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ORIGINAL PAPER

Phytoplankton odor modifies the response of *Euphausia superba* to flow

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Abstract
Antarctic krill, *Euphausia superba*, are critical components of the Antarctic food web as well as important targets for conservation and management. Krill behavior has important effects on demographic properties and aggregation characteristics, but remains incompletely known. Krill clearly respond to different environmental stimuli such as light, flow and chemicals, but few studies have quantified these behaviors. We examined the behavior of krill in well-quantified current speeds in a laboratory flume and examined interactions of phytoplankton odor and flow. Krill are sensitive to flow speeds as low as 1 mm s^{-1}, and flow polarizes krill swimming and orientation in the up-current direction. Phytoplankton odor increases the sensitivity of krill to flow, and induces area-restricted search behaviors that presumably allow krill to exploit food patches efficiently. The ability to quantify krill behavior could have important consequences for understanding demographic processes and the properties of krill aggregations.

Keywords Behavior · Chemical cues · Orientation · Palmer station · Rheotaxis

Introduction

Antarctic krill, *Euphausia superba*, are critical components of the Antarctic food web by linking phyto- and zooplankton production to a variety of large vertebrate predators such as fish, penguins and whales (Veit et al. 1993; Bernard and Steinberg 2013; Atkinson et al. 2014; Willis 2014). In addition to their ecological importance, *E. superba* is an important fisheries resource used for a variety of purposes with catch regulated by the Convention on the Conservation of Antarctic Marine Living Resources (CCAMLR; https://www.ccamlr.org/).

The ecological and economic importance of Antarctic krill has engendered interest in all facets of krill biology affecting their production and demography. Studies on energetics (e.g., Quetin et al. 1994; Haberman et al. 2003) and acoustic surveys of krill aggregations and attendant environmental properties (e.g., Lawson et al. 2008; Cox et al. 2010) are particularly common. Less common are studies on the behavioral responses of Antarctic krill to their environment, despite the fact that individual behavior seems important to explain fully krill demography and properties of krill aggregations (Nicol 2003).

Many zooplankton react strongly to light, chemicals or other aspects of their environment (Price 1989; Woodson et al. 2005). Such is the case for krill species, including *E. superba*, which have been shown to alter behavior in the presence of a variety of environmental cues including chemical and visual stimuli (Hamner et al. 1983; O'Brien 1987; Price 1989; Newman et al. 2003; Abrahamsen et al. 2010). These studies show krill respond with directed movements, feeding or aversive behaviors, and changes in swimming that potentially increase their access to food, or reduce their proximity to predators or potentially risky environments. Studies on *E. superba* typically have involved examining responses of aggregations to different cues, including phytoplankton, objects simulating predators, and fluid disturbances (Strand and Hamner 1990). Although these studies indicate the importance of behavioral responses for understanding krill ecology, they do not allow for quantitative linkages between cue intensity and response intensity necessary for predicting krill behavior in specific environments. Nonetheless, agent-based models incorporating extremely simple behavioral

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responses have provided insight into some aspects of krill distributions, particularly diel vertical migration (Cresswell et al. 2009). These studies make clear that the balance of attractive (e.g., food related) to aversive (e.g., light) stimuli result in a variety of demographic patterns. More detailed and accurate predictions are only possible with well-resolved relationships between environmental properties (light, flow, food abundance, predator cues) and behavior.

In an initial attempt to unravel these relationships between the environment and krill behavior, we studied the swimming responses of *E. superba* in well-controlled flows in the presence and absence of phytoplankton. Flow is ubiquitous environmental feature that often interacts with other cues to influence zooplankton behavior (Fields et al. 2012). Many zooplankton including macrozooplankton such as krill are attracted to phytoplankton patches, presumably by sensing released metabolites (Gill 1986). We defined the swimming speed and direction of krill to environmentally realistic flow speeds, and how flow speed interacts with the presence of food to determine responses. We find that even very slow flows polarize krill movement in an upstream direction and that the sensitivity of krill to flow is modified by the presence of algae. Thus, it is possible to quantify krill behavioral responses to environmental stimuli in a way that permits more detailed agent-based models capable of examining krill responses to cues in nature.

Materials and methods

Animal collection and maintenance

Krill were collected in the Palmer Deep canyon (PDC) using a 2×2 m^2 frame Metro net (750 µm mesh) towed obliquely at 100–150 m for 15 min. PDC is a highly productive coastal canyon near Palmer Station, Anvers Island, on the continental shelf of the West Antarctic Peninsula (WAP). It is characterized by enhanced primary production and elevated secondary biomass (Kavanaugh et al. 2015). These biological "hotspots" support large krill aggregations and are key foraging areas of penguin populations and marine mammals (Kohut et al. 2018). Captured krill were gently sorted into 20 L buckets and stored in onboard incubators for 24 h prior to reaching Palmer station. We captured additional krill directly offshore from Palmer station using a 2 mm mesh, 1 m diameter ring net towed obliquely from a Zodiac.

Krill were carefully transferred to a 2.4 m dia × 1.2 m deep circular tank at the National Science Foundation's Palmer Station. Krill were supplied continuously with ambient seawater. They were fed every other day on natural plankton assemblages by passing flowing (2 L min^{-1}) seawater through a 20 µm mesh for roughly 4 h. The mesh was rinsed into 2 L of ambient seawater and the resulting highly concentrated suspension dispensed into the tank. This always elicited vigorous feeding behavior as revealed by rapid directional swimming and visible expansion of the feeding basket. Nearly all krill used in the experiments were observed to have food in their gut, and there was minimal mortality during the course of the experiments. Krill used in the experiment were 4–6 cm long and each animal was only used once.

Flume

Krill were challenged with different velocities in the presence and absence of phytoplankton in a small recirculating flume (Fig. 1). This flume used two small aquarium pumps (Little Giant NK-2) to create current speeds of roughly 1 to 40 mm s^{-1} measured in the working section. Pumps were located in the tail section of the flume and pumped water via tygon tubing to the upwelling section where it entered at the bottom. The upwelling section was divided by a roughly 8 cm tall partition spanning the width of the flume, which served to dampen the turbulence created by the pump. Water then flowed through a 4-inch-long straightening section with a roughly 2.5 mm cell size (packed plastic straws) to further condition the flow before it entered the contraction section manufactured from stainless steel. This provided a uniform flow into the working section, which was roughly 32×18 cm (lx w). The walls of the working section were masked with opaque black plastic. The upstream end of the working section was a stainless steel mesh with a roughly 5 mm mesh size, which primarily served to prevent krill from entering the contraction section. The downstream end of the working section was a tailgate over which flow passed to enter the section containing the two pumps. Each pump was isolated by a stainless steel partition to dampen vibration. Valves on the pump output regulated flow velocity. All components other than the contraction section, partition, and upstream barrier of the working section were made from Plexiglas.

Experiments

The flume was filled to a 12.5 cm height with ambient seawater immediately prior to the start of a trial. Five krill were randomly selected and transferred gently into the working section of the still flume and allowed to acclimate for 15 min. The pumps were started and the krill were allowed 1 min to adjust to their new conditions. Krill behavior then was recorded for 15 min using a commercial digital video recorder (Sony HDR–CX760V) mounted directly above the working section so that the working section spanned nearly the entire field of view. We measured water temperature when krill were first introduced into the flume and when we ceased recording. Ambient temperatures ranged from 2–4

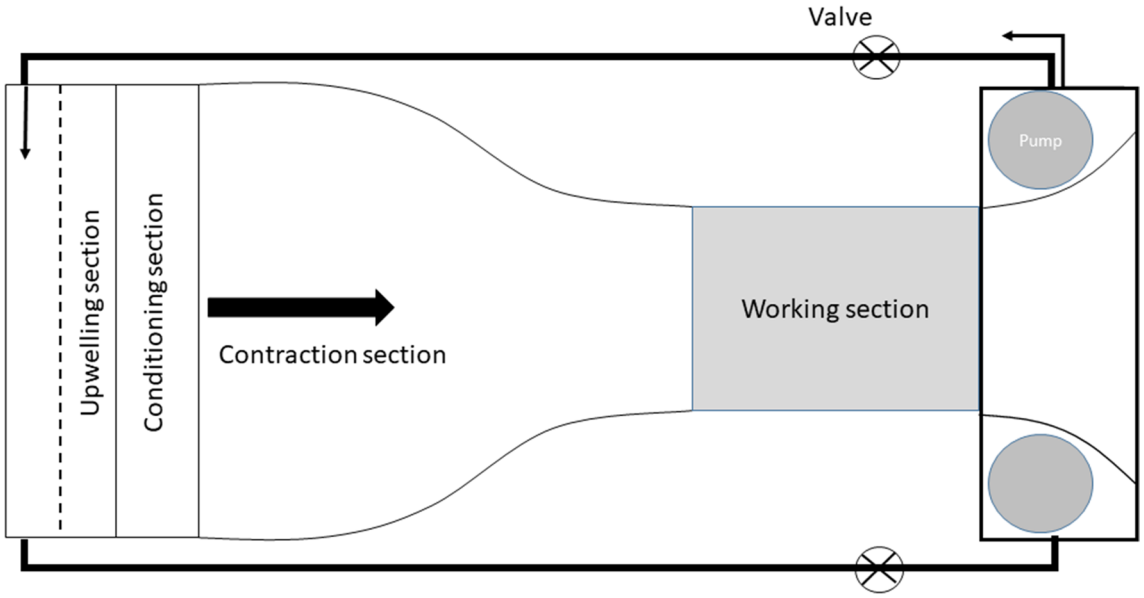

Fig. 1 Flume used to test behavioral reactions of krill. Arrows give the flow direction

°C and there was never more than a 0.8 °C change over the course of the experiment. Flume water was changed completely between trials.

Flow was controlled by valves, and we selected conditions that provided reproducible flows ranging from the minimum that could easily be measured with our equipment to the maximum possible speed of roughly 40 mm s^{-1}. We initially measured flows at different valve settings by timing neutrally buoyant dye, but we confirmed all velocity measurements using video image analysis upon return to Georgia Tech (see below). We filmed dye after the conclusion of a number of trials in different conditions to quantify the variation in nominal conditions experienced by krill, for each velocity setting.

We performed two separate sets of experiments; responses only to flow and responses to flow as a function of the presence of phytoplankton. The experiments utilizing only flow allowed us to identify approximate lower response thresholds and response patterns, and we used a subset of these velocities for the second experiment involving phytoplankton. The set of experiments involving only flow used current speeds of 0, 3.7, 8.0, 17.0, 37.4 mm s^{-1}, with flow speed being defined by digital analysis after all the trials were completed (see below). Speed treatments were randomly determined for each trial, with four trials per velocity treatment.

Phytoplankton suspensions were created as described above for feeding. A single stock solution was created and used throughout the entire experiment (3 days), and was gently aerated and held at 2 ºC in the dark during this time. Duplicate chlorophyll measurements were made at the start and end of the experiment by fluorescence (Smith et al. 1981), yielding a value of 12.19 µg chl a L^{-1}.

Trials with phytoplankton were conducted at velocities of 3.7 and 8.0 mm s^{-1}. The former was the approximate lower threshold for responses to current speed whereas the latter was in the approximately linear region of the intensity-response curve. (see "Results"). Phytoplankton treatments consisted of three different odor landscapes: thin filaments (1–2 mm), uniform background and no phytoplankton. Thin filaments were produced by injecting the concentrate through a 1.5 mm (O.D.) pipette with the tip bent so that it was oriented parallel to the flow, at a release rate of 1.5 mL $minute^{-1}$ controlled by a syringe pump. Visual inspection showed this resulted in a coherent steam that diffused very slowly, and was not mixed into the flow unless disrupted by krill or their flow fields. The uniform concentration was created by adding 22.5 mL of the concentrate (the same volume injected into the flume in the filament trials) during the filling process. Logistical concerns made it difficult to randomize both phytoplankton treatment and flow speed simultaneously. Therefore, we conducted trials with phytoplankton in two blocks, one at each flow speed, and randomized phytoplankton treatment within each flow speed treatment. There were six replicates for each phytoplankton condition at a flow speed of 3.7 mm s^{-1}, and 5 replicates for each phytoplankton condition at 8.0 mm s^{-1}.

Video analysis

We extracted position, angle, and swimming speed of the krill at multiple time points using DLTdv5 software (Tyson

2008). Velocity and angle were calculated using the frame of reference and scale defined by the working section, which was completely visible in all trial records. All data were obtained when krill were not contacting flume walls or each other, and free from contact for at least 30 s prior to measurements.

We scored each krill's position within the flume by dividing the working section into four equal parts along the x (streamwise) direction. Each krill was scored 1–4 according to the section it occupied, with 1 being the most upstream, and 4 the most downstream, section. The positions for all krill were measured five times, at 0, 3, 6, 9, 12, 15 min from the start of the trial. The angle of each krill relative to the flow was determined by digitizing one point on the rostrum and a second point on the telson. Angles were calculated relative to the flow and ignored left–right distinction, that is angles varied from 0° (directly upstream) to 180° (directly downstream). The analysis of position showed little effect of time (see "Results"), so analysis of angles occurred at 3, 6, 9, 12, 15 min. We also digitized the head and tail position of one randomly chosen krill over 30–60 frames to obtain swimming speed. This required us to follow one krill continuously over the entire trial so that we could identify it as the same individual. Velocity was measured at roughly 0, 4, 8, 12 min, as it was more difficult to find video segments of this length where we could follow the animal continuously while it was free from any interactions with walls or conspecifics. Note that we report krill swimming velocity relative to the ground and uncorrected for flow velocity.

We periodically concluded each trial by gently injecting a small amount of neutrally buoyant dye at the beginning of the working section, which allowed us to determine flow speed by following the dye front. Dye was injected at mid depth and multiple positions in the working section (always at least 2 cm away from the wall). Three–five replicate velocity measurements were taken for each trial where we computed speed, and mean treatment speeds were based on measurements in four replicate trials. This resulted in standard deviations of less than ca. 10% of the calculated mean speed for all conditions (see "Results").

Statistical analysis

Results were analyzed using one-way ANOVA. Flow speed was categorical rather than numeric for several reasons; the initial analysis suggests an exponential relationship over this range, but it is impossible to include 0 in an exponential model. Second, it is not clear that this range (1 order of magnitude) is sufficient to resolve fully the relationship between the variables. A categorical model is more conservative in detecting a relationship and we accepted the loss of the ability to define a slope in favor of a simpler approach.

Since we cannot identify individual krill from time point to time point (except for swimming speed measurements), we averaged position and angle for the 4 krill at each time point and then used this as the unit of observation. Thus, all analysis was a mixed model repeat measures design (time) with trial as a random factor. Each flow was analyzed separately for the trials with phytoplankton, with the main effect being phytoplankton treatment (background, filament, none). It is not possible to use a 2-way analysis for experiments with flow, and phytoplankton because this design was not fully randomized. Only swimming speed and swimming angle were analyzed for trials with phytoplankton. For all analysis, significant ANOVA effects were followed by Tukey HSD tests to define sub-sets of the data that were not significantly different from each other. Angle was arcsine transformed prior to analysis.

Results

Post-trial processing of video records resulted in calculated speeds of 0, 3.7 ± 0.4, 8.0 ± 0.8, 17 ± 1.0, 37.4 ± 2.1 mm s^{-1} (mean ± Std. Dev, $n = 5$ measurements per velocity treatment). Krill placed in the working chamber rapidly aligned to the flow when present and swam mainly upstream. The krill often reached the mesh separating the working area from the contraction section, where they swam in place until changing direction or drifting downstream. All krill remained at mid-depth and swam for the entire trial duration.

Krill responded to increasing flow speed by an increasing tendency to be found upstream (Fig. 2). The repeat

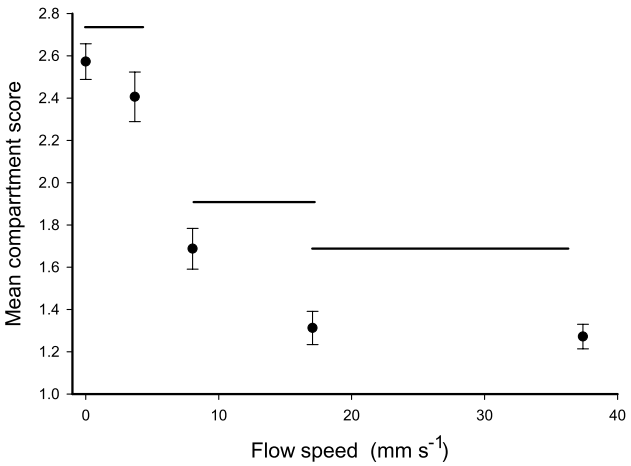

Fig. 2 Location of krill, *Euphausia superba*, in flume trials at different flow speeds. Data shows location of krill (mean ± SE, $n = 75$) as a function of flow speed. 1 is the most downstream flume section, whereas 4 is the most upstream flume section. Lines above the symbols indicate data not significantly different based on Tukey's HSD post hoc test

measures ANOVA of krill position showed an effect of flow speed, but not time or speed*time ($F_{4,15}=31.67$, $p<0.0001$; $F_{5,75}=0.78$, $p>0.5$; $F_{20,75}=0.91$, $p>0.5$ for flow, time, flow*time, respectively). Krill in the two lowest flow speeds had little apparent preference for position within the flume, and maintained themselves roughly in the middle of the working section (Fig. 2; Tukey post hoc test). In contrast, krill in higher flow speeds (> 8.0 mm s^{-1}) were more likely to be found in the upstream sections of the flume. Krill at the two highest current speeds displayed similar behavior and were predominantly positioned in the most upstream portion of the flume.

Krill swimming angle became more polarized in the upstream direction as flow velocity increased (Fig. 3). Flow speed, but not time or flow*time significantly affected swimming angle ($F_{4,15}=131.4$, $p<0.0001$; $F_{3,42}=0.46$, $P>0.5$; $F_{12,42}=0.75$, $p>0.1$ for flow, time and flow × time, respectively). The average angle declined from roughly 80° to roughly 10° at the highest flow speed. The importance of flow as a polarizing cue is particularly clear under no-flow conditions, where krill frequently swam towards the tail gate or across the flume width. Even the lowest flow setting caused a substantial change in swimming angle, resulting in krill aligned more directly upstream. Krill exposed to flow speeds greater than or equal to 8.0 mm s^{-1} had a strong upstream orientation.

Swimming speed of krill increased significantly with flow speed (Fig. 4), but not time or flow*time ($F_{4,15}=17.7$, $p<0.001$; $F_{4,52}=0.14$, $p>0.5$; $F_{16,52}=15.8$, $p>0.1$ for flow, time and flow*time, respectively). Krill swimming in flow

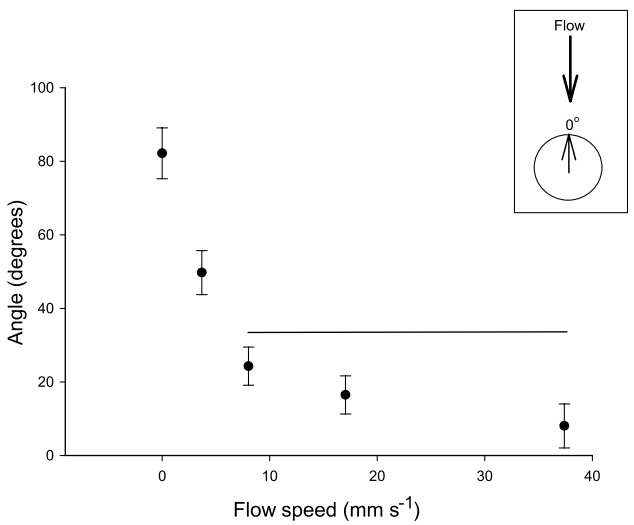

Fig. 3 Swimming angle of krill, *Euphausia superba*, in flume trials at different flow speeds. Data shows angle of krill (mean ± SE, $n=42$) as a function of flow speed. Lines above the symbols indicate data not significantly different based on Tukey's HSD post hoc test. Inset (top right) indicates the calculated angle relative to the flow, with an angle of 0 degrees corresponding to a heading directly upstream

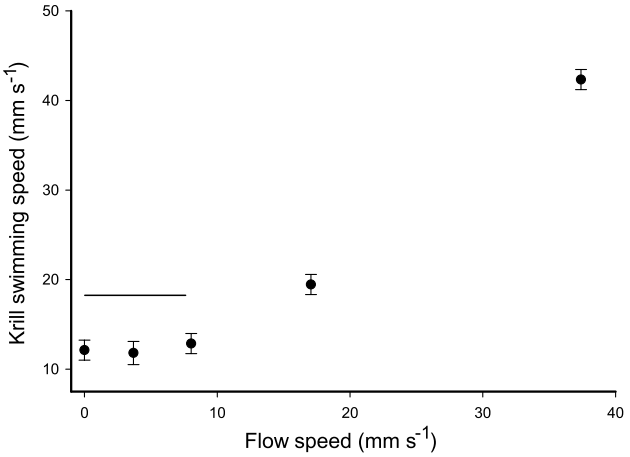

Fig. 4 Swimming speed of krill, *Euphausia superba*, in flume trials at different flow speeds. Data shows swimming of krill (mean ± SE, $n=52$) as a function of flow speed. Lines above the symbols indicate data not significantly different based on Tukey's HSD post hoc test

speeds less than or equal to 8.0 mm s^{-1} were roughly constant at approximately 12 mm s^{-1}, and increased substantially thereafter. The relationship between swimming speed and flow speed was roughly linear at flow speeds greater than or equal to 17 mm s^{-1}. Swimming speed peaked at roughly 40 mm s^{-1} at the highest flow speed.

Phytoplankton treatment had an interactive effect with flow on the alignment of krill (Fig. 5). At the lowest speeds (3.7 mm s^{-1}) phytoplankton treatment significantly altered the alignment of krill to flow (Fig. 4; $F_{2,15}=6.17$, $p<0.025$; $F_{4,60}=0.32$, $p>0.5$; $F_{8,60}=0.51$, $p>0.5$ for phytoplankton, time and phytoplankton*time, respectively). Krill in the presence of either phytoplankton filaments or background concentrations had angles less aligned to the flow direction compared to the flow-only treatment. The effect of filaments was weaker than that produced by the background condition. The overall pattern displayed at the higher flow speed resembled that occurring at the lower flow, and angles in the presence of phytoplankton were higher than with flow alone. However, there was no significant effect of phytoplankton treatment, time or their interaction, although the interaction term was marginally insignificant ($F_{2,12}=2.17$, $p<0.15$ $F_{4,48}=1.05$, $p<0.25$; $F_{8,48}=1.09$, $p<0.1$ for phytoplankton, time and phytoplankton*time, respectively). Krill in the filament treatment had a tendency to decrease their swimming angle over time.

Krill swimming speed was a more complex function of flow and phytoplankton treatment than observed for swimming angles (Fig. 5). At the lower flow speed, there was a significant effect of phytoplankton treatment and a time × phytoplankton interaction, with a marginally insignificant effect of time itself ($F_{2,16}=8.85$; $p<0.01$; $F_{3,48}=2.44$, $p<0.075$; $F_{6,48}=5.45$, $p<0.001$

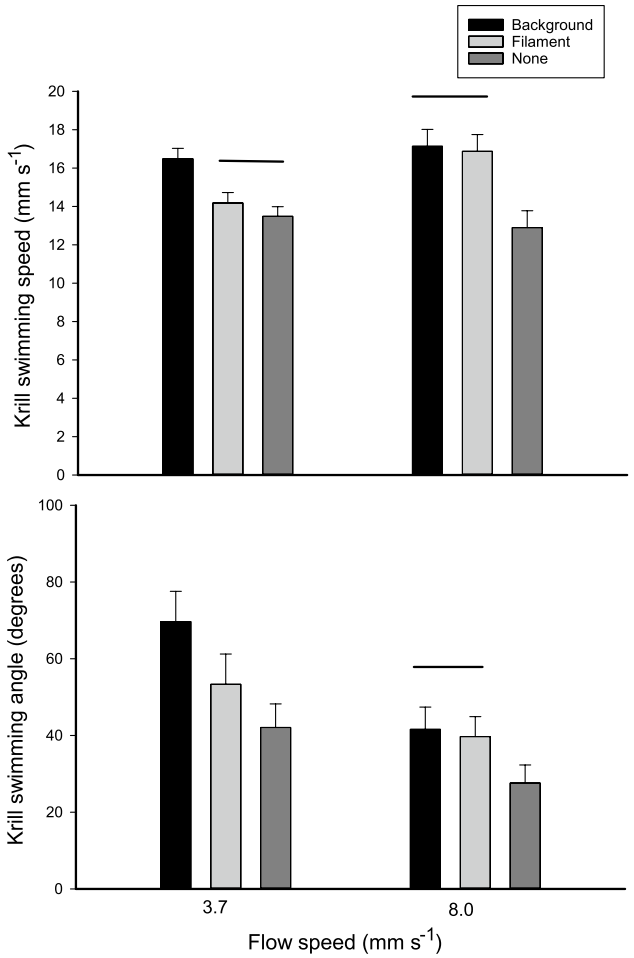

Fig. 5 Behavior of krill, *Euphausia superba*, in the presence of phytoplankton. Top panel shows krill swimming speed in the presence of phytoplankton filaments, background presence, or absence at two different flow speeds, with treatment indicated by bar fill. Bottom panel shows krill swimming angle (0 degrees indicates krill swimming directly upstream) in the presence of phytoplankton filaments, background presence, or absence at two different flow speeds, with treatment indicated by bar fill. Data shows mean values ± SE, with $n = 48,36$ for top and bottom panels, respectively. Lines above the symbols indicate data not significantly different based on Tukey's HSD post hoc test

for phytoplankton, time and phytoplankton*time, respectively). Inspection of individual treatment means suggest that krill in the phytoplankton treatments only, are swimming more slowly over time. At the higher flow speed, the only significant effect again was phytoplankton treatment ($F_{2,12} = 7.29$; $p < 0.01$; $F_{3,36} = 1.84$, $p < 0.1$; $F_{6,36} = 0.64$, $p > 0.5$ for phytoplankton, time and phytoplankton*time, respectively). Krill in the presence of either phytoplankton treatment swam significantly faster (Fig. 5).

Discussion

Individual krill respond to flow and the combination of phytoplankton and flow with a variety of behaviors indicating these cues have salience for the animal, and have consequences for krill distributions and properties of krill aggregations. Even extremely low flow velocities on the order of 1 mm s^{-1} cause krill to align with the current and swim upstream, with increasingly strong responses in alignment and position as flow velocity increases. Although the upper threshold was not tested, this study provides behavioral thresholds for low flow regimes that have not been determined previously. The lower threshold measured in this study is consistent with the limited measurements of krill (*Meganyctiphanes norvegica*) mechanosensitivity that indicate some receptors respond to flow speeds as low as 0.25 mm s^{-1} (Patria and Wiese 2004).

Alignment to current direction has consequences for both individuals and aggregations and has been observed in other contexts. *E. superba* in a large respirometry flow chamber (35 cm dia by 45 cm length) align to current at velocities from 20 to 180 mm s^{-1} (Swadling et al. 2005), suggesting krill in our flume were not simply constrained by the flow device. Individuals aligned to the current experience less drag and decreased energetic costs of swimming, conferring obvious advantages particularly as flow velocity increases. Marr (1962) provides a lovely and poetic account of coordinated swimming against the current by swarming krill. He observes krill maintain a coherent group that holds station for "several hours" while swimming up-current. Alignment to the current polarizes krill along a particular axis, and may facilitate the coordinated movement and tight packing structure seen in *E. superba* schools, although flow does not seem required to elicit schooling (Kawaguchi et al. 2010).

Swimming into the current has other advantages beyond schooling by affecting both food gathering and predator avoidance. It increases the chance of encountering food entrained within the flow, whereas holding position in the water column allows krill to decrease the encounter rate with larger predators that move independent of the flow (Gerritsen and Strickler 1977). The increasing swimming speed of krill in response to increasing flow velocity obviously cannot continue indefinitely. However, Antarctic krill are extremely strong swimmers capable of sustaining speeds of roughly 150 mm s^{-1} (Kils 1981) and are able to swim up-current (in schools) in flows up to 200 mm s^{-1} (Lawson et al. 2008). Swadling et al. (2005) report that krill make upstream progress in flows of 30–50 mm s^{-1} and hold station at flow velocities of 80–170 mm s^{-1}. We were unable to produce more rapid flows in our flume without reducing water depth, so could not define the response of krill at these higher velocities.

Adding phytoplankton changes the response to flow in ways presumably geared towards increasing the ability of krill to locate and exploit food. Krill in the presence of phytoplankton swim more rapidly, in essence lowering the flow velocity threshold. More rapid swimming increases the rate at which krill might locate dense phytoplankton patches and increases the volume water filtered over time, both of which enhance intake rate. Krill also are less aligned with the flow when phytoplankton are present suggesting a greater turning rate in the presence of food, which would serve to prevent krill from transiting out of algal patches. These responses likely are mediated by chemical detection, as krill seem acutely sensitive to a variety of natural and anthropogenic odors (Hamner et al. 1983; Strand and Hamner 1990).

These behavioral changes are consistent with observations on other zooplankton as well as studies examining krill aggregation structure in various conditions. For instance, copepods in the presence of algal thin layers show area-restricted search typified by increased turning rates and velocities, which keep them in the vicinity of the phytoplankton layer (Tiselius 1992; Woodson et al. 2005). Such responses are distinct from the way that these zooplankton respond to the shear flow component alone (Fields and Yen 1997; Woodson et al. 2005). The krill *Thysanoessa raschii* increases swimming speed (but not turning) in algal patches (Price 1989). *E. superba* rapidly follow phytoplankton scent trails, and aggregations in the lab become less coherent as individuals encounter phytoplankton patches and began feeding (Strand and Hamner 1990). Both *Thysanoessa* and *Euphasia* respond to the loss of contact with phytoplankton or its scent with abrupt directional changes. We expected to see differences in the response of krill to phytoplankton filaments vs. background odor reflecting orientation to discrete filaments, but the small spatial scale of the experimental apparatus might have been limiting.

It is increasingly accepted that krill are not passive particles, but respond dynamically to their physical and biological environment (Cresswell et al. 2007; Lawson et al. 2008; Cox et al. 2011; Tarling and Thorpe 2014). Decades of observations of krill school movements and structure suggest a variety of physical and biological factors are important, but none are completely explanatory. Krill schools can be associated with hydrogeographic discontinuities such as the shelf-slope break (Santora et al. 2012), near fronts, or strong flow gradients (Cresswell et al. 2007; Lawson et al. 2008), but do not necessarily track prevailing flows or currents (Tarling and Thorpe 2014). Krill aggregations also may be associated with areas of high chl a abundance but this is not invariably true (Lawson et al. 2008). Aggregation structure is variable with respect to length, area, volume and packing density (Hamner and Hamner 2000; Cox et al. 2011). This variability suggests understanding individual responses reflecting the integration of different environmental features is necessary to explain school properties and distributions. Agent-based modeling has promise as a way to generate predictive models by examining how individual behaviors in particular environments affect group dynamics (Cresswell et al. 2007, 2009). Decisions made at the level of the individual ultimately govern the cohesiveness and dynamics of the school. The results of this investigation indicate that acquiring data necessary for scaling up from individual behaviors to aggregate properties is experimentally tractable. This will require examining how individuals react to different combinations of flow, aversive and attractive stimuli (chemicals, light), and how individual responses to these conditions are modified when individuals form groups.

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Compliance with ethical standards

Conflict of interest The authors declare they have no conflicts of interest regarding this work.

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