

Predator-enhanced diel vertical migration in a planktonic dinoflagellate

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ABSTRACT: Diel vertical migration (DVM) is a common and conspicuous behavior amongst planktonic organisms. In the case of dinoflagellates, both light and nutrients have been shown to regulate DVM, although the role of predators (grazers) has been understudied. Here we report the results of an experimental study using a system of 'plankton mini-towers' to examine the DVM behavior of the marine planktonic dinoflagellate *Akashiwo sanguinea*. *A. sanguinea* undertook a pronounced reverse DVM (down during the night, up during the day) in both the absence and presence of copepod predators (*Acartia* spp.). In the presence of copepods, however, the amplitude of the DVM was enhanced, providing the dinoflagellate with greater spatial separation from its 'normally' migrating predator. We briefly discuss the causes (cues) and ecological consequences of predator-enhanced DVM in dinoflagellates.

KEY WORDS: Dinoflagellate · Vertical distribution · Diel vertical migration · Nutrients · Light · Predator avoidance

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INTRODUCTION

Diel vertical migration (DVM) behavior is common and widespread among planktonic organisms in marine, estuarine, and freshwater systems, and can have profound consequences for pelagic ecosystems, e.g. by modulating the vertical flux of material and energy (Cushing 1951, Longhurst & Harrison 1988, Mincks et al. 2000, Steinberg et al. 2000, Legendre & Rivkin 2002, Hannides et al. 2009, Bollens et al. 2011a). DVM behavior is thought to have a variety of both proximate and ultimate causes (i.e. immediate cues and adaptive significances, respectively). For mesozooplankton such as copepods and cladocerans, it is now widely held that predator evasion often plays a critical role (Bollens & Frost 1989a,b, Lampert 1989, Bollens et al. 1993, Hays 2003), although non-biological factors such as light, transparency, and UV radiation can also have important effects (Forward 1988, Ringelberg 2010, Williamson et al. 2011).

Dinoflagellates also often undertake DVM, although usually in a pattern that is opposite or reverse to that of most zooplankton, i.e. they reside near the surface during the day and at depth during the night (Eppley et al. 1968, Blasco 1978, Cullen & Horrigan 1981, Ault 2000, Schofield et al. 2006, Jephson & Carlsson 2009). A wide range of field, laboratory, and modeling studies have shown that both nutrients and light influence dinoflagellate DVM (Heaney & Furnass 1980, Cullen & Horrigan 1981, Kamykowski 1981, MacIntyre et al. 1997, Kamykowski et al. 1998, Erga et al. 2003, Doblin et al. 2006, Ji & Franks 2007, Ralston et al. 2007). However, the role of predators (grazers) in triggering or enhancing DVM in dinoflagellates has largely gone unstudied.

Here we report the results of a replicated and well-controlled experimental study using a system of 'plankton mini-towers' that have been successfully deployed to study DVM in a range of other planktonic organisms (Speckmann et al. 2000, Lougee et al. 2002, Bochsansky & Bollens 2004, Clay et al. 2004,

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Ignoffo et al. 2005, Bochsansky et al. 2010, Breckenridge & Bollens 2010). Again, the role of both nutrients and light in regulating DVM in dinoflagellates cannot be denied (see references above), but here we test for the additional effect of predators (copepods) on enhancing the DVM behavior of the dinoflagellate *Akashiwo sanguinea*.

MATERIALS AND METHODS

Culturing and collection of organisms

A clone of the dinoflagellate *Akashiwo sanguinea* (strain no. SPMC 140) was obtained from Shannon Point Marine Center, Anacortes, Washington, USA, and maintained in a growth chamber at Washington State University, Vancouver, Washington. The growth chamber was set to 19°C and a 12:12 h light:dark cycle using 400 W high pressure sodium (HPS) lamps, 400 W metal halide lamps, and incandescent bulbs. Cells were cultured using sterile techniques under an ultraviolet hood in 10 d cycles with f/2 media (–Si) and 31 ppt artificial seawater (ASW: autoclaved Milli-Q water and Instant Ocean® sea salt).

Wild copepods were collected at high tide from Yaquina Bay, Oregon, USA (24 May 2010) and the lower Columbia River estuary in Astoria, Oregon (20 September 2010) with vertical tows of a 73 µm, 0.5 m diameter ring net. Back in the laboratory, adult female copepods of the genus *Acartia* were sorted from the net zooplankton and acclimated for 1 d to experimental temperature and salinity conditions (19°C, 31 ppt).

Experimental design and setup

Two separate 24 h experiments (25 to 26 May 2010 and 21 to 22 September 2010) were performed using a set of 2 columnar tanks as described by Bochsansky & Bollens (2004), where the control tank contained only dinoflagellates and the treatment tank contained dinoflagellates plus copepods. Experiments tested for the effects of light (diel cycle) and copepod predators (presence/absence) on the vertical distribution of *Akashiwo sanguinea*. This set of 2 m tall (5 cm deep × 8 cm wide) tanks allowed for high-resolution sampling of vertical distribution of dinoflagellates using an external fluorometer, and of copepods using an automated, continuously recording video microscope. Three

vertical fluorescence profiles, consisting of point collections at 10 cm intervals, were taken manually at midnight and midday with a Wet Labs Handheld DFLB fluorometer, and from these, a single average vertical fluorescence profile was calculated. A panning video microscope system, consisting of an infrared camera and diode mounted on a vertically traveling cradle, connected to a VCR, was used to determine cm-scale vertical distributions of copepods every hour.

Suspended 20 cm above each tank were 400 W HPS lamps on a 12:12 h light:dark cycle. Light intensity was controlled using neutral density screens, and diffusers were placed between the HPS lamps and the tanks to mimic light quality in an aquatic environment. Light intensity was set within the ranges for *Akashiwo sanguinea* described by Matsubara et al. (2007); mean ± SE surface intensity was $116.7 \pm 15.53 \mu\text{mol m}^{-2} \text{s}^{-1}$ (n = 4) and mean bottom intensity was $4.7 \pm 0.29 \mu\text{mol m}^{-2} \text{s}^{-1}$ (n = 4). The HPS lamps, video microscopes, and VCRs were controlled through a set of programmable switches linked to a desktop computer running an automation program. Nutrients ($\text{PO}_4 = 2 \mu\text{M}$, $\text{NO}_3 = 53 \mu\text{M}$) were homogeneously distributed and were similar to concentrations found in Monterey Bay, California, USA (Ryan et al. 2010).

Acartia spp. are known omnivores that are capable of feeding on dinoflagellates (Rollwagen Bollens & Penry 2003, Gifford et al. 2007). Our preliminary feeding experiments showed that *Acartia* readily fed on *Akashiwo sanguinea* and produced fecal pellets as a result, consistent with observations of other calanoid copepods (Kang & Poulet 2000, Murray & Marcus 2002). Expected dinoflagellate growth and copepod grazing during the experiments were estimated from Matsubara et al. (2007) and Kiørboe et al. (1985), respectively, and then prey (dinoflagellate) and copepod abundances were chosen so as to minimize the impact of grazing during the experiments (e.g. a ~5% reduction of dinoflagellates), while still maintaining natural predator densities of ~10 copepods l^{-1} .

Cultured dinoflagellates at densities of $\sim 2.15 \times 10^6$ cells were gently mixed into the nutrient-rich ASW and then, with the aid of a funnel, gently placed into the treatment and control tanks until nearly full (~180 cm depth). The experiments began 2 h later (21:00 h), when adult female copepods (64 in Expt 1, 94 in Expt 2) were added with a small volume (<50 ml) of ASW to the surface of each treatment tank. Midnight sampling of dinoflagellates and cope-

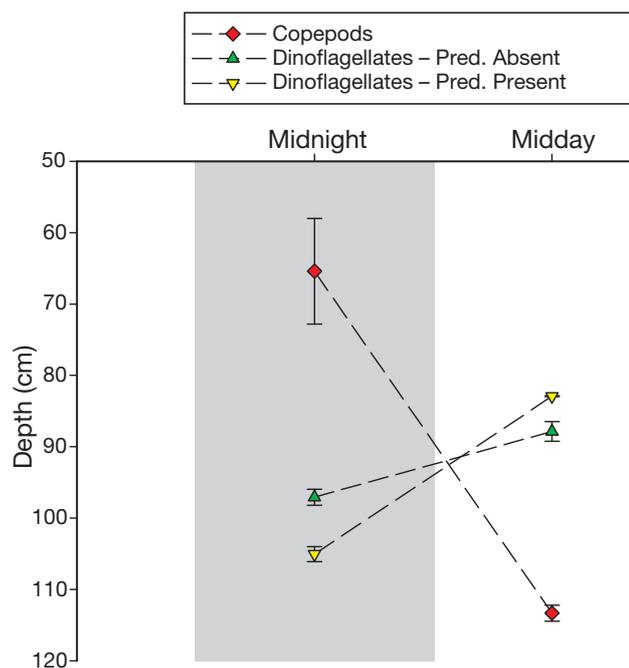


Fig. 1. *Akashiwo sanguinea* and *Acartia* spp. Diel vertical migration (DVM) of the dinoflagellate *A. sanguinea* and the copepods *Acartia* spp. Mean (± 1 SE) weighted mean depth during midnight and midday of copepods (red diamonds), dinoflagellates in the absence of predators (green triangles), and dinoflagellates in the presence of predators (yellow triangles). The copepods undertook 'normal' DVM and the dinoflagellates 'reverse' DVM, with the latter being enhanced (i.e. of greater magnitude) in the presence of predators

pods occurred about 5 h later (02:00 h), and midday sampling 12 h after that (14:00 h). A final water column total fluorescence reading was collected 24 h after the initiation of each experiment (21:00 h on Day 2), to allow for calculation of total grazing losses over 24 h.

Subsequent taxonomic identification of these copepods indicated that the vast majority were *Acartia* (*Acartiura*) spp., but a few (5%) were *Acartia tonsa*. The subgenus *Acartiura* consists of a group of 3 species of copepods that cannot be reliably distinguished, and thus identification is typically left at the subgenus level (Bradford 1976, Bollens et al. 2011b). Both *A. tonsa* and *A. (Acartiura)* spp. have similar patterns of 'normal' DVM (Schallek 1942, Lance 1962, Stearns & Forward 1984, Bollens et al. 1992, Kouassi et al. 2001), that is, up during the night and down during the day, and were therefore considered suitable for our experiments.

Statistical analyses

Weighted mean depths (WMDs) of copepods and dinoflagellates in each tank at midday and midnight of each experiment were calculated from video counts and water column fluorescence profiles, respectively, using the following equation (Bollens et al. 1993, Rollwagen-Bollens et al. 2006):

$$\text{WMD} = \frac{\sum(A_i \cdot Z_i)}{\sum(A_i)} \quad (1)$$

where i is each depth sampled, A is the fluorescence or copepod abundance value, and Z is the depth. The WMDs of dinoflagellates at midday and midnight (light effect), and in the presence and absence of copepods (predator effect), were combined from the two 24 h experiments, and were subsequently analyzed using 2-way analyses of variance (ANOVAs; Type III sum of squares and $\alpha = 0.05$).

RESULTS AND DISCUSSION

The copepods in our experimental tanks undertook 'normal' DVM (up at night, down during the day) in response to a diel light cycle (Fig. 1). In contrast, the dinoflagellate *Akashiwo sanguinea* undertook 'reverse' DVM (down during the night, and up during the day; Fig. 1, Table 1). Dinoflagellate DVM occurred both in the absence and the presence of copepod predators, but the amplitude of the migration was greater (i.e. enhanced) in the presence of the copepods (Fig. 1, Table 1, as evidenced by the significant Light Condition \times Copepods term). The ANOVA indicated no significant copepod effect alone (Table 1) because the direction of the dinoflagellate response to copepods varied depending on the presence or absence of light; dinoflagellates moved higher during the day and lower during the night, in a pattern that was reverse or opposite that of the normally migrating copepods. That is, the pres-

Table 1. *Akashiwo sanguinea*. Summary of results of 2-way ANOVA of *A. sanguinea* weighted mean depths. Significant p-values (< 0.05) are shown in **bold**

Source	df	Seq. SS	Adj. SS	Adj. MS	F	p
Light condition	1	490.67	490.67	490.67	233.23	0.000
Copepods	1	4.65	4.65	4.65	2.21	0.211
Light condition \times Copepods	1	83.60	83.60	83.60	39.74	0.003
Error	4	8.42	8.42	2.10		
Total	7	587.34				
S = 1.45046, R ² = 98.57%, R ² (adj.) = 97.49%						

ence of copepod predators had the effect of enhancing or strengthening the reverse DVM of the dinoflagellates, over and above the effect of light alone. This resulted in the dinoflagellates experiencing greater spatial separation from their predators during both day and night. Although we cannot know the exact amount by which dinoflagellate mortality is reduced by this predator-evasion behavior, it has been shown for zooplankton that only a very small reduction in predation mortality is required to offset the energetic costs of diel vertical migration (e.g. Frost 1988, Ohman 1990).

The role of both nutrients and light in modulating DVM in dinoflagellates has been the focus of many previous field, experimental, and modeling studies. That light attracts some dinoflagellates to the surface during the day, and that the presence of higher nutrients at depth can induce some dinoflagellates to descend to depth during the night (e.g. below the nutricline), has been well established (see references in the 'Introduction'). What is new about our study is that it implicates predator (grazer) evasion as an additional factor influencing DVM in dinoflagellates.

Quenette (2010) performed similar experiments as those reported here, but with one important difference: most copepod predators were cultured rather than collected from the wild. Quenette (2010) found a very strong effect of light on the vertical distribution of *Akashiwo sanguinea*, but an inconsistent effect of copepod predators. Indeed, the results of Quenette (2010) led us to suspect that wild copepods might behave (i.e. swim and migrate) more naturally than cultured copepods, and that the dinoflagellates might therefore be more likely to respond to wild predators. The results reported herein bear this out; in the presence of wild, normally migrating copepod predators, dinoflagellates enhanced their reverse DVM behavior (Fig. 1, Table 1).

One obvious question that arises is whether depth-specific grazing might, in and of itself, have caused changes in the vertical distribution of the dinoflagellates, i.e. by disproportionately removing cells at one depth and thereby giving the false appearance that the population of dinoflagellates moved to a different depth, farther away from the copepods. Although we could not measure depth-specific grazing losses in our plankton towers, we were able to measure water column total losses due to grazing. Grazing impact over the course of the experiments, estimated using reduction in water column total fluorescence over 24 h, was estimated to be 8.4%. This level of grazing can be applied to various vertical dis-

tribution patterns to test for the possible effects on WMD. Whereas we observed an 8 cm change in the WMD of the dinoflagellates in the first 5 h due to the copepod treatments, the effect of grazing losses on WMD would be far less than this, ranging from 0 (if grazing occurred at all depths in proportion to prey abundance) to a theoretical maximum of 2.9 cm (if grazing losses were concentrated entirely within a 10 cm stratum at one end of the dinoflagellate distribution and all remaining dinoflagellates occurred within the 10 cm stratum at the opposite end of the distribution). In all cases, the effect of grazing losses on WMD (0 to 2.9 cm) are far less than the observed effect of copepods on dinoflagellate WMD (8 cm). In short, the low levels of grazing that occurred during our experiments could not have caused the observed changes in dinoflagellate distribution through cell removal alone. Rather, dinoflagellates must have sensed the presence of their predators and actively moved away from them, i.e. they migrated to shallower depths during the day and greater depths during the night (Fig. 1) so as to evade their predators.

This in turn raises the question of how *Akashiwo sanguinea* might sense the presence of copepods. Chemoreception and mechanoreception, individually or in combination, are both possibilities. Dinoflagellates have been shown to use chemoreception to detect prey (Buskey 1997) and predators (Burkholder et al. 1995, Cancellieri et al. 2001) and to use mechanoreception to detect potential predators (White 1979, Anderson et al. 1988, von Dassow et al. 2005). In crustacean zooplankton, there is now a rich body of work on chemoreception of predator-released kairomones (see reviews by Lass & Spaak 2003 and Williamson et al. 2011), and to a lesser degree, of mechanoreception of predator cues (e.g. Bollens et al. 1994, Woodson et al. 2007). The question of how *A. sanguinea* sense their copepod predators, however, remains open.

This newly reported behavioral response in dinoflagellates, viz. predator-enhanced reverse DVM, could have important ecological consequences at the individual (physiological), population (growth and mortality), community (predator-prey), and ecosystem (flux) levels. Indeed, DVM behavior in dinoflagellates, when coupled with that of their predators and other higher trophic levels, could result in a 'cascade of migrations' throughout the food web, with important consequences for pelagic biogeochemical cycling (Bollens et al. 2011a). In any event, both the causes (cues) and ecological consequences of predator-enhanced DVM in dinoflagellates warrant further investigation.

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