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# Predator-induced diel vertical migration in a planktonic copepod

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**Abstract.** Predator evasion is the most commonly hypothesized reason for diel vertical migrations undertaken by a wide variety of planktonic organisms in lakes and seas, yet direct evidence remains elusive. We tested the predation hypothesis by exposing enclosed populations of a marine copepod *Acartia hudsonica* to caged or free-ranging individuals of their natural predator, the planktivorous fish *Gasterosteus aculeatus*. After little more than a week, adult copepods changed their vertical distribution and migration behavior depending on the presence or absence of predation. Only free-ranging fish induced vertical migration in the copepod population. Caged fish had no effect, indicating that vertical migration was not a simple chemically mediated response of copepods to the predator. Rather, copepods seemed to react to the presence of predators by other means, perhaps visual or mechanical stimuli, and to exhibit a downward escape response which, because encounters with visually orienting fish occur chiefly in the daytime, effectively limited the copepods' occurrence in the upper water column to the night-time hours. Alternatively, because fish imposed heavy mortality on copepods, it is possible that selective predation altered the proportions of individuals with fixed, genetically determined migration behaviors. We suggest experiments to distinguish these alternatives.

## Introduction

Diel vertical migration, widespread among planktonic animals in lakes and seas, is an important class of animal migration (Rankin, 1985). Typically, migrators inhabit the surface layer at night and make vertical excursions of a few to tens or hundreds of meters to spend the daylight hours in deep water. Though not all planktonic species migrate, those that do are often abundant, causing major diel changes in the composition of the surface plankton assemblage (Rodriguez and Mullin, 1986; Dorazio *et al.*, 1987) and imposing diel cyclicity to grazing and fluxes of particles and nutrients out of the surface layer (Welschmeyer *et al.*, 1984; Dorazio *et al.*, 1987; Longhurst and Harrison, 1988). Among the several hypotheses advanced to explain the adaptive significance of diel vertical migration in planktonic animals (Kerfoot, 1985), recent field studies (Stich and Lampert, 1981; Williamson and Magnien, 1982; Fancett and Kimmerer, 1985; Gliwicz, 1986a, b; Luecke, 1986; Dorazio *et al.*, 1987; Lampert, 1987; Dini and Carpenter, 1988) and theoretical studies (Ohman *et al.*, 1983; Frost, 1988; Gabriel and Thomas, 1988; Mangel and Clark, 1988) favor predator evasion: prey species avoid visually orienting predators by entering the surface layer only under the cover of darkness.

To test the hypothesis that predators induce diel vertical migration in zooplankton, we experimentally manipulated predation on enclosed populations of the marine planktonic copepod *Acartia hudsonica* Pinhey using its natural predator, the three-spined stickleback *Gasterosteus aculeatus* Linnaeus. *Gasterosteus aculeatus* is a visually orienting, predominantly diurnally foraging, zooplanktivorous fish (Wootton, 1984; Jakobsen and Johnsen, 1987). The

experiment was done in Jakles Lagoon, a small (2.6 ha) marine lagoon on San Juan Island, WA, USA. The site was chosen because (i) both the zooplankton and fish assemblages exhibit remarkably low diversity, with *A.hudsonica* (see Ueda, 1986) and its predator *G.aculeutus* being the overwhelming dominants (Landry, 1978); (ii) previous sampling indicated diel vertical migration by *A.hudsonica*; and (iii) the lagoon is shallow (max. depth, 3.9 m), facilitating the use of enclosures that span the depth range of the copepods. We hypothesized that if fish predation was responsible for the observed diel vertical migration in *A.hudsonica*, then enclosed populations of the copepod should diverge in their vertical distribution and diel migration depending on the presence or absence of free-ranging, actively feeding fish. Additionally, enclosed populations of *A.hudsonica* were exposed to caged fish to test the hypothesis that chemical exudates released by fish, or associated with their feeding activity, could induce vertical migration in the copepod.

## Materials and methods

We deployed nine 2600 l enclosures in linear array on the south side of a raft. The cyclindrical enclosures (1.0 m dia. × 3.3 m depth, closed at bottom) were constructed of 1.5 m wide panels of 10 mil (0.25 mm) woven polyethylene stitched together with double seams using natural fiber thread. They were pre-soaked in filtered seawater for about 10 days, rinsed with freshwater, then refilled with filtered (73 μm) seawater, pumped from ~1.5 m depth, and allowed to stand for 48 h before the experiment began. At night on June 9, 1988 the contents of three vertical plankton hauls (0.5 m diameter net, 110 μm mesh, closed cod end), made from within 15 cm of the bottom to the surface in the lagoon, were placed in each enclosure, giving an expected initial density of *A.hudsonica* of ~0.75 natural density.

On the same night, nine adult *G.aculeatus* (standard length, 42–54 mm) from the lagoon were added to each of six enclosures. Previous observations (Landry, 1978) suggest that this was about 3× natural density. In three enclosures the fish ranged freely. In each of the other three enclosures, three fish were enclosed in each of three cylindrical, pre-soaked, PVC cages (15 cm dia., 12 cm deep, 216 μm mesh screen on top and bottom) and the cages were suspended at 0.65, 1.65 and 2.65 m respectively. Caged fish were fed near midday each day with a small subsample of the live catch of a vertical plankton haul (0.3 m dia. net, 150 μm mesh) in the lagoon. The remaining three enclosures, serving as controls, received no fish. The treatments (free fish, caged fish and control) were assigned at random to the enclosures.

Beginning on June 10, we determined the vertical distribution of *A.hudsonica* in each enclosure near midday (prior to feeding the caged fish) and near midnight on days 1, 2, 5, 8 and 9; the lagoon was similarly sampled on days 2, 5 and 9. Sampling of enclosures was limited to noon and midnight to minimize depletion of copepod populations. Although such sampling probably adequately characterized day and night vertical distribution of adult copepods (Landry, 1978), behavioral subtleties such as twilight migration/midnight sinking

phenomena would not have been detected. However, neither Stearns (1986) nor Ueda (1987) observed migration behavior of this sort in species of *Acartia*.

Samples were obtained from the enclosures and lagoon with a multiple water bottle sampler, consisting of four clear tubes (extruded acrylic, 6.7 cm inside dia. × 1 m long, fitted with spring-loaded end caps) mounted end-to-end but orthogonally on the four sides of a 4.5 m long aluminum square tube (2.5 × 2.5 cm). To minimize disturbance of the water column during sampling, the vertically oriented sampler was lowered slowly, with tubes open, to a depth of ~115 cm above the bottom; after a brief pause the sampler was lowered quickly 1 m and the end caps on the tubes were remotely closed, simultaneously collecting 3 (enclosures) or 4 (lagoon) samples. At each sampling time a single vertical series of samples was collected from each enclosure; duplicate vertical series of samples were taken from the lagoon, except for the night of day 9 when only one vertical series was collected. Depth ranges of samples from enclosures were 0.15–1.15, 1.15–2.15 and 2.15–3.15 m; those from the lagoon were 0–0.75, 0.75–1.75, 1.75–2.75 and 2.75–3.75 m. Samples were concentrated on a 73 μm sieve and preserved in 10% formalin–seawater solution. We counted all adult *A.hudsonica* in each sample.

Except for measuring Secchi depth in all enclosures on day 2, no other sampling of the enclosures was done during the experiment. At the end of the experiment (day 10), the vertical distribution of temperature (YSI temperature-conductivity probe) and Secchi depth were determined for each enclosure. Then the enclosures were stirred with the Secchi disk and a single vertical haul (30 cm dia. net, 150 μm mesh) was taken from each. As the enclosures were emptied by pumping, the nine fish in each free fish enclosure were captured and preserved. Zooplankton samples were subsampled by pipette or plankton splitter and replicate subsamples were analyzed for abundance of all types of zooplankton. Gut contents of three fish from each free fish enclosure were analyzed.

## Results

### *Vertical distribution and abundance of* A.hudsonica *in the lagoon*

During the experiment, the vertical distributions of adult female and male *A.hudsonica* exhibited a day–night difference in the lagoon (Figure 1). Three-way analysis of variance of abundances (log transformed) for days 2 and 5 together yielded only one highly statistically significant interaction (depth × time of day, Table I), which we interpret as evidence of diel vertical migration by the copepods. Although we consistently caught significantly more copepods at night than in the daytime in the lagoon, this was probably not due to daytime avoidance of the sampler. In this study the deepest sample excluded the bottom-most 15 cm of the water column to avoid contamination with interfacial sediments. Previous observations in the lagoon (Landry, 1978) as well as our data (Figure 1) suggest aggregation of copepods toward the lagoon floor in the daytime. In preliminary trials with the water bottle sampler, we obtained equal day and night catches integrated over the water column when the deepest bottle penetrated the sediments. We infer that most copepods were very near, some

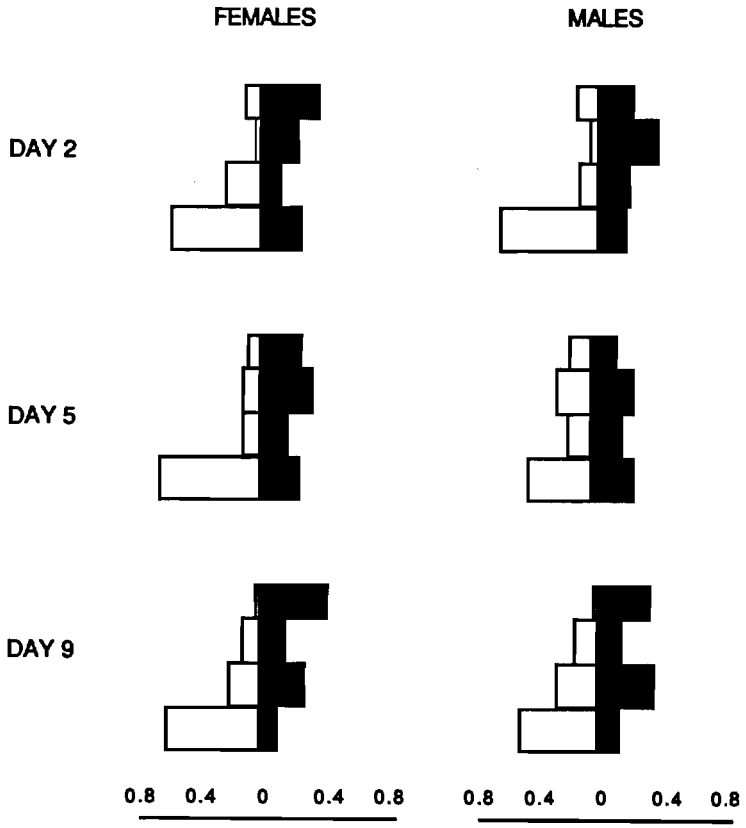


**Fig. 1.** Vertical distributions of adult females and adult males of *A. hudsonica* in Jakles Lagoon; days correspond to those for the enclosure experiment. Each daytime (clear) and night-time (blackened) vertical distribution is the mean of duplicate vertical series of samples, except for the night-time of day 9 (only one vertical series). The depth range of each histogram is 0–3.75 m. Scales are proportions of the copepod populations in the four sampled layers.

**Table I.** Three-way ANOVA tables for abundance (log transformed) of adult females and adult males of *Acartia hudsonica* in Jakles Lagoon

| Source of variation | Females | | | Males | |
|---|---|---|---|---|---|
| | df | MS | *F* | MS | *F* |
| Day | 1 | 3.49 | 29.1*** | 4.65 | 36.0*** |
| Depth | 3 | 1.59 | 13.3*** | 1.13 | 8.7*** |
| Time of day | 1 | 19.34 | 161.2*** | 12.7 | 98.0*** |
| Day × depth | 3 | 0.17 | 1.4 | 0.13 | 1.0 |
| Depth × time of day | 3 | 1.72 | 14.3*** | 0.89 | 7.0*** |
| Day × time of day | 1 | 0.21 | 1.8 | 0.16 | 1.2 |
| Day × depth × time of day | 3 | 0.14 | 1.2 | 0.39 | 3.0* |
| Error | 16 | 0.12 | | 0.13 | |

Analyses based on data for days 2 and 5 were combined (day 9 was excluded because only one night-time vertical series of samples was taken).
*** Probability that observed *F* value occurred by chance is <0.01; * probability that observed *F* value occurred by chance is between 0.05 and 0.1; all other *F* values are not significant ($P > 0.1$).

perhaps on, the lagoon floor in the daytime and migrated up into the water column at night (cf. Stearns, 1986). Between days 2 and 9 of the experiment the abundance of copepods in the lagoon increased (females by 2.9 times, males by 2.5 times).

*Vertical distribution and abundance of* A.hudsonica *in the enclosures*

We summarize analysis of the 270 samples collected in the enclosure experiment by presenting, for each treatment on each day, the mean abundances, mean vertical distributions and calculated mean depths of populations of *A.hudsonica*. The mean vertical distributions are portrayed as proportions of the total population in each of the three sampled layers, because, unlike the results for the lagoon, there was no consistent difference between daytime and night-time catches integrated over the water column. Diel vertical migration was inferred when the daytime mean depth of copepods was significantly greater than their night-time mean depth (using *t*-tests presented in the tables to follow). By this criterion inferred absence of diel vertical migration does not, however, preclude continuous interchange of copepods between layers; our sampling would not detect such behavior (Pearre, 1979a). Females and males showed somewhat different responses in the enclosures.

*Adult females.* Over the course of the experiment changes in abundance of adult females varied dramatically between enclosures in which copepods were exposed to fish predation and those where copepods were protected from fish (Figure 2A). Taking as initial abundance the mean for days 1 and 2 and as final abundance the mean for days 8 and 9, abundance of females increased by 415% in control enclosures and 518% in caged fish enclosures, but decreased by 12% in the free fish enclosures. Significant shifts in vertical distribution accompanied these changes in abundance.

On days 1 and 2 the females in the control and caged fish enclosures exhibited diel vertical migration (Figure 3, Table II). Females in the free fish enclosures showed, on the same days, somewhat weaker diel differences in vertical distribution, being more strongly aggregated at depth both day and night (Figure 3). On day 5 the day and night vertical distributions of females in all treatments were no longer significantly different based on calculated mean depths (Table II), suggesting a relaxation of migration behavior. However, in all enclosures on day 5 (Figure 3) a larger proportion of females occurred in the surface layer at night than in the daytime; vertical migration still appeared to be present, but was not statistically detectable by our mean depth comparison. By days 8 and 9, females in the control and caged fish enclosures were apparently non-migratory (Table II) and the daytime mean depths of populations were shallower than on days 1 and 2 (Table III). In sharp contrast, in the free fish enclosures a significant difference between daytime and night-time mean depths of females was now evident (Figure 3, Table II), indicating reinforcement of diel vertical migration. Moreover, daytime mean depths were unchanged from days 1 and 2 (Table III).

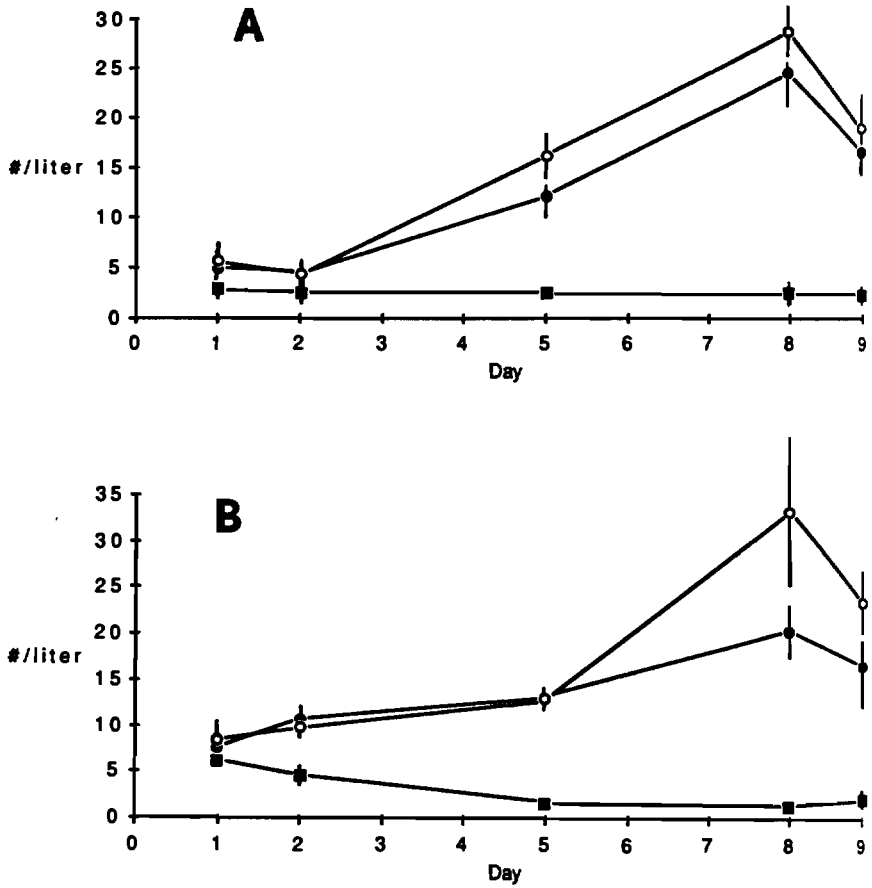


**Fig. 2.** Mean abundances of adult females (**A**) and adult males (**B**) of *A.hudsonica* in experimental enclosures. Each point is the mean of day and night abundances (±SE) in the three enclosures for each treatment (●, control; ○, caged fish; ■, free fish).

The absence of any significant differences in vertical distributions between the control and caged fish enclosures (Figure 3, Table II) shows that the vertical distribution of copepods was not affected by the mere presence of fish. The caged fish remained healthy, indicating adequate diffusion of oxygen into the cages. They also actively fed when presented with food each day and regularly produced fecal material (based on daily observations at time of feeding). Any dissolved products from fish feeding or exudation should have been dispersed by diffusion and stirring during retrieval of the sampler and daily recovery of the cages for feeding.

*Adult males.* Abundance of adult males also varied strongly depending on exposure to free-ranging fish (Figure 2B). Taking as initial and final abundances the means for days 1 and 2 and days 8 and 9, respectively, abundance of males

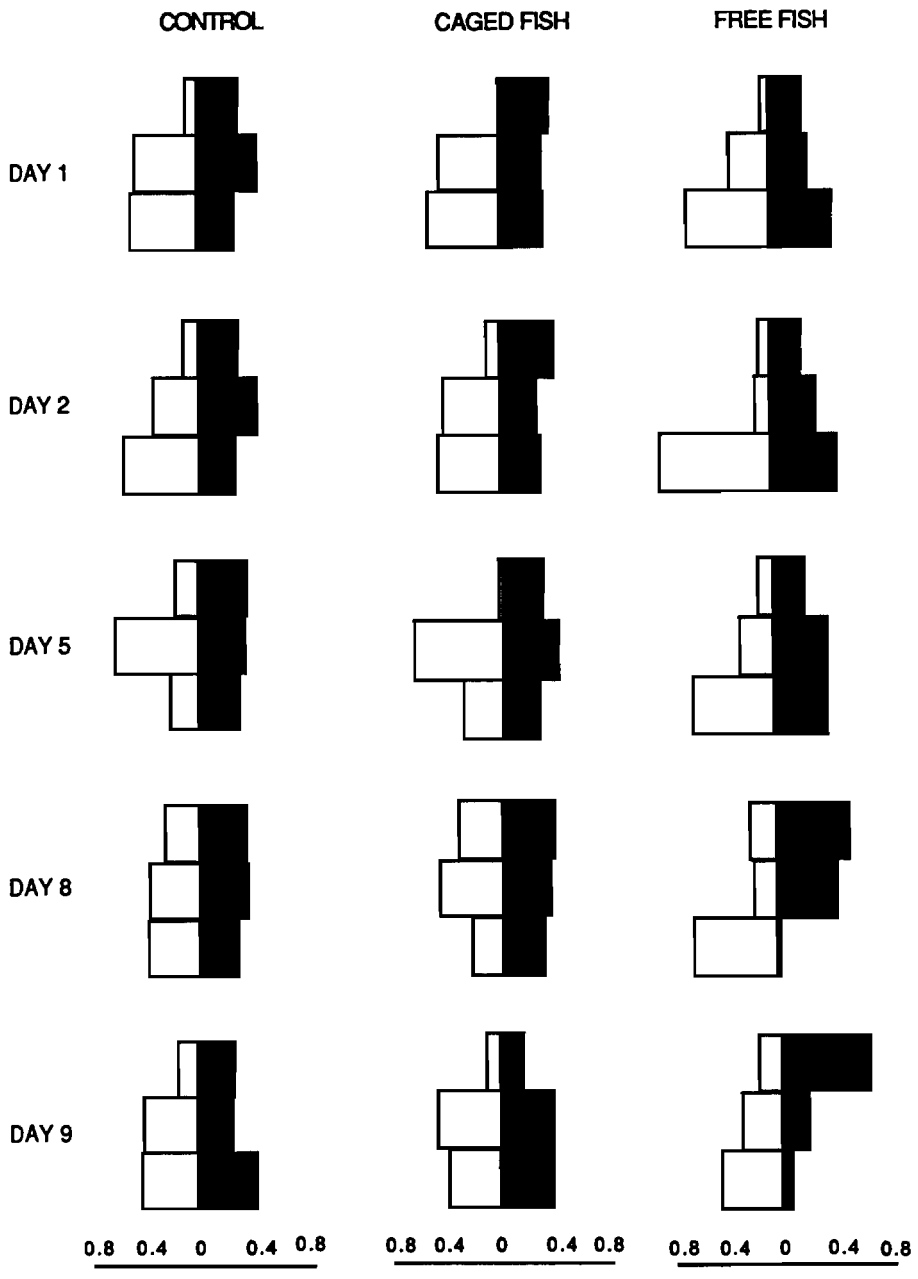


**Fig. 3.** Vertical distribution of adult females of *A.hudsonica* in experimental enclosures. Each daytime (clear) and night-time (blackened) vertical distribution is the mean of three enclosures for each treatment (control, caged fish, free fish). Variability among triplicates within treatments is indicated by weighted mean depths (WMD) in Table II. The depth range of each histogram is 0.15–3.15 m. Scales are proportions of the copepod populations in the three sampled layers.

**Table II.** Daytime and night-time mean depths (in m) of adult females of *Acartia hudsonica* in experimental enclosures

| Day | Time | Treatment | | | | | |
|---|---|---|---|---|---|---|---|
| | | Control | | Caged fish | | Free fish | |
| | | WMD | MD | WMD | MD | WMD | MD |
| Day 1 | D | 2.04,2.04,2.03 | 2.04 | 2.49,2.01,2.03 | 2.18 | 2.46,2.05,2.10 | 2.20 |
| | N | 1.55,1.60,1.76 | 1.64** | 1.56,1.51.1.65 | 1.57** | 1.84,1.79,2.01 | 1.88* |
| Day 2 | D | 2.21,1.98,2.06 | 2.09 | 1.94,2.15,1.92 | 2.00 | 2.32.2.32,2.39 | 2.34 |
| | N | 1.57,1.59,1.90 | 1.69** | 1.52,1.51,1.63 | 1.55** | 1.52,2.08,2.10 | 1.90* |
| Day 5 | D | 1.83,1.86,1.35 | 1.68 | 2.08,1.79,1.89 | 1.92 | 1.90,2.40,2.11 | 2.14 |
| | N | 1.70,1.70,1.38 | 1.59 | 1.39,1.79,1.71 | 1.63 | 2.13,1.65,1.65 | 1.81 |
| Day 8 | D | 1.93,1.69,1.75 | 1.79 | 1.65,1.48,1.52 | 1.55 | 1.87,1.79,2.52 | 2.06 |
| | N | 1.46,1.92,1.41 | 1.60 | 1.48,1.75,1.51 | 1.58 | 0.98,1.22,1.24 | 1.15** |
| Day 9 | D | 1.83,1.97,1.98 | 1.93 | 1.69,2.07,2.00 | 1.92 | 1.90,2.32,1.65 | 1.96 |
| | N | 1.77,2.24,1.44 | 1.82 | 1.95,1.93,1.75 | 1.88 | 0.88,1.01,1.20 | 1.03** |

Weighted mean depth, WMD = $(\sum n_i d_i)/\sum n_i$, where $n_i$ is abundance (no. 3.5 $l^{-1}$) at depth $d_i$ ($d_1$ = 0.65, $d_2$ = 1.65, $d_3$ = 2.65 m) in each of three replicate enclosures. MD (mean depth, day or night) is the mean of the three values of WMD. Day and night mean depths (MD) were compared by the *t*-test (4 df) for each treatment.

**Probability that observed difference between day and night mean depth occurred by chance is <0.05; *probability that observed difference between day and night mean depth occurred by chance is between 0.05 and 0.1; for all other pairs, day and night mean depths are not significantly different ($P > 0.1$).

**Table III.** Daytime mean depths (in m) of adult females and adult males of *Acartia hudsonica* on days 1 + 2 and days 8 + 9 of the enclosure experiment

| | Days 1 + 2 | Days 8 + 9 | *t* |
|---|---|---|---|
| Females | | | |
| Control | 2.06 | 1.86 | 3.40** |
| Caged fish | 2.09 | 1.74 | 2.64** |
| Free fish | 2.27 | 2.01 | 1.70 |
| Males | | | |
| Control | 2.24 | 2.07 | 1.89 |
| Caged fish | 2.18 | 2.17 | 0.03 |
| Free fish | 2.12 | 2.03 | 0.43 |

Mean depths are based on the 6 values of WMD given for each pair of days in Tables II and IV. Mean compared by *t*-test (*t*, 10 df).

**Probability that observed difference between mean depths occurred by chance is <0.05; for all other pairs the mean depths are not significantly different ($P > 0.1$).

increased by 208% in control enclosures and 301% in caged fish enclosures, but decreased by 68% in free fish enclosures. Although these changes paralleled those for adult females, the vertical distributions of males were different.

On days 1, 2 and 5 the males in all enclosures exhibited similar patterns of vertical distribution, but only those in the control enclosures on day 1 and caged

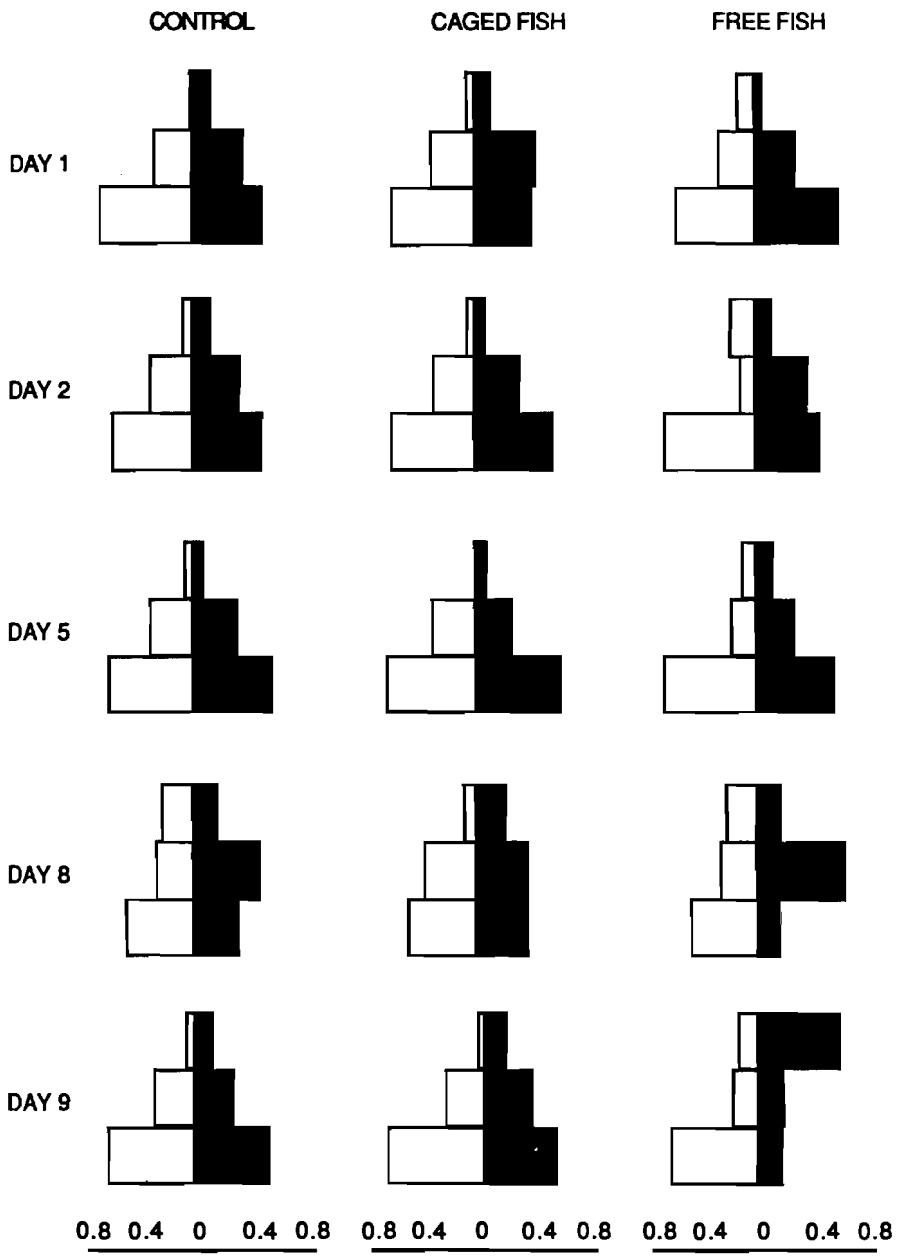


**Fig. 4.** Vertical distribution of adult males of *A. hudsonica* in experimental enclosures. Each daytime (clear) and night-time (blackened) vertical distribution is the mean of three enclosures for each treatment (control, caged fish, free fish). Variability among triplicates within treatments is indicated by weighted mean depths (WMD) in Table IV. The depth range of each histogram is 0.15–3.15 m. Scales are proportions of the copepod populations in the three sampled layers.

**Table IV.** Daytime and night-time mean depths (in m) of adult males of *Acartia hudsonica* in experimental enclosures

| Day | Time | Treatment | | | | | |
|---|---|---|---|---|---|---|---|
| | | Control | | Caged fish | | Free fish | |
| | | WMD | MD | WMD | MD | WMD | MD |
| Day 1 | D | 2.33,2.29,2.31 | 2.31 | 2.47,2.17,1.96 | 2.20 | 1.57,2.30,2.45 | 2.11 |
| | N | 1.90,2.03,2.12 | 2.02** | 1.88,1.92,2.09 | 1.96 | 2.29,2.18,2.19 | 2.22 |
| Day 2 | D | 2.36,2.05,2.10 | 2.17 | 2.11,2.20,2.14 | 2.15 | 2.03,2.08,2.30 | 2.14 |
| | N | 1.98,2.05,2.07 | 2.03 | 1.89,1.86,2.10 | 1.95* | 2.02,2.08,1.92 | 2.01 |
| Day 5 | D | 2.28,2.14,2.20 | 2.21 | 2.58,2.18,2.15 | 2.30 | 2.09,2.45,2.18 | 2.24 |
| | N | 2.24,2.23,2.03 | 2.17 | 2.15,2.22,2.31 | 2.23 | 2.12,1.98,2.24 | 2.11 |
| Day 8 | D | 1.93,1.91,1.90 | 1.91 | 1.98,2.14,2.10 | 2.07 | 1.77,1.79,2.15 | 1.90 |
| | N | 1.74,1.82,1.87 | 1.81* | 1.47,1.91,2.07 | 1.82 | 1.79,1.65,1.48 | 1.64 |
| Day 9 | D | 2.15,2.27,2.26 | 2.23 | 2.18,2.34,2.30 | 2.27 | 2.32,2.65,1.48 | 2.15 |
| | N | 2.07,2.23,1.92 | 2.07 | 1.80,1.98,2.24 | 2.01 | 0.98,1.40,1.26 | 1.21* |

Weighted mean depth, WMD = $(\sum n_i d_i)/\sum n_i$, where $n_i$ is abundance (no. 3.5 $l^{-1}$) at depth $d_i$ ($d_1$ = 0.65, $d_2$ = 1.65, $d_3$ = 2.65 m) in each of three replicate enclosures. MD (mean depth, day or night) is the mean of the three values of WMD. Day and night mean depths (MD) were compared by *t*-test (4 df) for each treatment.

**Probability that observed difference between day and night mean depth occurred by chance is <0.05; *probability that observed difference between day and night mean depth occurred by chance is between 0.05 and 0.1; for all other pairs, day and night mean depths are not significantly different ($P > 0.1$).

fish enclosures on day 2 had statistically detectable diel vertical migrations (Figure 4, Table IV). In all enclosures males tended to aggregate, much more strongly than females, toward the bottom at both day and night (cf. Figures 3 and 4). On day 8 there were indications of changes in vertical distributions (in particular, shallower daytime and night-time distributions), but only in the control enclosures were day and night vertical distributions marginally significantly different, and even then the actual depth difference (10 cm) was very small (Table IV). On day 9 males in the control and caged fish enclosures were non-migratory. However, in the free fish enclosures a conspicuous, though marginally statistically significant, difference between daytime and night-time mean depths of the males was evident (Figure 4, Table IV), suggesting development of a diel vertical migration similar to that observed in females on days 8 and 9. In contrast to adult females, the daytime vertical distribution of males in control and caged fish enclosures on day 9 was essentially the same as that on days 1 and 2.

No significant difference was observed between vertical distributions of males in control and caged fish enclosures (Figure 4, Table IV), indicating that the mere presence of fish did not affect the vertical distribution of copepods.

*Temperature, transparency and other zooplankton in the enclosures*

In all enclosures, temperature decreased essentially linearly with depth from

about 19.6°C at the surface to 15.7°C at 3 m; a similar temperature gradient was observed in the lagoon, though at all depths temperature was ~1°C lower. On day 2 the average Secchi depth was 2.7 m (SE 0.10 m, no significant differences among treatments). On day 10 the Secchi disk was barely visible at the bottom (3.3 m) in all enclosures.

*Acartia hudsonica* dominated the zooplankton in all enclosures. The species composition in free fish enclosures (Table V) was representative of the other enclosures. None of the other zooplankton species that occurred in abundance are potential predators of copepodid stages and adults of *A.hudsonica.*

*Prey and estimated feeding rates of sticklebacks in free fish enclosures*

*Acartia hudsonica* was the numerically dominant prey organism in the guts of the nine fish analyzed (Table V). Note that all developmental stages of the copepod were consumed by fish.

The data in Figure 2 permit estimation of the maximum potential feeding rate of fish on adult *A.hudsonica.* From the increase in abundance of adults in control and caged fish enclosures the rate of increase ($k$, day$^{-1}$) for adults, in the absence of fish predation, can be calculated from

$$k = (\ln A_t - \ln A_0)/t$$

where $A_0$ and $A_t$ are initial and final abundances of adults (female or male) and $t$ is time. $A_0$ was taken as the mean of days 1 and 2 and $A_t$ as the mean of days 8 and 9 for the six enclosures; thus $t = 7$ days. The rates of increase were 0.22 day$^{-1}$ for females and 0.13 day$^{-1}$ for males. At the temperatures prevailing during the experiment, this increase reflects recruitment from immature stages, some probably as young as nauplius stage VI (Landry, 1978), which were present in the inoculum to the enclosures.

Assuming that these growth rates apply to copepods in the free fish enclosures, then mortality rates ($m$, day$^{-1}$) can be calculated from

$$m = k - (\ln A'_t - \ln A'_0)/t$$

where $A'_0$ and $A'_t$ are initial and final abundances of adults (female or male) in free fish enclosures, and $k$ and $t$ are as above. $A'_0$ was taken as the mean of days 1 and 2 and $A'_t$ as the mean of days 8 and 9 for the three free fish enclosures. The mortality rates were 0.24 day$^{-1}$ for females and 0.30 day$^{-1}$ for males.

Given that the mortality of adult copepods in the free fish enclosures was due entirely to predation by fish, and making the conservative assumption that fish eat only adult copepods, then the mortality rates specify the required average feeding rates of the fish. In the case of adult females, whose abundance was ~2.5 l$^{-1}$ in the free fish enclosures, applying the finite mortality rate of 21% day$^{-1}$ to the total female population of 6500 per enclosure requires that about 1365 females be consumed by fish per day, or 152 females per fish per day if all nine fish fed on females. Average abundance of adult males was 3.2 l$^{-1}$;

**Table V.** Percentage composition of zooplankton in the water column of the three free fish enclosures (day 10) and abundance of prey types in the stomach contents of three fish from each free fish enclosure

| Taxa | Enclosure 1 | | | | Enclosure 2 | | | | Enclosure 3 | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Water column (%) | Fish 1 | Fish 2 | Fish 3 | Water column (%) | Fish 1 | Fish 2 | Fish 3 | Water column (%) | Fish 1 | Fish 2 | Fish 3 |
| *A.hudsonica* | | | | | | | | | | | | |
| Ad. females | 10 | 10 | | 1 | 15 | 51 | 31 | 5 | 17 | | 53 | 55 |
| Ad. males | 18 | 4 | | | 12 | 23 | 27 | 1 | 10 | | 10 | 13 |
| Copepodids | 46 | | 1 | 2 | 48 | 16 | 127 | 8 | 32 | 9 | 16 | 46 |
| Nauplii | 12 | | 236 | 2 | 16 | 1694 | 774 | 88 | 22 | 2052 | 435 | 138 |
| Other copepods | | | | | | | | | | | | |
| Harpacticoids | 10 | 1 | 13 | 2 | 4 | 3 | 1 | 2 | 3 | | 6 | 3 |
| Cyclopoids | 1 | | | | | | | | 2 | | | |
| Juv. *Corophium* | 1 | | 1 | | | | | | | 1 | | |
| Oikopleura | | | | | 5 | | 2 | | 2 | | | |
| Polychaeta larvae | | | | | 1 | | | | 11 | | | |
| Nematoda | 1 | | | | | | | | 1 | | | |

Abundances of copepod nauplii in the water column were underestimated because of the coarse mesh of the net used to sample the zooplankton.

therefore each fish must have consumed ~240 males $day^{-1}$, giving a total daily consumption of ~400 adult copepods $fish^{-1}$ $day^{-1}$.

Since some potential recruits to the adult stage must have been eaten as immature stages by the fish (Table V) and copepods must have reproduced in the enclosures, the calculated rate of consumption must be an overestimate of the number of adult copepods eaten but an underestimate of the total number of copepods consumed. Nevertheless, the required feeding rate may be compared with observed feeding rates of *G.aculeatus* by converting the rates to specific ingestion rates. If the average dry weight of adult *A.hudsonica* is 5 μg (Landry, 1978), then a daily consumption of 400 copepods corresponds to 2 mg $fish^{-1}$. A 50 mm stickleback has a dry wt of ~250 mg (Wootton, 1976), giving a weight-specific ingestion rate of ~0.8% $day^{-1}$, well within the observed range for fish of that size feeding at 15–20°C (Wootton, 1984).

## Discussion

Our manipulations of fish predation were accompanied by two striking changes in the enclosed populations of *A.hudsonica*. First, when fish were excluded (control and caged fish enclosures), populations of adult copepods increased substantially, while in enclosures with free-ranging fish, copepod populations declined at rates requiring daily mortality losses well within the known feeding capabilities of *G.aculeatus*. Second, associated with these unequivocal effects of presence or absence of fish predation were changes, occurring over little more than a week, in vertical distribution and diel vertical migration of copepods. The observed changes indicate that fish predation was a direct causal factor in diel vertical migration of the copepods.

Vertical migrations reducing spatio-temporal overlap between prey and predator could arise and be maintained by two alternative predator–prey interactions (Stein, 1979; Ohman, 1988). In some species of planktonic animals, diel vertical migration is variable on a time scale of weeks to months (Kozhov, 1963; Narver, 1970; Stich and Lampert, 1981; Gliwicz, 1986b; Frost, 1988). Since different patterns of vertical migration are heritable in some species of zooplankton (Weider, 1984; Dumont *et al.*, 1985; DeMeester and Dumont, 1988), such long-term temporal changes in migration behavior could be the result of changes in the relative proportions of different, genetically determined, behavioral types within a population. Predators could cause such shifts in population behavior by imposing differential mortality on subpopulations with different migration patterns (Pearre, 1979b). We will refer to this induction mechanism as a genotypic response of the copepod population to fish predation.

Alternatively, predators could cause simple, more immediate, avoidance reactions in their prey if they produce detectable signals or disturbances betraying their presence. For example, predators can, through the mediation of chemical exudates, elicit phenotypic morphological changes in their prey (Havel, 1987), and the possibility of chemical induction of phenotypic behavioral changes in prey must also be considered (Petranka *et al.*, 1987; Kats *et al.*, 1988; Dodson, 1988). Chemically mediated induction can be discounted as

a possibility in our experiment because there was no difference in vertical distributions of copepods in control and caged fish treatments. However, predators could produce mechanical disturbances, or even visual cues, which are detected and cause escape reactions by prey, eventually leading the prey to avoid regions of their habitat where and when predatory activity is intense (Sih, 1986). We will refer to this induction mechanism as a phenotypic response of copepods to fish predation. Changes in vertical distribution and migration may occur at potentially very different rates depending on whether genotypic or phenotypic responses are induced in the prey.

A role for phenotypic behavioral flexibility in migration behavior of adult females is strongly suggested by differences among the treatments on the first two days of the experiment. While a highly significant diel vertical migration was evident in control and caged fish enclosures, the migration of females was weaker in the free fish enclosures due to a substantial fraction of the population being strongly aggregated at depth day and night. This suggests that females exposed to free-ranging fish sensed the presence of the predators, and after one or more encounters and escapes from foraging fish descended to depth and remained there. Escape reactions may have been elicited by visual cues or mechanical disturbances (Buskey *et al.*, 1986; Paffenhöfer and Stearns, 1988), but encounters would have been most frequent in the daytime since the fish feed visually.

We suggest that the diel vertical migration exhibited by females in control and caged fish enclosures on days 1 and 2 represented persistence of behavior induced by their recent experience with fish in the lagoon. During days 5–9 of the experiment, the diel vertical migration seemed gradually to wane, due largely to shallower daytime vertical distribution of females. Females may have sensed the absence of predatory threat, which must have been by some means other than olfaction, and in response, spread upward in the water column even in the daytime. What would be the motivation for copepods to occupy the water column in the daytime? We can only speculate, but it is generally assumed that in a deep, well stratified water column diel vertical migration reflects foraging by the copepods on their preferred food, phytoplankton in the case of *Acartia* (Paffenhöfer and Stearns, 1988; Uchima, 1988), which is more abundant near the surface than at depth. Even for the shallow water column of Jakles Lagoon there is evidence of vertical stratification of phytoplankton (Hardy, 1971). Because swimming and feeding are distinctly different activities in *Acartia* (Rosenberg, 1980), it may also be that movement off the bottom is necessary for the copepods to feed (Stearns, 1986). When visual predators are absent such movement may occur any time, day or night, when hunger motivates copepods to feed. Under these circumstances a diel vertical migration should not be evident (Pearre, 1979b).

Hunger motivation would also drive females in the free fish enclosures to ascend. Although some females occurred at shallow depths in the daytime on days 8 and 9, many more were up at night. This suggests that encounters with fish kept copepods down in the daytime and that ascents occurred chiefly at night because of reduced interaction with fish. Curiously, in the few species of

*Acartia* so far studied, adults feed mainly at night (Stearns, 1986). Copepods may move up into the water column and forage nocturnally because they are then less conspicuous to visual predators.

The apparently different rates at which adult females responded to the presence and absence of actively foraging fish may reflect the asymmetry of costs associated with different behaviors. A copepod migrating down in the absence of fish might experience retarded development and growth (Frost, 1988), but its survival is not evidently threatened. In contrast, not migrating down in the presence of fish could mean death. An innate, rapid, evasive response to foraging predators has obvious survival value.

In contrast to adult females, adult males showed no detectable behavioral response to release from fish predation in the control and caged fish enclosures. Yet the vertical distribution of males was distinctly different from that of females, and even from males in the lagoon, suggesting both behavioral flexibility in males and sex-specific patterns of vertical distribution controlled by different factors or processes. Moreover, the eventual emergence of a diel vertical migration in males in the free fish enclosures suggests a possible controlling mechanism. Adult males of *Acartia* have intrinsically shorter lifetimes than females (Landry, 1978) and significantly lower feeding rates (Conover, 1956), which may affect their vertical distribution. However, perhaps even more relevant is the fact that males mature faster than females (Landry, 1983), probably to ensure insemination of females immediately upon their molt to the adult stage. It is possible that vertical distribution of males is determined primarily by that of adult females (Parker, 1902). Elaborate mate-seeking behavior, apparently mediated by female pheromones, is known for a variety of planktonic calanoid copepods (e.g. Katona, 1973; Griffiths and Frost, 1976; Blades and Youngbluth, 1980; Jacoby and Youngbluth, 1983; Watras, 1983). Given the estimated intense mortality rates imposed by fish on both females and males, a complete turnover of the populations of adult females and males could have occurred in the free fish enclosures during the experiment. Newly molted females, mostly migratory by days 8 and 9, could have been present and attractive to adult males, with the possible consequence that the vertical distribution of males changed as they oriented toward aggregations of females.

Flexible behavioral responses of individuals could thus account for the changes in vertical distribution and diel vertical migration of *A. hudsonica*. However, in the case of adult females particularly, we cannot entirely rule out a population response based on shifts in relative proportions of individuals with different, genetically fixed, migration behaviors. For example, although the diel vertical migration exhibited by females in control and caged fish enclosures on days 1 and 2 could represent persistence of behavior induced by recent experience with fish in the lagoon, it could also be the expression of a genetically fixed migration behavior. Similarly, the subsequent relaxation of vertical migration by females in these enclosures could be due to behavioral changes in individuals, as inferred above, or it could be due to proportional changes in fixed, genetically determined behavioral types. Nothing is known about a possible genetic basis for variability in vertical distribution and migration

behavior in *A.hudsonica* or any other planktonic copepod. Nor, as pointed out by Pearre (1979a), can a pattern of genetically determined behavior be defensibly inferred from our data on vertical distributions. Given these uncertainties, we briefly consider hypothetical mechanisms for a genotypic response and suggest ways to disprove the hypotheses in future experiments.

If the relaxation of diel vertical migration by females in control and caged fish enclosures was due to proportional changes in genetically determined behavioral types, then these types must have experienced differential recruitment. Such differential recruitment would have had to be based on differences in development rates, since there was no obvious source of differential mortality in these enclosures. Because there was a vertical temperature gradient in the enclosures, behavioral types could have had different development rates if they persistently occupied different depths in the enclosures. For example, based on the effect of temperature on development rate in *A.hudsonica* (Landry, 1978, Table I), at the temperatures prevailing in the enclosures development would be ~13% faster in a non-migratory, surface-dwelling subpopulation (experiencing mean temperature of 19°C) than in a migratory subpopulation (experiencing a mean temperature of 17.8°C). The significance of such a difference to our results could only be evaluated by knowing the abundances of the developmental stages of the behavioral types, non-migratory and migratory, that could reach the adult stage during the course of the experiment. This information could not be easily obtained for any copepod population. However, this ambiguity could be eliminated in a future experiment by inoculating the enclosures with only the oldest copepodid stages (ideally copepodid V) and adults, since these are the most strongly migratory stages of *A.hudsonica* (Landry, 1978), and keeping the experiment short enough (<2 weeks) that offspring produced by adults would not reach the adult stage. Initial observations would establish the proportion of the female population, all older stages combined, which is migratory. If migration behavior is genetically fixed, then in the absence of predation there should be no subsequent change in the proportion of migratory female individuals in the population.

A genotypic response could also have been the basis of reinforcement of the diel vertical migration by adult females in the free fish enclosures; copepods in these enclosures did, after all, suffer undeniably heavy predation mortality. Such a shift could have arisen through differential predatory selection if fish imposed greater mortality on non-migratory copepods occurring up in the water column in the daytime. Although some adult females clearly were consumed by fish, we do not know how the estimated total mortality in these enclosures was distributed among adult and subadult stages. Nor do we know whether adult females occurring in the enclosures on day 9 were among the adults present in the inocula to these enclosures. An unequivocal test of the hypothesis that fish predation acts as a differential selective force on genetically fixed behavioral types requires a modification of our experimental design. If, in the presence of fish predation, a genotypic response is involved in the shift in vertical distribution and intensification of diel vertical migration, then the time scale of the behavioral change should depend on the mortality rate imposed by the fish.

Performing the experiment with different initial numbers of copepods (again, only the oldest copepodid stages and adults), but fixed numbers of free ranging fish, would permit evaluation of the dependence of time scale of the behavioral change on mortality rate. If there is no dependence, then the genotypic response can be rejected as a mechanism for the induction of diel vertical migration in *A.hudsonica* by fish.

## Conclusions

The diel vertical migration induced in *A.hudsonica* by *G.aculeatus* appeared to be a behavioral response enabling the copepod to avoid its visually orienting predator. This response was not due to the presence of chemical exudates from the fish. Rather, copepods seemed to react to the presence of predators by other means, perhaps visual or mechanical stimuli, and to exhibit a downward escape response which, because encounters with visually orienting fish occur chiefly in the daytime, effectively limited the copepods' occurrence in the upper water column to the night-time hours. However, because fish imposed heavy mortality on copepods, we cannot discount the possibility that selective predation altered the proportions of individuals with fixed, genetically determined behaviors.

Our results illustrate the potentially complicated effects of manipulation of fish predation on the vertical distribution of zooplankton, even in a seemingly relatively simple enclosure experiment. Experiments must be interpreted in terms of population growth phenomena, and the unambiguous choice of alternative hypothetical explanations will be possible only under carefully controlled initial conditions. Phenotypic and genotypic determinations of migration behavior warrant attention. Sex-related differences in vertical distribution and migration should be anticipated.

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