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1-2018

Resilience in Moving Water: Effects of Turbulence on the Predatory Impact of the Lobate Ctenophore *Mnemiopsis leidyi*

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Resilience in moving water: Effects of turbulence on the predatory impact of the lobate ctenophore *Mnemiopsis leidyi*

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Abstract

Despite its delicate morphology, the lobate ctenophore *Mnemiopsis leidyi* thrives in coastal ecosystems as an influential zooplankton predator. Coastal ecosystems are often characterized as energetic systems with high levels of natural turbulence in the water column. To understand how natural wind-driven turbulence affects the feeding ecology of *M. leidyi*, we used a combination of approaches to quantify how naturally and laboratory generated turbulence affects the behavior, feeding processes and feeding impact of *M. leidyi*. Experiments using laboratory generated turbulence demonstrated that turbulence can reduce *M. leidyi* feeding rates on copepods and *Artemia* nauplii by > 50%. However, detailed feeding data from the field, collected during highly variable surface conditions, showed that wind-driven turbulence did not affect the feeding rates or prey selection of *M. leidyi*. Additional laboratory experiments and field observations suggest that the feeding process of *M. leidyi* is resilient to wind-driven turbulence because *M. leidyi* shows a behavioral response to turbulence by moving deeper in the water column. Seeking refuge in deeper waters enables *M. leidyi* to maintain high feeding rates even under high turbulence conditions generated by wind driven mixing. As a result, *M. leidyi* exerted a consistently high predatory impact on prey populations during highly variable and often energetic wind-driven mixing conditions. This resilience adds to our understanding of how *M. leidyi* can thrive in a wide spectrum of environments around the world. The limits to this resilience also set boundaries to its range expansion into novel areas.

The comb jelly *Mnemiopsis leidyi*, endemic to the Atlantic coast of North and South America including the Gulf of Mexico (GESAMP 1997), is a voracious predator and a very successful invasive species, now reaching a near global

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distribution (Costello et al. 2012). A highly specialized feeding current allows *M. leidyi* to entrain large volumes of water with exceptionally high prey capture efficiencies (Costello et al. 1999; Colin et al. 2010). Predation by *M. leidyi* populations have been repeatedly estimated to remove > 100% of the prey standing stock on a daily basis (e.g., Finenko et al. 2006; Kideys et al. 2008; Roohi et al. 2008; Riisgård et al. 2012) which has led to documented cascading effects with changes in food web structure and functioning in native (Nelson 1925; Kremer 1979; Mountford 1980; Sullivan and Gifford 2007) as well as invaded (Kideys 2002; Riisgaard et al. 2012) habitats. Even though *M. leidyi* has been shown to thrive under different environmental conditions, it remains unclear under which circumstances or in which areas it can exert the highest grazing impacts and which abiotic factors might govern its distribution or could set a limit to its range expansion, especially in invaded habitats.

The high predatory impacts of *M. leidyi* are based on its ability to rapidly ingest a wide array of prey and effectively convert food into growth and offspring. Previous research demonstrates that the mechanics of prey capture strongly influence prey selection and final diet composition of *M. leidyi* (Costello et al. 1999; Waggett and Costello 1999; Colin et al. 2010). The mechanics of *M. leidyi* prey capture require it to strike a delicate hydrodynamic balance—maintenance of adequate feeding current strength to entrain prey while not producing shear deformation levels that alert approaching copepods to the ctenophore's presence. The solution appears to be generation of a low velocity, laminar current characterized by shear deformation rates below copepod detection thresholds (Colin et al. 2010). One consequence of this delicate hydrodynamic equilibrium is that *M. leidyi* predation is likely to be highly sensitive to variations in ambient hydrodynamic conditions such as wind driven turbulence in surface waters. So far, low levels of turbulence have been shown to interfere with the feeding current of *M. leidyi* (Sutherland et al. 2014). This suggests that ambient turbulence can disrupt the encounter processes and reduce feeding proficiency, thereby limiting population growth. For anchovy larvae it has been shown that high turbulence can dramatically reduce recruitment strength by diluting preferred food items (Lasker 1975). On the other hand, encounter rates for fish larvae such as cod are increased under experimental high turbulence regimes, leading to higher feeding rates (as reviewed in Kiørboe 1997).

How do natural flows affect *M. leidyi* feeding process? Unfortunately, most studies of *M. leidyi* feeding mechanics have used laboratory, still water conditions. A recent study, however, showed that low levels of turbulence elicit a behavioral response by *M. leidyi*, causing them to increase their swimming speeds (Sutherland et al. 2014). Consequently, we envision different scenarios where low to moderate turbulence may either increase or decrease feeding proficiency. Increased swimming could lead to increased encounter rates, and therefore, ingestion rates on prey. However, if turbulence disrupts post-encounter capture abilities, then any level of turbulence may decrease ingestion rates. To resolve these different possible outcomes, turbulence and its effects on *M. leidyi* feeding need to be quantified at the relevant scales to assess the influence of turbulence on feeding at both the individual and population scales. Turbulence has long been understood as one of the critical forces influencing planktonic processes (e.g., Margalef 1978; Lazier and Mann 1989; Kiørboe 1993) and quantifying turbulence at the relevant size and temporal scales has been recognized as critical for understanding how turbulence affects feeding interactions of pelagic organisms (Yen et al. 2008; Jumars et al. 2009).

The goal of this study was to evaluate the impact of turbulence on the feeding process and in situ predatory impact of *M. leidyi*. To this end, we used a novel combination of laboratory and field studies at the individual and population level to directly quantify how turbulence changes the behavior, feeding rates and predatory impact of *M. leidyi*. The intent of this combined approach is to provide a mechanistic understanding of turbulent effects on *M. leidyi* so that we can better predict the types of environments in which *M. leidyi* is capable of exerting high predatory controls and hence, which areas would be of concern for future expansion of this highly successful invasive species.

Methods

Laboratory turbulence feeding experiments

The effect of high turbulence levels on clearance rates of *M. leidyi* was investigated under laboratory controlled conditions using evasive (copepod *Acartia tonsa*) and non-evasive (*Artemia salina*) prey types. Experiments were performed in 38 L glass aquaria which were separated into an experimental chamber of 28-L and two turbulence-generating chambers with one VorTech MP10w ES EcoSMART (EcoTech Marine, U.S.A.) propeller pump, each (Supporting Information Figs. S1, S2). The pumps (flow rate range of 0.75–6 $m^3\ h^{-1}$) were set to the lowest flow rate and operated in the short pulsed mode. This mimicked high turbulence reef conditions, which were confirmed to be similar to natural turbulence conditions (Supporting Information Fig. S2). To ensure that animals were not entrained into the pumps, they were screened off from the experimental chamber with 100 μm nitex mesh divide that had constant water flow over the front of the divide, using submersible aquarium pumps with a maximum flow rate of 600 L h^{-1} (Supporting Information Fig. S1).

Turbulence in the tank was quantified using both an Acoustic Doppler Velocimeter (ADV, Fixed Stem Nortek AS©; measurements made in 16 positions in the tank) and using digital particle image velocimetry (DPIV; Sutherland et al. 2014). Measurements were made in three positions in the tank. Turbulence dissipation rate, ε, using the ADV was calculated from the root-mean-square (RMS) velocities (cm s^{-1}),

$$\text{RMS} = \sqrt{u_{\text{rms}_x}{}^2 + u_{\text{rms}_y}{}^2 + u_{\text{rms}_z}{}^2} \ \text{ where}$$

$$u_{\text{rms}_x} = \sqrt{\frac{\sum u_x{}^2 - (\sum u_x)^2/n}{n-1}} \tag{1,2}$$

with *n* being the number of measurements in the 5 min sampling interval (e.g., Pekcan-Hekim et al. 2016). The energy dissipation rate ($m^2\ s^{-3}$) was calculated as $\varepsilon = A_1 \frac{\text{RMS}^3}{l}$ with *l* being the water depth and A_1 a constant of the order 1 (Moum 1996).

DPIV video was collected by adding 5 μm hollow glass beads which were illuminated with a vertically positioned laser sheet using a 532 nm high power portable laser (Laserglow technologies), and recorded at 500 frames s^{-1} using a high-speed digital video camera (Photron Fastcam 1024 PCI). Two-dimensional velocities of illuminated particles in the laser sheet were analyzed using sequential images and a

cross-correlation algorithm with shifting overlapping interrogation windows (DaVis 7.2 software, LaVision, U.S.A.) following published protocols (Colin et al. 2010; Sutherland et al. 2014). Turbulence dissipation rate from DPIV was calculated from the u and w velocity vectors directly (De Jong et al. 2009).

$$\varepsilon_{PIV} = 4\nu \left[\left\langle \left(\frac{\partial u}{\partial x}\right)^2 \right\rangle + \left\langle \left(\frac{\partial w}{\partial z}\right)^2 \right\rangle + \left\langle \frac{\partial u}{\partial x}\frac{\partial w}{\partial z} \right\rangle + \frac{3}{4}\left\langle \left(\frac{\partial u}{\partial x}\frac{\partial w}{\partial z}\right)^2 \right\rangle \right]$$

(3)

where ν is the kinematic viscosity of the seawater. Random measurement error (e.g., from noise in the PIV data) was addressed using a correction to isolate noise in the DPIV measurements by comparing dissipation rate estimates for multiple interrogation window sizes (Tanaka and Eaton 2007). Dissipation rates derived from DPIV are 2D approximations and assumes turbulence is homologous and isotropic.

Both the ADV and the DPIV methods yielded similar dissipation rate estimates at 7.8×10^{-4} and 2.5×10^{-4} m^2 s^{-3}, respectively. In comparison, field sampling during turbulent ($n = 17$) conditions used for gut content analyses showed a similar range for high turbulence days with an average dissipation rate of 1.2×10^{-4} m^2 s^{-3}, while low turbulence days were two orders of magnitude lower with 6.53×10^{-6} m^2 s^{-3}.

A total of 22 laboratory turbulence replicate incubations were performed. Each incubation contained three *M. leidyi* and 150 prey, leading to an initial prey concentration of 5.3 ind L^{-1}. The water in the experimental units was changed after each experiment and consisted of 10-μm filtered seawater at a temperature of 21 ± 1°C and a salinity of 32.

Before each incubation *M. leidyi* were starved for 12 h and acclimatized in the experimental turbulence chamber for a minimum of 30 min until all animals showed normal swimming behavior and had opened their lobes. All prey were individually sorted under a stereomicroscope with adult *A. tonsa* (C6) originating from field samples and *A. salina* from newly hatched laboratory cultures. All prey were visually checked to be alive and actively swimming. Thereafter, prey were added and the water gently stirred to ensure even prey distribution. To avoid accumulation of prey due to phototaxis, the aquaria were individually covered with black plastic foil during the entire experiment. In order to detect a feeding signal and to ensure that we can assume near constant prey concentration over time, *M. leidyi* size and incubation time was chosen so that a maximum of 1/3 of the aquarium was cleared. The average animal size was 24.4 ± 1.9 mm (range: 19–29 mm oral-aboral length) with an incubation time of 2 h. Upon termination, *M. leidyi* were removed from the aquaria and remaining prey were concentrated via reverse filtration using a 55 μm meshed funnel and preserved with acidified Lugol solution at a final concentration of 2%. Animals were morphologically inspected at the end of the experiments. In total, 5 out of 66 animals showed signs of damage and thus the three experiments with damaged animals were removed from the analyses.

Handling controls for each aquarium were performed regularly (i.e., prey with no *M. leidyi*) and used to calculate initial prey concentrations for each aquarium. Overall, prey re-capture in handling controls was very high ($98.9\% \pm 1.9\%$; $n = 13$). Clearance rates (F, L ind^{-1} h^{-1}) were calculated based on prey disappearance in the experimental aquaria.

Laboratory behavior turbulence tank experiments

To investigate the effect of turbulence on *M. leidyi* behavior, animals were incubated in an experimental chamber mimicking a turbulence gradient in the field (Supporting Information Fig. S3). To generate a turbulence gradient, a standing wave was generated at the surface using a motor with a plate rotating at 1.8 ± 0.02 revolutions s^{-1} and an attached rigid plunger. The motor rotated the plunger in and out of the water within a 175.5-L glass aquarium filled with 10-μm filtered seawater at ambient temperature and salinity (23°C, 32 PSU).

Turbulence levels decreased with depth (Supporting Information Fig. S3) and were measured using two-dimensional DPIV as described above and following the methods of Sutherland et al. (2014). DPIV measurements were conducted at eight different depth strata from the surface to the bottom of the aquarium using the methods described above.

Six replicate 20 min incubations were conducted for this experiment. Each incubation contained 10 similar-sized, field caught (Woods Hole, Massachusetts, U.S.A.) *M. leidyi* (with an oral-aboral length of ca. 2.5–3.5 cm) placed in filtered seawater. Before each incubation *M. leidyi* were starved for 24 h and acclimated in the incubation tank in still water for 10 min. Non-turbulent treatments were generated by only switching on the motor but without attaching the plunger.

The behavior of *M. leidyi* was video recorded using a Sony HDV 1080i MiniDV Progressive digital video camera and a Vario Sonar Carl Zeiss 1.6/4.4–52.8 objective at 30 frames s^{-1} overlooking the entire aquarium. For analyzing the depth distribution and swimming speed of individuals over time, video sequences were exported as tiff files and every 100th or 300th image analyzed for turbulent and non-turbulent treatments, respectively. These frames were extracted from 5 min sequences in the middle of ca. 20 min recordings of turbulent and non-turbulent conditions. In each frame, the position and orientation of each *M. leidyi* was quantified by digitizing the position of the mouth and anal pore of *M. leidyi* using ImageJ (National Institutes of Health, U.S.A.). The velocity was calculated as the change in the position of the mouth over time. Because DPIV measurements required different illumination than the behavior measurements we were not able to quantify the water velocity at the same time as the swimming velocity. This prevented us from being able to quantitatively separate out the effects of flow from swimming velocity. The net-to-gross-displacement ratio (NGDR) was calculated by taking the ratio of the distance between *M. leidyi*'s position at the beginning and ending of

a 1 min interval (net distance) divided by the total distance *M. leidyi* traveled during the interval (gross distance).

In situ observations of turbulence effects on *M. leidyi*

Feeding and behavior were also investigated in the field. To investigate the effect of in situ turbulence on feeding in *M. leidyi*, field sampling was conducted on days experiencing a range of wind speeds in Woods Hole, Massachusetts, U.S.A. (41.524627, −70.673104) in August of 2012 (Supporting Information Table S1). Sampling was done from a pier and the data that were collected during each sampling (Supporting Information Table S1) were: (1) environmental data throughout the water column (i.e., salinity, temperature, wind speed and velocity profiles using an Acoustic Doppler Velocimeter, ADV, Fixed Stem Nortek AS©); (2) *M. leidyi* for gut content analysis; and (3) plankton tows for biological background data of *M. leidyi* abundances and sizes and zooplankton prey abundances. Sampling was conducted within 2 h at the same location.

For turbulence sampling, an ADV was rigidly attached to a mounting apparatus that was subsequently lowered by 0.3 m depth intervals. This allowed for profiling the water column from the surface to 0.3 m above the seafloor. Depending on water heights, a total of 10–13 discrete depth strata were sampled for each profile. ADV sampling was conducted by triplicate measurements for each discrete depth strata with recordings of 3–5 min each. Turbulent dissipation rate (m^2 s^{-3}) was calculated as described above from the root-mean-square (RMS) velocities (cm s^{-1}) and the average of the triplicate measurements are reported along with their standard deviation (SD). Wind data during the 1–2 h sampling period were taken from the weather station next to the sampling pier (WHOI Dock).

For gut content analysis, 15–24 *M. leidyi* were individually collected by hand from the pier and immediately analyzed within 2–5 min for gut contents on site using a stereomicroscope (Rapoza et al. 2005). In total 423 *M. leidyi* individuals were analyzed for gut contents.

Plankton tows for biological background sampling consisted of replicated 500 μm oblique plankton tows (0.5 m diameter), with an attached flow meter, where the net was towed obliquely throughout the entire water column from the surface to a maximum depth of 4 m, leading to sampled water volumes of 3–26 m^{-3}. The volume sampled varied depending on overall *M. leidyi* abundance in the water column. From these tows we measured *M. leidyi* abundances and size distributions (oral-aboral length, mm). Additional duplicate 100-μm oblique plankton tows (same methods and location as *M. leidyi* tows) were conducted to measure total zooplankton abundances. Samples were individually preserved in 4% borax buffered formalin ($n = 48$). Abundances per cubic meter were estimated from flow meter recordings and checked against expected values based on the net tow distance.

Zooplankton samples were analyzed from replicated formalin preserved samples and identified to the lowest taxonomic level and averages of both nets were used for further analyses. Pearre's electivity index (*E*) was calculated for all major prey items (Pearre 1982) using gut contents and average zooplankton prey availability from the field (Costello and Colin 2002). The values of *E* range from 1 to −1 and reflect the relative selection for or against a prey item, respectively. Only significant *E* values are displayed and tinnids, protozoans and invertebrate eggs were disregarded due to potential sampling bias using a 100 μm plankton mesh. Larvaceans were the only prey not present in the zooplankton samples but found in some guts. Other prey items were present in samples but not observed in the gut contents, including cladocerans, echinoderm larvae, and hydromedusae. All gut contents ($n = 423$) were standardized using published gut digestion times (Table 1, Supporting Information Table S2) and temperature corrected to a standard temperature of 20°C (Hansen et al. 1997b). Carbon specific daily ingestion rates (I_{cs}) for all prey items were calculated as:

$$\text{Ingestion rate} = \left(\frac{N_i}{D_i}\right) 24 C_i \qquad (4)$$

where N_i is the number of prey of species *i* present in the gut, D_i is the prey specific temperature corrected digestion time and C_i the prey specific carbon content (Table 1). Dividing, the ingestion rate, *I*, by the concentration of prey, *P*, in the water column yields the clearance rate, *F*, where:

$$\text{Clearance rate} = I/P \qquad (5)$$

Dividing *I* by C_{Mn}, *M. leidyi* carbon content, yields the carbon specific daily ration for different prey types. Oral-aboral lengths were converted to carbon (Robinson and Graham 2014) and carbon content of prey items were retrieved from the literature (Table 1). To estimate the predatory impact of *M. leidyi*, we used the half-life time ($\tau_{1/2}$) of the most abundant prey, the copepod *A. tonsa*. The half-life is a community clearance proxy and indicates how long it would take the *M. leidyi* community (in days) to reduce the copepod population to 50%, not considering recruitment. This has frequently been calculated for *M. leidyi* in other ecosystems (e.g., Riisgård et al. 2012) and is computed as:

$$\text{Half life time} = \frac{\ln 2}{\mu} \qquad (6)$$

where μ is the mortality rate, which is *F* multiplied by the respective concentration of *M. leidyi*. A key advantage of this metric is that it provides a common measure for comparing predatory impact across communities of variable abundance.

In situ behavioral analyses

To investigate the behavioral response of *M. leidyi* to different turbulence levels in the field, we used both video

Table 1. Average carbon content (μgC) of different zooplankton groups present in *M. leidyi* gut content analyses and zooplankton samples from Woods Hole, NE U.S.A. during August 2012 - with general copepodite weight (excluding cyclopoids) averaged (bold). Digestion times (h^{-1}), temperature corrected to 20°C (Hansen et al. 1997b) averaged over all available literature regressions (*see* Supporting Information Table S2 for detail). If no digestion times were available, digestion times of similar prey types were used. References are indicated by numbers and given below.

Species/group	μgC ind^{-1}	References carbon content	Digestion time (h)
A. tonsa - C6 Copepod	5	Berggreen et al. (1988)	
Temora longicornis - C6 Copepod	13	Hay et al. (1991)	
Oithona similis - C6 Copepod	0.6	Sabatini and Kiørboe (1994)	
Copepodites: average	**2.1**	See below	
Harpacticoid copepods	2	Martinussen and Båmstedt (1995)	
A. tonsa	2.5	Berggreen et al. (1988)	
Paracalanus parvus - C4	1.5	Hay et al. (1991)	
Temora longicornis - C4	2.5	Hay et al. (1991)	
Cyclopoid copepods* - general	0.8	Hay et al. (1991)	
Herpacticoid copepods - general	2	Martinussen and Båmstedt (1995)	
Copepod – general			2[1–6]
Copepod nauplii	0.17	Berggreen et al. (1988), Granhag et al. (2011)	0.6[1–4]
Amphipod	10	Martinussen and Båmstedt (1995)	2[8]
Barnacle nauplii	2.5	Rodhouse and Roden (1987)	0.9[1]
Barnacle cypris	11	Rodhouse and Roden (1987)	2[8]
Crab zoea	10	Harms et al. (1994)	2[8]
Crab megalope	80	Harms et al. (1994)	2[8]
Cladocerans	2	Rodhouse and Roden (1987)	2[2]
Polychaete larvae	4.3	Uye (1982)	0.2[3]
Mollusc larvae	2.2	Uye (1982)	1.8[3,7]
Ascidian larvae	3.3	Bennett and Marshall (2005)	0.4[8]
Larvaceans[†]	3	Lombard et al. (2009)	0.4[2,5]
Rotifers, Protozoans	0.23	Hansen et al. (1997a)	0.2[3]
Tintinnid, *Favella* sp.	0.055	Loret et al. (2000), Granhag et al. (2011)	
Tintinnid – general			0.5[2,3]
Nematode	0.055	Assuming the same as for Tintinnida	2[8]

* Cyclopoid copepods were only present in field samples.
[†] Corresponds to *Oikopleura dioica* with a trunk length of 750 μm.
1. Larson (1987), 2. Granhag et al. (2011), 3. Sullivan (2009), 4. Stanlaw et al. (1981), 5. Javidpour et al. (2009), 6. Reeve (1980), 7. Purcell et al. (1991), 8. Assumed.

observation by SCUBA diving and depth stratified sampling. To video *M. leidyi* behavior in situ we used our self-contained underwater velocimetery apparatus (SCUVA; Katija et al. 2008). Dives were performed on multiple days under varying surface wind conditions. Each dive was to 8 m where individual *M. leidyi* were video recorded for several minutes. The video was analyzed for different behavioral parameters and the dissipation rate of the water around the *M. leidyi* was quantified using the DPIV methods described above except natural particles in the water column were used as tracers. There is the potential for in situ DPIV measurements of dissipation rate to have added noise as a result of uncontrollable factors such as motile plankton. While there are no available methods to correct for these motions this added noise is likely minimal since the average velocity of the water was greater than 1 cm s^{-1} on the calmest days

and this is an order of magnitude greater than the swimming velocities of most motile plankton.

In an effort to relate *M. leidyi* vertical distribution to surface wave conditions we analyzed depth stratified plankton samples that were collected on 3 d (20 August 2008, 23 August 2008, and 29 August 2008) from the R/V *Tioga* (WHOI) in Vineyard Sound near Woods Hole, Massachusetts, U.S.A. Depth stratified sampling was done using a 500 μm mesh Multiple Opening and Closing Net Environmental Sampling System (MOCNESS) where three discrete depth strata were sampled per station (0.5 m, 6 m, and 12 m). Filtered water volumes ranged between 190 m^{-3} and 500 m^{-3} with 21–630 *M. leidyi* analyzed per net. The % of the *M. leidyi* population at the surface was calculated as the number of *M. leidyi* in the uppermost sampling net compared to the entire sampled population at that station and plotted as a
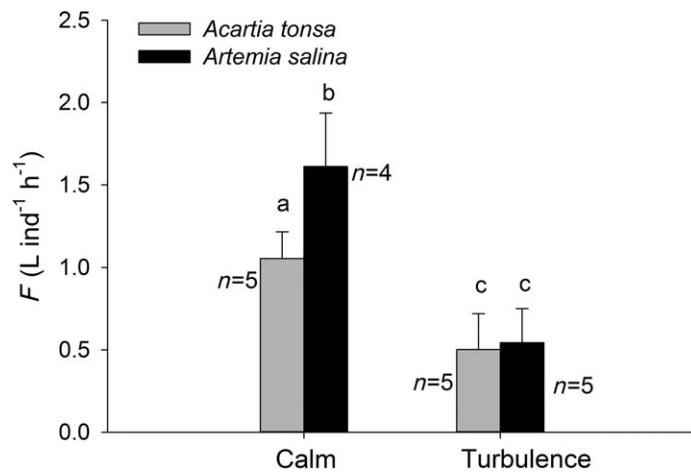
Fig. 1. Effects of artificial turbulence on feeding in the laboratory (Dissipation rate = 5.1×10^{-4} m^2 s^{-3}). Treatments with different letters above each bar were significantly different (Tukey–Kramer Post-hoc analysis, $p < 0.05$). Experimental turbulence reduced *M. leidyi* feeding rates.

function of wave height (cm). Estimated wave heights were visually estimated from the ship and recorded at the exact time of the sampling. As no direct wind measurements were available on board, wave heights were our best measure of local wind driven turbulence, similar to previous investigations (e.g., Finelli et al. 2009).

Results

Laboratory experiments comparing the feeding rates of *M. leidyi* in calm vs. high levels of artificial turbulence (dissipation rate = 5.1×10^{-4} m^2 s^{-3}) demonstrated a strong effect of turbulence on the clearance rates of *M. leidyi* fed both passive and active prey (Fig. 1). In calm conditions *M. leidyi* had significantly greater clearance rates on the passive *A. salina* than on the highly reactive copepod *A. tonsa* (Two-way ANOVA, $p < 0.05$). However, turbulence reduced *M. leidyi*'s ability to feed on both types of prey and it eliminated the observed advantage that copepods had in calm conditions to avoid predation. Hence, under turbulent conditions escaping and non-escaping prey faced similar mortality rates due to *M. leidyi* feeding (Fig. 1).

A detailed examination of the gut contents of *M. leidyi* collected from the field (Figs. 2, 3) during different wind driven turbulence conditions (Fig. 4A) showed that the turbulence measured at the surface did not relate to measured predatory impact of *M. leidyi*. Specifically, clearance rates on all prey (Fig. 2A) and the most abundant prey item (Fig. 2C), the copepod *A. tonsa*, were unrelated to surface turbulence levels. A common index for predatory impact, half-life time ($\tau_{1/2}$), showed that *M. leidyi* is capable of removing copepods from the water column at high rates on even the windiest days (Fig. 2C). The amount of carbon *M. leidyi* ingested, relative to its body carbon also remained unchanged (Fig. 2D,E). During our sampling

period, larger *M. leidyi* (> 2 cm) on average ingested about 5% of their carbon mass while smaller *M. leidyi* (< 2 cm) ingested 50% of their carbon mass daily.

In addition to feeding rates, prey selection patterns (measured as Pearre's electivity, E) did not change in relation to surface turbulence (Fig. 3). The most abundant prey type found in the guts of *M. leidyi* were copepods and their nauplii stages. However, low electivity values demonstrate that this was because copepod prey were most abundant in the water column. In fact, most of the electivity values were rather low with considerable variability between individuals indicating that *M. leidyi* fed generally non-selectively on most types of prey available. This pattern did not appear to be affected by background turbulence. Other variables which could confound in situ feeding analyses, such as *M. leidyi* abundance or prey abundance, were also not affected by turbulence (Supporting Information Fig. S4A,B). However, independent of wind speed, we found that turbulence values measured as dissipation rate rapidly decreased with depth (Fig. 4A) and below 1.5 m no relationship between surface wind speed and dissipation rate values ($p > 0.05$) was observed (Fig. 4E).

In an effort to better understand the mechanistic basis of observed feeding patterns we conducted additional laboratory experiments and field observations to evaluate how background turbulence affected the behavior of *M. leidyi*. In the laboratory experiments turbulence was generated by a plunger at the surface which generated a standing wave and, similar to field observations (Fig. 4A), turbulence was greatest at the surface and rapidly declined with depth (Supporting Information Fig. S3). Turbulence had little overall effect on the behavioral parameters measured (Supporting Information Fig. S5) indicating that turbulence, even relatively high levels of turbulence, do not disrupt the foraging behavior of *M. leidyi*. The primary difference that was observed was that *M. leidyi* had increased swimming speeds under turbulent conditions (Supporting Information Fig. S5A,E,F; One-tailed Paired T-test comparing averages of all *M. leidyi* in tank, $n = 5$ experiments, $p < 0.005$). Surface fluid velocities (above 20 cm depth) were greater than *M. leidyi* swimming velocities and likely dominated the measured swimming velocities in the turbulence treatments. However, in the bottom third of the tank (below 35 cm depth) fluid velocities were well below *M. leidyi* swimming velocities. Therefore, the elevated swimming velocities of *M. leidyi* at the bottom of the tank were most likely due to behavioral effects and the velocity of *M. leidyi* along the bottom in turbulent treatments was still greater than twice their velocity in the calm treatments (One-tailed Paired T-test comparing averages of *M. leidyi* below 35 cm, $n = 5$ experiments, $p < 0.02$).

In the field we used video observations to quantify how swimming orientation and lobe opening (an indication of feeding behavior) of *M. leidyi* located below the surface (~ 8 m depth) were related to surface wind conditions. It appeared that their behavior at depth was not affected by wind conditions
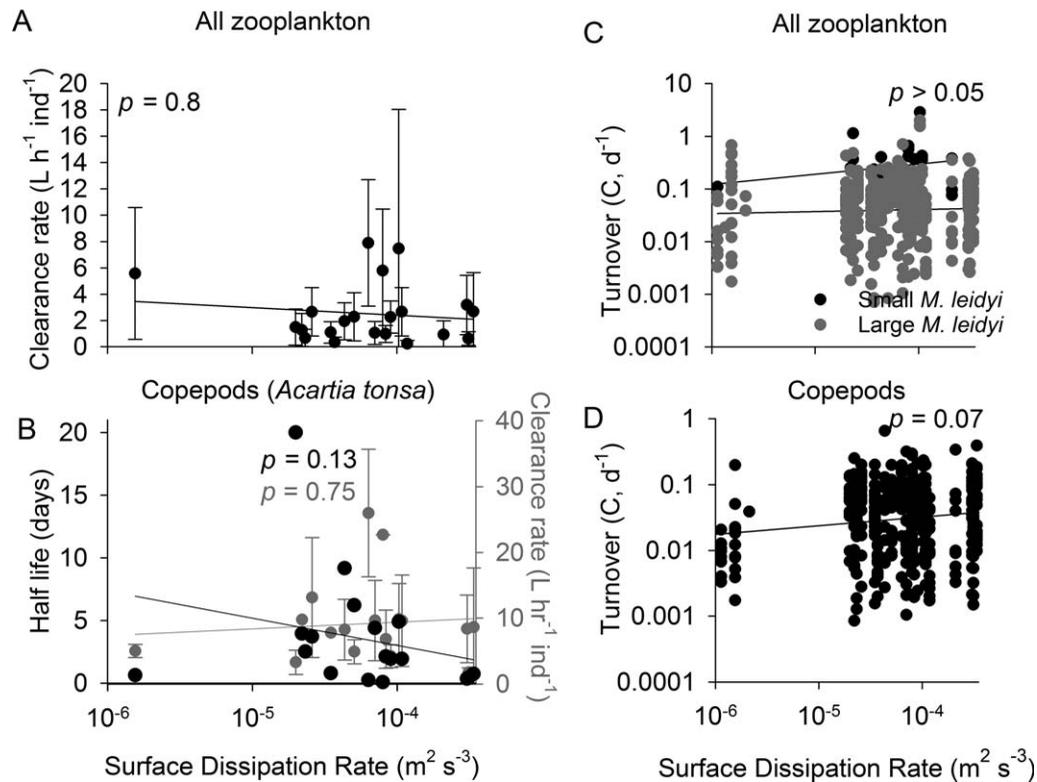
Fig. 2. Effects of surface turbulence conditions (dissipation rate) on *M. leidyi* feeding. (**A**) Relationship between clearance rates of *M. leidyi* on all zooplankton (excluding *A. tonsa*) and surface dissipation rate. (**B**) Effects of turbulence on *M. leidyi* clearance of *A. tonsa* copepods (most abundant copepod) and on the half-life time of the *A. tonsa* population (low values indicate high predatory impact). (**C, D**) The amount of carbon *M. leidyi* ingested per day normalized by their body carbon. In (**C**) small *M. leidyi* were < 2 cm in length.

and that their lobes were open in their feeding posture with full guts regardless of how windy it was at the surface (Fig. 5A,B,D). However, at depth (∼ 8 m depth), turbulence did not vary with surface wind speeds (Fig. 5C). Detailed ADV measurements demonstrate that below 1.5 m turbulence levels remained relatively constant and were not related to surface wind conditions (Fig. 4B–F). Therefore, even in shallow coastal systems, such as those around Woods Hole, *M. leidyi* have a refuge from wind driven turbulence at depths > 1.5 m (Fig. 4E). Short vertical migrations below 1.5 m allow *M. leidyi* reach conditions where they are able to function and feed normally.

Additionally, depth stratified field sampling suggested that in this region around Woods Hole *M. leidyi* avoid the surface when the sea-state is anything but calm (i.e., wave height < 30 cm; Fig. 6). While the sea-state data in this study is qualitative, it still demonstrates that the distribution of *M. leidyi* changes in response to the presence of any surface waves.

Discussion

Impact of natural turbulence on trophic ecology

The predatory impact of *M. leidyi* is the result of several combined features of its feeding strategy. In calm laboratory conditions, *M. leidyi* uses its auricular cilia to generate a slow, continuous and virtually undetectable feeding current that entrains and transports all types of prey between its oral lobes toward its auricles, including the most mechanosensitive copepod prey (Main 1928; Waggett and Costello 1999; Colin et al. 2010). The auricles are then able to scan the feeding current and sort out potential prey by diverting them toward the tentillae for capture (Colin et al. 2015). This strategy enables *M. leidyi* to process large volumes of fluid and capture unsuspecting prey items with remarkably high efficiency (capture efficiencies > 80% for all prey items; Waggett and Costello 1999; Colin et al. 2015) and feed as a generalist predator on most zooplankton prey available. Intuitively, it would seem that the delicate body and laminar feeding current of *M. leidyi* would not enable these ctenophores to thrive in dynamic coastal environments. However, empirical field data demonstrate that *M. leidyi* does indeed thrive in these systems. In fact, our field results demonstrate that most surface wind and wave conditions experienced around Woods Hole, Massachusetts have no impact on the predatory effect of *M. leidyi* in even shallow waters.

In the laboratory, high levels of turbulence inhibited the feeding mechanics of *M. leidyi* (Fig. 1). This suggests that high levels of turbulence are able to disrupt the feeding
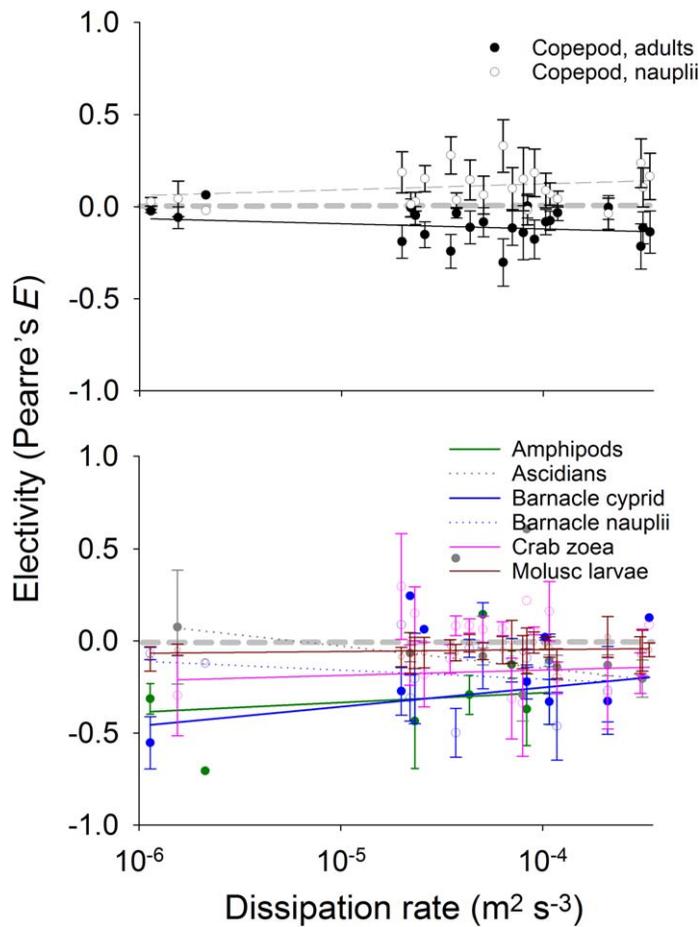
Fig. 3. In situ prey selection of *M. leidyi* collected during conditions with different levels of wind driven turbulence, expressed as Pearre's Electivity Index (*E*) averaged per turbulence level ($\pm$ SD) for (**A**) copepod adults and nauplii, the most prominent prey items present in the guts and (**B**) eight other most abundant prey found in the guts. Lines represent linear regressions ($p > 0.05$), none of which were significant.

process, but, based on our field sampling, the feeding mechanics of *M. leidyi* are robust enough for *M. leidyi* to maintain normal feeding rates and prey selection at the levels of turbulence they experience in the field. This was confirmed over a wide range of wind conditions. A detailed analysis of Woods Hole wind conditions during the summer and fall (seasons when *M. leidyi* are present in the water column) demonstrated that the range of wind speeds (1–5 m s^{-1}) encompassed greater than 95% of the cumulative wind speeds measured in Woods Hole through the summer and fall in 2012 (Sutherland et al. 2014). In other words, windier conditions occurred less than 5% of the time. Therefore, it appears that at this study site wind driven turbulence normally does not affect the predatory impact of *M. leidyi*. The study site in Woods Hole, Massachusetts is less windy than more exposed waters, such as those along the south shore of Martha's Vineyard (source: Martha's Vineyard Coastal Observatory) where windier conditions occur 20% of the

time (with mean wind speed = 4.8 $\pm$ 2.3 m s^{-1} compared to Woods Hole means wind speeds = 2.5 $\pm$ 1.4 m s^{-1}).

Feeding in a turbulent environment

What adaptations enable this delicate gelatinous predator to thrive in highly energetic coastal ecosystems? One important behavioral adaptation is the ability of *M. leidyi* to detect and avoid the surface during turbulent conditions. Our data support this for the waters around Woods Hole and it has been shown in different locations as well (Fig. 6; Miller 1974; Mutlu 1999; Purcell et al. 2001; Mianzan et al. 2010). In our study location, having the ability to avoid turbulent conditions near the surface appeared to be sufficient to provide *M. leidyi* refuge from the daily fluctuations in the wind driven turbulence that occur in surface waters. Only a short distance below the surface, turbulent dissipation rate values were much lower ($\sim 10^{-6}$ m^2 s^{-3}) and less variable (Fig. 4). As evidenced by our depth-stratified sampling, *M. leidyi* avoided surface waters during turbulent conditions. In Woods Hole, being below 2 m is sufficient for *M. leidyi* to avoid high turbulence, however, they would need to migrate to deeper depths in windier locations to find refuge from high turbulence.

Below the surface there is still some level of turbulence and because *M. leidyi* generates a very slow feeding current (~ 2 mm s^{-1} velocity), even the lowest observed dissipation rates are sufficient to degrade the feeding current (Sutherland et al. 2014). So as a compensatory response *M. leidyi* has been observed to increase swimming speeds, even in response to very low levels of turbulence (Supporting Information Fig. S5; Sutherland et al. 2014). We suggest that increased swimming is critical for *M. leidyi* to maintain feeding rates in turbulence. By swimming, *M. leidyi* shifts from being a hovering predator to a cruising predator. Studies with other suspension feeders such as copepods have demonstrated that hovering is more hydrodynamically favorable than cruising foraging because it generates higher encounter rates with prey (Kiørboe 2011). In contrast, cruising foraging by lobate ctenophores, such as *M. leidyi*, has the potential to greatly enhance encounter rates over hovering because ctenophores use different ctene rows for generating their feeding current than for swimming. The ctene rows which generate the feeding current, auricular ctenes, generate flow at 2 mm s^{-1} while the propulsive ctenes are capable of propelling *M. leidyi* at >5 mm s^{-1}, more than doubling the encounter rates with prey (Colin et al. 2010). However, for higher encounter rates to enhance ingestion rates, *M. leidyi* must capture encountered prey just as efficiently while swimming as while hovering.

Unlike other gelatinous predators, such as medusae, *M. leidyi* scans encountered fluids for prey by using its auricles to detect prey in its feeding current. This mechanism enables it to maintain high capture efficiencies even at high swimming speeds (Colin et al. 2015). Therefore, we argue the combination
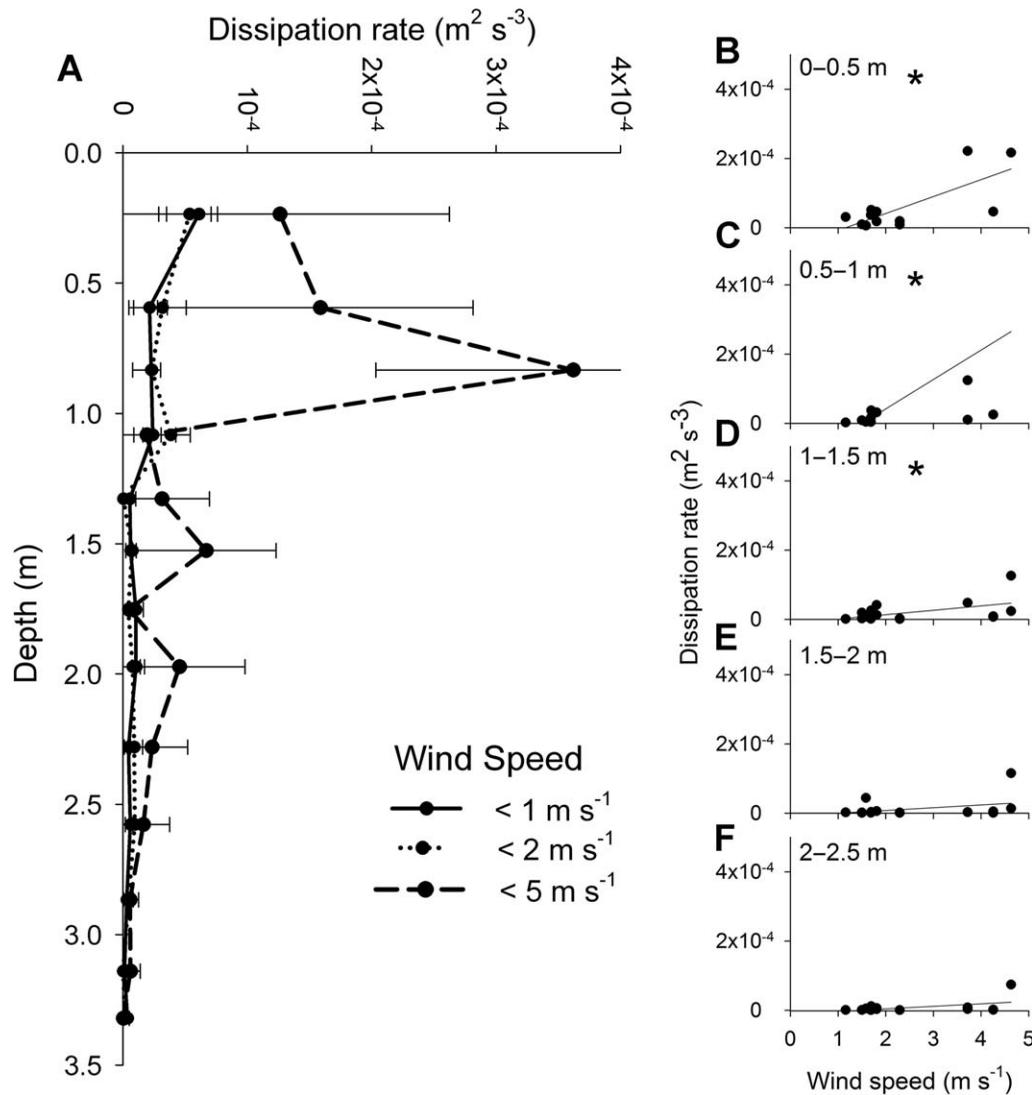
Fig. 4. Turbulence in the field. (**A**) Dissipation rate vs. depth taken from the Marine Biological Laboratory dock in the Vineyard Sound. Data was collected on multiple days between the dates of 01 August 2012–15 August 2012. Days were pooled based on wind conditions during sampling as measured from the WHOI weather station adjacent to the sampling location. (**B–F**) Regression analysis of dissipation rate vs. the wind speed when the measurements were recorded for different depth intervals. Below 1.5 m there was not a significant relationship between surface wind speed and turbulence mixing (Regression, $p > 0.05$). Asterisks indicate figures with significant regressions (Regression, $p < 0.05$).

of avoidance behavior, enhanced swimming speeds and sensory scanning are the key components of *M. leidyi*'s robust feeding mechanics which enable it to feed normally under a diverse range of environmental conditions.

General implications for studies on turbulence

The effects of turbulence on predator–prey interactions have been well studied both experimentally (e.g., Saiz and Kiørboe 1995; MacKenzie and Kiørboe 2000; Saiz et al. 2003; Adamík et al. 2006) and theoretically (Rothschild and Osborn 1988; Kiørboe and Saiz 1995; Lewis and Pedley 2001; Mariani et al. 2007). However, despite an abundance of laboratory studies showing a strong effect of turbulence when

compared to still water (Fig. 1, Saiz and Kiørboe 1995; MacKenzie and Kiørboe 2000; Saiz et al. 2003; Adamík et al. 2006), few studies have measured the effects of turbulence in the field (Saito and Kiørboe 2001; Visser et al. 2001; Reiss et al. 2002; Maar et al. 2006) and none of these were able to identify a strong effect of turbulence on feeding rates, regardless of feeding strategy. A likely explanation is that predators (and prey) are highly sensitive and responsive to turbulence and that, in most cases, the spatial heterogeneity of turbulence in nature provides areas of refuge from turbulence. The ability to respond and avoid turbulent layers in the water column has been well established for copepods (Lagadeuc et al. 1997; Incze et al. 2001; Reiss et al. 2002;
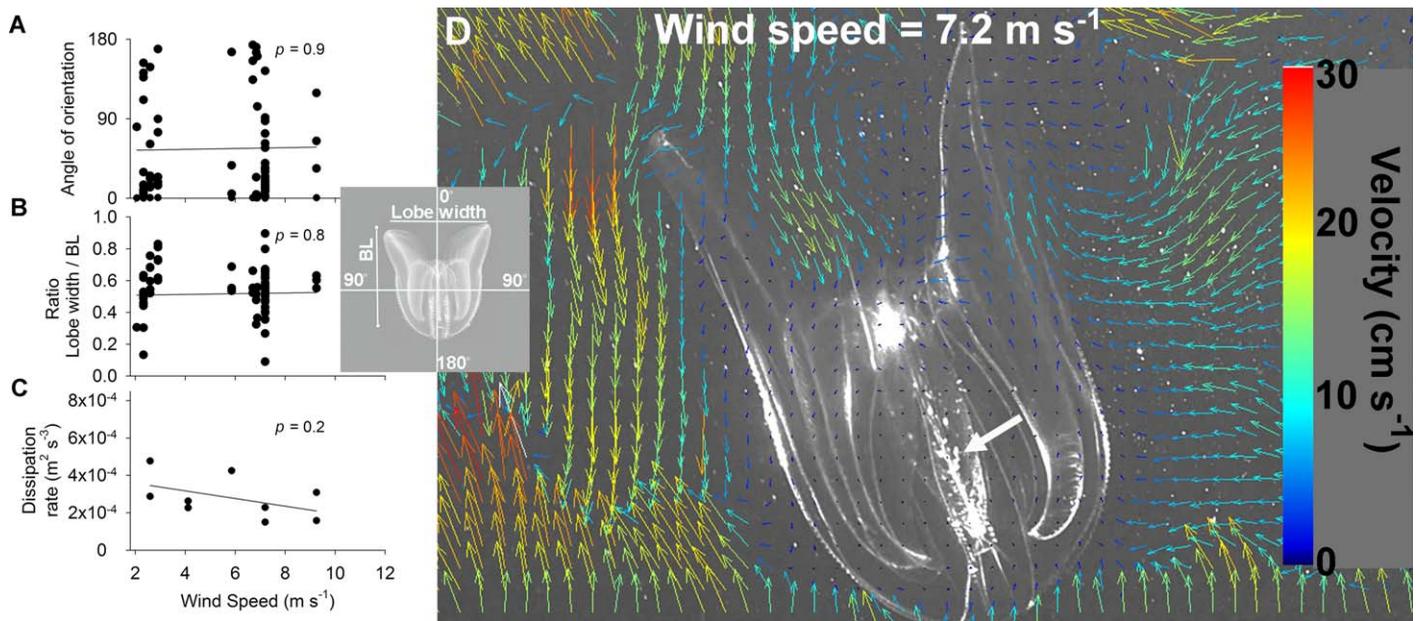
Fig. 5. In situ behavior of *M. leidyi* on days with different wind conditions. (**A**) *M. leidyi* angle of orientation in the water column from multiple days with different surface wind conditions. (**B**) How open *M. leidyi* lobes were positioned relative to their body length (BL) from multiple days with different surface wind conditions. (**C**) Turbulent dissipation rates measured from the DPIV taken at the depth where *M. leidyi* behaviors were quantified (about 8 m depth). Solid lines are linear regressions, none of which were significant ($p > 0.05$). (**D**) Single frame of a *M. leidyi* with velocity vectors showing surrounding ambient water velocity on a windy day with average wind speeds of 7.2 m s^{-1}. White arrow is pointing to large number white specks (prey items) in the gut of *M. leidyi*, illustrating that it is actively feeding with many prey in its gut.
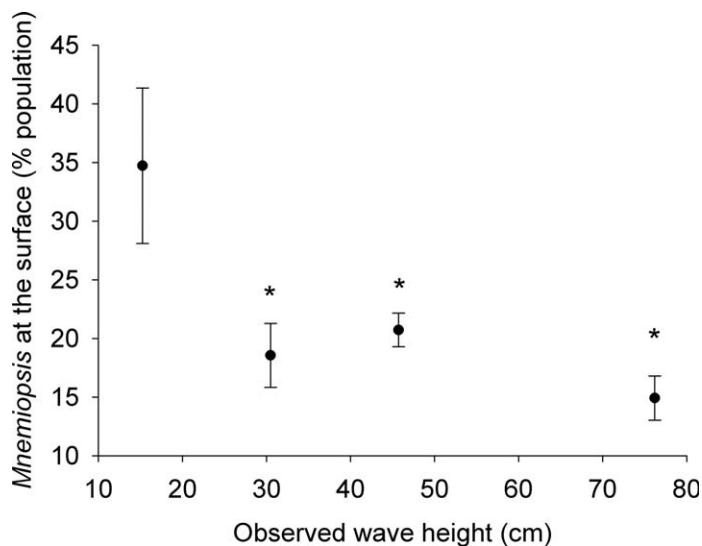

Fig. 6. The relative abundance of the *M. leidyi* population at the surface during days with different wind driven wave conditions. The greatest proportion of the population was at the surface on the calmest days (Student–Newman–Keuls post-hoc analysis, $n = 3$, $p = 0.016$). On windier days more *M. leidyi* were below the surface. Asterisks indicate wave heights with a greater proportion of *M. leidyi* below the surface (Student–Newman–Keuls post-hoc analysis, $n = 3$, $p < 0.05$). Error bars represent standard deviations.

Maar et al. 2006). Therefore, it might be reasonable to assume zooplankton predators are able to seek refuge from turbulent layers and feed normally at those refuge depths. If

so, the important question is not "what are the effects of turbulence on feeding," but rather, what are the effects of turbulence on energetics, predator–prey distributions (Franks 2001) and ultimately fitness of predators. For example, the predatory impact and prey selection of *M. leidyi* in the field do not change in relation to surface turbulence conditions. But what remains unknown, and perhaps more relevant, is how changes in behavior and distribution during turbulence affect prey availability, energetics, and population growth.

Implications for how turbulence may limit distribution of *M. leidyi*

The resilience of *M. leidyi* to wind-driven turbulence suggests that their distributions may be less limited by turbulence patterns than other environmental factors such as temperature or salinity that have been demonstrated to govern range expansion in invaded areas (Jaspers et al. 2011). It is difficult to envision systems where they are unable to find some refuge in the water column from turbulence, except, perhaps, in some localized regions where both wind and tidally driven turbulence lead to high turbulence throughout the entire water column. For example, the invasion history of *M. leidyi* indicates that some high turbulence areas remain uncolonized, but neighboring regions with more irregular coastlines harbor very high *M. leidyi* abundances. Regions along the English Channel exemplify this pattern. The south western Nord-pas-de-calais coast of France is one of the most

dynamic systems in the world with a tidal amplitude of up to 7 m (NOAA 2016). This high-turbulence are a remains uncolonized yet permanent *M. leidyi* populations are present to the south (e.g., Le Havre and the Bay of Seine, France; Antajan et al. 2014) and to the north along the Dutch and Belgium coast (van Walraven et al. 2013; Vansteenbrugge et al. 2015), especially in lagoon and harbors where abundances may reach 1 ind L^{-1} (van Walraven et al. 2013). One potential explanation is that extreme tidal amplitudes eliminate hydrodynamic refuges from turbulence and limit *M. leidyi* from attaining high feeding rates and, hence, the high reproduction rates which are required to establish large population sizes. However, studies quantifying turbulence at the relevant scales throughout the water column are rare. Since, on local scales, tidal mixing might be an important determinant setting limits to *M. leidyi* range expansion, we expect that physical parameters, such as turbulence profiles, will be important variables when predicting range expansion and invasion risk of *M. leidyi* for different habitats around the globe.

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Conflict of Interest

None declared.