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Diel vertical migration in zooplankton: rapid individual response to predators

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Abstract. While diel vertical migration in zooplankton has been shown recently to be a predator avoidance behavior, the mechanism by which predators induce and maintain such behavior has been debated. We report results of an *in situ* predator manipulation experiment during which enclosed populations of the marine planktonic copepod *Acartia hudsonica* rapidly changed their vertical distribution and diel migration behavior depending on presence or absence of the planktivorous fish *Gasterosteus aculeatus* These results point unambiguously to phenotypic behavioral plasticity of individual planktonic prey, not, as previously hypothesized, population-genetic level behavioral changes caused by selective fish predation, as the mechanism underlying changes in diel vertical migration in this copepod.

Introduction

Recent experimental manipulation of pelagic predator–prey systems in enclosures (Bollens and Frost, 1989b; Neill, 1990) provides conclusive evidence in favor of the hypothesis that diel vertical migration, widespread among planktonic animals in lakes and seas, can be a predator-avoidance behavior (Lampert, 1989). However, the mechanism by which predators induce and maintain such avoidance behavior remains uncertain. Predators could impose strong differential mortality on different genetically fixed behavioral types within the prey population, thereby selecting for types effecting avoidance of the predator, or alternatively, simply evoke immediate evasive reactions in individual prey (Stein, 1979; Gliwicz, 1986; Huntingford and Metcalfe, 1986; Ohman, 1988; Bollens and Frost, 1989b).

In an earlier experiment (Bollens and Frost, 1989b) we found adult males of the marine planktonic copepod *Acartia hudsonica* Pinhey to exhibit rapid evasive responses to one of its natural predators, the three-spine stickleback *Gasterosteus aculeatus* Linnaeus. In the case of adult female *A.hudsonica*, however, changes in behavior occurred more slowly (i.e. 3–5 days) and in the face of high rates of mortality and recruitment, suggesting that a population–genetic level response to predation could not be ruled out. Subsequently, phenotypic plasticity in diel vertical migration behavior was shown to occur in several freshwater zooplankters, including copepods (Neill, 1990), daphnids (Leibold, 1990; Ringelberg, 1991) and *Chaoborus* larvae (Dawidowicz *et al.*, 1990; Tjossem, 1990). Here we present direct experimental evidence that diel vertical migration in adult female *A.hudsonica* represents an immediate, flexible evasive response of individual prey elicited by a diurnally foraging visual predator.

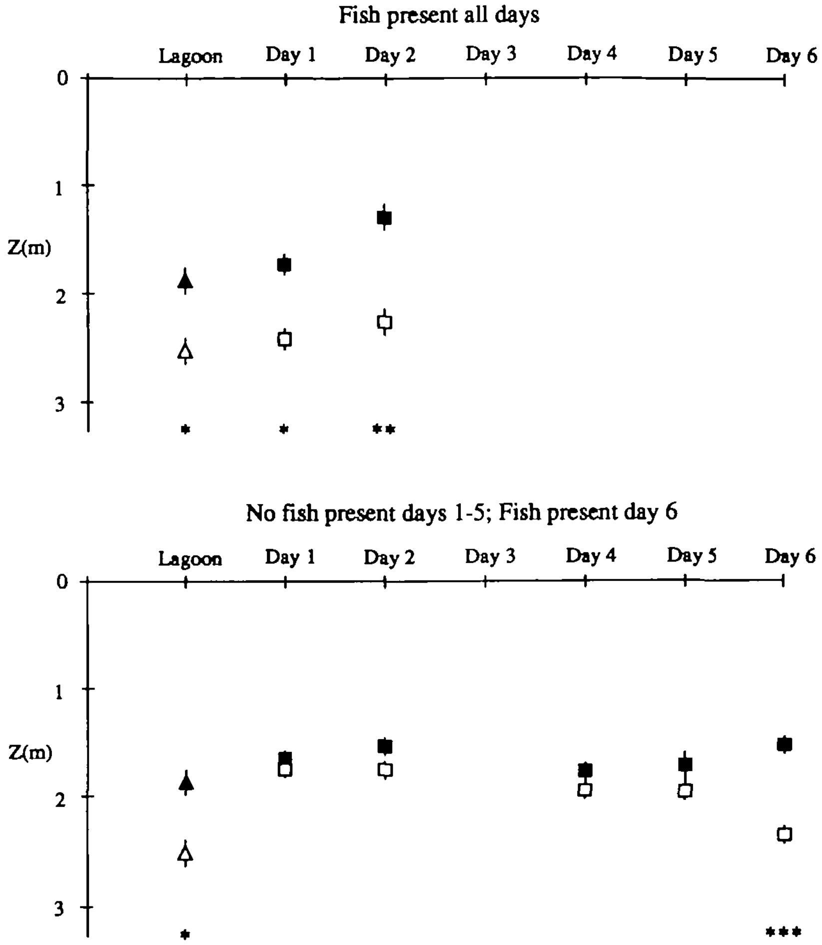
Method

We manipulated enclosed populations of the marine planktonic copepod *Acartia hudsonica* Pinhey and one of its natural predators, the three-spine stickleback *Gasterosteus aculeatus* Linnaeus, a visually orienting, predominantly diurnally foraging, zooplanktivorous fish (Wootton, 1984; Delbeek and Williams, 1987; Jakobsen and Johnsen, 1987). Eight 2600 l enclosures, 1.0 m diameter × 3.3 m deep [see Bollens and Frost (1989b) for details] were deployed in a linear array along the southern side of a raft moored in the center of Jakles Lagoon (48°28'N, 122°59'W, 2.6 ha, 3.9 m maximum depth), a temperate marine lagoon. On the night of May 2, 1990, populations of adult *A.hudsonica*, collected with a coarse mesh (0.253 μm) net to exclude immature stages, were established at natural densities in all eight enclosures. Immature stages were excluded so as to obviate the confounding effect of recruitment during the experiment (e.g. Bollens and Frost, 1989b). Nine adult *G.aculeatus* from the lagoon were added to each of four enclosures. The remaining four enclosures received no fish. The two treatments ('fish' and 'no fish') were randomly assigned to the eight enclosures.

Beginning on May 3, we sampled for vertical distribution of *A.hudsonica* in each enclosure near midday and near midnight on days 1, 2, 4 and 5. We used a multiple water bottle sampler [see Bollens and Frost (1989b) for details] to simultaneously sample three depth strata in the enclosures (0.15–1.15, 1.15–2.15 and 2.15–3.15 m). Immediately after sampling all eight enclosures on the night of day 5, nine adult *G.aculeatus* were introduced into each of the four 'no fish' enclosures, and these four enclosures were sampled near midday and midnight on days 6 and 7. The lagoon population of *A.hudsonica* was similarly sampled just prior to and immediately after the experiment (0–0.8, 0.8–1.8, 1.8–2.8 and 2.8–3.8 m depth strata). Samples were concentrated on a 73 μm sieve and preserved in 10% Formalin–seawater solution. We counted all adult female *A.hudsonica* in each sample. Transparency, thermal stratification, and abundance of phytoplankton (chlorophyll *a*) were determined in all enclosures on days 1, 5 and 7. Daytime weather conditions were consistent during the course of the experiment, with clear and mostly sunny skies, and a light to moderate breeze. The moon was waxing from ¾ full on day 1 to full on day 7.

Results

We summarize data from the 64 lagoon samples and the 240 enclosure samples using midday and midnight mean depths of adult female *A.hudsonica* in the lagoon and each of the two experimental treatments (Figure 1). While the total number of animals sampled in any one deployment of the corer was highly variable (Figure 2), no consistent differences occurred between day and night series of samples. In the lagoon copepods exibited diel vertical migration, as evidenced by the statistically significant difference in midday and midnight mean depths (Figure 1). The copepods in the lagoon were very near the lagoon floor in the daytime and dispersed throughout the water column during the night (Bollens and Frost, 1989b). On days 1 and 2 of the experiment the copepods in the 'fish' enclosures likewise exhibited diel vertical migration, with both midday


Fish present all days

No fish present days 1-5; Fish present day 6

Fig. 1. Vertical distribution of adult females of *A. hudsonica* in Jakles Lagoon (triangles) and in enclosures (squares) of two experimental treatments ('fish', upper panel; 'no fish', lower panel). Symbols are means (±1 SE) of noon (open) and midnight (solid) weighted mean depths for replicate series of samples in the lagoon ($N = 8$) or for replicate enclosures ($N = 4$). Z is depth (m). Noon and midnight mean depths were compared by t-test (one-tailed, $2N - 2$df) for lagoon and for each enclosure on each day. ***, probability that observed difference between day and night means depths occurred by chance is <0.001, **, $0.001 < P < 0.01$; *, $0.01 < P < 0.05$; for all other pairs, day and night mean depths not significantly different ($P > 0.05$) Because of predation by fish, abundances of copepods in each sample were sufficiently high (≥5) to reliably detail vertical distributions only on days 1 and 2 in the four 'fish' enclosures, and on days 1, 2, 4, 5 and 6 (immediately after introduction of fish) in the 'no fish' enclosures. Weighted mean depths were calculated as WMD = $(\Sigma n_i d_i)/\Sigma n_i)$, where n_i is abundance (number/3.5 l) at depth d_i ($d_1 = 0.65$, $d_2 = 1.65$, $d_3 = 2.65$ m in the enclosures, $d_1 = 0.40$, $d_2 = 1.30$, $d_3 = 2.30$, $d_4 = 3.30$ m in the lagoon)

and midnight distributions, and thus magnitude of vertical migration, being very similar to the lagoon population (Figure 1). In contrast, copepods in the 'no fish' enclosures did not show vertical migration on any of the first four sampling days (days 1, 2, 4 and 5; Figure 1). However, on day 6, immediately after introduction

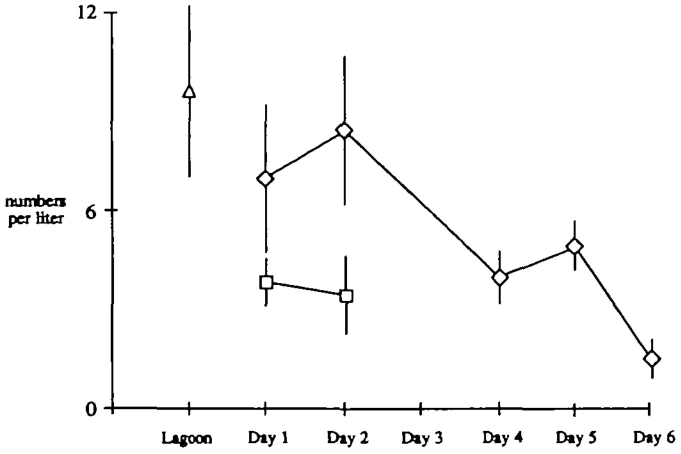


Fig. 2. Mean abundances of adult females of *Acartia hudsonica* in Jakles Lagoon (triangles) and in enclosures of two experimental treatments ('fish', squares, 'no fish', diamonds) Each symbol is the mean (±1 SE) of noon and midnight abundances (lagoon, $N = 16$; enclosures, $N = 8$).

of fish to the 'no fish' enclosures, the copepods again began to vertically migrate, and did so with a magnitude very similar to that of populations in the lagoon and 'fish' enclosures (Figure 1).

No statistically significant differences in transparency or thermal stratification of the water column occurred between treatments or dates. Abundance of chlorophyll *a* was consistently high in the enclosures, increasing slightly with depth on day 1 and being higher in the 'fish' versus 'no fish' enclosures on day 5 (Figure 3).

Discussion

The change in migration behavior of *A.hudsonica* from migratory in the lagoon to nonmigratory in the 'no fish' enclosures on day 1 occurred in the absence of significant mortality (predators excluded) or recruitment (only adults stocked in the enclosures) (Figure 2). Thus the cessation of migration could only have occurred as a result of individual copepods responding to the absence of predators, and exhibiting marked phenotypic flexibility in their behavior. The resumption of migration behavior of *A.hudsonica* coincident with introduction of fish into the 'no fish' enclosures (nonmigratory on day 5 in the absence of fish, migratory on day 6 in the presence of fish) likewise occurred very rapidly (12–24 h), but was also accompanied by significant mortality (69%) of copepods (Figure 2). Thus while we cannot rule out a population-genetic level response as the mechanism underlying resumption of this diel vertical migration, the initial cessation of the behavior, occurring as it did in the absence of recruitment or mortality, points unambiguously to phenotypic behavioral plasticity of individuals as the mechanism underlying changes in migration behavior.

Furthermore, the difference in migration behavior between treatments on day

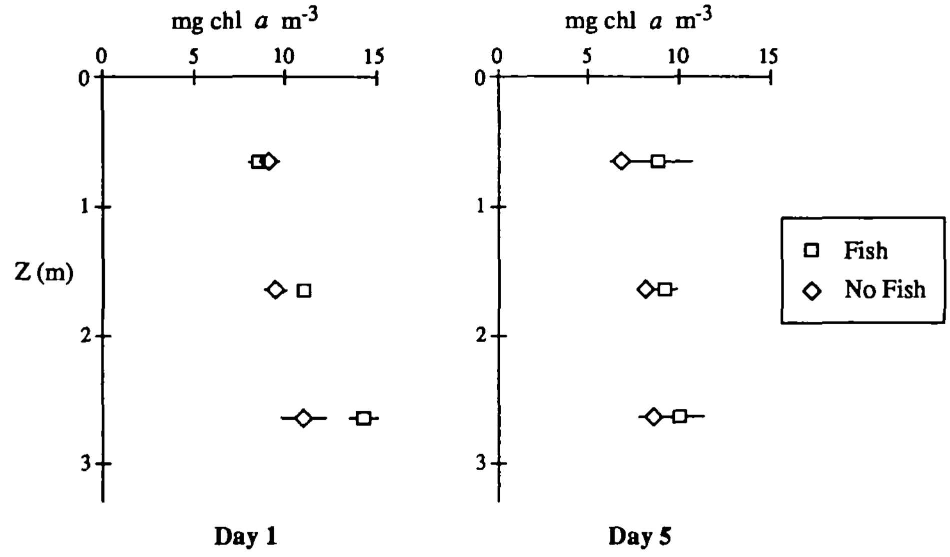


Fig. 3. Abundance of chlorophyll *a* in enclosures of two treatments on days 1 and 5 of the experiment Each point is the mean (±SE) of four replicate enclosures and is located at the mid-point of each depth stratum sampled A two-way ANOVA testing effects of treatment ('fish' versus 'no fish') and depth (upper, middle and lower water column) on abundance (log transformed) of chlorophyll *a* for each day indicated significant effects due to depth on day 1 and treatment on day 5 (probability that observed *F* value occurred by chance is $<0\,05$); all other effects, including interactions, not significant ($P > 0\,05$)

1 cannot be attributed to effects of food resources on diel vertical migration behavior (e.g. Johnsen and Jakobsen, 1987; Gliwicz and Pijanowska, 1988), as no significant differences in abundance of chlorophyll *a* occurred between treatments at this time (Figure 3). Rather, this difference in migration behavior can only be accounted for by individual copepods responding to the presence or absence of fish. Previous experimentation on this predator–prey system (Bollens and Frost, 1989b) suggests that such changes in predator avoidance behavior are not elicited by chemical cues, as has been found for several freshwater zooplankters (Dawidowicz *et al.*, 1990; Neill, 1990; Tjossem, 1990; Ringelberg, 1991), but rather are mediated by visual cues or mechanical stimuli.

It is worth noting that our two predator manipulation experiments resulted in different rates of behavioral response in *A.hudsonica* to release from predation [i.e. 3–5 days in June 1988 (Bollens and Frost, 1989b) versus 1 day in May 1990 (this report)]. We postulate that there is an element of past experience, or conditioning, in the rate at which *A.hudsonica* responds to the absence of predators. The principal predators of adult *A.hudsonica* in Jakles Lagoon are three-spine sticklebacks (Landry, 1978; Bollens *et al.*, 1991). These planktivorous fish exhibit an annual life cycle, with spawning occurring in April/May, and young-of-the-year fish becoming abundant in open water by June (Bollens *et al.*, 1991). Thus copepods in June will experience greater predatory threat (i.e. conditioning) than copepods in May, and might therefore be expected to respond more slowly to the removal of predators. This hypothesis is amenable to testing by releasing the copepods from predation under conditions of even higher ambient predator abundance, e.g. August (Bollens *et al.*, 1991). If conditioning does indeed affect the rate of behavioral response in *A.hudsonica*, copepods should respond to the exclusion of predators more slowly in August than they did in June (i.e. >3–5 days).

Rapid evasive responses by individual prey to predators may be much more common and effective in pelagic environments (Orr, 1981) than previously supposed, and such behavioral flexibility may underlie many cases of diel vertical migration, both freshwater and marine, in which the behavior is seasonally or geographically variable (Bollens and Frost, 1989a; Ohman, 1990). On the other hand, a population-genetic level response of prey to predators may still be suspected in instances where migratory behavior is demonstrably genetically fixed (De Meester and Dumont, 1988) or appears to be a stereotyped behavior in a population. For example, a recent predator manipulation experiment (Neill, 1990) showed that the migration behavior of larval phantom midges (*Chaoborus* spp.) persisted for weeks despite the absence of their predators, presumably fish (Luecke, 1986). Such cases of inflexible vertical migration behavior may still be attributable to predator evasion; it will just be more difficult to disprove the inducing role of predators.

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