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Phototaxis in Two Shallow-Water *Zeuxo* Species (Crustacea: Tanaidacea)

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Different crustacean species can differ in their response to light. In Tanaidacea, a small group of aquatic, benthic crustaceans, previous studies suggested that several species may be positively phototactic based on their attraction to nocturnal light traps, but no experimental investigations of phototaxis had been conducted on this group. Here we show experimentally that two species in the genus *Zeuxo* are phototactic but exhibit opposite reactions to light; *Zeuxo ezoensis*, which inhabits the blades and stipes of seaweeds, was positively phototactic, whereas *Zeuxo molybi*, which inhabits muddy sediments overlying bedrock, was negatively phototactic. This differential response may reflect differences in photoenvironment between these species' microhabitats.

Key words: benthos, habitat segregation, intertidal, Peracarida, Tanaididae

INTRODUCTION

The crustacean order Tanaidacea, comprising around 1500 described species (Anderson, 2020), is widely distributed geographically (all oceans) and vertically (intertidal to ca. 9000 m depth). Tanaidaceans show various modes of life, occurring interstitially in sea bottoms and in deep-sea sunken woods, occupying the insides of empty gastropod shells and dead barnacle tests, or inhabiting the surfaces of marine vertebrates (McClain and Barry, 2014; Chim et al., 2016; Kakui, 2016; Kakui et al., 2017a; Tanabe et al., 2017). Various ecological studies have focused on the relationship between tanaidacean assemblages and their abundance on the one hand and environmental factors such as depth and substrate type (e.g., seagrasses vs. corals) on the other (e.g., Nakamura and Sano, 2005; Takada et al., 2012; Błażewicz-Paszkowycz and Siciński, 2014; Cházaro-Olvera et al., 2018). However, few studies have investigated what features of tanaidaceans determine or restrict their habitats. One example is Kakui et al. (2017b), which found differences between two *Apseudes* species in the types of bottom substrate into which they can burrow.

Species in *Zeuxo*, one of the most species-rich tanaidacean genera in shallow waters (cf. Anderson, 2020), construct tubes with silk in or on various substrates, including the surfaces of seaweeds and seagrasses, sea-bottom sediments, shell gravels, and the insides of empty gastropod shells attached to macroalgae (Nakaoka et al., 2001; Edgar, 2008; Kakui, 2016; Kakui et al., 2017a, 2021; García-Herrero et al., 2017). While multiple congeneric species that seem to occupy different microhabitats often occur sympatrically (cf. Kakui, 2016), it is unknown how such niche partitioning is mediated.

Phototaxis—positive or negative—may be one factor related to crustacean habitat choice. Watanabe et al. (2008) and Borowsky (2011), for example, documented that interstitial ostracods and cave-dwelling amphipods show negative phototaxis, which may explain their preference for dark habitats. Chan et al. (2016) and Kakui (2016) reported the collection of unidentified tanaidaceans at night with light traps, indicative of positive phototaxis.

Observations of captive individuals of *Zeuxo ezoensis* Okamoto, Oya, and Kakui, 2020, which inhabits the surfaces of seaweeds, and *Zeuxo molybi* Okamoto and Kakui, 2022, which inhabits muddy sediment overlying bedrock, suggested that these species might exhibit different reactions to light. In this study, we investigated whether these two species are phototactic.

MATERIALS AND METHODS

Animals

Zeuxo ezoensis individuals used in this study (19 males and 19 females) were collected on 3 September 2018 at Oshoro, Hokkaido. We used captive-bred individuals of *Z. molybi* (22 males and 13 females) due to the difficulty in preparing a sufficient number of wild-caught individuals; they were descendants of individuals collected at Kominato, Chiba on 17 May 2018 that had been hatched in an aquarium and were maintained at 21°C, 14 h L/10 h D, and fed porphyrized dry feed for crayfish (JAN code 4971618829092; Kyorin, Japan) every 3 days.

Prior to experiments, each individual was isolated in filtered seawater in a petri dish and kept at room temperature (ca. 26°C) and in constant darkness for 3 days without feeding to attempt to standardize the light regime before experimental treatments.

Experimental design

Experiments were conducted in a dark room at ca. 26°C and were carried out in two time periods: "Day," between 8:00 and 12:00; and "Night," between 20:00 and 24:00. Isolated individuals

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were subjected to light/dark adaptation prior to experimental treatments: “light”, in which they were exposed to white light for at least 1 hour; and “dark”, in which they were put in the dark for at least 1 hour. For each individual, we carried out four illumination treatments (Day-light [Dl], Day-dark [Dd], Night-light [Nl], and Night-dark [Nd]) and corresponding control treatments (Dlc, Ddc, Nlc, and Ndc respectively). For each individual (*Z. ezoensis*, 19 males and 19 females; *Z. molybi*, 22 males and 13 females) eight treatments were conducted over a span of 2 days. The experiment is diagrammed in Fig. 1, which shows the timeline for two conspecific individuals.

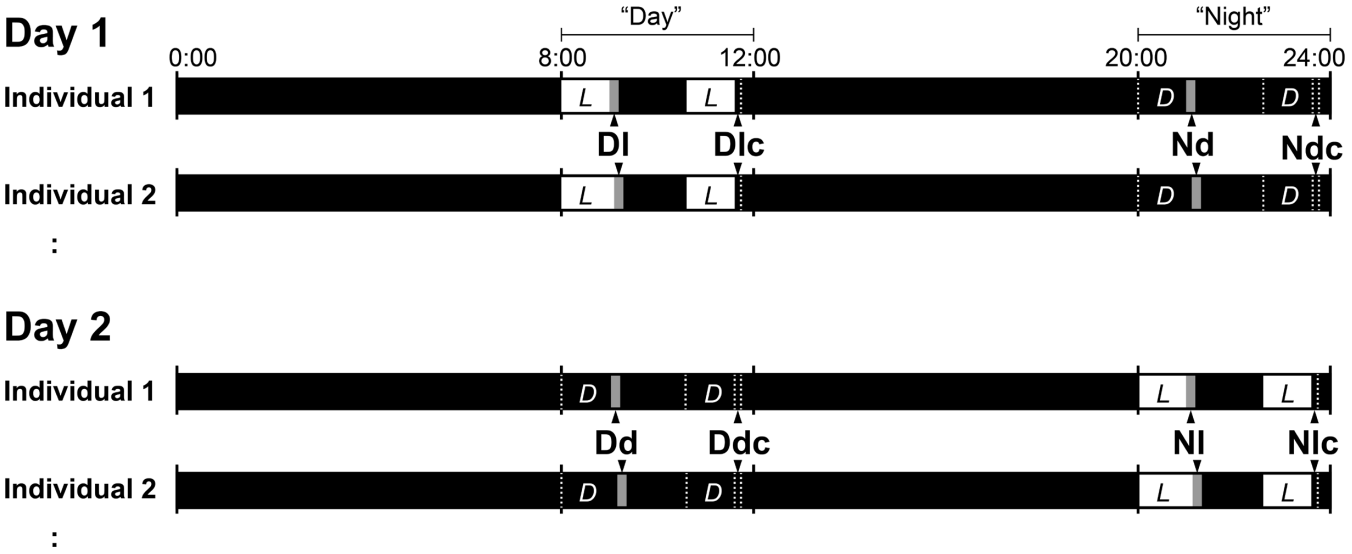

Fig. 1. Diagram showing the design of the phototaxis experiment. Periods during which individuals were kept in the dark are indicated by black (periods labeled “*D*” indicate dark adaptation periods). Periods during which individuals were kept in a light box for light adaptation are shown in white (labelled “*L*”). The periods for the illumination treatments are shown in gray. The periods for treatments are indicated with arrowheads. Because we conducted the experiment for multiple individuals partly simultaneously, the lengths of some periods in the diagram are not proportional to actual time. Treatments: Dd, Day-dark; Ddc, Day-dark control; Dl, Day-light; Dlc, Day-light control; Nd, Night-dark: Ndc, Night-dark control; Nl, Night-light; Nlc, Night-light control.

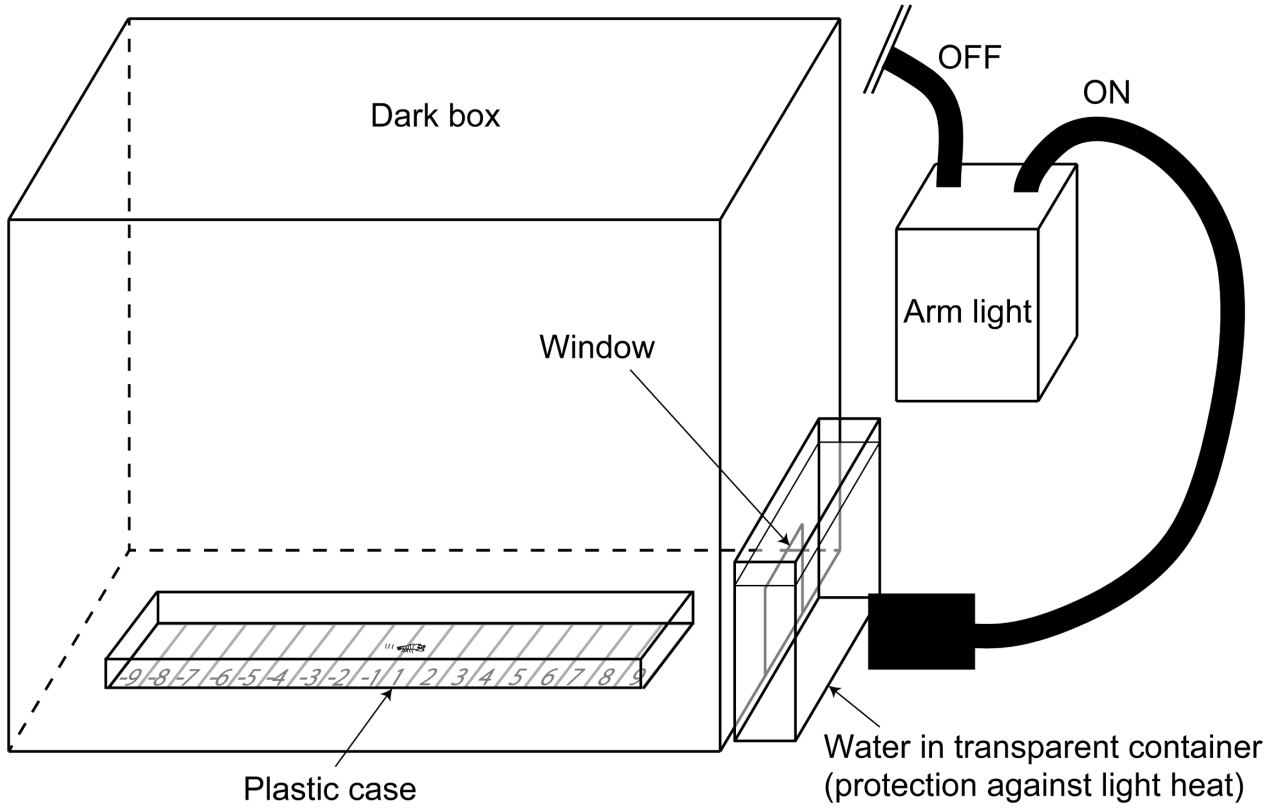

Fig. 2. Apparatus for the phototaxis experiment.

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The experimental apparatus is diagrammed in Fig. 2. Open, transparent-plastic cases (18 cm long × 2 cm wide × 0.5 cm high) were used for observing responses; they were marked off into 18 sections, each 1 cm long, with section –9 the farthest from the light and section 9 closest to it. The case was filled with filtered seawater and placed inside a dark box with a window. An individual was placed on the border between sections –1 and 1, i.e., at the center of the case. After each experiment, the case was washed with deionized water, wiped with a Kimwipe, and refilled with filtered seawater for another experiment. We placed one plastic case in the dark box for illumination treatment and placed several cases simultaneously in the dark box for control treatment.

In illumination treatments, immediately after an individual was put in the case, an arm light STA-B2 (STC Inc., Osaka, Japan; 130 lumens, 6500 K) was turned on. Two minutes later, the individual's position (section) was recorded; after the experiment, the individual was returned to its petri dish in the dark. In control treatments, the section where the individual was positioned was recorded (with aid of a flashlight) 2 minutes after the individual was placed in the case under the dark condition.

Statistical analyses

Statistical analyses were performed with R version 4.1.1. By using the function lmer in the lme4 package (Bates et al., 2015) in R, the effect of illumination on the position of individuals was tested for fit to linear mixed-effects (LME) models by maximizing the restricted log-likelihood (REML), with sex (male or female), illumination (test or control), time period (day or night), and prior adaptation (light or dark) as fixed effects, and individual ID as a random effect.

RESULTS

The results of the experiments are illustrated in Fig. 3, with raw data presented in Supplementary Table S1. In both *Z. ezoensis* and *Z. molybi*, the positions of individuals after treatments show no interaction with sex, time period, or prior

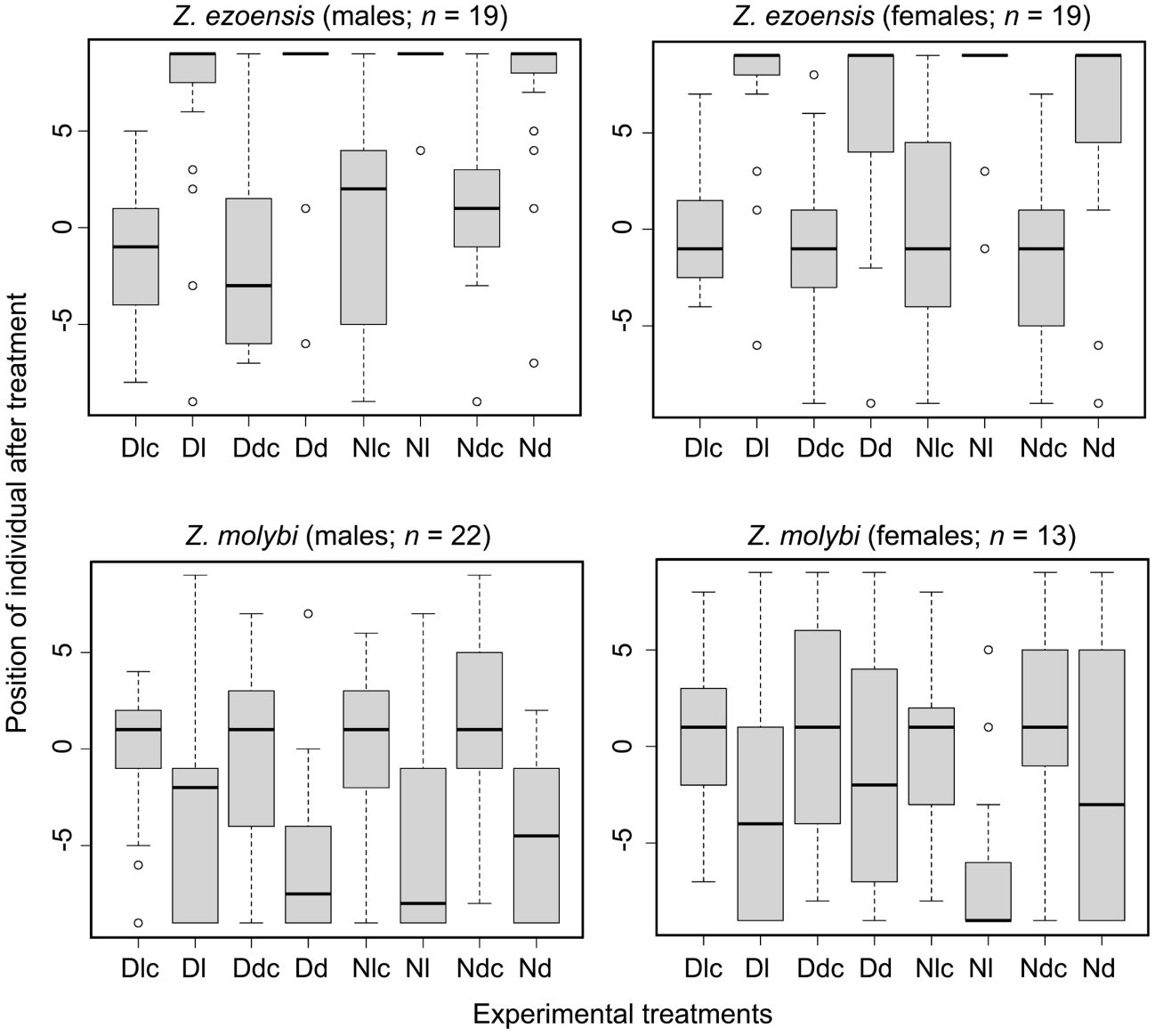

Fig. 3. The results of the phototaxis experiment. The boxplots show the median values (black bars), first and third quartiles (bottom and top bars for boxes), outliers (small circles), and minimum and maximum values excluding outliers (ends of whiskers). The vertical axis indicates the positions of individuals after experimental treatments; the positive direction is toward the light source. Treatments: Dd, Day-dark; Ddc, Day-dark control; Dl, Day-light; Dlc, Day-light control; Nd, Night-dark: Ndc, Night-dark control; Nl, Night-light; Nlc, Night-light control.

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Table 1. Results of the LME analysis for experiments on *Z. ezoensis*.

	Value	Std. error	DF	*t*-value	*P*-value
Intercept	–1.423236	0.5758169	256	–2.471681	0.0141
Male/Female	0.561038	0.5123759	35	1.094974	0.281
Test/Control	7.358108	0.5121887	256	14.366011	0
Day/Night	0.885135	0.5121887	256	1.728143	0.0852
Light/Dark	0.533784	0.5121887	256	1.042162	0.2983

Table 2. Results of the LME analysis for experiments on *Z. molybi*.

	Value	Std. error	DF	*t*-value	*P*-value
Intercept	1.642308	0.7990144	242	2.055417	0.0409
Male/Female	–1.078671	0.798256	33	–1.351285	0.1858
Test/Control	–4.592857	0.5631937	242	–8.155023	0
Day/Night	–0.321429	0.5631937	242	–0.570725	0.5687
Light/Dark	–0.735714	0.5631937	242	–1.306326	0.1927

adaptation (*P*-values for the LME are listed in Tables 1 and 2). *Zeuxo ezoensis* individuals were closer to the light source after the illumination treatment than after the control treatment (LME, $P < 0.0001$). In contrast, *Z. molybi* individuals were farther from light source after the illumination treatment than after the control treatment (LME, $P < 0.0001$).

DISCUSSION

We found that both *Zeuxo* species examined are phototactic under captive conditions. This is the first study experimentally demonstrating phototaxis in any tanaidacean species. Our study, however, used only white light of uniform intensity, and we cannot rule out that the behavior of individuals might be different if the light wavelength or intensity were different. Other environmental factors such as temperature, salinity, dissolved chemicals, or the presence of other organisms might also affect behavior. We used captive individuals of *Z. molybi* in this study (note: we preliminarily observed captive-bred individuals of *Z. ezoensis* approaching a light source). Additional data from experiments under both captive and wild conditions will be necessary for a more complete understanding of phototaxis in these animals.

Zeuxo ezoensis and *Z. molybi* showed opposite responses to light; the former was positively phototactic whereas the latter was negatively phototactic. Both species are tube dwellers, but they differ ecologically in several ways, one of which is microhabitat. *Zeuxo ezoensis* weaves nests on blades and stipes of seaweeds such as *Sargassum* spp. and *Neorhodomela aculeata* (Kakui et al., 2017a; Hayakawa and Kakui, 2022), and its habitat is essentially the water column. In contrast, *Zeuxo molybi* is benthic, constructing nests in bottom sediment overlying bedrock (Okamoto and Kakui, 2022). The light conditions are different between these two microhabitats, brighter in the water column and darker in the bottom sediment.

Negative phototaxis in *Z. molybi* is consistent with its presumed microhabitat; this trait will keep this species inside the sediment. Positive phototaxis would seem to be disadvantageous for *Z. ezoensis*; they dwell inside a tube, and positive phototaxis might lure them outside the tube, where predation risk is higher. It is unknown how *Z. ezoensis* copes with positive phototaxis yet remains in a tube. That most tanaidaceans exist as benthic infauna suggests their ancestral habitat was benthic (see also Kakui et al., 2021), and that the acquisition of positive phototaxis by epiphytic species such as *Z. ezoensis* may have allowed microhabitat expansion from the darker infaunal habitat to the brighter epiphytic habitat.

It is unknown how this difference in phototaxis between these two congeners arose. However, as their common ancestor likely showed only one of the possible responses to light (positively or negatively phototactic, or not phototactic), we speculate that evolutionary changes in phototaxis have occurred and are adaptive to particular (micro) habitats. To verify this hypothesis, more comprehensive studies on phototaxis in *Zeuxo* and its allies, and the ecologies of the species involved, are needed.

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COMPETING INTERESTS

We declare no competing interests.

AUTHOR CONTRIBUTIONS

NO identified the tanaidaceans, conducted the experiments, and carried out statistical analyses. KK reared the tanaidaceans. NO and KK conceived and designed the study, collected the tanaidaceans, contributed to writing the manuscript, and have read and approved the final draft.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available online. (URL: https://doi.org/10.2108/zs220118)

Supplementary Table S1. Positions of individuals after experimental treatments.

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