property that influences female mortality, I have separated the susceptibilities of ovigerous and non-ovigerous females as well as males. It is the purpose of this paper to rank them with respect to encounter probability, escape ability, and mortality.

Methods

Two different experiments were carried out aiming to show corresponding results at the individual and populational level. In the first series of experiment, the performance of individual copepods when confronted with fish was observed. Zebrafishes (*Brachydanio rerio*) were used as predators since they are easy to handle and accept the close appearance of a human observer. In another laboratory experiment these observations were controlled by studying sex-specific mortality in pure *Eudiaptomus*-populations exposed to predation by zebrafish and young-of-the-year roach (*Rutilus rutilus*).

The zebrafishes (2.8–3.1 cm std. length) came from a laboratory stock held at the department, while the roaches (2.2–2.8 cm std. length) were caught with a sweep net in Lake Mjörn, southwest Sweden. All fish were held in 60 l tanks for two weeks prior to start of experiments and were fed with commercial fish fodder and, once a day, a natural zooplankton assemblage. They were not fed within the last 12 h before an experiment.

The copepods were collected with a net (100 μm mesh size) in Lake Stora Stockelidsvatten, a small forest lake (3 ha) in southwest Sweden with dense populations of roach and perch. They were stored at about natural population densities in large buckets in the laboratory. Single individuals were caught in a sieve, picked out with a pipette and placed in cells of tissue culture dishes where sex and the adult stage were controlled using a dissecting microscope. New copepods were collected from the lake every third day during the experiments.

Observation of predation sequence

One ovigerous female, one non-ovigerous female and one male, were placed together in a small tank (23 by 13 cm and 3.5 cm of water, normal indoor light and temperature) and ten minutes later one zebrafish was added. Encounters, attacks, escapes and ingestions were noted, as well as the number of evasive jumps the copepods performed in each escape event. Time to encounter of first prey was measured with a hand watch. The experiment was interrupted if the fish did not encounter a copepod within five minutes, otherwise the interactions were continuously recorded until all three copepods were ingested. Except for one observation side the tank was coated with white paper. The experiment was repeated 75 times, always with an 'unused' zebrafish as predator.

Mortality in population

50 ovigerous females, 50 non-ovigerous females and 50 males were placed in a tank (47 by 38 cm and 14 cm of water, normal room light) and 10 minutes later a single zebrafish or three individuals of roach were added. The fishes were allowed to prey on the copepods during 40 minutes. Thereafter the tank was rapidly but gently emptied through a number of siphons; remaining copepods were collected in sieves (25 μm mesh) attached to the siphons and immediately fixed in Lugol's solution.

The experimental procedure was carefully checked to ensure that eggs at no time were produced or hatched and that copepods were not lost. To reduce the risk of hatching and production of eggs, tank water was somewhat cooled (16–18 °C) and the duration of the experiment was kept to a minimum. All copepods and egg sacs were obtained when the method was tested in five replicates without fish. If hatching occurred, in the methodological control as well as in the experiments, it should have been detected by the presence of nauplius larvae in the sieved water. The experiment was repeated 10 times with zebrafish and 14 times with roach.

Results

Observation of predation sequence

Out of the total of 75 sequences recorded, ovigerous females were the first encountered prey in 34, non-ovigerous in 22, and males in 19. This is not a significantly biased ratio ($0.10 < p < 0.20$, χ^2-test) but, when comparing the prey types two and two, regardless of when the third was encountered, the result shows that ovigerous females are more often encountered before both non-ovigerous females ($0.01 < p < 0.05$) and males ($0.01 < p < 0.05$), while there is no difference between the two later categories (Table 1). An independent measure of encounter probability, the time elapsed between the introduction of the fish into the tank and its first encounter with prey gives the same pattern. This encounter time (mean ± SE) is 47.4 ± 8.6 seconds when ovigerous females are the first encountered prey ($n = 34$), for non-ovigerous females 58.6 ± 12.6 seconds ($n = 22$), and for males 60.5 ± 13.3 seconds ($n = 19$).

The experiment gave no indication of differences in the predators attack rate against the prey categories. More than 99% of the encountered copepods were pursued, and all of these were attacked, except those that escaped during the predators approach.

The paired comparisons show that both of the female categories are superior escapers to the males, as measured by the number of replicates in which they had a higher escape success (Table 1). An analysis of some components of escape performance shows that there was a significant difference in the number of evasive jumps made by the copepods in the capture events ($F_{2,148} = 8.973$, $p < 0.001$, Randomized complete block ANOVA). Males performed significantly fewer evasive jumps than both ovigerous ($p < 0.01$, Duncan's new multiple-range test) and non-ovigerous females ($p < 0.01$), but this difference can be explained by whether or not the copepods initiated an escape reaction at all. In 44 of the 225 capture attacks, the copepods never made any evasive jumps. These 44 catches were not evenly distributed among the prey categories; 3 was directed against ovigerous females, 14 against non-ovigerous females, and 27 against males ($p < 0.05$ for all two and two comparisons, χ^2-test). When once escaping there was no significant difference in the number of evasive jumps performed.

Ovigerous females was the first captured prey in 37, non-ovigerous in 15, and males in 23 replicates ($0.001 < p < 0.01$, χ^2-test). When again making the comparison two and two, the only significant difference in mortality in this experiment is between ovigerous and non-ovigerous females (Table 1).

It should be noted that, despite the great difference in mortality among the female prey types, the total number of first captured females, irrespective of reproductive state, is very close to what is expected if fish predation is random (observed = 52, expected = 50) with respect to sex of prey.

Table 1. A comparison of encounter frequenties, escape abilities, evasive jumps, and survival in males, non-ovigerous, and ovigerous females of *Eudiaptomus gracilis* when preyed upon by zebrafish. 75 replicates were performed in a small tank. One copepod of each of the three categories were simultaneously offered to the predator and the predation cycle was observed and registered until all copepods were ingested.

Encounter frequenties	No. of replicates	Frequency		p (χ2-test)
Non-ovig. encountered before male	40	0.533		n.s.
Ovig. encountered before male	47	0.627		<0.05
Ovig. encountered before non-ovig.	47	0.627		<0.05
Escape ability	Escaped when attacked more times than opposite category (No. of replicates)		No measured difference in escape ability (No. of replicates)	p (sign test)
	Non-ovig.	Male		
Non-ovig. vs male	37	17	21	0.0096
	Ovig.	Male		
Ovig. vs male	40	23	12	0.0434
	Ovig.	Non-ovig.		
Ovig. vs non-ovig.	26	29	20	n.s.
No. of evasive jumps	Ovig.	Non-ovig.	Males	p (ANOVA)
In capture event (mean ± SE, $n = 75$)	2.9 ± 0.2	2.4 ± 0.2	1.6 ± 0.2	<0.001
Survival	No. of replicates	Frequency		p (χ2-test)
Non-ovig. captured before male	34	0.453		n.s.
Ovig. captured before male	41	0.547		n.s.
Ovig. captured before non-ovig.	50	0.667		<0.01

Mortality in population

The mortality of the different prey categories of the *Eudiaptomus*-population is depicted in figure 1. Both zebrafish and roach preyed selectively ($p < 0.001$ and $p < 0.05$ respectively, Randomized complete block ANOVA). In the zebrafish experiment all means differ significantly; ovigerous females were preyed upon more than both males and non-ovigerous females, and males were preferred before non-ovigerous females ($p < 0.01$ in all cases, Duncan's new multiple-range test). In the roach experiment there was no difference between males and ovigerous females, males were preyed upon more than non-ovigerous females ($p < 0.01$), while the difference between the female categories is on the significance limit ($p < 0.0502$).

The mortality of both female categories taken together doesn't differ significantly from male mortality. When preyed upon by zebrafish, total female mortality is greater than expected during random choice in 7 replicates and male mortality greater in 3 replicates. In the roach experiment

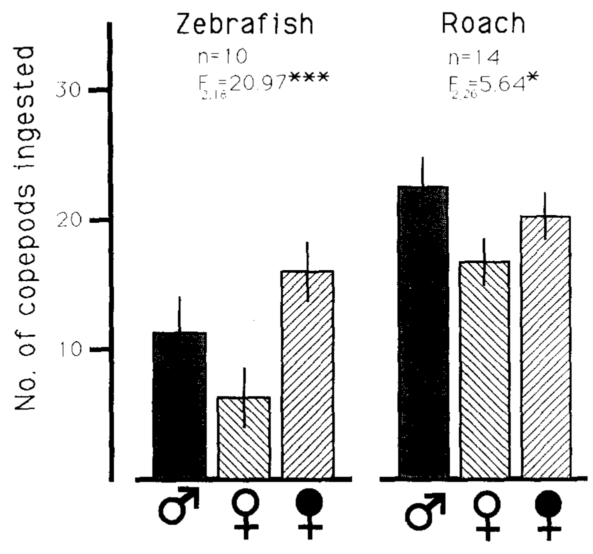

Fig. 1. Number of males, non-ovigerous, and ovigerous females (filled symbols) of *Eudiaptomus* ingested by one zebrafish or three individuals of roach during 40 minutes in a tank experiment (mean ± SE). The initial copepod population consisted of 50 individuals per category in each replicate. All the means, except between ovigerous females and males in the roach experiment, are significantly different (Duncan's new multiple-range test).

male mortality are greater in 8 replicates and total female mortality greater in 5 replicates.

Discussion

The main results may be stated and explained as follows:

1. My prime conclusion is that the sex-specific susceptibility to fish predation in *Eudiaptomus* is affected both by differences in visibility and in escape ability between males and females.
2. All experiments ranked males as more susceptible than non-ovigerous females. This may be due to their inferior escape ability which possibly emanates from their habit not to perform evasive jumps immediately upon mechanical disturbances in the water. Males do not perform fewer evasive jumps than females when once escaping.
3. All experiments ranked ovigerous females as more susceptible than non-ovigerous. This is best explained by the visible egg sac which gives ovigerous females a higher encounter rate with the predator. Although non-ovigerous females were less escape inclined than ovigerous there was no difference in their escape success.
4. Ovigerous females were ranked as more susceptible than males only in one of the zebrafish experiments. They could not be ranked in the roach experiment, which should be pointed out since roach, unlike zebrafish, is a main natural predator on *Eudiaptomus*.
5. Neither experiment showed significant differences in male and overall female mortality but from the significant difference in susceptibility between ovigerous and non-ovigerous females follows that the sex-specific mortality should have been dependent on the reproductive condition in the experimental population.

Although this study shows that both encounter frequencies and escape reactions influences sex-specific mortality in *Eudiaptomus*, the result can not be used to quantify their relative importance with accuracy under natural conditions. The difference in encounter rates between the prey categories in these experiments may have been underestimated because of the small water volume used. Especially in the predation sequence study a significant part of the reactive field of the fish is 'outside' the tank. The greater the reaction distance to a prey category, the larger portion of the reactive field will be screened off and therefore the measured difference in encounter frequency will be lower than the true difference. This will reduce the role of encounter in comparison to escape behaviour. On the other hand, it might be argued that the size of the tank also restrict the copepods opportunity to escape out of the reactive field in relation to their visibility. The greater the reaction distance, the smaller is the refuge to escape to inside the tank, but this interference is probably of minor importance in this study since the major difference in sex-specific escape success can be explained by whether or not the copepods escaped at all.

The few previous studies on sex-specific mortality in diaptomids exposed to fish predation are not concordant. In a series of papers on the timing of diapausing egg production Hairston and coworkers (Hairston *et al.*, 1983; Hairston, 1987) point out and show the significant mortality risk associated with the female ovigerous condition. They also use the increase of the male proportion in a natural population of *Diaptomus sanguineus* as an index of sunfish predation on ovigerous females (Hairston & Munns, 1984). None of my experiments gave significant differences between male and female mortality. However, there is strong evidence for the disadvantage of the highly visible ovigerous females, as compared to non-ovigerous, in my study. This also supports the opinion that fish predation is the selective force behind the strong vertical migrating behaviour of ovigerous females of *Eurytemora hirundoides* (Vourinen *et al.*, 1983; Vourinen, 1987). Heavy fish predation on ovigerous females has also been proposed to select for gut passage resistance in cyclopoid eggs (Gliwicz & Rowan, 1984).

Maly (1970) reported higher male mortality of *Diaptomus oregonensis* when exposed to guppies, and since males were more active and fastswimming he presumed that this was an effect of a higher encounter rate. Although I did not directly measure the activity of the different prey categories in my experiment I could not detect any male disadvantage neither in encounter rate nor in encounter time.

Besides differences in experimental setup, different preferences of the fish species used, and the evident possibility that there in fact exists real differences in sex-specific susceptibilities to fish predation among these different diaptomid species, there are some other points that should be made when discussing this discordance.

First; as a consequence of the abrupt change in susceptibility between the ovigerous and non-ovigerous states, it follows that the relative sex-specific mortality should depend on the frequency of females reproducing. That is, the relative predation pressure on females should increase with the proportion of females carrying eggs. In my experiment 50% of the females were ovigerous. Maly (1970) gives no information about the frequency of ovigerous females while Hairston *et al.* (1983) reports female biased mortality in a natural population when 40% of the females carried eggs.

Second; by invoking the difference in escape ability, the sex-specific mortality may be affected by the attack efficiency of the predator. An inefficient predator should be relatively more successful in capturing males than in capturing the more escape inclined females. The capture success of an efficient fish may be less dependent on the escape ability of the prey; their impact on the sex-specific mortality should to a greater extent be governed by encounter rates. This predicted efficiency dependence may be important when comparing different planktivorous fish species. Winfield & Townsend (1983) showed that roach and bream (*Abramis brama*) differed in efficiency in capturing encountered ovigerous and non-ovigerous cyclopoid copepods. They proposed that the ovigerous-biased attack efficiency of roach, the less efficient predator, was due to impaired acceleration and manoevrability in prey individuals carrying the burden of egg sacs.

The attack efficiency, and hence the effect on sex-specific copepod mortality, may also differ between individuals within a predator population. This may have consequences for the seasonality of sex-specific mortality in diaptomids. It is reasonable to assume that attack efficiency of a planktivorous fish is increasing as it grows from newly hatched fry to adulthood. In temperate lakes predation from inexperienced newborn young fish in spring and early summer may then be relatively more directed towards the less-escaping sex and, as the season pass and the predator grows, turn more against the most encountered prey.

Origin of sex-specific escape performance

Why do the sexes differ in escape ability? One answer is that it may be a secondary effect of differences in body size (in these experiments mean female cephalothoraxlength = 0.83 mm, mean male = 0.75 mm). A larger female may be a more successful escaper than a smaller male since she may put more power into the escape jumps. This size factor may, however, by counterbalanced by another inversely scaled relationship. The success of an encountered copepod to escape visually feeding fish is still dependent on its visibility; a smaller, less conspicuous male, has a shorter distance to go when trying to escape out of the reactive field of a fish.

An alternative view is that escape ability may be selected as a trait (traits) of its own and that differences in escape ability is not just a consequence of body size. Existing life history theory states that in species without male parental care, selection favours male adaptations that lead to high intrasexual competitive ability for mates (Trivers, 1972).

The component of escape performance that showed the most apparent difference between males and females in my experiment was the inclination or ability to make evasive jumps in time when fish attacked. Both female categories did significantly better than males in this respect. This difference may have evolved by assymmetries in intrasexual selection for mate recognition. A strong evasive reaction is an advantage for both sexes when confronted with a predator, but it may be of unequal value when detecting and locating the opposite sex.

The mechanisms of mate encounter in *Eudiaptomus* is not understood in detail but males of other calanoid genera seem to use hydrodynamical cues (Watras, 1983) or pheromones left in the females swimming track (Katona, 1973; Griffiths & Frost, 1976) to identify potential mates at a distance. If a male is to approach a female he cannot just escape when her movement cause mechanical disturbances in the water. As proposed by Gerritsen (1978, 1980) when accounting for the 'stop and listen' behaviour of male *Cyclops scutifer*, he would at least have to spend some time to analyse the information given in the swimming wake. Sexual selection may then favour a higher escape threshold in males since it decreases the probability of escaping from a potential mate. Females, on the other hand, may afford to always escape from all encountered males except when she is receptive.

The hypothesis that escape performance may be connected to the copepods motivation to mate has further support in my results. The two female types did not differ in overall escape success, but non-ovigerous females were less escape inclined than ovigerous females. Since remating is necessary for the production of each viable clutch in diaptomids (Watras, 1983) this is the predicted outcome, assuming that not all the gravid and non-ovigerous females in the experiment were already successfully mated. Female diaptomid copepods vary between gravid and non-gravid conditions which is distinct from ovigerous/non-ovigerous states (Watras & Haney, 1980) but it seems less probable that ovigerous females are able, and hence motivated to mate, since the egg sac would make it impossible for the male to transfer the spermatophore to her urosome.

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