

Roger Williams University
DOCS@RWU

Feinstein College of Arts & Sciences Faculty Papers

Feinstein College of Arts and Sciences

2012

Predator-Induced Vertical Behavior of a Ctenophore

Josefin Titelman
University of Oslo

Lars Johan Hansson
University of Gothenburg

Trygve Nilsen
University of Bergen

Sean Colin
Roger Williams University, scolin@rwu.edu

John H. Costello
Providence College

Follow this and additional works at: http://docs.rwu.edu/fcas_fp

 Part of the [Biology Commons](#)

Recommended Citation

Titelman, Josefin, Lars Johan Hansson, Trygve Nilsen, Sean P. Colin, and John H. Costello 2012. Predator-Induced Vertical Behavior of a Ctenophore. *Hydrobiologia* 690(1):181-187.

This Article is brought to you for free and open access by the Feinstein College of Arts and Sciences at DOCS@RWU. It has been accepted for inclusion in Feinstein College of Arts & Sciences Faculty Papers by an authorized administrator of DOCS@RWU. For more information, please contact mwu@rwu.edu.

Predator-induced vertical behavior of a ctenophore

**Josefin Titelman, Lars Johan Hansson,
Trygve Nilsen, Sean P. Colin & John
H. Costello**

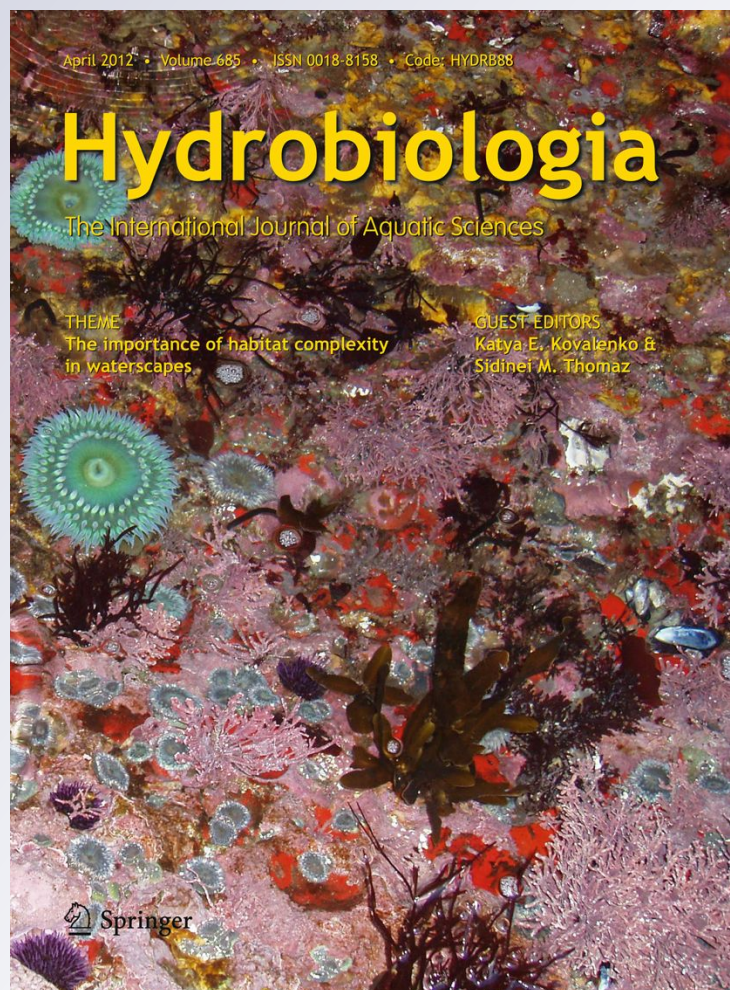
Hydrobiologia

The International Journal of Aquatic
Sciences

ISSN 0018-8158

Hydrobiologia

DOI 10.1007/s10750-012-1056-6



Your article is protected by copyright and all rights are held exclusively by Springer Science+Business Media B.V.. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your work, please use the accepted author's version for posting to your own website or your institution's repository. You may further deposit the accepted author's version on a funder's repository at a funder's request, provided it is not made publicly available until 12 months after publication.

Predator-induced vertical behavior of a ctenophore

Josefin Titelman · Lars Johan Hansson ·
Trygve Nilsen · Sean P. Colin · John H. Costello

© Springer Science+Business Media B.V. 2012

Abstract Although many studies have focused on *Mnemiopsis leidyi* predation, little is known about the role of this ctenophore as prey when abundant in native and invaded pelagic systems. We examined the response of the ctenophore *M. leidyi* to the predatory ctenophore *Beroe ovata* in an experiment in which the two species could potentially sense each other while being physically separated. On average, *M. leidyi* responded to the predator's presence by increasing variability in swimming speeds and by lowering their vertical distribution. Such behavior may help explain

field records of vertical migration, as well as stratified and near-bottom distributions of *M. leidyi*.

Keywords *Beroe* spp. · *Mnemiopsis leidyi* · Ctenophore · Behavior · Vertical distribution · Predator–prey

Introduction

The ctenophore *Mnemiopsis leidyi* (A. Agassiz, 1865) persists in high numbers during the summer to winter, both in its native range along the American Atlantic coasts (Costello et al., 2006; 2012) and in invaded habitats like the Black and Caspian Seas (Vinogradov et al., 2005), the North Sea (Riisgård et al., 2007), the Baltic Sea (Javidpour et al., 2009), and the Mediterranean Sea (Fuentes et al., 2010). The recent invasions of northern European waters have stimulated heightened interest in the role of *M. leidyi* as a competitor and predator of crustacean zooplankton, fish eggs, and larvae (e.g., Colin et al., 2010; Jaspers et al., 2011). An understanding of its ecology also requires quantification of its role as prey, but such studies are sparse (e.g., Oviatt & Kremer, 1977; Purcell & Cowan, 1995; Kreps et al., 1997; Hosia et al., 2011; Hosia & Titelman, 2011).

Although *M. leidyi* remains among the most frequently studied gelatinous plankton, the sensory and behavioral ecology involved in its distributions and its interactions with prey and predators remains poorly understood (Purcell & Cowan, 1995). Many

Guest editors: J. E. Purcell, H. Mianzan & J. R. Frost / Jellyfish Blooms: Interactions with Humans and Fisheries

J. Titelman (✉)
Department of Biology, University of Oslo, PO Box 1066,
Blindern, 0316 Oslo, Norway
e-mail: e.r.j.titelman@bio.uio.no

L. J. Hansson
Department of Marine Ecology-Göteborg, University
of Gothenburg, Box 461, 405 30 Göteborg, Sweden

T. Nilsen
Department of Mathematics, University of Bergen,
PO Box 7800, 5020 Bergen, Norway

S. P. Colin
Environmental Sciences and Marine Biology, Roger
Williams University, Bristol, RI 02809, USA

J. H. Costello
Biology Department, Providence College,
549 River Ave, Providence, RI 02918-0001, USA

predators exploit lobate ctenophores (Oviatt & Kremer, 1977; Condon & Steinberg, 2008; Hosia & Titelman, 2011). Despite its various post-encounter escape behaviors (reviewed in Titelman et al., 2007), *M. leidy* is vulnerable to predation or partial predation from gelatinous predators (e.g., Purcell & Cowan, 1995; Kreps et al., 1997; Hosia et al., 2011). In particular, ctenophores in the genus *Beroe* feed on many ctenophores (reviewed in Purcell, 1991). Population control on various ctenophore species have been implicated from field studies in the northwestern Atlantic Ocean (*Beroe ovata* Bruguière, 1789; in Swanberg, 1974; Purcell et al., 2001), the Black Sea (*B. ovata*; in Stone, 2005; Vinogradov et al., 2005), Norwegian coastal waters (*Beroe cucumis* Fabricius, 1780; in Falkenhaus, 1996), and the North Sea (*Beroe gracilis* Künne, 1939; in Greve & Reiners, 1988).

Upon encountering a predator such as *Beroe* spp, a prey ctenophore stands little chance of survival (Swanberg, 1974; Harbison et al., 1978; Falkenhaus, 1996; Hosia et al., 2011). The chemical presence of prey ctenophores triggers search behavior of *Beroe* spp. and engulfment occurs almost instantaneously upon encounter (Swanberg, 1974; Falkenhaus & Stabell, 1996; Hosia et al., 2011). The ability to remotely detect predators could enhance survival probability. Jellyfish exude various dissolved chemicals into the environment (Hansson & Norrman, 1995; Riemann et al., 2006; Titelman et al., 2006; Pitt et al., 2009) that could potentially be used as cues. Some ctenophores possess chemoreceptors (Horrige, 1965; Kass-Simon & Hufnagel, 1992; Aronova & Alekseeva, 2002, 2003). However, documented escape behaviors from predators by *M. leidy* are generally elicited after direct contact. Such escape behaviors include altering swimming direction and speed (Kreps et al., 1997), as well as tearing away and losing tissue when caught by predators (Purcell & Cowan, 1995; Kreps et al., 1997; Hosia & Titelman, 2011). Responses, such as crumpling, to remote fluid disturbances also exist (Moss et al., 2004). In contrast, escape strategies such as migration and vertical habitat shelters in response to perceived risk are virtually unexplored for ctenophores (e.g., Esser et al., 2004), despite being widespread amongst zooplankton (e.g., reviews in Ohman, 1988; Hays, 2003), including scyphozoan jellyfish (Albert, 2011). Chemical cues from jellyfish can induce vertical behavior in crustacean zooplankton (McKelvey & Forward, 1995;

Cohen & Forward, 2003). In our experimental study, we test the hypothesis that *M. leidy* may remotely perceive risk from predatory ctenophores and adjust their vertical position accordingly.

Methods

Mnemiopsis leidy and *B. ovata* were collected from Eel Pond, Woods Hole, Massachusetts, USA on the same day as the experiment in August 2008. Experiments were conducted at the Marine Biological Laboratory in natural sea water (22°C, 32‰) that was collected at the same time as the specimens. In our experimental setup, *M. leidy* and *B. ovata* ctenophores potentially could sense each other remotely, while being spatially separated. The experiment consisted of two treatments (predator: with *B. ovata*, and control: without *B. ovata*), each with three replicates. The order of the experimental trials was randomized (control, predator, predator, control, predator, control) and trials were conducted immediately after one another.

The setup consisted of a 5-l glass aquarium (25 × 25 × 8 cm, length × height × width) with a holder for the predator at the top of the aquarium (Fig. 1). The holder was a funnel made from a PET bottle with the bottom cut off and was centered at the top of the aquarium with the neck (2.2-cm diameter) facing downward about 9 cm below the surface. The submerged part of the holder created a 150-ml isolation chamber where *B. ovata* could be placed. Water could exchange freely between the holder and the rest of the tank, but *B. ovata* could not escape from the holder. The setup was lit from the side with cold white light. The experiment was video recorded in 2D at 30 frames s⁻¹ with a SONY HDV camera (HVR-Z7U) equipped with a Carl Zeiss 1.6/4.4–52.8 lens.

In each of the six experimental trials, the tank was first filled with seawater and then 10 *M. leidy* (total length 31.9 ± 9.3 mm, mean ± SD) were added. The water level was then adjusted to a set mark (0.9 cm from the top). *M. leidy* were allowed to acclimatize for 10 min. Each *B. ovata* was rinsed in seawater to avoid addition of already released chemicals, and then gently poured with a glass beaker into the holder together with a small amount of filtered seawater (total volume 150 ml). In the control treatment, 150 ml of water was poured into the holder. The introduction of

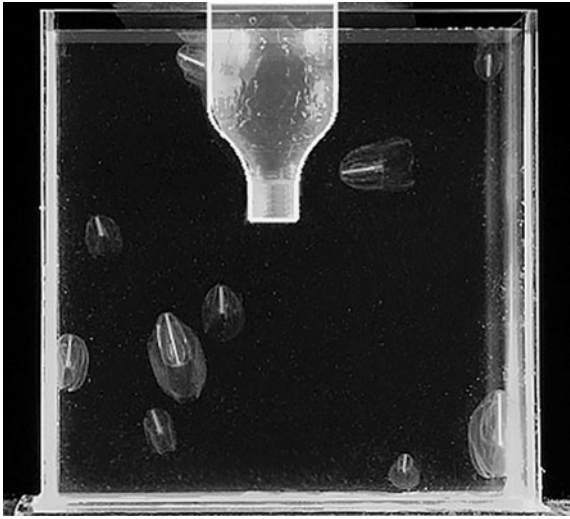


Fig. 1 Experimental tank with funnel containing one *Beroe ovata* predator at top center and 10 *Mnemiopsis leidyi* ctenophores in the water. The outlines of the holder and ctenophore guts have been enhanced for clarity

B. ovata or the water was considered to be the start of the experiment. The setup was then left undisturbed and video recorded for about 30 min. Each treatment was replicated 3 times using new water and animals. The aquarium was rinsed with hot water and then with natural seawater between trials. To avoid contamination by *B. ovata* chemicals, we used different bottles and transfer jars for the predator and control treatments. The volume of *B. ovata* was measured after each trial (41 ± 18 ml, mean \pm SD), and *M. leidyi* total body lengths were measured from the videos. There were no differences in mean *M. leidyi* length between trials (ANOVA, $F_{5,54} = 0.426$, $P = 0.829$). The flow patterns in the tank were not quantified; however, we assume that the water circulation caused by 10 *M. leidyi* in the tank by far exceeded that of one *B. ovata* (Colin et al., 2010).

The position of each *M. leidyi* in the tank at 1-s intervals was determined manually from the video recordings using Image J (Rasband, 2008), with the aboral apex of the ctenophore as the tracking point. The x, y coordinates were smoothed by a running average of 3 steps prior to calculations. To compare positions and motility parameters between the predator and the control treatments, we first calculated each parameter for every individual in all replicates. All statistical analyses, including those for test assumptions, were done by SPSS (14.0), R (R Development Core Team,

2008), or SigmaPlot (10.0 or 11.0). The position of each ctenophore in the tank during the ~ 30 min of experimentation can be considered independent of their initial position because *M. leidyi* could easily swim across the tank (personal observations) (e.g., Kreps et al., 1997). There were no significant differences in initial distribution between tanks at t_0 (Kruskal–Wallis, $\chi^2 = 9.590$, $df = 5$, $P = 0.088$). All individual *M. leidyi* were tracked over time (1,780 s after stimulus introduction).

Results

The motility tracks appeared to differ between the two treatments. In the controls, *M. leidyi* used both the upper and lower parts of the tank and generally wandered over much of the available space during the observation period (Fig. 2). In contrast, in the predator treatments, many individuals displayed seemingly more convoluted tracks with a smaller vertical component than those observed in the controls and longer residence times at the lower part of the tank. The variability in apparent behavior was analyzed by considering the data of vertical movement as two panels of time series (one for each treatment) (Fig. 2). The vertical motions of the individuals (“ups and downs”) were cyclic but without a fixed frequency (Fig. 2). We therefore modeled the correlations in locations for the individual *M. leidyi* as an autoregressive process of order 2 (AR, $P = 2$). This was done by the function *gls* from the package *nlme* (Pinheiro et al., 2008) of R (R Development Core Team, 2008) to the data in Fig. 2. We used time as a covariate and included tank as a factor variable to account for any possible differences between the six trials. We then compared the fits from a homogenous model, in which we forced the variances within the two treatments to be equal, with a heterogeneous model, in which we allowed unequal variance for the two treatments (i.e., $H_0: \sigma_{\text{predator}} = \sigma_{\text{control}}$ vs. $\sigma_{\text{predator}} \neq \sigma_{\text{control}}$ are equal). These models differed significantly from one another (L ratio = 12.26, $df = 10, 11$, $P = 0.0005$), indicating a significant effect of treatment on individual variability in vertical position (Fig. 2). The better heterogeneous model yielded $\Phi_1 = 0.767$ and $\Phi_2 = -0.107$.

In the second set of analyses, we examined how position (x, y) changed as a function of time (t_i) by using the average tank values ($n = 3$ per treatment) for each time step. To examine the dynamics of these

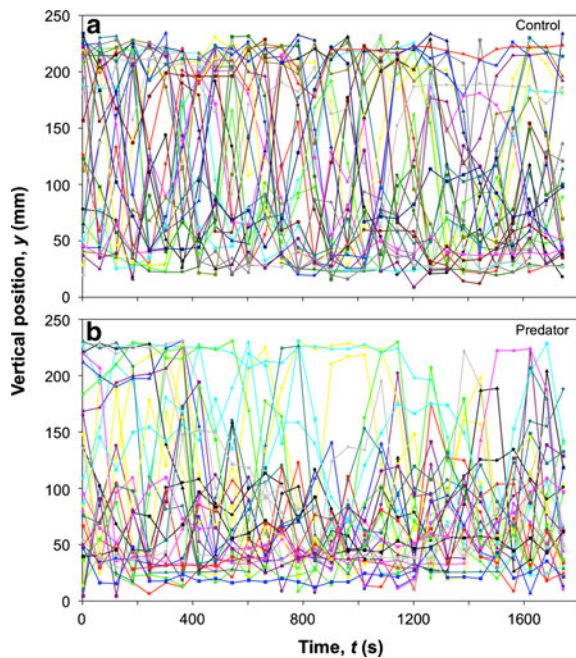


Fig. 2 Vertical positions of *Mnemiopsis leidyi* ctenophores in the water column as a function of time for all individuals in the controls (a) and in *Beroe ovata* predator treatments (b). Line color indicates individual *M. leidyi*, and symbol type represents the three replicate tanks. Data are only shown for every 60 s for clarity

parameters over time, we plotted the difference between the maximum and minimum values observed from t_0 to t_i . Patterns were analyzed by fitting the hyperbolic function $f(t) = \frac{at}{b+t}$ to the data. This confirmed that *M. leidyi* in the predator treatment were located lower in the tank than in the controls (Fig. 3). The variability in the mean vertical position of animals in the predator treatment generally decreased with time (cf Fig. 2). The dependency of the fitted coefficients a and b on treatment was tested by comparing mixed effects models with and without the factor treatment and including a random tank effect. This analysis was done using the *nlme* package (Pinheiro et al., 2008) in *R* (R Development Core Team, 2008). Treatment had a significant effect on a and b (L ratio = 14.12, $P = 0.0009$); *M. leidyi* in the predator treatment took longer to explore the vertical range of the aquarium ($b_{\text{control}} = 160$ s vs. $b_{\text{predator}} = 178$ s) and, on average, they used less of the vertical range than did *M. leidyi* in the control treatment ($a_{\text{control}} = 233$ mm, $a_{\text{predator}} = 204$ mm;

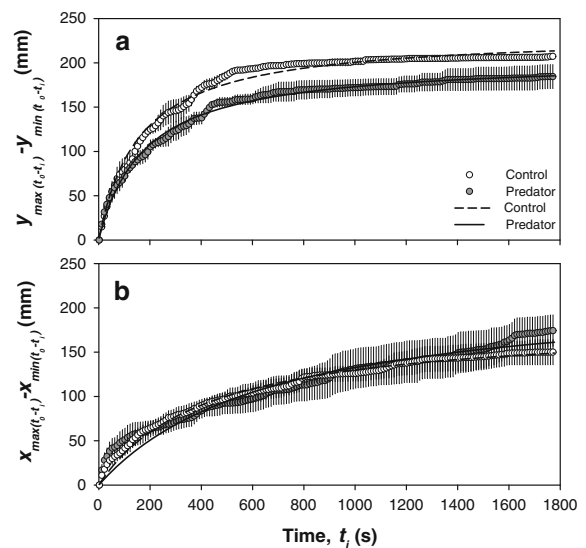


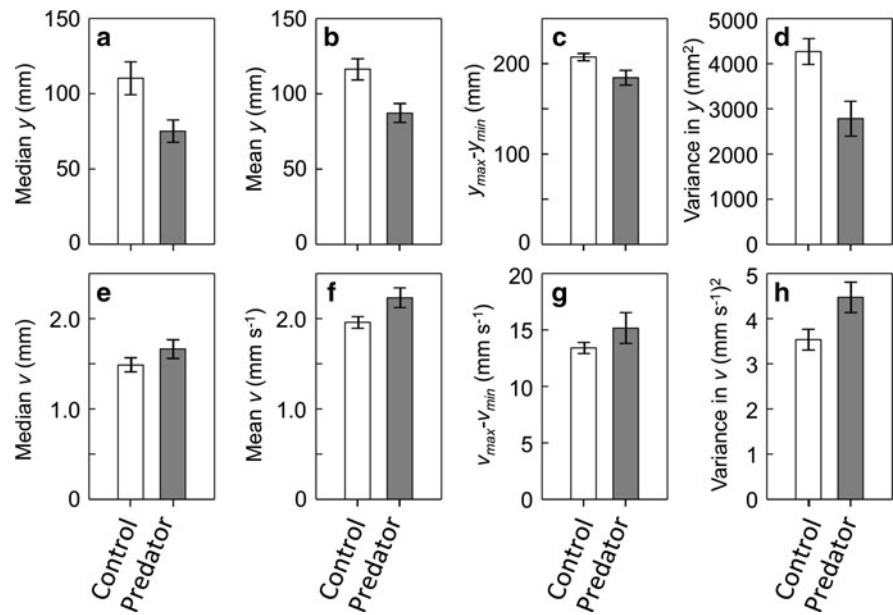
Fig. 3 Spans of vertical, y (a) and horizontal, x (b) distances covered by *Mnemiopsis leidyi* ctenophores as a function of time in the predator and the control treatments. Data points are mean values from the replicates \pm SE ($n = 3$). Every 10th data point is shown for clarity. a–b Curve fits ($f(t) = \frac{at}{b+t}$) yielded the following coefficients \pm SE for a: $a_{\text{control}} = 232.7 \pm 0.32$, $b_{\text{control}} = 159.8 \pm 1.15$, $R^2 = 0.95$, and $a_{\text{predator}} = 203.9 \pm 0.51$, $b_{\text{predator}} = 178.2 \pm 2.20$, $R^2 = 0.87$; for b: $a_{\text{control}} = 183.7 \pm 0.99$, $b_{\text{control}} = 415.0 \pm 7.03$, $R^2 = 0.82$, and $a_{\text{predator}} = 222.3 \pm 2.51$, $b_{\text{predator}} = 674.2 \pm 18.89$, $R^2 = 0.66$. $P < 0.0001$ for all coefficients and curve fits

Fig. 3a). As expected, there was no significant effect of treatment on horizontal placement (Fig. 3b).

In both treatments, *M. leidyi* alternated between slow and faster swimming. When at the bottom of the tank, the ctenophores either rested with their lobe tips at the bottom or moved upwards intermittently with sinking at regular intervals. Similarly, animals were often stationary at the surface for some time before descending. Although plots of mean speed over time suggested few differences, there was higher variation in speed in the predator treatment than in the controls (data not shown, but see Fig. 4).

We tested for differences in vertical position (y) and speed (v) parameters (mean, median, max–min, and variance) in the time-integrated data (Fig. 4). The analyses conducted for the individual variances of vertical position and speed become relevant when animals alter their behavior with time (i.e., all variables here) or when differences in mean or median values are expected to be small because the control treatment is expected to be uniformly distributed

Fig. 4 Individual median (a), mean (b), maximum–minimum (c), and variance (d) in vertical (y) position of *Mnemiopsis leidyi* ctenophores, and median (e), mean (f), maximum–minimum (g), and variance (h) of their speed (v) as a function of treatment. Bars represent mean \pm SE of all 30 *M. leidyi* in each treatment. Data for each *M. leidyi* were integrated over 1,775 s



across the entire measured range (i.e., x , y). To test if ctenophore behavior differed in the two treatments, we fitted linear models to each of the dependent variables using the *nlme* package (Pinheiro et al., 2008) of *R* (R Development Core Team, 2008). We included size as a covariate, added a random component to account for any possible tank effects, and allowed for unequal variance. The test without and with the factor treatment included (i.e., models with 5 and 6 degrees of freedom, respectively) were compared by likelihood tests. We found a significant treatment effect on several vertical distribution and speed parameters. Median y (L ratio = 5.045, P = 0.025) and mean y (L ratio = 4.263, P = 0.039) differed between treatments (Fig. 4a, b). Treatment also affected $y_{max} - y_{min}$ (L ratio = 5.906, P = 0.015), but not the variance in y (L ratio = 2.240, P = 0.135) (Fig. 4c, d). Although *M. leidyi* in the predator treatment explored a large part of the tank (Fig. 4c), they spent much less time in the top section than did the *M. leidyi* in the controls (Fig. 4a, b). Treatment had a significant effect on individual variance in speed (L ratio = 4.959, P = 0.026), with *M. leidyi* in the predator treatment being more variable. In contrast, treatment effects on other median v (L ratio = 1.419, P = 0.234), mean v (L ratio = 3.078, P = 0.079), and $v_{max} - v_{min}$ (L ratio = 1.473, P = 0.225) were not significant (Fig. 4e, h). We found no effects of individual size of *M. leidyi*.

Discussion

The statistical analyses assume that *M. leidyi* in the same tank behaved independently of one another, or in other words that the experimental signal was caused by the treatment itself and not by a dominant *M. leidyi*. Although opportunities for physical interactions occurred in a tank of this size, dominant group behavior in ctenophores has not been documented in the literature.

We demonstrate a suite of behavioral responses of *M. leidyi* to the presence of their predator, *B. ovata*. Our results suggest that lobate ctenophores may actively use remote signals and alter their behavior to avoid risky habitats. In contrast to previously documented escape behaviors of *M. leidyi*, which occur post-encounter, vertical positioning may enhance survival by limiting predator encounters. Such avoidance behaviors are common among smaller pelagic crustaceans (Titelman & Fiksen, 2004) and have been suggested for the ctenophore *Pleurobrachia pileus* (Esser et al., 2004). *M. leidyi* populations may be dense both close to the bottom and the surface (Miller, 1974; Costello & Mianzan, 2003). Vertically heterogeneous distributions in nature may also be attributed to both passive downward mixing and active surface avoidance during periods of heavy wind mixing, because high turbulence supposedly interferes with maintenance of the feeding position (Miller,

1974; Purcell et al., 2001; Mianzan et al., 2010). Also, *M. leidyi* tolerates hypoxia well (Thuesen et al., 2005) and may utilize poorly oxygenated deep water layers for spatial refuge (Decker et al., 2004). Nevertheless, our experiment suggests that predation risk may be involved in governing behavior of *M. leidyi*.

Probably, chemical cues from the predator *B. ovata* triggered a response from *M. leidyi*. The alternative explanation that fluid disturbance caused by the predator elicited a response seems unlikely because *M. leidyi* themselves created considerable fluid motion (Colin et al., 2010) in both treatments. Regardless of the nature of the cue involved, our results indicate that *M. leidyi* may actively adjust their position in the water column in response to remote cues and perceived risk from predators. *M. leidyi* responded to the predator presence by altering directional movement, reducing their vertical range, changing their motility patterns, and increasing the variability in swimming speed. Given that *M. leidyi* responds behaviorally to at least one of its major predators, *B. ovata*, and reacts by adjusting its swimming behavior and position in an experimental water column, it seems likely that vertically distinct distribution patterns of lobate ctenophores in the field may also be influenced by risk-sensitive behaviors.

Acknowledgments We thank J. E. Skjæraasen, P. Tiselius, E. Selander, T. Andersen, and reviewers for constructive comments. This is a contribution to Baltic Zooplankton Cascades (BAZOOCA) program funded by Baltic Organizations Network for funding Science, European Economic Interest Grouping (BONUS EEIG). We received financial support from Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (FORMAS), Sweden (grant numbers 2007-1105 to LJH and JT; 2006-1054 and 2008-1586 to JT), the National Science Foundation, USA (grant numbers OCE-0350834 and OCE-0623508 to JHC; OCE-0351398 and OCE-0623534 to SPC.), Stiftelsen Konung Carl XVI Gustafs 50-årsfond för vetenskap, teknik och miljö (to JT), and Birgit och Birger Wählströms minnesfond (to JT).

References

- Albert, D. J., 2011. What's on the mind of a jellyfish? A review of behavioural observations on *Aurelia* sp. jellyfish. *Neuroscience and Biobehavioral Reviews* 35: 474–482.
- Aronova, M. Z. & T. M. Alekseeva, 2002. Second messengers in the locomotor-sensory system of first multicellulars. The IP3-containing compartments in chemoreceptor cells of the comb jelly *Beroë cucumis* from data of cytochemical study. *Journal of Evolutionary Biochemistry and Physiology* 38: 318–329.
- Aronova, M. Z. & T. M. Alekseeva, 2003. Development of chemoreceptor cells in oral epithelium of adult jelly-fish *Beroë cucumis*. *Journal of Evolutionary Biochemistry and Physiology* 39: 714–723.
- Cohen, J. H. & R. B. Forward Jr., 2003. Ctenophore kairomones and modified aminosugar disaccharides alter the shadow response in a larval crab. *Journal of Plankton Research* 25: 203–213.
- Colin, S. P., J. H. Costello, L. J. Hansson, J. Titelman & J. O. Dabiri, 2010. Stealth predation and the predatory success of the invasive ctenophore *Mnemiopsis leidyi*. *Proceedings of the National Academy of Sciences of the United States of America* 107: 17223–17227.
- Condon, R. H. & D. K. Steinberg, 2008. Development, biological regulation, and fate of ctenophore blooms in the York River estuary, Chesapeake Bay. *Marine Ecology Progress Series* 369: 153–168.
- Costello, J. H., K. M. Bayha, H. W. Mianzan, T. A. Shiganova & J. E. Purcell, 2012. Transitions of *Mnemiopsis leidyi* (Ctenophora: Lobata) 3 from a native to an exotic species: a review. *Hydrobiologia*. doi:10.1007/s10750-012-1037-9.
- Costello, J. H. & H. W. Mianzan, 2003. Sampling field distributions of *Mnemiopsis leidyi* (Ctenophora, Lobata): planktonic or benthic methods? *Journal of Plankton Research* 25: 455–459.
- Costello, J. H., B. K. Sullivan, D. J. Gifford, D. Van Keuren & L. J. Sullivan, 2006. Seasonal refugia, shoreward thermal amplification, and metapopulation dynamics of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. *Limnology and Oceanography* 51: 1819–1831.
- Decker, M. B., D. L. Breitbart & J. E. Purcell, 2004. Effects of low dissolved oxygen on zooplankton predation by the ctenophore, *Mnemiopsis leidyi*. *Marine Ecology Progress Series* 280: 163–172.
- Esser, M., W. Greve & M. Boersma, 2004. Effects of temperature and the presence of benthic predators on the vertical distribution of the ctenophore *Pleurobrachia pileus*. *Marine Biology* 145: 595–601.
- Falkenhaus, T., 1996. Distributional and seasonal patterns of ctenophores in Malangen, northern Norway. *Marine Ecology Progress Series* 140: 59–70.
- Falkenhaus, T. & O. B. Stabell, 1996. Chemical ecology of predator-prey interactions in ctenophores. *Marine and Freshwater Behavior and Physiology* 27: 249–260.
- Fuentes, V. L., D. L. Angel, K. M. Bayha, D. Atienza, D. Edelist, C. Bordehore, J. M. Gili & J. E. Purcell, 2010. Blooms of the invasive ctenophore, *Mnemiopsis leidyi*, span the Mediterranean Sea in 2009. *Hydrobiologia* 645: 23–37.
- Greve, W. & F. Reiners, 1988. Plankton time-space dynamics in German Bight—a systems-approach. *Oecologia* 77: 487–496.
- Hansson, L. J. & B. Norrman, 1995. Release of dissolved organic carbon (DOC) by the scyphozoan jellyfish *Aurelia aurita* and its potential influence on the production of planktic bacteria. *Marine Biology* 121: 527–532.
- Harbison, G. R., L. P. Madin & N. R. Swanberg, 1978. On the natural history and distribution of oceanic ctenophores. *Deep Sea Research* 25: 233–256.

- Hays, G. C., 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503: 163–170.
- Horridge, G. A., 1965. Non-motile sensory cilia and neuromuscular junctions in a ctenophore independent effector organ. *Proceedings of the Royal Society B* 162: 333–350.
- Hosia, A. & J. Titelman, 2011. Intraguild predation between the native North Sea jellyfish *Cyanea capillata* and the invasive ctenophore *Mnemiopsis leidyi*. *Journal of Plankton Research* 33: 535–540.
- Hosia, A., J. Titelman, L. J. Hansson & M. Haraldsson, 2011. Interactions between native and alien ctenophores: *Beroe gracilis* and *Mnemiopsis leidyi* in Gullmarsfjorden. *Marine Ecology Progress Series* 422: 129–138.
- Jaspers, C., J. Titelman, L. J. Hansson, M. Haraldsson & C. Ditlefsen, 2011. The invasive ctenophore *Mnemiopsis leidyi* poses no direct threat to Baltic cod eggs and larvae. *Limnology and Oceanography* 56: 431–439.
- Javidpour, J., J. Molinero, J. Peschutter & U. Sommer, 2009. Seasonal changes and population dynamics of the ctenophore *Mnemiopsis leidyi* after its first year of invasion in the Kiel Fjord, Western Baltic Sea. *Biological Invasions* 11: 873–882.
- Kass-Simon, G. & L. A. Hufnagel, 1992. Suspected chemoreceptors in coelenterates and ctenophores. *Microscopy Research and Technique* 22: 265–284.
- Kreps, T. A., J. E. Purcell & K. B. Heidelberg, 1997. Escape of the ctenophore *Mnemiopsis leidyi* from the scyphomedusa predator *Chrysaora quinquecirrha*. *Marine Biology* 128: 441–446.
- McKelvey, L. M. & R. B. Forward Jr, 1995. Activation of brine shrimp nauplii, photoreponses involved in diel vertical migration by chemical cues from visual and non-visual planktivores. *Journal of Plankton Research* 17: 2191–2206.
- Mianzan, H. W., P. M. Martos, J. H. Costello & R. A. Guerro, 2010. Avoidance of hydrodynamically mixed environments by *Mnemiopsis leidyi* (Ctenophora: Lobata) in open-sea populations from Patagonia, Argentina. *Hydrobiologia* 645: 113–124.
- Miller, R. J., 1974. Distribution and biomass of an estuarine ctenophore population, *Mnemiopsis leidyi* (A. Agassiz). *Chesapeake Science* 15: 1–8.
- Moss, A. G., B. Wells & L. Muellner, 2004. A mechanosensory system that controls feeding in adult *Mnemiopsis*. *Hydrobiologia* 530–531: 145–153.
- Ohman, M. D., 1988. Behavioral responses of zooplankton to predation. *Bulletin of Marine Science* 43: 530–550.
- Oviatt, C. A. & P. M. Kremer, 1977. Predation on the ctenophore, *Mnemiopsis leidyi*, by butterflyfish, *Periplus triacanthus*, in Narragansett Bay, Rhode Island. *Chesapeake Science* 18: 236–240.
- Pinheiro, J., S. DebRoy, D. Sarkar & The R Core team, 2008. nlme: linear and nonlinear mixed effects models. R package version 3.1-89.
- Pitt, K. A., D. T. Welsh & R. H. Condon, 2009. Influence of jellyfish blooms on carbon, nitrogen and phosphorous cycling and plankton production. *Hydrobiologia* 616: 133–149.
- Purcell, J. E., 1991. A review of cnidarians and ctenophores feeding on competitors in the plankton. *Hydrobiologia* 216–217: 335–342.
- Purcell, J. E. & J. H. Cowan, 1995. Predation by the scyphomedusan *Chrysaora quinquecirrha* on *Mnemiopsis leidyi* ctenophores. *Marine Ecology Progress Series* 129: 63–70.
- Purcell, J. E., T. A. Shiganova, M. B. Decker & E. D. Houde, 2001. The ctenophore *Mnemiopsis* in native and exotic habitats: U.S. estuaries versus the Black Sea basin. *Hydrobiologia* 451: 145–176.
- R Development Core Team, 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. ISBN 3-900051-07-0 [available on internet at <http://www.R-project.org>].
- Rasband, W. S., 2008. Image J. U. S. National Institutes of Health, Bethesda, MD [available on internet at <http://imagej.nih.gov/ij/>, 1997–2011]. Accessed 23.08.2008.
- Riemann, L., J. Titelman & U. Båmstedt, 2006. Links between jellyfish and microbes in a jellyfish dominated fjord. *Marine Ecology Progress Series* 325: 29–42.
- Riisgård, H. U., L. Bøttiger, C. V. Madsen & J. E. Purcell, 2007. Invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark) in late summer 2007—assessment of abundance and predation effects. *Aquatic Invasions* 2: 395–401.
- Stone, R., 2005. Attack of the killer jellies. *Science* 309: 1805–1806.
- Swanberg, N., 1974. The feeding behavior of *Beroe ovata*. *Marine Biology* 24: 69–76.
- Thuesen, E. V., L. D. Rutherford & P. L. Brommer, 2005. The role of aerobic metabolism and intragel oxygen in hypoxia tolerance of three ctenophores: *Pleurobrachia bachei*, *Bolinopsis infundibulum* and *Mnemiopsis leidyi*. *Journal of Marine Biological Association of the United Kingdom* 85: 627–633.
- Titelman, J. & Ø. Fiksen, 2004. Ontogenetic vertical distribution patterns in small copepods: field observations and model predictions. *Marine Ecology Progress Series* 284: 49–63.
- Titelman, J., L. Gandon, A. Goarant & T. Nilsen, 2007. Intraguild predatory interactions between the jellyfish *Cyanea capillata* and *Aurelia aurita*. *Marine Biology* 152: 745–756.
- Titelman, J., L. Riemann, T. A. Sørnes, T. Nilsen, P. Griekspoor & U. Båmstedt, 2006. Turnover of dead jellyfish: stimulation and retardation of microbial activity. *Marine Ecology Progress Series* 325: 43–58.
- Vinogradov, M. E., E. A. Shushkina & T. A. Lukasheva, 2005. Population dynamics of the ctenophores *Mnemiopsis leidyi* and *Beroe ovata* as a predator–prey system in the near-shore communities of the Black Sea. *Oceanology* 45(Suppl 1): S161–S167.