

Life history responses of *Amphiascus tenuiremis* (Copepoda, Harpacticoida) to mimicked predation*

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ABSTRACT: Potential demographic effects of life stage or gender specific predation on population size and composition were investigated using populations of a laboratory-reared benthic harpacticoid copepod, *Amphiascus tenuiremis* cf. Mielke, 1974. Control populations initially contained 100 copepodites, 100 adult males and 100 adult females. In the experimental treatments, one of these components was reduced by 90 or 50 % to mimic 30 or 17 % once-in-time predation impact. Number of nauplii, copepodites, adult males, adult females and total population size was recorded for each population after 21 d (1 generation). Abundance increased in all populations, and at both levels removal of females (female treatment) resulted in significant decreases in final total abundance. Copepodite and male removal had no significant effect on total population size. Final population composition was also affected by treatment. In the 90 % removals final abundances of nauplii were significantly lower in female removal treatments. At the 50 % removal level, final number of nauplii and copepodites was lower in female treatments only. Number of males was significantly lower in male treatments at both levels of removal, as was number of females in female treatments. Female specific predation had the greatest effect on these copepod populations. Total population size decreased because number of nauplii (which comprised 75 to 80 % of each population) was significantly decreased. High reproductive potential, as indicated in up to 28-fold increases in population size over 1 generation, intimated that the observed changes in population size and composition would not be enduring. Predation, imitated herein by removal, would play a small role in determining population structure of *A. tenuiremis*.

INTRODUCTION

In their discussion of the ecological role of meiofaunal harpacticoid copepods, Hicks & Coull (1983) asked how predation by higher trophic levels influenced the structuring of benthic copepod populations. In recent years, research in meiofaunal ecology has expanded to include field and laboratory studies addressing this question (reviewed by Coull & Palmer 1984). The full spectrum of results, from no significant impacts to declining abundance and threatened viability of the copepod population, have been observed. Predation by hydroids (Heip & Smol 1976), and a

variety of fishes (Reise 1979, Alheit & Schiebel 1982, Hicks 1984, Sogard 1984, Gee et al. 1985, Gee 1987) did not appear to significantly alter copepod population size for some epibenthic harpacticoid copepods. Other epibenthic harpacticoid copepods experienced significant abundance declines associated with fish or shrimp predation (Feller & Kaczynski 1975, Bell & Coull 1978, Sibert 1979, Bell 1980, Dethier 1980, Warwick et al. 1982, Coull & Wells 1983, Hicks 1985, Smith & Coull 1987, Palmer 1988, Ellis & Coull 1989, Nelson & Coull 1989). Laboratory experiments imitating predation (Hoppenheit 1975a, b, 1976, Dethier 1980) indicated that constant predation pressure affected abundance and composition of a single species copepod population. The complexity of the question is evident.

This study examines the question of effects of one-time predation on certain aspects of population demo-

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graphics by mimicking controlled predation on a single species population of meiobenthic copepod in a laboratory setting. The null hypothesis tested was that this kind of predation had no effect on population size or stage composition. Confounding factors such as interspecies competition (for food and space), chemical and physical environmental variations over time and space, immigration, emigration and disturbance are minimized by the experimental design. Intraspecific density-related effects are unlikely to influence the outcome, as estimated maximum final density of 10 000 copepods per chamber (224 copepods per 10 cm²) was similar to mean copepod densities in North Inlet, South Carolina, USA, which was the source of these specimens (Coull & Dudley 1985).

The experimental copepod *Amphiascus tenuiremis* (Brady & Robertson, 1875) cf. Mielke (1974) is an epibenthic, euryhaline harpacticoid. *A. tenuiremis* conforms to the common harpacticoid copepod life history pattern (Lang 1948) with 6 naupliar and 6 copepodite stage. The sixth copepodite is the sexually mature adult. Clasped pairs may involve Stage 5 females but copulation does not occur and eggs are not extruded until after the fifth copepodid molt. Eggs are carried externally in sacs, from which the nauplii hatch and crawl away.

Body size and behaviour may contribute to stage- or gender-specific natural predation on *Amphiascus tenuiremis*. Mature female copepods are generally larger in size than any other population component, especially when in copula or carrying eggs. Bodiou & Villiers (1979) reported that the mean size of harpacticoids in goby stomachs was larger than that in the source population and epibenthic harpacticoids were the most commonly observed in the goby. In the laboratory, adult female *A. tenuiremis* spend more time than nauplii, copepodites or males on top of the substrate, in the water column and underneath the water surface. If this behaviour is representative of field populations, then higher relative predation risk to females is likely. Adult males, on the other hand, are smaller and thus at less predation risk. Copepodites exhibit behaviour similar to that of adults but are even smaller than male adults, and thus assume lower predation risk. Nauplii spend most of the time on or in the sediment, rarely venturing into the water column, thereby reducing risk from visually cued predators. This behaviour pattern may result in high exploitation by predators like spot *Leiostomus xanthurus* which take bites of sediment and filter out organisms for consumption (Billheimer & Coull 1988). The probable primary predators of this copepod are immature estuarine fishes (Ellis & Coull 1989, Nelson & Coull 1989, Feller et al. 1990) some of which may use visual cues for prey location. The experiments reported below

provide new information about the population composition of *A. tenuiremis*, and the potential role of predation in determining its population dynamics.

MATERIALS AND METHODS

The original source of *Amphiascus tenuiremis* stock was North Inlet (Georgetown, South Carolina, USA; 33°19'N, 79°10'W) where it inhabits sand and mud communities in *Spartina alterniflora* Loisel salt-marshes. Seasonal patterns of abundance, gender and life stage ratios are not fully known but this species proved to be easy to maintain in laboratory cultures (following Chandler 1986) and possessed high reproductive potential.

Preliminary experiment. The generation time of *Amphiascus tenuiremis* was determined by observing 10 gravid females and 10 mating pairs, isolated in individual small petri dishes. These cultures were maintained under the same feeding and environmental conditions as the removal experiments (see below) except that these preliminary experiments were carried out under static conditions, not in the flow-through seawater system. Cultures were examined daily and every individual enumerated by stage and/or gender. Mean generation time (egg to egg) was 20.8 d (range 20 to 23 d) under these static conditions. Thus, we selected 21 d, 1 generation, for our mimicked predation experiments.

Mimicked predation experiments. Predation was mimicked by reducing initial number of 1 of the 3 starting components: adult (gravid and non-gravid) females, adult males and copepodites, and is referred to as 'treatment'. The treatments were called 'female', 'male' and 'copepodite', respectively. Nauplii were not included in initial composition due to the inability to obtain the large numbers required.

We conducted 6 experiments: 3 at 90 % removal of the target population with controls (no removal), and 3 at 50 % removal of the target population with controls (Table 1). Thus each experiment consisted of 2 replicates of the controls and 2 replicates of 3 treatments (Table 1). Ninety percent removal represented 30 % decrease in initial population size and 50 % removal represented 17 % decrease. These removal levels were selected to provide a wide range of one-time 'predation' impact without completely eliminating the target component. Control populations did not have any component removed, and contained 100 copepodites (sex unknown), 100 males and 100 females (approximately 50/50 ovigerous and non-ovigerous). Three experiments, with 2 replicates each, were performed separately and sequentially at the 2 removal levels (Table 1). For example, experiments with 90 %

Table 1. *Amphiascus tenuiremis*. Initial composition of experiments, and number of individuals per chamber. Maximum abundance, in control populations, equaled 300 copepods. Each experiment (90 % removal) and 50 % removal was repeated 3 times

Treatment	Replicate	Number of each component		
		Copepodites	Males	Females
90% Removal level (Expts 1, 2 & 3)				
Control	1	100	100	100
	2	100	100	100
Copepodite	1	10	100	100
	2	10	100	100
Male	1	100	10	100
	2	100	10	100
Female	1	100	100	10
	2	100	100	10
50% Removal level (Expts 4, 5 & 6)				
Control	1	100	100	100
	2	100	100	100
Copepodite	1	50	100	100
	2	50	100	100
Male	1	100	50	100
	2	100	50	100
Female	1	100	100	50
	2	100	100	50

removal (Expts 1, 2 & 3) used initial population sizes of 210 copepods, involving reduction of the 'treatment' component from 100 individuals to 10 individuals. Similarly, 50 % removal level experiments (Expts 4, 5 & 6) initially contained 250 copepods with reduction of the 'treatment' component from 100 to 50 individuals (Table 1). All experiments were performed in an environmentally-controlled laboratory, using the flow-through artificial seawater/culture system designed by Chandler (1986). Salinity averaged 30 ppt, temperature ranged from 22 to 24 °C and daily photoperiod was 14 h of light and 10 h of darkness.

Eight experimental chambers were constructed from cylindrical plastic finger bowls, 10.2 cm (inner diameter) wide by 4 cm deep. A 12 cm length of 0.6 cm diameter Tygon tubing was snugly inserted into a drainhole 1 cm from the top of each dish, and a filter made of 44 µm Nitex mesh was cemented across the inside of the opening. This prevented organisms from escaping but did not inhibit drainage, and could be easily aspirated clean of algae and waste materials after each feeding. Surface area was 81.7 cm² and with water level at 3 cm (determined by drainhole height), habitable volume was 254.8 cm³.

Food in all experiments was frozen, concentrated suspensions of the unicellular alga *Isochrysis galbana*

(Chrysophyceae, Chrysophyta). Frozen, concentrated algal suspension was brought to room temperature and agitated (to break up cell clumps). An equal volume of well-mixed suspension was pipetted into each experimental chamber every third day in the 21 d experimental period. Rations were calculated to feed to excess in order to minimize potential influence of food deprivation on reproductive capacity (Ustach 1982, Vilela 1984) and population composition (Hicks & Coull 1983).

In preparation for each of the 6 experiments, 8 chambers were connected to the seawater system and allowed to fill. An aliquot of autoclaved 44 µm sieved sediment (prepared following the procedure in Chandler 1986) was homogenized in seawater and poured into each chamber. After 6 to 8 h settling time, each chamber contained a smooth layer of sediment 3 mm thick. Chamber filters were aspirated clean of excess fine sediment to facilitate water drainage, prior to addition of organisms.

Control and treatment populations were assembled from stock cultures. Stock specimens were obtained from muddy sediments from North Inlet, approximately 2 yr (30 generations) prior to the experiments. Stock populations were maintained under the same environmental conditions in a flow-through seawater system, with excess food. Complete assembly of a single experiment required 6 to 8 h of sorting, necessitating precautions to minimize pre-experiment alteration of population composition. During the sorting period, each treatment was assembled in a separate watch glass, supplied with food and placed in a constant environment chamber, awaiting the start of the experiment. When all 8 populations (per experiment) were assembled, the contents of each watch glass were gently washed into its randomly assigned chamber in the array connected to the seawater system.

After 21 d, the population in each of the 8 chambers was terminated and fixed in a 4 % formaldehyde solution containing Rose Bengal. All copepods were enumerated by life stage and gender in the following categories: nauplius, copepodite, adults. Adults were enumerated as male, gravid female and non-gravid female. Detailed enumeration of the 6 naupliar and 5 immature copepodite (juvenile) stages was not performed.

Data analyses. The original experimental ANOVA model was 2-factor (level of removal and treatment) with a blocking factor (experiment). There was significant interaction between the factors level and experiment, which prohibited statistical comparisons between the 2 levels of removal. Additionally, variability among experiments (of the same level) was often more significant than effects of level of removal, especially at the 90 % level, where Expt 3 had signifi-

cantly fewer individuals than Expts 1 & 2. However, the pattern of treatment effects was not significantly different ($F = 2.18$, $p = 0.1183$) in Expt 3 from that in Expt 1 or 2. Therefore, data from Expt 3 were included in statistical comparisons. At the 50 % level, inter-experimental differences were also present but the pattern of treatment effects was similar. Sources of variability could not be specifically identified but pooling gravid and non-gravid females in the female treatments and the unknown ages and gender ratios of the copepodites could have contributed to this variability. The stock population which was the source of all experimental subjects was 30 generations old and was presumed to have a stable age distribution and to be nearly genetically uniform. Due to the high inter-experiment variability at each level, analyses of variability were confined to inter-treatment comparisons of population abundance, population composition and gender ratio. Therefore, the original theoretical model changed from blocked, 2-factor, with experiment as the blocking factor, to 3-factor, with level, experiment and treatment as factors:

$$Y_{ijk} = u_{ijk} + \text{Level}_i + \text{Experiment}_j + \text{Treatment}_k + E_{ijk}$$

where u = overall mean; E_{ijk} = variation between experiments; $i = 2$ (90 % or 50 %); $j = 3$ (1, 2 or 3; 4, 5 or 6); $k = 4$ (control, copepodite, male or female).

All data analyses were performed using SAS Institute (1985) statistical analysis programs. Population size variance and population composition variance were compared within level of removal among treatments using Tukey's multiple comparison of means procedure ($\alpha = 0.05$). In all analyses, values for Replicate 1 and Replicate 2 of each experiment were averaged for use in comparisons.

Population abundance data were \log_{10} transformed to meet ANOVA assumptions of normal distribution. Population composition was compared using abundance of each component and gender ratio (number of females per male).

Estimates of daily rate of predator impact on a single component were calculated from the percentage of copepods initially removed (90 or 50 % out of 300) of the experiments. Using raw data, the following quantities were calculated:

$$\text{Maximum percent impact} = \frac{\text{copepods removed}}{\text{initial abundance}} \times 100$$

$$\text{Minimum percent impact} = \frac{\text{copepods removed}}{\text{final abundance}} \times 100$$

Estimated mean percent impact was the average of maximum and minimum percent impact. Estimated daily mean percent impact (dmipi) was obtained by

dividing the mean percent impact by 21, the number of days that each experiment ran.

RESULTS

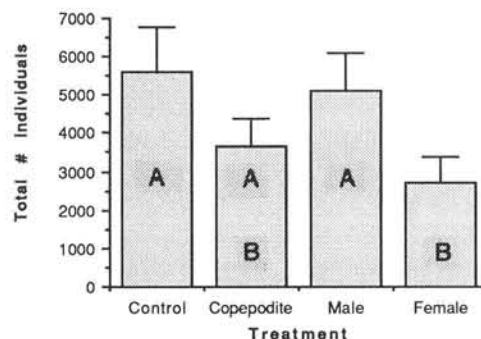
Total population abundance

Final total population size after 1 generation was greater than initial population size in all treatments. In each instance, the magnitude of increase (final total abundance/initial total abundance) was greater than a factor of 10 (Table 2).

Table 2. *Amphiascus tenuiremis*. Mean increase in abundance (times initial) over 1 generation (21 d) in the laboratory

Treatment (Component removed)	Increase in abundance	
	90 % removal	50 % removal
Control	28.6	18.0
Copepodite	17.4	14.8
Male	24.4	16.4
Female	12.8	12.5

A. Population sizes in the 90% level treatments



B. Population sizes in the 50% level treatments

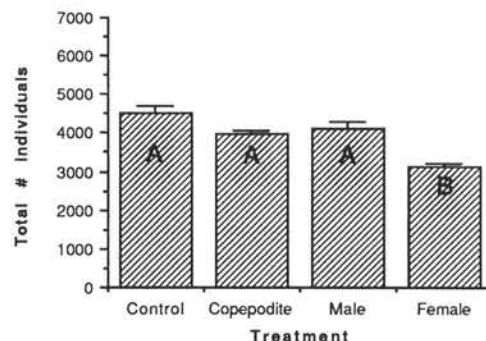


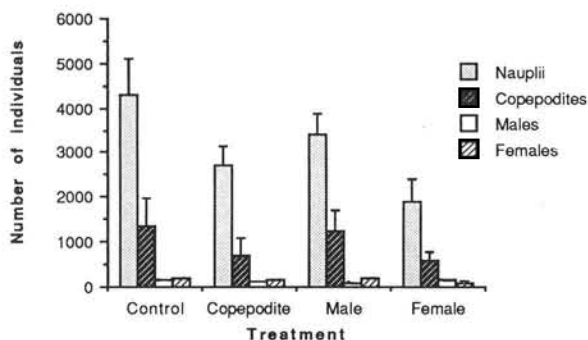
Fig. 1. Mean abundance ($n = 6$ for each bar) at end of 21 d for control (no removal), copepodite, male and female removal populations. Error bars = 1 SE of mean. Bars with similar letters are not significantly different from each other (Tukey's multiple comparison procedure; experiment-wise error rate ≤ 0.05)

Final population abundance was significantly different among treatments at both the 90 and 50 % removal levels. At both removal levels, female removal resulted in total abundance which was significantly lower than that in controls (Fig. 1).

Population composition

There were treatment effects on abundance of each component (Fig. 2). At the 90 % removal level (Table 3) mean number of nauplii and females was each significantly lower in the female removal treatment and mean number of males was lower in the male removal treatments. Only mean number of copepodites was not significantly different across all treatments (Table 3). At the 50 % removal level, mean number of nauplii, copepodites and females each was significantly lower in the female treatment and mean number of males was lower in the male treatment (Table 3, Fig. 2).

A. Composition in 90% level treatment populations



B. Composition in the 50% treatment populations

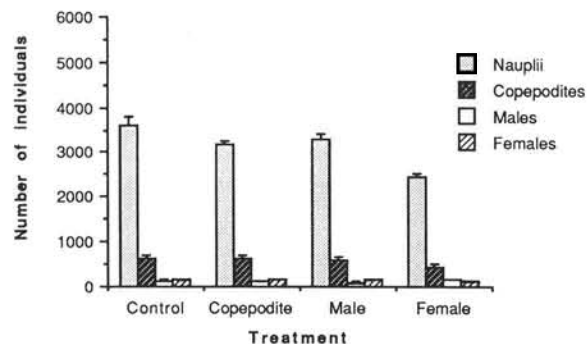


Fig. 2. Mean abundance + 1 SE at end of 21 d of nauplii, copepodites, males and females in the control (no removal), copepodite, male and female removal treatments. See Table 3 for multiple comparison results on these values

Table 3. *Amphiascus tenuiremis*. Mean abundance of life history stage (nauplii, copepodites, males, females at end of 21 d in controls (C), copepodite removal (J), male removal (M) and female removal (F) treatments. Values with a common underline are not significantly different from each other for the particular life history stage (Tukey's multiple comparison procedure; experiment-wise error rate ≤ 0.05): e.g. in the 90 % removal experiments the mean number of nauplii at 21 d was 4295 in the controls, 3419 in the male removals, 2717 in the copepodite removals and 1894 in female removals and only the number of nauplii in the female treatment was significantly different

Life history stage	Mean abundance			
90 % Removal level				
Nauplii	C	M	J	F
	4295	3419	2717	1894
Copepodites	C	M	J	F
	1373	1245	684	568
Males	C	F	J	M
	147	137	113	75
Females	M	C	J	F
	195	181	140	90
50 % Removal level				
Nauplii	C	M	J	F
	3608	3295	3155	2436
Copepodites	C	J	M	F
	626	607	562	431
Males	F	C	J	M
	144	125	121	89
Females	M	C	J	F
	155	149	137	103

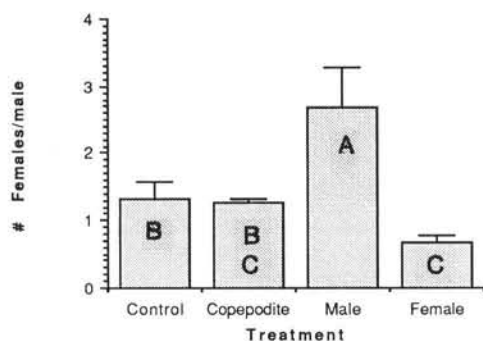
Gender ratio

There were treatment effects on gender ratio at each removal level (Fig. 3). At the 90 % removal level, gender ratio was significantly higher in male removal treatment populations than in copepodite removal, female removal treatment or control populations. Gender ratio was also significantly different between control and female treatment populations. At the 50 % removal level, gender ratio was significantly higher in male treatments and lower in female treatment populations, compared to control and copepodite removal treatment populations, which were not significantly different from each other (Fig. 3).

Daily mean percent impact

At the 90 % removal level, treatment effects were not definitive (Table 4), but at the 50 % removal level female removal treatment had a significantly higher

A. Mean gender ratio in the 90% level treatments



B. Mean gender ratio in the 50% level treatments

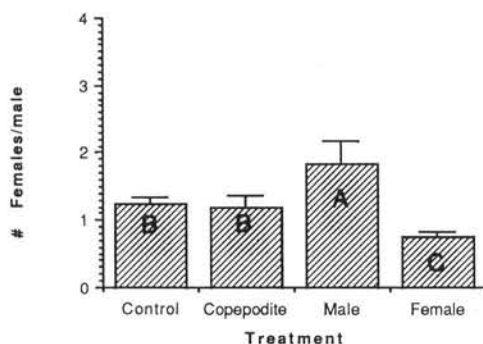


Fig. 3. Mean gender ratios ($n = 6$ for each bar) at end of 21 d for control, copepodite, male and female removal treatments. Error bars are ± 1 SE

impact on the population (Table 4) than the removal of any other single population component.

DISCUSSION

Effects of removal on total population abundance

Each population increased in abundance by a factor (mean final abundance/initial abundance) greater than 10-fold (Table 2), independent of treatment, indicating the high potential fecundity of *Amphisascus tenuiremis* in the optimal environmental conditions provided. Only the initial removal of females from the population had an effect on subsequent population size (Fig. 1), primarily due to either significant decreases in number of nauplii produced or high naupliar mortality, compared to number of nauplii in the other treatments and controls (Fig. 3). Reduction of number of adult males did not have similar effects. Females of most harpacticoids (and presumably *A. tenuiremis*) have the ability to store sperm (Hicks & Coull 1983) and thus reduce dependence of uninterrupted egg production on continuous presence or high density of males.

Table 4. Results of ANOVA comparison of daily mean percent impact (dmpi) at 90 and 50 % removal levels. See Table 3 for definition of 'component removed' letters. Tukey results with the same letter are not significantly different at $\alpha = 0.05$

Component removed	DMPI	Tukey result
90 % Removal level		
C	0.763	B
M	0.770	B
J	0.789	A B
F	0.876	A
50 % Removal level		
C	0.423	B
M	0.426	B
J	0.427	B
F	0.435	A

Copepodite removals had little effect on total population abundance (Fig. 2, Table 3) because the percentage of copepodites removed (30 and 17 % for 90 and 50 % removal, respectively) was lower than copepodite mortality rates. Recruitment (survival of nauplii) was less than 17 % so that the impact of mimicked predation could not be distinguished from low recruitment. Feller (1980) reported 25 % copepodite mortality for *Huntemannia jadensis* and estimates of 33 to 36 % copepodite mortality were obtained from a life table for *Tisbe holothuriae* (Bergmans 1981).

Naupliar reductions were not performed in our experiments, but initial removal of nauplii should not have had significant effects on final total abundance, given the known high naupliar mortality in harpacticoids. D'Apolito & Stanczyk (1979) calculated 85 % naupliar mortality for *Euterpina acutifrons* in the laboratory. Feller (1980) observed 32 to 100 % naupliar mortality for *Huntemannia jadensis* and Bergmans (1981) reported 44 % naupliar mortality for *Tisbe holothuriae*. Fleeger (1979) and Palmer (1980) concluded that high death rates for *Microarthridion littorale* were due to high naupliar mortality because nauplii were the numerically dominant life stage. Based on these findings, the highest removal level employed herein (30 %) would not have significantly affected final naupliar abundance. A *posteriori* confirmation is evident in our estimated naupliar survival (mean final percentage of copepodites), which ranged from 14 to 16 %. Population size was most reduced by initial removal of females, due to significant decreases in number of nauplii. Predation or any disturbance which selectively impacts females, the population component which controls the reproductive capacity of *Amphisascus tenuiremis*, has the highest potential to decrease population abundance.

Effects of removal on population composition

Low juvenile survival (nauplii and copepodites, combined) was indicated in the low final adult male and female abundances, which were lower than copepodite and nauplii abundance in all treatments (Fig. 2) despite the high reproductive potential of *Amphiascus tenuiremis* (Table 2). Male replacement was low in the male removal treatments and female replacement was depressed in the female removals (see gender ratios, Fig. 3). In each of these treatments, the 100 copepodites and many more maturing nauplii should have been able to replace the 90 adult males or females removed. Thus, survival to adulthood must have been less than 17 % (loss of 90 individuals out of 300). *A. tenuiremis* completes its life cycle in 21 ± 1 d under these conditions so all of the initially-present copepodites and some early-hatched nauplii could have matured within the experimental period. The low final abundances of adults, coupled with high reproductive potential (Table 2) indicated low survival of nauplii and copepodites. High adult mortality could potentially be responsible for the low adult numbers, but our observations on stock-cultured *A. tenuiremis* indicate they live 60 to 90 d. Thus there is no *a priori* reason to assume increased adult mortality in our treatments. In our experiments, mean final number of adults ranged from 6.0 to 15.8 % of the final total population size.

Under the experimental conditions, *Amphiascus tenuiremis* did not display any compensating mechanism to combat the effects of 90 or 50 % loss of its reproductive potential. If it had, there would have been no treatment effects on population size, composition or gender ratio. *Tisbe holothuriae* use compensation mechanisms in response to imitation predation: 90 % weekly population reduction reduced egg development rate and naupliar mortality and increased survival of males (Hoppenheit 1975b, 1976). *A. tenuiremis* may not have these mechanisms. Our experiments were probably too short a duration (1-generation) treatments for compensating mechanisms to be invoked.

While our 2 levels of predation each elicited responses from the copepod populations, the levels of impact imposed were not different enough to delineate upper and lower boundaries of potential effects on population size and composition. The less severe of the 2 treatments caused responses similar to the severe treatment. Impacts of greater than 90 % removal of copepodites or males would be required to show significant abundance/composition effects. Similarly, impacts of less than 50 % removal of females would be required to determine level of no effects.

Types of potential responses to predation pressure

Natural copepod assemblages have been found to be highly variable in species composition and temporal abundance (e.g. Hicks 1979, Hicks & Coull 1983, Gee & Warwick 1984, Coull & Dudley 1985, Johnson & Scheibling 1986, Palmer 1988). Using highly controlled populations, limited diversity taxocenoses (e.g. laboratory-raised monocultures or assemblages) or naturally occurring low diversity assemblages should help to separate effects of environmental and genetic variation from effects of the imposed experimental treatments. To date, few studies of the population dynamics of harpacticoid monocultures have been conducted. Dethier (1980) conducted field and laboratory studies of *Tigriopus californicus*, which inhabits high intertidal pools with few other occupants. She reported significant decreases in abundance of the copepod due to predation by fish or sea anemones during periods of 1 to 4 d. Such effects, which are basically the primary reactions to a disturbance, may indicate that the organisms did not or could not compensate by altering reproductive rates. These types of effects which do not appear to involve any response by the affected organisms are defined herein as 'first order effects', or 'passive responses' and are associated with short term or rare, intermittent disturbances. Potential for long-term changes in population composition was addressed by Hoppenheit (1975b, 1976) in a series of predation-imitation experiments with *Tisbe holothuriae*. His results, over an observation period of 24 wk, indicated that significant alterations of the population resulted from long-term, constant predation pressure. He observed changes in gender ratios, egg viability rates and naupliar and male mortality – effects which probably indicate that compensating mechanisms had been invoked. We define the efforts of a disturbed population to restore demographic parameters to pre-disturbance levels or values, especially under conditions of constant predation pressure, as 'second order effects' or 'active responses'. These types of mechanisms would eventually become a part of the evolutionarily stable strategy of the population if predation was constant and persistent for a long enough time.

The 1-generation time course of our experiments does not allow for long-term compensating mechanisms *sensu* Hoppenheit (1975b, 1976) and our results are obviously first order effects, despite the fact that the experiments covered 100 % of the generation time (defined as long term; (Wilson & Bossert 1971). The observed effects of stage or gender specific predation were only passive responses, involving reduction of total abundance and nauplii. *Amphiascus tenuiremis* most likely does not possess the physiological flexibility to alter fecundity within

1 generation and more than 1 generation would be required to stabilize gender ratio after catastrophic demographic perturbation.

Predation impact

It is generally assumed that predation is a continuous or regularly occurring event and not a one time event as we mimicked. Yet we are unaware of quantitative data on the predation frequency on a harpacticoid population in the field. The presence of copepods in predator guts over time does not unequivocally mean that the same prey population was eaten each time. In the southeastern United States schools of harpacticoid feeding juvenile spot *Leiostomus xanthurus* swim onto a mudflat, feed on some portion of the flat (often a very small portion of 1 or 2 m) and swim off. Observing 1 mudflat over 4 d we did not observe another spot school on that flat, indicating that at least over 4 d there was not a continuous predation impact on the resident harpacticoids, yet juvenile spot almost always have harpacticoids in their guts (Feller et al. 1990). Whether the fish returned to the same mudflat within 21 d (the time of our experiment) is unknown. Thus while we mimicked a once in time predation event, we did so because of our observations on feeding spot in South Carolina. Our experiments then should be viewed as simulating natural conditions but perhaps at a low predation rate.

Impact of predator exploitation on copepod populations has been calculated for a variety of predators ranging from juvenile flatfish (Hicks 1985) to shrimp

(Gee 1987). A summary of estimated predator effects on various field populations of harpacticoid copepods is presented in Table 5. In each example, a single species was the dominant prey item and represented a large proportion of the copepod assemblage. Estimates of daily consumption rate of the dominant predators ranged from 0.01 to 3.45 %. In each case, the author concluded that predation at the above-stated rates would not significantly alter the respective copepod population.

In our experiments, female removal at the 90 % removal level resulted in the highest daily mean percent impact removal level, 0.876 % d⁻¹, and female removal at the 50 % removal level, 0.435 % d⁻¹ (Table 4). These values are comparable to published estimates of predation impact where there was little or no observable effects on the copepod populations. Therefore, the changes which were observed in abundance and composition of the populations of *Amphiascus tenuiremis* should not be long lasting. These first order effects would have probably been eliminated within the next few generations, given the high reproductive potential of this copepod. Since compensating mechanisms were not involved with *A. tenuiremis*, we conclude that the imitated predation pressure which we invoked was not severe or long enough to require such strategies. Daily predation pressures of 12.8 and 7.1 % on *Tisbe holothuriae* populations (Hoppenheit 1976) resulted in compensation mechanisms: rates are 4 to 200 times higher than reported field values. Our field-comparable results suggest that *A. tenuiremis* did not, or would not, require alteration of physiological parameters to cope with predation.

Table 5. Selected literature on predator impacts on benthic harpacticoid copepods

Predator	Prey	Removal by predator (% d ⁻¹)	Conclusion	Source
Tomtate <i>Haemulon aurolineatum</i>	<i>Longipedia helgolandica</i>	0.02	Predicted no impact at 0.1 % d ⁻¹	Alheit & Scheibel (1982)
Spotted dragonet <i>Callionymus pauciradiatus</i>	Harpacticoids	0.05 – 3.45	No impact at 3 × observed fish density	Sogard (1984)
Juvenile flatfish	<i>Parastenhelia megarostrum</i>	0.38	No impact	Hicks (1985)
Plaice <i>Pleuronectes platessa</i>	<i>Asellopsis intermedia</i>	0.012 – 0.097	None, unless predator abundance 1000 × higher	Gee (1987)
Shrimp <i>Crangon crangon</i>	"	0.015 – 0.097	"	"
Gobies <i>Pomatoschistus microps</i> and <i>P. minutus</i>	"	0.015	"	"
Gobies, plaice, shrimp	"	0.01 – 0.10	"	"

Gobies and blennies are reported to preferentially prey on large or female benthic copepods (Bodiou et Villiers 1979, Coull & Wells 1983, respectively) but a flatfish selectively preyed on nauplii (Hicks 1984). If size or gender-specific predation on harpacticoids is commonplace in the field, and our controlled mimicked predation is indicative, then only the removal of females would have an effect on population size. If the prey copepod has the ability to reproduce rapidly (*sensu* *Amphiascus tenuiremis*), then predation effects on demographic parameters should not be long lasting, unless the predation pressure is continuous. Most harpacticoid copepods apparently have the ability to out-reproduce any removal due to predation.

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LITERATURE CITED

- Alheit, J., Schiebel, W. (1982). Benthic harpacticoids as food for fish. *Mar. Biol.* 76: 141–147
- Bell, S. S. (1980). Meiofauna-macrofauna interactions in a high salt marsh habitat. *Ecol. Monogr.* 50: 487–505
- Bell, S. S., Coull, B. C. (1978). Field evidence that shrimp predation regulates meiofauna. *Oecologia* 35: 141–148
- Bergmans, M. (1981). A demographic study of the life cycle of *Tisbe furcata* (Baird 1837) (Copepoda, Harpacticoida). *J. mar. biol. Ass. U. K.* 61: 691–705
- Billheimer, L. E., Coull, B. C. (1988). Bioturbation and recolonization of meiobenthos in juvenile spot (Pisces) feeding pits. *Estuar. coast. Shelf Sci.* 27: 335–340
- Bodiou, J. Y., Villiers, L. (1979). La predation de la meiofaune par les formes juveniles de *Deltentosteus quadrimaculatus* (Teleostei, Gobiidae). *Vie Milieu* 28–29: 143–156
- Chandler, G. T. (1986). High density culture of meiobenthic harpacticoid copepods within a muddy substrate. *Can. J. Fish. Aquat. Sci.* 43: 53–59
- Coull, B. C., Dudley, B. W. (1985). Dynamics of meiobenthic copepod populations: a long term study (1973–1983). *Mar. Ecol. Prog. Ser.* 24: 219–229
- Coull, B. C., Palmer, M. A. (1984). Field experimentation in meiofaunal ecology. *Hydrobiologia* 118: 1–19
- Coull, B. C., Wells, J. B. J. (1983). Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. *Ecology* 64: 1599–1609
- D'Apolito, L. M., Stancyk, S. E. (1979). Population dynamics of *Euterpina acutifrons* (Copepoda: Harpacticoida) from North Inlet, South Carolina, with reference to dimorphic males. *Mar. Biol.* 54: 251–260
- Dethier, M. N. (1980). Tidepools as refuges: predation and limits of the harpacticoid copepod *Tigriopus californicus* (Baker). *J. exp. mar. Biol. Ecol.* 42: 99–111
- Ellis, M. J., Coull, B. C. (1989). Fish predation on meiobenthos: field experiments with juvenile spot *Leiostomus xanthurus* Lacepede. *J. exp. mar. Biol. Ecol.* 130: 19–32
- Feller, R. J. (1980). Development of the sand dwelling meiobenthic harpacticoid copepod *Huntemannia jadensis* Poppe in the laboratory. *J. exp. mar. Biol. Ecol.* 46: 1–15
- Feller, R. J., Coull, B. C., Hentschel, B. T. (1990). Meiobenthic copepods: tracers of where juvenile *Leiostomus xanthurus* (Pisces) feed? *Can. J. Fish. Aquat. Sci.* 47: 1913–1919
- Feller, R. J., Kaczynski, V. W. (1975). Size selective predation by juvenile chum salmon on epibenthic prey in Puget Sound. *J. Fish. Res. Bd Can.* 32: 1419–1429
- Fleeger, J. W. (1979). Population dynamics of three estuarine meiobenthic harpacticoids (Copepoda) in South Carolina. *Mar. Biol.* 52: 147–156
- Gee, J. M. (1987). Impact of epibenthic predation on estuarine intertidal harpacticoid populations. *Mar. Biol.* 96: 497–510
- Gee, J. M., Warwick, R. M. (1984). Preliminary observations on the metabolic and reproductive strategies of harpacticoid copepods from an intertidal sandflat. *Hydrobiologia* 118: 29–37
- Gee, J. M., Warwick, R. M., Davey, J. T., George, C. L. (1985). Field experiments on the role of epibenthic predators in determining prey densities in an estuarine mudflat. *Estuar. coast. Shelf Sci.* 21: 429–448
- Heip, C., Smol, N. (1976). On the importance of *Protohydra leuckarti* as a predator of meiobenthic populations. In: Persoone, G., Jaspers, E. (eds.) *Proc. 10th Eur. mar. biol. Symp.* Universa Press, Wetteren, 2: 285–296
- Hicks, G. R. F. (1979). Pattern and strategy in the reproductive cycles of benthic harpacticoid copepods. In: Naylor, E., Marshall, R. G. (eds.) *Cyclic phenomena in marine plants and animals.* Pergamon Press, Oxford, p. 139–147
- Hicks, G. R. F. (1984). Spatio-temporal dynamics of a meiobenthic copepod and the impact of predation-disturbance. *J. exp. mar. Biol. Ecol.* 81: 47–72
- Hicks, G. R. F. (1985). Biomass and production estimates for an estuarine meiobenthic copepod, with an instantaneous assessment of exploitation by flatfish predators. *N.Z. J. Ecol.* 8: 125–127
- Hicks, G. R. F., Coull, B. C. (1983). The ecology of marine meiobenthic copepods. *Oceanogr. mar. Biol. A. Rev.* 21: 67–125
- Hoppenheit, M. (1975a). Zur Dynamik exploitierter Populationen von *Tisbe holothuriae* (Copepoda, Harpacticoida). I. Methoden, Verlauf der Populationsentwicklung und Einfluß der Wassererneuerung. *Helgoländer wiss. Meeresunters.* 27: 235–253
- Hoppenheit, M. (1975b). Zur Dynamik exploitierter Populationen von *Tisbe holothuriae* (Copepoda, Harpacticoida). II. Populationdichte, Wachstum und Ausbeute. *Helgoländer wiss. Meeresunters.* 27: 377–395
- Hoppenheit, M. (1976). Zur Dynamik exploitierter Populationen von *Tisbe holothuriae* (Copepoda, Harpacticoida). III. Reproduktion, Geschlechtsverhältnis, Entwicklungsdauer und Überlebenszeit. *Helgoländer wiss. Meeresunters.* 28: 109–137
- Johnson, S. C., Schiebling, R. E. (1987). Structure and dynamics of epifaunal assemblages on intertidal macroalgae *Ascophyllum nodosum* and *Fucus vesiculosus* in Nova Scotia, Canada. *Mar. Ecol. Prog. Ser.* 37: 209–227
- Lang, K. (1948). *Monographie der Harpacticiden*, I and II. Hakan Ohlsson, Lund
- Nelson, A., Coull, B. C. (1989). Selection of meiobenthic prey by juvenile spot (Pisces): an experimental study. *Mar. Ecol. Prog. Ser.* 53: 51–57
- Palmer, M. A. (1980). Variation in life history patterns between intertidal and subtidal populations of the meiobenthic copepod *Microarthridion littorale* Poppe. *Mar.*

- Biol. 60: 159–165
- Palmer, M. A. (1988). Epibenthic predators and marine meiofauna: separating predation, disturbance and hydrodynamic effects. *Ecology* 69: 1251–1259
- Reise, K. (1979). Moderate predation on meiofauna by macrobenthos of the Wadden Sea. *Helgoländer wiss. Meeresunters.* 36: 453–465
- SAS Institute (1985). SAS user's guide: statistics version 5. SAS Institute, Cary, North Carolina
- Sibert, J. (1979). Detritus and juvenile salmon production in the Nanaimo estuary: II. Meiofauna available as food to juvenile chum salmon (*Oncorhynchus keta*). *J. Fish. Res. Bd Can.* 36: 497–503
- Smith, L. D., Coull, B. C. (1987). Juvenile spot (Pisces) and grass shrimp predation on meiobenthos in muddy and sandy substrates. *J. exp. mar. biol. Ecol.* 105: 123–136
- Sogard, S. M. (1984). Utilization of meiofauna as a food source by a grassbed fish, the spotted dragonet, *Callionymus pauciradiatus*. *Mar. Ecol. Prog. Ser.* 17: 183–191
- Ustach, J. F. (1982). Algae, bacteria and detritus as food for the harpacticoid copepod, *Heteropsyllus pseudonunni* Coull and Palmer. *J. exp. mar. Biol. Ecol.* 64: 203–214
- Vilela, M. H. (1984). Production experiments of the marine harpacticoid *Tigriopus brevicornis* Muller, reared on various feeding regimes. *Bol. Inst. Nac. Invest. Pescas, Lisboa* 11: 83–115
- Warwick, R. M., Davey, J. T., Gee, J. M., George, C. L. (1982). Faunistic control of *Enteromorpha* blooms: a field experiment. *J. exp. mar. Biol. Ecol.* 56: 23–31
- Wilson, E. O., Bossert, W. H. (1971). A primer of population biology. Sinauer Associates Inc., Publishers, Sunderland, Massachusetts

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