

Photo-dependent population dynamics of *Stentor coeruleus* and its consumption of *Colpidium striatum*

M.W. Cadotte, S. Jantz, and D.V. Mai

Abstract: The predatory protozoan *Stentor coeruleus* Ehrenberg, 1830 is known to show photosensitivity and photodispersion, avoiding regions of high light intensity as an antipredation strategy. This physiological and behavioral response to light likely has demographic consequences. We manipulated light intensity to determine population responses of *S. coeruleus* and the resulting effects on its prey *Colpidium striatum* Stokes, 1886. We show that *S. coeruleus* maintained the highest population density under ambient light levels and low densities under both high and no light treatments. The results from the no light treatment were surprising because little work has been done on possible important behavioral and physiological processes cued by light. These results add power to the use of *S. coeruleus* as a model predator system to test ecological dynamics and processes associated with predation.

Résumé : Le protozoaire prédateur *Stentor coeruleus* Ehrenberg, 1830 est connu pour sa photosensibilité et sa photodispersion; il évite les régions de forte intensité lumineuse par stratégie anti-prédatrice. Cette réaction physiologique et comportementale à la lumière a vraisemblablement des conséquences démographiques. Nous avons manipulé l'intensité lumineuse pour déterminer les réactions démographiques chez *S. coeruleus* et les effets qui en découlent chez sa proie *Colpidium striatum* Stokes, 1886. Nous montrons que *S. coeruleus* maintient une densité maximale de population aux niveaux ambiants de lumière et des densités faibles dans des conditions de lumière élevée et d'absence de lumière. Les résultats obtenus en l'absence de lumière sont surprenants, car il y a eu peu de travail sur les processus comportementaux et physiologiques importants possibles qui dépendent des signaux lumineux. Ces résultats confirment la valeur de l'utilisation de *S. coeruleus* comme système modèle de prédateur dans le but de vérifier des dynamiques écologiques et des processus associés à la prédation.

[Traduit par la Rédaction]

Introduction

Predator-prey interactions are an essential component to understanding species interactions (e.g., Holt 1977; Chase et al. 2002). A key tool for testing predator effects on prey communities has been to use artificial aquatic microcosms consisting of free-living protozoans and rotifers (Robinson and Edgemon 1989; Lawler and Morin 1993; Balciunas and Lawler 1995; Holyoak and Lawler 1996; Kaunzinger and Morin 1998; Amezcua and Holyoak 2000; Holyoak 2000; Petchey 2000; Jiang and Kulczycki 2004; Cadotte and Fukami 2005; Jiang and Morin 2005; Cadotte et al. 2006). Specifically, several use the omnivorous heterotrophic proto-

zoan *Stentor coeruleus* Ehrenberg, 1830) to examine how a generalist predator structures prey communities (Cadotte and Fukami 2005; Jiang and Morin 2005; Cadotte et al. 2006).

Stentor coeruleus is a free-swimming, blue-green, unicellular ciliate that exhibits photo-sensitivity and photodispersal, where individuals swim away from light sources and collect in dimly lit areas (Mast 1906; Tartar 1961; Tao et al. 1994; Miyake et al. 2001, 2003; Menzies et al. 2004). Under light onset, *S. coeruleus* individuals stop normal swimming and begin a brief period of backward swimming before swimming in a new direction (Tao et al. 1994; Menzies et al. 2004). Individuals keep re-adjusting their swimming trajectories until they end up in a locale that is below the light threshold for the photophobic response (Tartar 1961). Furthermore, under normal conditions, *S. coeruleus* uses a holdfast to attach to substrate to commence feeding. High light intensity will cause individuals to cease feeding, release the holdfast, and disperse (Tartar 1961).

This response to light has long interested physiologists and behavioral biologists (Mast 1906; Cole 1907; Fabczak and Fabczak 1995; Kuhlmann 1998; Fabczak 2000), as photo-responses in simple organisms have profound evolu-

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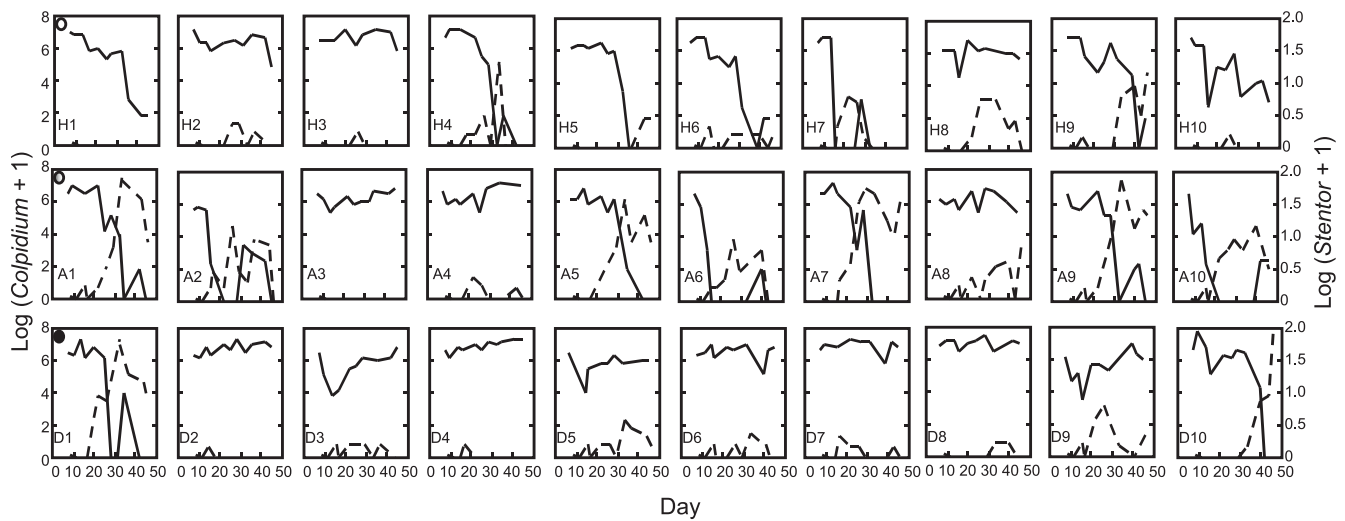
M.W. Cadotte,^{1,2,3} S. Jantz,³ and D.V. Mai.³ Department of Ecology and Evolutionary Biology, University of Tennessee, Knoxville, TN 37996, USA.

¹Corresponding author (e-mail: cadotte@lifesci.ucsb.edu).

²Present address: Department of Ecology, Evolution and Marine Biology, University of California, Santa Barbara, CA 93106, USA.

³All authors contributed equally to the work presented.

Fig. 1. Predator–prey population dynamics in each replicate. Light treatment results in differing temporal abundances (per millilitre) for both *Stentor coeruleus* (predator, broken line) and *Colpidium striatum* (prey, solid line). Top row corresponds to high light treatment, the middle row to ambient light, and bottom row to no light. Two replicates, H1 and A3, were excluded from analyses, since *S. coeruleus* apparently failed in establishing a population.



tionary consequences. The photo-receptor pigment that induces the light response, i.e., stentorin, is likely an adaptation that aids in reducing predation risk by avoiding high light areas where *S. coeruleus* would be easily located by visual predators, as well as producing cytotoxins that have been shown to have some protective value against predators and that are toxic to *S. coeruleus* (Miyake et al. 2001). While *S. coeruleus* shows these adaptations for predation avoidance, it is also a predator of smaller ciliates and rotifers (Cadotte and Fukami 2005; Cadotte et al. 2006). Thus, energy and time devoted to avoiding predation may have consequences on the ability of *S. coeruleus* to consume prey and should result in a reduced impact on prey populations. Little is known how these light responses affect the consumption rates and population dynamics of *S. coeruleus*. Because of its strong response to light, the predatory effect of *S. coeruleus* should be reduced under high light conditions.

In this paper, we examine the effects of light on the population dynamics of *S. coeruleus* and its predation rates on *Colpidium striatum* Stokes, 1886. We hypothesize that if light is detrimental to *S. coeruleus* then predation on *C. striatum* will be reduced and *S. coeruleus* populations will show reduced growth rates.

Materials and methods

Biological communities consisted of 100 mL of sterilized medium in loosely sealed, clear, glass containers. The medium contained 0.55 g·L⁻¹ of protozoa pellets (Carolina Biological Supply, Burlington, North Carolina), 0.05 g·L⁻¹ of powdered vitamins, and two sterilized wheat seeds as a source of slowly released nutrients in spring water (Crystal Springs, Flowery Branch, Georgia). Prior to addition of *C. striatum*, the stock medium was inoculated with bacteria (*Bacillus cereus* Frankland and Frankland, 1900; *Bacillus subtilis* (Ehrenberg, 1835) Cohn, 1900; *Proteus vulgaris* Hauser, 1885; *Serratia marcescens* Bizio, 1823) from stock cultures. After inoculation with bacteria, the stock medium

Table 1. Results of repeated-measures ANOVAs for *S. coeruleus* and its prey *C. striatum*.

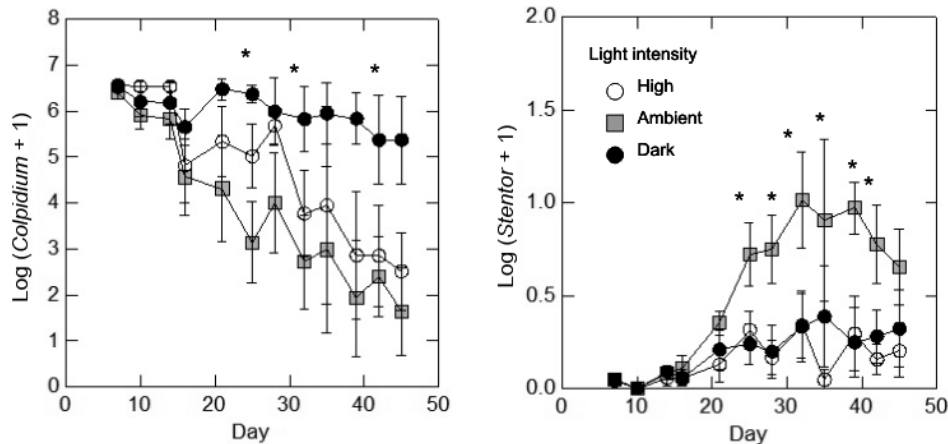
Source	df	Sums of squares	F	P
<i>S. coeruleus</i>				
Light	2	5.69	6.67	0.005
Error	25	10.66		
Time	8	9.37	6.84	<0.001*
Time × light	16	3.55	2.14	0.053*
Error	200	20.73		
<i>C. striatum</i>				
Light	2	190.25	4.91	0.016
Error	25	484.01		
Time	8	255.92	11.99	<0.001*
Time × light	16	83.89	1.96	0.096*
Error	200	533.76		

*Greenhouse–Geisser corrected P values.

was inoculated with microflagellates and other unidentified bacteria species prior to the initiation of the experiment. Unidentified bacteria species were assumed to have an equal distribution among all treatments and communities. Approximately 100 individuals of *C. striatum* were added to each community and they were allowed time to reach carrying capacity before the addition of 15 *S. coeruleus* individuals, except to communities 8, 9, and 10 of the dark treatment because of insufficient numbers in the stock cultures. In these communities, the number of individuals added were 12, 8, and 5, respectively. All living cultures were obtained from Carolina Biological Supply.

Experimental treatments consisted of 10 biological communities each under conditions of high light, ambient light (control), and no light. For the high light treatment, two 25 W fluorescent bulbs were placed 28 cm above five biological communities covered with clear, sterile petri dishes for a total of four bulbs and a 24 h photoperiod at about

Fig. 2. Mean abundance (per millilitre) of *C. striatum* and *S. coeruleus* across time for the three light treatments. Asterisks refer to significant differences based on Tukey's post hoc tests from repeated-measures ANOVA.



$48 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Light levels were quantified with a Quantum meter (QMSW-SS; Apogee Instruments Inc., Logan, Utah). For the ambient light treatment, communities were covered with sterile petri dishes and were exposed to the fluorescent lights of the laboratory, approximately 3.048 m overhead, with a 24 h photoperiod at about $3 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Dark communities were covered with sterilized aluminum foil, as well as cardboard cylinders at $0 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Dark communities were exposed to room lights for a brief time during sampling only.

Sampling

Twice per week, 5 mL of medium were removed from each gently homogenized community and replaced with an equal amount of fresh medium. From the 5 mL aliquot, a 2 μL sample was used to count the number of individuals of *C. striatum*, whereas the entire 5 mL aliquot was used to count the number of individuals of *S. coeruleus*. Individuals were counted using a Leica stereomicroscope (Leica Microsystems Inc., Bannockburn, Illinois). Abundances for both species were converted to numbers of individuals per millilitre.

Statistical analyses

We used repeated-measures ANOVA to determine if light level had significant effects on the abundance of *S. coeruleus* and *C. striatum*. We removed two replicates in which *S. striatum* appeared to fail establishment (Figs. 1H1, 1A3). An assumption for the repeated-measures *F* test is that the variance-covariance matrix has compound symmetry. When there is departure from compound symmetry, corrections, which modify degrees of freedom, have been proposed by Huynh-Feldt and Greenhouse-Geisser. We used these corrections in determining *P* values. ANOVAs were done using SAS[®] version 9.1 (SAS Institute Inc. 2003).

Results

Depending upon light level, qualitatively different predator-prey dynamics were observed (Fig. 1). For both the high and no light treatments (Fig. 1), *S. coeruleus* generally maintained low population sizes and only a few replicates showed predator-prey cyclic population dynamics.

However, most of the replicates in the ambient light treatment revealed classic predator-prey cyclic dynamics and *S. coeruleus* periodically obtained high densities (Fig. 1).

Repeated-measures ANOVA revealed significant differences among treatments (Table 1). *Colpidium striatum* maintained the highest abundance in the no light treatment and the lowest in the ambient treatment, whereas *S. coeruleus* maintained higher average abundances in the ambient light treatment (Fig. 2).

Discussion

Based on our reading of the literature (e.g., Tao et al. 1994), we hypothesized that the high light treatment would negatively impact the ability of *S. coeruleus* to adequately consume *C. striatum*. However, we observed the highest abundances in the ambient treatment, indicating that both high and no light negatively impacted *S. coeruleus*. Besides being the first study to examine the population effects of photophobic behavior in *S. coeruleus*, this study shows the positive effects of low light levels on the population dynamics of *S. coeruleus*. However, without mechanistic experiments it is difficult to ascertain the reason for the positive light effects. *Stentor coeruleus* cells may use light to generally orient themselves (Kuhlmann 1998), and therefore may need light to initiate other processes such as feeding.

Predator-prey dynamics

What this study reveals is that an adaptation for predator avoidance can affect a species' ability to consume prey. Predator avoidance behavior has been repeatedly shown to be associated with costs, such as reduced foraging times (Werner et al. 1983; Mittelbach 1988). The case studied here is different than most studies of predation avoidance in that species in other studies are usually responding to a direct cue of the presence of a predator (e.g., visual, olfactory, etc.). In the present study, *S. coeruleus* has apparently evolved predation avoidance, not in response to the actual presence of the predator but rather to a cue associated with increased predation risk. For species inhabiting intermediate trophic positions, such as *S. coeruleus*, the benefit from avoiding predators must, in the long run, be more beneficial than the loss of potential prey.

The fact that the feeding efficiency and population dynamics of *S. coeruleus* are photo-dependent presents an opportunity. *Stentor coeruleus* is increasingly being used as a model laboratory system to test ecological theory about predator–prey dynamics and trophic interactions (e.g., Cadotte and Fukami 2005; Jiang and Morin 2005; Cadotte et al. 2006). The results presented here should strengthen this role as a model system, since the strength of predation and trophic interactions can be directly tested, not by using differing species but with the same species, by altering light intensity.

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