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Chemical, mechanical and visual cues in the vertical migration behavior of the marine planktonic copepod *Acartia hudsonica*

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Abstract. Recent experimental evidence in both marine and freshwater systems indicates that predators can induce vertical migration behavior in individual zooplankters, yet the specific cues by which zooplankters sense their predators appear to vary. *In situ* manipulation experiments were carried out with enclosed populations of the marine planktonic copepod *Acartia hudsonica* to re-examine the potential role of chemical cues in the behavior of *A.hudsonica*, and to test explicitly for the role of mechanical or visual stimuli in triggering vertical migration behavior in this species. Adult female copepods were induced to vertically migrate (descend) when exposed to fish mimics during the day, but no such response occurred when the copepods were exposed to fish mimics during the night. Moreover, copepods exhibited no changes in vertical distribution when exposed to water which, having recently held a natural predator (the threespine stickleback, *Gasterosteus aculeatus*), was presumed to be laden with predator-produced chemical exudates. Predator-mediated mechanical or visual cues, or a hierarchy of both, are responsible for eliciting vertical migration behavior in adult female *A.hudsonica*. These results, together with those of other investigations demonstrating the inducing role of chemical exudates, indicate that the stimuli eliciting vertical migration in zooplankton can be expected to vary between species.

Introduction

A wide variety of marine and freshwater planktonic organisms undertake diel vertical migration, changing their vertical distribution in the water column on a 24-h cycle. While recent field manipulation experiments with both marine (Bollens and Frost, 1989b, 1991) and freshwater (Neill, 1990, 1992) zooplankton have demonstrated the role of predators in inducing and maintaining diel vertical migration behavior, the exact cues by which migratory zooplankton sense their predators appear to vary.

For instance, chemical exudates produced by predators were shown recently to trigger changes in vertical migration behavior in several species of zooplankton, including cladocerans (Dodson, 1988; Ringelberg, 1991a,b; Dawidowicz and Loose, 1992; De Meester, 1993; Loose, 1993; Loose *et al.*, 1993), chaoborid larvae (Dawidowicz *et al.*, 1990; Tjossem, 1990; Dawidowicz, 1993), brine shrimp larvae (Forward and Hettler, 1992; Forward and Rittschof, 1993) and freshwater copepods (Neill, 1990, 1992). In contrast, the marine copepod *Acartia hudsonica* vertically migrated only when in direct contact with free-swimming, actively feeding fish (the threespine stickleback, *Gasterosteus aculeatus*), and was unaffected by the presence of caged fish which were presumed to be producing chemical exudates. This was indirect evidence that *A.hudsonica* sensed predators by mechanical or visual stimuli (Bollens and Frost, 1989b).

In light of the growing body of evidence that predator-mediated chemical

exudates can induce migratory behavior of zooplankton, we recently undertook a series of experiments re-examining the potential role of chemical cues in the behavior of *A.hudsonica*. We also tested explicitly for the role of mechanical or visual stimuli in triggering vertical migration behavior.

Method

Enclosed populations of the marine planktonic copepod *A.hudsonica* Pinhey were manipulated in three experiments in Jakles Lagoon (48°28′N, 122°59′W, 2.6 ha, 3.9 m maximum depth) during May 1993. Eight 2600 l (1.0 m diameter × 3.3 m deep), woven polyethylene enclosures [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 the lagoon. On the evening of 5 May 1993, several hundred threespine sticklebacks (*G.aculeatus* Linnaeus) were collected from the lagoon using a pelagic trawl (described in Bollens *et al.*, 1992). *Gasterosteus aculeatus* is a visually orienting, predominantly diurnally foraging (Wootton, 1984), zooplanktivorous fish (Jakobsen and Johnsen, 1987; Hangelin and Vuorinen, 1988; Horsted *et al.*, 1988; Williams and Delbeek, 1989; Ibrahim and Huntingford, 1989a,b). *Gasterosteus aculeatus* was shown previously to be a dominant predator of *A.hudsonica* in Jakles Lagoon (Landry, 1978; Bollens *et al.*, 1992). These fish were placed in a temporary holding pen (3 mm stretch mesh) in the lagoon for use in subsequent experiments.

Experiment 1 tested for the effect of predator-released chemical exudates on the vertical distribution of *A.hudsonica*. On the afternoon of 7 May 1993, all eight enclosures were filled with seawater pumped from ~2 m depth in the lagoon and filtered through a 72 μm mesh net. Filtered (73 μm) seawater was also placed in two, 240 l plastic tubs (soaked previously in the lagoon for 24 h) and placed on the north side of the raft. On the night of 7 May 1993, all enclosures were stocked with adult *A.hudsonica* at one-half natural density, collected from the lagoon by making repeated vertical (3.5 m depth to the surface) hauls with a coarse mesh (253 μm) net to exclude immature stages. At the same time, one of the two tubs received 50 *G.aculeatus* from the holding pen, as well as live zooplankton collected by making four vertical hauls with a 253 μm, 0.5 m diameter net; this resulted in fish and zooplankton densities in the tub of ~100 and 10 times natural densities, respectively (Bollens *et al.*, 1992). Because the exact nature of fish-generated chemical exudates capable of eliciting behavioral responses in zooplankton prey has not yet been identified (e.g. Forward and Rittschof, 1993; Loose *et al.*, 1993), we could not monitor for their presence or absence during the experiment; but we assume that the high densities of healthy, actively feeding fish in the tubs generated high concentrations of fish exudates.

On 8 May 1993, each of the eight enclosures was randomly assigned to one of two treatments: Fish Exudates or No Fish Exudates. Each of the four Fish Exudates enclosures had 1% of the seawater (23 l) removed from the surface and replaced with the same volume from the tub containing *G.aculeatus*; this fish-treated water was passed through a 5 μm woven bag filter before gently

being added to the surface of each Fish Exudate enclosure. The four No Fish Exudates enclosures all underwent similar transfers of 1% by volume, except that the newly added, filtered (5 μm) seawater came from the tub containing no fish. One hour after the transfer of water in each enclosure, we sampled for vertical distribution of *A.hudsonica* using a multiple water bottle sampler [see Bollens and Frost (1989b) for details] that simultaneously sampled three depth strata (0.15–1.15, 1.15–2.15 and 2.15–3.15 m). This sampling procedure (water transfers followed by sampling for the vertical distribution of *A.hudsonica*) was carried out in each enclosure near noon on three consecutive days (8–10 May).

Experiment 2 tested for an effect of mechanical disturbance associated with the removal and addition of seawater. Because of logistic constraints associated with field manipulation experiments of this magnitude, we were unable to empty and re-establish populations of copepods in the enclosures between each experiment. Rather, when a given treatment was found after 3 days to have no effect on the copepods (this was possible because samples were processed and data analyzed statistically within 12 h of sample collection), the experiment was terminated and the next experiment initiated by randomly assigning the enclosures to new treatments. Thus, on 11 May 1993, experiment 2 was begun by randomly reassigning six of the eight enclosures (the two remaining enclosures were used for a separate, unrelated purpose) to one of two new treatments: Mixing and No Mixing. The three enclosures comprising the Mixing treatment received reciprocal transfers of filtered (5 μm) seawater from the fishless tub (just as in the No Fish Exudates treatment of experiment 1 above); the three enclosures comprising the No Mixing treatment received no water transfers. These six enclosures were sampled for the vertical distribution of *A.hudsonica* near noon on three consecutive days (11–13 May).

Experiment 3 tested for the effect of mechanical disturbances, such as those produced by actively feeding zooplanktivorous fish. On 19 May 1993, six enclosures were randomly reassigned to one of two new treatments: Fish Mimics and No Fish Mimics. Each of the three enclosures comprising the Fish Mimics treatment underwent 20 min of exposure near noon and midnight to seven, 15-cm-long rubber fish lures (previously soaked in the lagoon for 24 h) fastened ~33 cm apart in vertical series on a monofilament line attached to a wood dowel, and moved in a saltatory manner through the upper 2 m of each enclosure to simulate the 'striking' of actively feeding sticklebacks. The fish mimics were deployed by a person standing on the north side of each enclosure, such that the only shadows cast in the enclosures were from the mimics or the wood dowel. Each of these enclosures was sampled for the vertical distribution of copepods immediately after exposure to the fish mimics. The three enclosures comprising the No Fish Mimics treatment received no manipulations. These six enclosures were sampled for the vertical distribution of *A.hudsonica* near noon on three consecutive days (19–21 May) and near midnight on the last two consecutive nights (20 and 21 May).

Zooplankton samples from the enclosures 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 (Secchi disk depth) and

thermal stratification (using a YSI temperature probe) of the water column were determined in all enclosures on 10, 13 and 21 May.

We used the vertical series of samples in each enclosure on each date to calculate a weighted mean depth (WMD), or center of mass, as WMD = $(\sum n_i d_i)/\sum n_i$, where n_i is abundance (number/3.5 l) at depth d_i (d_1 = 0.65 m, d_2 = 1.65 m, d_3 = 2.65 m). These data are provided in Appendix I. A model I two-way ANOVA (Sokal and Rohlf, 1981) was performed on the data from each experiment to test for effects of treatment and time (date) on copepod WMD.

Results

There was no significant effect of chemical exudates on the daytime vertical distribution of *A.hudsonica* (Table I, Figure 1), nor was there a significant effect

Table I. Two-way ANOVA table for daytime weighted mean depths of adult female *A.hudsonica* in enclosures during the fish exudates experiment. Treatment = Fish Exudates versus No Fish Exudates; time = date

Source of variation	df	SS	MS	*F*s
Treatment	1	0.16	0.16	2.47 ns
Time	2	0.16	0.08	1.25 ns
Treatment × time	2	0.07	0.03	0.51 ns
Error	18	1.16	0.06	
Total	23	1.55		

Analyses based on data from four replicates for each of two treatments (Fish Exudates; No Fish Exudates) and 3 days. ns = probability that the observed *F* value occurred by chance is >0.05, i.e. non-significant.

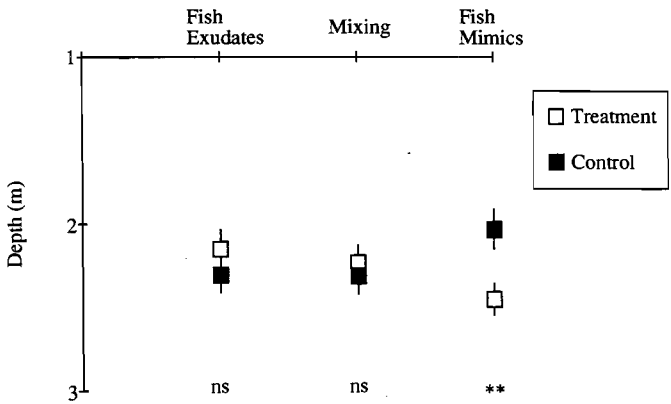

Fig. 1. Daytime vertical distribution of adult females of *A.hudsonica* in field enclosures in Jakles Lagoon, Washington, USA during three experiments in May 1993. Each experiment included replicate (3–4) control and treatment enclosures sampled daily over the course of 3 days. Symbols are means (±1 SE) of WMD values calculated as described in the text. Data within treatments and across dates were combined because of the absence of any significant time × treatment interactions (Tables I–III). Asterisks designate the level of significance (**, $P < 0.01$; ns, $P > 0.05$) of treatment effects (Tables I–III).

of mechanical mixing due to water transfers on the daytime vertical distribution of *A.hudsonica* (Table II, Figure 1). Moreover, in neither of these experiments were there any significant time (= date) or time × treatment interaction effects (Tables I and II).

There was a highly significant effect of fish mimics on the daytime vertical distribution of *A.hudsonica* (Table III, Figure 1). However, no such effect of fish mimics was seen in the night-time vertical distributions of the copepods (Table IV). Although there were significant time (= date) effects (i.e. slight shoaling) on both daytime and night-time vertical distributions during the

Table II. Two-way ANOVA table for daytime weighted mean depths of adult female *A.hudsonica* in enclosures during the mixing experiment. Treatment = Mixing versus No Mixing; time = date

Source of variation	df	SS	MS	*F*s
Treatment	1	0.01	0.01	0.19 ns
Time	2	0.09	0.05	1.32 ns
Treatment × time	2	0.00	0.00	0.07 ns
Error	12	0.42	0.03	
Total	17	0.52		

Analyses based on data from three replicates for each of two treatments (Mixing; No Mixing) and 3 days. ns = probability that the observed *F* value occurred by chance is >0.05, i.e. non-significant.

Table III. Two-way ANOVA table for daytime weighted mean depths of adult female *A.hudsonica* in enclosures during the fish mimic experiment. Treatment = Fish Mimics versus No Fish Mimics; time = date

Source of variation	df	SS	MS	*F*s
Treatment	1	0.79	0.79	13.91 **
Time	2	0.71	0.35	6.27 *
Treatment × time	2	0.26	0.13	2.30 ns
Error	12	0.68	0.06	
Total	17	2.43		

Analyses based on data from three replicates for each of two treatments (Fish Mimics; No Fish Mimics) and 3 days. ** Probability that the observed *F* value occurred by chance is between 0.001 and 0.01; * probability that the observed *F* value occurred by chance is between 0.01 and 0.05; ns is non-significant.

Table IV. Two-way ANOVA table for night-time weighted mean depths of adult female *A.hudsonica* in enclosures during the fish mimic experiment. Treatment = Fish Mimics versus No Fish Mimics; time = date

Source of variation	df	SS	MS	*F*s
Treatment	1	0.03	0.03	1.11 ns
Time	1	0.43	0.43	15.75 **
Treatment × time	1	0.05	0.05	1.64 ns
Error	8	0.22	0.03	
Total	11	0.73		

Analyses based on data from three replicates for each of two treatments (Fish Mimics; No Fish Mimics) and 2 nights. ** Probability that the observed *F* value occurred by chance is between 0.001 and 0.01; ns is non-signifiant.

mimics experiment (Tables III and IV), in neither case were there significant time × treatment interaction effects.

The magnitude of the effect of fish mimics on the daytime vertical distribution of adult female *A.hudsonica* (mean WMD of all Fish Mimics enclosures − mean WMD of all No Fish Mimics enclosures = 0.40 m) was similar to the magnitude of the effect of free-swimming fish in an earlier enclosure experiment (0.57 m; Bollens and Frost, 1991).

No statistically significant differences in transparency or thermal stratification of the enclosed water columns occurred between treatments or dates.

Discussion

The absence of an effect of predator-released chemical exudates on the vertical distribution of *A.hudsonica* corroborates the findings of Bollens and Frost (1989b). In this earlier study, caged fish were distributed evenly throughout the water column, fed actively when presented with food, produced fecal material and otherwise appeared healthy; these fish were therefore presumed to be producing chemical exudates that were adequately mixed within the enclosures due to twice-daily sampling with the multiple water bottle sampler and daily retrieval of the fish cages to the surface for feeding. Yet the possibility existed that the absence of an effect of caged fish in this earlier study could have been an artifact of the experimental set-up, e.g. production of exudates at all depths rather than predominantly in the surface where visual feeders would be expected to concentrate in nature. We doubt that the distributional pattern of the exudates was a factor, however, given that other investigators have observed a positive effect of exudates on exudate-sensitive zooplankton by both homogeneously distributing (e.g. Dodson, 1988; Tjossem, 1990; Forward and Hettler, 1992; Forward and Rittschof, 1993) or stratifying (e.g. Neill, 1990; Loose, 1993) the predator-treated water in the experimental chambers. Nevertheless, to obviate such a potential bias in the present study, fish-treated water was gently introduced into the surface of the enclosures. Yet, just as in the earlier study (Bollens and Frost, 1989b), there was no effect on the vertical distribution of *A.hudsonica*.

Although sampling was carried out only once each day (1 h after transferring water), this should have been an adequate period of time to elicit a response, as other investigators have found that exudate-sensitive zooplankton respond behaviorally in as little as a few minutes (Dodson, 1988; Ringelberg, 1991a,b) and the response persists for ≥4 h (Dodson, 1988; Neill, 1990; Loose, 1993).

It is possible that slight changes in the vertical distribution of *A.hudsonica* occurred due to either fish exudates or mixing that were too small to be detected by our sampling [i.e. 'effect size' as in Rotenberry and Weins (1985)]. Even if such undetectable and slight changes did occur, however, they would have been substantially less than those due to fish mimics (Figure 1) or free-ranging fish in enclosures or in nature (Bollens and Frost, 1989b, 1991; Bollens *et al.*, 1992). Thus, based on this and earlier (Bollens and Frost, 1989b) findings, we conclude

that vertical migration behavior in *A.hudsonica* is not induced by chemical exudates from its natural predator, the threespine stickleback.

Our results with fish mimics provide the first direct experimental evidence in support of a mechanical or visual cue for the induction of downward daytime vertical migration in *A.hudsonica*. Mechanoreception is known to be common among copepods (e.g. Strickler and Bal, 1973; Strickler, 1975; Landry, 1980; Legier-Visser *et al.*, 1986; Yen *et al.*, 1992 and references therein). In marine copepods, escape responses such as 'jumps' or 'hops' were elicited by physical interactions with real (Yen, 1988; Kils, 1992) and simulated predators (Haury *et al.*, 1980; Gill, 1985; Gill and Crisp, 1985). Migratory behavior per se has not, however, been documented in response to mechanical stimuli [although see Orr (1981) for possible community-level effects].

Visual stimuli may also play a role. While most calanoid copepods have simple, non-image-forming eyes, they are sensitive to changes in light intensity, and this could be important in predator avoidance and/or vertical migration behavior (Forward, 1988). Indeed, Buskey *et al.* (1986) found *Acartia tonsa* to exhibit short bursts of rapid swimming when exposed to ephemeral shadows, such as might be cast by predators. With regard to these two possibilities (i.e. mechanical and visual cues) in *A.hudsonica*, the absence of a night-time effect due to the fish mimics suggests an underlying role for visual cues, although an hierarchical effect of mechanical cues and light is also possible.

Can these results from *A.hudsonica* be generalized to marine copepods as a group? Perhaps not. For instance, Barrientos Chacon De Avendano (1980) found mechanoreceptive sensory hairs to be more numerous and chemoreceptors less numerous on the first antennae in three species of *Acartia* (*A.longiremis*, *A.grani* and *A.discandata*) compared to other marine copepods such as *Calanus finmarchicus*, *Eucalanus pileatus* and *Centropages furcatus*. Indeed, chemical cues are known to function in several species of marine copepods as aids in mate recognition (e.g. Katona, 1973; Griffiths and Frost, 1976; Blades and Youngbluth, 1980; Jacoby and Youngbluth, 1983) and feeding (e.g. Poulet and Marsot, 1978; Poulet and Ouellet, 1982; Poulet and Gill, 1988). Thus, the possibility that predator-mediated chemical cues can trigger behavioral responses in other marine copepods, such as has been shown for the freshwater copepod *Diaptomus kenai* (Neill, 1990, 1992), should not be discounted unless evidence exists to the contrary.

In summary, our results show that mechanical or visual cues, or a hierarchy of both, underlie predator-induced vertical migration in *A.hudsonica*. These results, together with those of other investigations demonstrating the inducing role of chemical exudates, indicate that the stimuli eliciting vertical migration in zooplankton can be expected to vary between species.

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Appendix I. Weighted mean depths (WMD, see the text for details) of adult female *A.hudsonica* in each enclosure sampled during three experiments in May 1993 in Jakles Lagoon, Washington, USA

Experiment 1	Treatment Fish Exudates					Control No Fish Exudates				
	WMDs				Mean WMD	WMDs				Mean WMD
Day 1	2.49	2.26	1.79	2.13	2.17	2.40	2.20	1.86	2.39	2.21
Day 2	1.97	1.73	1.92	2.40	2.00	2.38	2.45	2.09	2.30	2.30
Day 3	2.52	2.08	1.92	2.57	2.27	2.57	2.18	2.36	2.55	2.42
2	Mixing					No Mixing				
	WMDs				Mean WMD	WMDs				Mean WMD
Day 1	2.11	2.45	2.65		2.30	2.17	2.00	2.50		2.28
Day 2	2.16	2.57	2.48		2.33	2.32	2.32	2.43		2.36
Day 3	2.45	2.40	2.22		2.34	2.26	2.39	2.47		2.37
3	Fish Mimics					No Fish Mimics				
	WMDs				Mean WMD	WMDs				Mean WMD
Day 1	2.43	2.57	2.57		2.52	2.21	2.15	2.49		2.28
Day 2	2.41	2.58	2.53		2.51	1.74	2.62	2.40		2.25
Day 3	2.65	2.27	2.13		2.35	1.56	1.53	1.70		1.59
Night 2	1.45	1.43	1.68		1.52	1.80	1.54	1.89		1.74
Night 3	1.01	1.32	1.46		1.26	1.33	1.16	1.23		1.24