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Environmental conditions influence the frequency of prey responses to predation risk

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ABSTRACT: Predators can strongly influence prey populations and the structure and function of communities by altering the foraging behavior and/or habitat selection of prey. For these nonlethal predator effects to occur, prey must be able to detect and respond to cues indicating predation risk. The ability of prey to detect and respond to predator signals likely varies with environmental conditions. To better understand how the environment can modify nonlethal predator effects by influencing the frequency of prey responses to predators, we examined how hydrodynamic conditions influence predator avoidance behavior in the dogwhelk *Nucella lapillus*, a carnivorous snail found on rocky intertidal shores. When confronted with predation risk, such as that signaled by water-borne chemical cues released by predatory green crabs, *N. lapillus* often reduce their movement and foraging activity. Using laboratory flumes, we explored how flow velocity and turbulence influenced responses by *N. lapillus* to predator risk cues. The influence of hydrodynamic conditions on predator avoidance behavior were nonlinear. *N. lapillus* responded to predators most frequently in intermediate flow velocities but less so in high and low velocities, suggesting that the effects of flow on predator avoidance behaviors are complex. Abiotic factors like flow can strongly influence the behavioral responses of intermediate consumers, which may propagate to other trophic levels via trait-mediated trophic cascades.

KEY WORDS: *Carcinus maenas* · Dogwhelk · Green crab · Hydrodynamics · Intermediate consumer · Non-consumptive predator effect · *Nucella lapillus* · Predator avoidance behavior

INTRODUCTION

In the presence of cues signaling predation risk, prey often decrease foraging behavior, increase refuge use, and/or alter their habitat selections to reduce their vulnerability to consumers (Trussell et al. 2003, Turner & Montgomery 2003, Werner & Peacor 2003, Grabowski 2004, Valeix et al. 2009). Responding to risk may reduce prey growth or fecundity (Harvell 1990, Palmer 1990, Kats & Dill 1998, Nakaoka 2000, Bernot & Turner 2001), and may have community level effects by generating trait-mediated trophic cascades that have a positive effect on the prey's resources (e.g. Trussell et al. 2003, Grabowski 2004). Thus, understanding how prey evaluate and respond to predation risk has been a key focus of behavioral and community ecology (reviewed by Werner & Peacor 2003, Preisser et al. 2005). While many studies have examined the types of signals prey use to detect and evaluate risk (reviewed by Chivers & Smith 1998, Kats & Dill 1998, Werner & Peacor 2003), few studies have explored how environmental conditions influence prey behavioral responses to predation risk by altering prey detection capability (but see Malmqvist & Sackmann 1996, Abrahams & Kattenfeld 1997, Smee & Weissburg 2006, Smee et al. 2008).

Predator avoidance behaviors are often costly (Harvell 1990, Palmer 1990, Kats & Dill 1998, Nakaoka 2000, Bernot & Turner 2001), and thus the ability of prey being able to use reliable sensory cues that accurately reflect risk levels before initiating predator avoidance strategies is a valuable trait (Kats & Dill 1998). In aquatic systems, predators and prey often detect one another via reciprocal detection of water-borne chemical cues (Zimmer & Butman 2000, Weissburg et al. 2002, Zimmer & Zimmer 2008). As these chemical signals are propelled by currents, hydro-

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dynamic forces such as flow velocity and turbulence can influence the structure of chemical odor plumes (Weissburg 2000, Webster & Weissburg 2001) as well as the perception of the odor plumes by predators (Weissburg & Zimmer-Faust 1993, Powers & Kittinger 2002, Weissburg et al. 2003, Ferner et al. 2005, Ferner & Weissburg 2005) and prey (Smee & Weissburg 2006, Smee et al. 2008). Therefore, in chemically mediated predatory interactions, hydrodynamic conditions likely dictate the strength and frequency of prey responses to predators by altering their perceptive ability (Smee & Weissburg 2006, Smee et al. 2008, 2010).

Here we examine how hydrodynamic conditions affect the responses of an intermediate consumer to predation risk. In rocky intertidal systems, green crabs *Carcinus maenas* initiate trophic cascades by either consuming *Nucella lapillus* (dogwhelks, hereafter *Nucella*) or causing changes in *Nucella*'s foraging activity and refuge behavior (e.g. increased use of refuge habitats) (Trussell et al. 2003, 2006). In both scenarios, green crabs can have positive indirect effects on *Nucella*'s resources (mussels and barnacles), but recent evidence suggests that the nonconsumptive effects of green crabs are more important (Trussell et al. 2006). Because *Nucella* clearly respond to chemical signals emanating from predatory green crabs, they are an excellent model system to explore how hydrodynamics affect assessment of predation risk and subsequent foraging decisions. Our results suggest that flow conditions strongly influence *Nucella*'s responses to green crab predators and that the environment can have complex effects on the role that nonlethal predator effects play in these communities.

MATERIALS AND METHODS

General protocol. In the presence of green crab predators, *Nucella* decrease their activity (Vadas et al. 1994). Therefore, we used *Nucella* movement frequency as a proxy for response to perceived predation risk. Behavioral assays were conducted in flumes at the Darling Marine Center (DMC) in Walpole, ME, USA, and at Texas A&M University – Corpus Christi (TAMU-CC) in Texas, USA. We measured the effects of hydrodynamic conditions on *Nucella* behavior by comparing the frequency of *Nucella* movements in the presence and absence of green crab risk cues. The flume at the DMC is useful for behavioral investigations because specimens can be collected from nearby study sites and readily assayed with minimal disturbance. However, the DMC flume is incapable of producing flows above 8.0 cm s^{-1}, so we utilized the TAMU-CC flume, which is capable of producing the higher flow velocities necessary for some of our experiments.

DMC flume. Behavioral assays were conducted in a flow-through laboratory flume (2.2. m long, 0.53 m wide, 0.1 m deep) at the DMC that reliably reproduced free-stream flow velocities between 3.0 and 8.0 cm s^{-1} (see Smee & Weissburg 2008 for detailed flume description). Ceramic tiles lined the entire bottom of the flume to simulate the natural rocky substratum typically occupied by *Nucella* in the field. Flow-through seawater pumped from the Damariscotta River, ME, USA, was delivered to the flume and then released back into the river. The Damariscotta River is a well-mixed estuary with little variation in both salinity (32 to 34) and temperature (10 to 15°C) during the summer months.

TAMU-CC flume. We also conducted behavioral assays in a recirculating laboratory flume at TAMU-CC. The flume was 4.25 m long, 0.75 m wide and was able to reliably reproduce free-stream flow velocities between 0.5 and 25 cm s^{-1} at a water depth of 20 cm. Ceramic tiles identical to those used in the DMC flume were used to form the substratum. The flume was filled with seawater drawn from a local estuary that had passed through sand, UV, and carbon filtration systems as well as a 50 µm biological filter before it entered the flume. Water was chilled to ~13°C, and salinity was maintained at ~32, values that are similar to that experienced by organisms in the DMC flume.

Hydrodynamic methods. Flow conditions were measured in both flumes to ensure behavioral assays were conducted in similar and reproducible flow regimes. Flow was measured in each flume using an acoustic Doppler velocimeter (ADV; Vectrino model, NortekUSA) and vendor-supplied software. Free-stream flow velocity was measured 7 and 15 cm above the substratum in Maine and Texas, respectively, for 5 min at a sampling rate of 10 Hz for each flow condition. Flow velocity and turbulence were also measured 3 cm above the substratum in each flume to quantify the near-substratum hydrodynamic conditions experienced by *Nucella*. Previous authors have used this height because it is within the range used by benthic organisms for chemosensory sampling (e.g. Smee & Weissburg 2006). As above, flow velocity was measured for 5 min at 10 Hz at this height.

ADVs measure 3-dimensional flow velocity, and the net flow velocity (U) was calculated using the formula $U = \sqrt{(u^2 + v^2 + w^2)}$ where u, v, and w are the velocity components in the x, y, and z dimensions, respectively. Turbulence was calculated using the root mean square (RMS) of the velocity time series. As with flow velocity, RMS was combined in the x, y, and z dimensions for each 5 min measurement period using the formula $RMS = \sqrt{(RMS_u^2 + RMS_v^2 + RMS_w^2)}$ where these values represent the RMS levels in the x, y, and z dimensions, respectively.

Hydrodynamic environment in the field. Flow velocities were measured *in situ* using Vector model ADVs (NortekUSA) and vendor-supplied software at 6 different sites in the Damariscotta River to ensure that the velocity ranges and RMS measured in behavioral assays were similar to those experienced by *Nucella* in the field. Flow velocities in the field ranged from ~0 at slack tide to 1.2 m s^{-1}, and RMS ranged from ~0 to 0.17 m s^{-1}, similar to values reported by Leonard et al. (1998).

Animal collection and care. Organisms used in behavioral assays were collected from the Damariscotta River and held in flowing seawater tables (i.e, holding tanks) at the DMC. Green crabs *Carcinus maenas* were captured using lobster traps, SCUBA, and recreational crab nets, and were maintained on an ad libitum diet of *Nucella,* mussels *Mytilus edulis*, and clams *Mercenaria mercenaria*. *Nucella* were collected by hand and maintained on an ad libitum diet of barnacles *Semibalanus balanoides* and mussels. Water temperature ranged from 12 to 16°C, and salinity remained at ~32 in the seawater tables. *Nucella* were acclimated for 24 h in seawater tables and used in behavioral assays within 1 wk of collection. Each snail was used in a single behavioral assay before being returned to the river, except for those organisms used as food for green crabs. Green crabs were fed and acclimated for at least 48 h before being used in behavioral assays and were used within 2 wk of collection. Green crabs were only used in a single assay before being released.

For experiments conducted in Texas, green crabs and *Nucella* were collected from the Damariscotta River and shipped overnight in refrigerated containers to TAMU-CC. There they were housed in insulated tanks with filtered, circulating seawater chilled to ~13°C. Green crabs and *Nucella* were similarly housed and fed in Texas as in Maine. In all assays conducted at TAMU-CC, organisms were used in a single assay and were then humanely euthanized and discarded in a land-based facility. TAMU-CC Institutional Animal Care and Use Committee approved this protocol.

Behavioral assay. The experimental area of each flume was lined with 15 × 15 cm ceramic tiles to mimic the rocky habitat encountered by *Nucella*. Tiles were spaced 1.5 cm apart to provide crevices similar to those in which *Nucella* are typically found in the field (S. I. Large pers. obs.). Because *Nucella* reduce movement and increase use of crevices or other refuge habitats in the presence of predation risk (Gosselin & Bourget 1989, Vadas et al. 1994, Trussell et al. 2003), we utilized movement as a proxy for risk response. Small *Nucella* (<20 mm, with a thin shell lip) are more vulnerable to crab predation than larger snails (Hughes & Elner 1979, Vadas et al. 1994) and moved more frequently than larger individuals in our preliminary assays. Hence, small *Nucella* were used in behavioral assays.

To begin the assay, *Nucella* were placed in the crevice between the tiles. A refuge habitat was selected as the starting location for 3 reasons: (1) *Nucella* were commonly collected from crevices and other refuge habitats (e.g. mussel beds) in the field; (2) we wanted to determine if *Nucella* would leave a refuge habitat in the presence of predators; (3) starting *Nucella* in a refuge removes potential observational ambiguity. That is, if snails were not started in a refuge and found to be actively moving, it would not be possible to determine if the *Nucella* were unresponsive to the predator and foraging or detecting the predator and seeking refuge. Thus, starting snails in a refuge allowed us to assess *Nucella* response to predators as well as mimic the location these snails were most often collected from in the field.

In each assay, 3 *Nucella* were placed into a crevice within the experimental area and allowed to acclimate for 5 min. After the 5 min acclimation period, *Nucella* were observed for 20 s and were either recorded as moving, or not. All observable activity including climbing from refuge, lifting or rotating their shells, or crawling within the crevice was scored equally. After the initial observation, a tethered predator or the tethering apparatus without a predator (control) was introduced at a fixed distance upstream from the *Nucella* being observed. Observations were made for 20 s at 5 min intervals for 30 min. Thus, each *Nucella* could have been observed moving a maximum of 7 times during each assay.

Additional trials were performed in Texas to verify that *Nucella* behaviors were similar between Maine and Texas after shipping. In these assays (U = 4 cm s^{-1}), we compared *Nucella* responses to controls and predators between assays performed in Maine and Texas using a 2-way ANOVA with experimental location (Maine or Texas) and risk level (crab present or absent) as the main effects. These data met ANOVA assumptions. No significant differences in *Nucella* behaviors in Maine and Texas were found (see Behaviour in Maine and Texas) so the behavioral data from both flumes were combined for subsequent analyses.

Data collection and analysis. Since *Nucella* are usually found in groups throughout the intertidal zone in the Damariscotta River (S. I. Large pers. obs.), groups of *Nucella* were used in our behavioral assays. To insure that interactions between individual *Nucella* did not bias results, a series of assays were performed with a single versus a group of *Nucella.* The responses of individual *Nucella* to the presence of green crabs was compared to those exhibited by groups of 3 snails using a 2-way ANOVA where risk level (predator or control) and prey density (1 or 3 *Nucella*) were fixed factors (Sokal & Rohlf

1995). These data met ANOVA assumptions. There was a significant effect of risk but no significant density or interaction effect. The lack of a significant conspecific density effect suggests that interactions between *Nucella* did not affect their response to predation risk. Therefore, we treated each *Nucella* as an independent replicate in behavioral assays.

Response of *Nucella* to predators in differing flow conditions. To determine the effect of flow velocity and turbulence on *Nucella* behavioral responses to predators, our behavioral assays were performed in different flow regimes. Green crabs were presented to *Nucella* as a predator stimulus in 5 different flow velocities (0, 4, 8, 12, and 20 cm s^{-1}), all of which are within the natural range experienced by *Nucella* (Leonard et al. 1998, S. I. Large unpubl. data). For each flow velocity, 1 male green crab (mean carapace width ± SD: 75.7 ± 5.0 mm) was placed either 0.5 or 1.0 m upstream from the *Nucella*. This distance from the predator cue defined the level of risk where 0.5 m was considered high risk, 1.0 m as low risk, and a no-predator control as no risk. For each flow velocity, *Nucella*'s responses to 3 risk treatments (i.e. no, low, high) were replicated at least 10 times (3 *Nucella* per trial) with treatments randomly interspersed.

As flow velocity increases, turbulence also increases. In high velocity trials, turbulent mixing of odor plumes or a faster advection rate of chemical signals may have affected *Nucella*'s perceptive ability. To determine if *Nucella*'s perceptive ability is altered by higher flow velocity or increased turbulence, the substrate roughness was increased to generate turbulence in slower flows, thereby decoupling turbulence from flow velocity (see Weissburg & Zimmer-Faust 1993, Jackson et al. 2007). Gravel (diameter ± SD: 2.5 ± 0.25 cm) was placed in the flume in lieu of ceramic tiles to create a longer hydraulic roughness length. Flow was maintained at an intermediate level of $U = 8$ cm s^{-1}.

We define a flow treatment as a set of behavioral assays performed at 1 flow velocity and over 1 substrate type. *Nucella* responses in the 6 flow treatments were compared using a 2-way ANOVA with flow treatment and risk level (none, high, low) as fixed factors (Sokal & Rohlf 1995). If we detected a significant interaction between flow and risk, risk level was compared within each flow treatment using a simple main effects test to ascertain the variation in risk responses at a given flow. Since *Nucella* movement decreases in fast flows, this analysis allowed us to compare differences in predator avoidance responses between risk levels at each flow condition and avoid ambiguity of a decrease in movement caused by predator detection versus reduced movement due to hydrodynamic forces (e.g. drag). For each flow treatment, variance between risk levels was compared with nested 1-way ANOVAs with each risk level (none, high, low) as a fixed factor. Each set of flow treatments was conducted at different points in time and no-predator controls were interspersed within all risk treatments. This approach allowed us to precisely measure how *Nucella* response to risk is affected by flow velocity and/or turbulence. Post hoc analysis of power ($1 - \beta$) for each 1-way ANOVA was performed to minimize the risk of Type II error using G*Power (Faul et al. 2007). All data met ANOVA assumptions of normality and equal variances. Pair-wise differences in treatments were compared using Tukey-Kramer post hoc tests (Sokal & Rohlf 1995).

Since prey density did not affect *Nucella* responses, a nested ANOVA (see Smee & Weissburg 2006) was used to compare the effects of predator treatment and trial nested within treatment on the number of *Nucella* movements (Sokal & Rohlf 1995). A nested ANOVA was used to show if variations in *Nucella* responses were affected by variability in cue quality or quantity across replicate treatments, which is a source of uncontrolled variation in the experiments. The p-value for the nest effect was >0.2 in all experiments, indicating that *Nucella* in different groups were reacting similarly to the same treatments. The lack of a significant nest effect enabled individual snail responses to be grouped within treatments to test the significance of the main effect using the pooled error variance (Sokal & Rohlf 1995). The absence of a nest effect suggests that cues from predators and *Nucella* responses were not significantly different between replicate trials. Since the nest effect was not significant nor was *Nucella* behavior when assayed individually or in groups, individual snail responses were treated as independent replicates. All statistical analyses were performed using SPSS software for Windows, and all data met assumptions of ANOVA.

RESULTS

Hydrodynamic conditions

All flow velocities and RMS values were well within the range *Nucella* experience in the field and roughly similar between Texas and Maine flumes (Table 1). As expected, turbulence increased with flow velocity and substrate coarseness.

Behavior in Maine and Texas

Nucella responses to controls and predators were not significantly different between assays performed in Maine and those in Texas (Fig. 1). *Nucella* moved significantly less in the presence of green crabs (2-way

ANOVA, $F_{1,89} = 9.48$, $p < 0.01$), but flume location had no effect ($F_{1,89} = 0.45$, $p = 0.50$), and there was no interaction between these factors ($F_{1,89} = 0.30$, $p = 0.58$).

Density

We compared grouped and individual *Nucella* movements in the presence of a tethered green crab predator and a no-predator control to verify that *Nucella* reactions to consumers were independent. The number of observed movements for each snail was treated as an individual measurement. The presence of a green crab caused a significant reduction in *Nucella* movement ($F_{1,67} = 14.83$, $p < 0.001$), but effects of *Nucella* density ($F_{1,67} = 0.003$, $p = 0.96$) and interactive effects between density and risk ($F_{1,67} = 0.12$, $p = 0.73$) were not detected (Fig. 2). Thus, interactions between *Nucella* were not influencing their reactions to green crab predators.

Table 1. Flow conditions measured in flumes in Maine (DMC) and Texas (TAMU-CC), USA. RMS = root mean square (for the full definition see 'Hydrodynamic methods')

Flume and substrate	Free-stream flow (cm s^{-1})	RMS (cm s^{-1})
DMC		
Tile	0.0	0.00
Tile	3.8	0.65
Tile	7.2	0.92
Gravel	6.9	1.15
TAMU-CC		
Tile	3.6	0.47
Tile	8.7	0.62
Tile	12.5	0.86
Tile	19.4	2.66

Behavioral response to predators in differing hydrodynamic conditions

A 2-way ANOVA revealed a significant interaction ($F_{10,677} = 6.68$, $p < 0.001$) between the effects of risk level ($F_{5,677} = 15.42$, $p < 0.001$) and flow treatment ($F_{2,677} = 29.98$, $p < 0.001$) (Fig. 3). To separate these effects, we compared risk levels within each flow condition using 1-way ANOVAs. Without flow ($U = 0$ cm s^{-1}), there was no significant difference in *Nucella* behavior between predator risk levels and the control ($F_{2,139} = 0.38$, $p = 0.68$, $1 - \beta = 0.99$) (Fig. 4). Similarly, in 12 cm s^{-1} flow ($F_{2,72} = 2.76$, $p = 0.07$, $1 - \beta = 0.99$) and 20 cm s^{-1} flow ($F_{2,57} = 1.78$, $p = 0.17$, $1 - \beta = 0.99$), we detected no significant differences in *Nucella* behavior among the no, low, and high risk treatments (Fig. 4). In the slower flow treatments, compared to no-predator controls, risk significantly reduced the frequency of *Nucella* movements, regardless of the distance the green crabs were placed upstream. Differences between risk conditions as determined by Tukey-Kramer post hoc tests are reported in Fig. 4.

In the 8 cm s^{-1} flow treatment over tile, *Nucella* movement was reduced by ~50% in response to both high and low risk levels ($F_{2,130} = 36.44$, $p < 0.001$) (Fig. 4). However, *Nucella* did not respond differently between low and high predator risk levels in slower (4 cm s^{-1}; $F_{2,129} = 20.25$, $p < 0.001$) and more turbulent (8 cm s^{-1} with gravel; $F_{2,133} = 20.85$, $p < 0.001$) flow conditions (Fig. 4). We observed the least amount of movement in the highest risk level at 8 cm s^{-1} flow (Fig. 4).

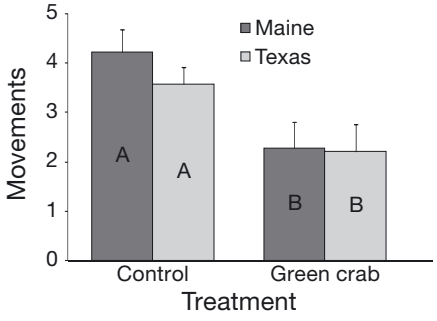

Fig. 1. Number of *Nucella* movements (mean + SE) in response to control and green crab treatments in flumes located in Maine and Texas. A 2-way ANOVA revealed that *Nucella* movements were significantly decreased in response to green crab predators ($p < 0.01$, $n = 90$), but flume location was not significantly different ($p = 0.50$, $n = 90$), nor was there an interaction between these factors ($p = 0.58$, $n = 90$). Letters denote pair-wise differences as determined with a Tukey-Kramer post hoc test

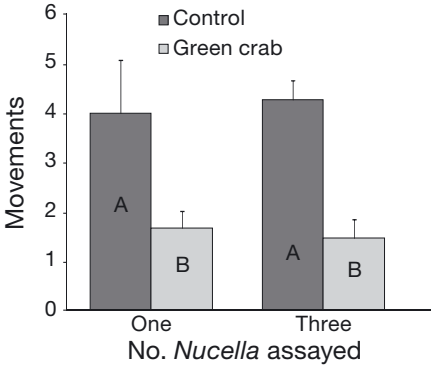

Fig. 2. Number of *Nucella* movements (mean + SE) in response to control and green crab treatments when assayed individually or in groups of 3. A 2-way ANOVA revealed that the presence of a green crab caused a significant increase in *Nucella* responses ($p < 0.001$, $n = 68$), but effects of *Nucella* density ($p = 0.96$, $n = 68$) and interactive effects between density and risk ($p = 0.73$, $n = 68$) were not detected. Letters denote pair-wise differences as determined with a Tukey-Kramer post hoc test

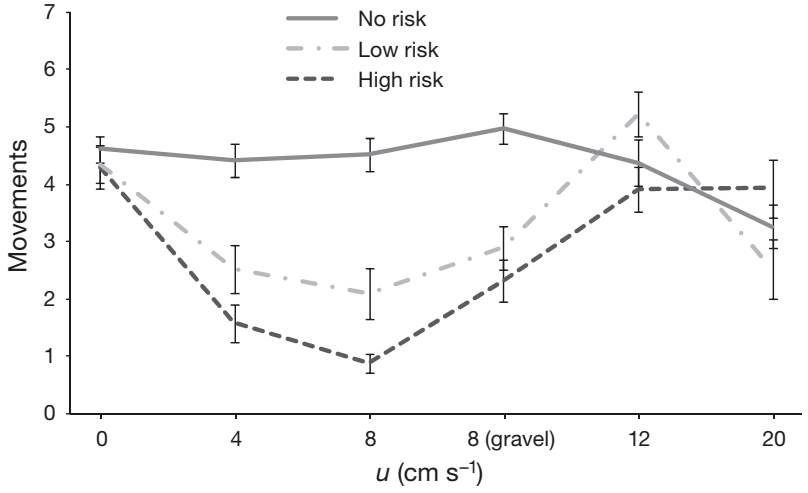

Fig. 3. Number of *Nucella* movements (mean ± SE) in response to control and green crab treatments at different flows (u = flow velocity) and risk levels. No predator = no risk, predator 1.0 m upstream = low risk and predator 0.5 m upstream = high risk. All assays were performed on tiled surfaces except where gravel is indicated as surface cover

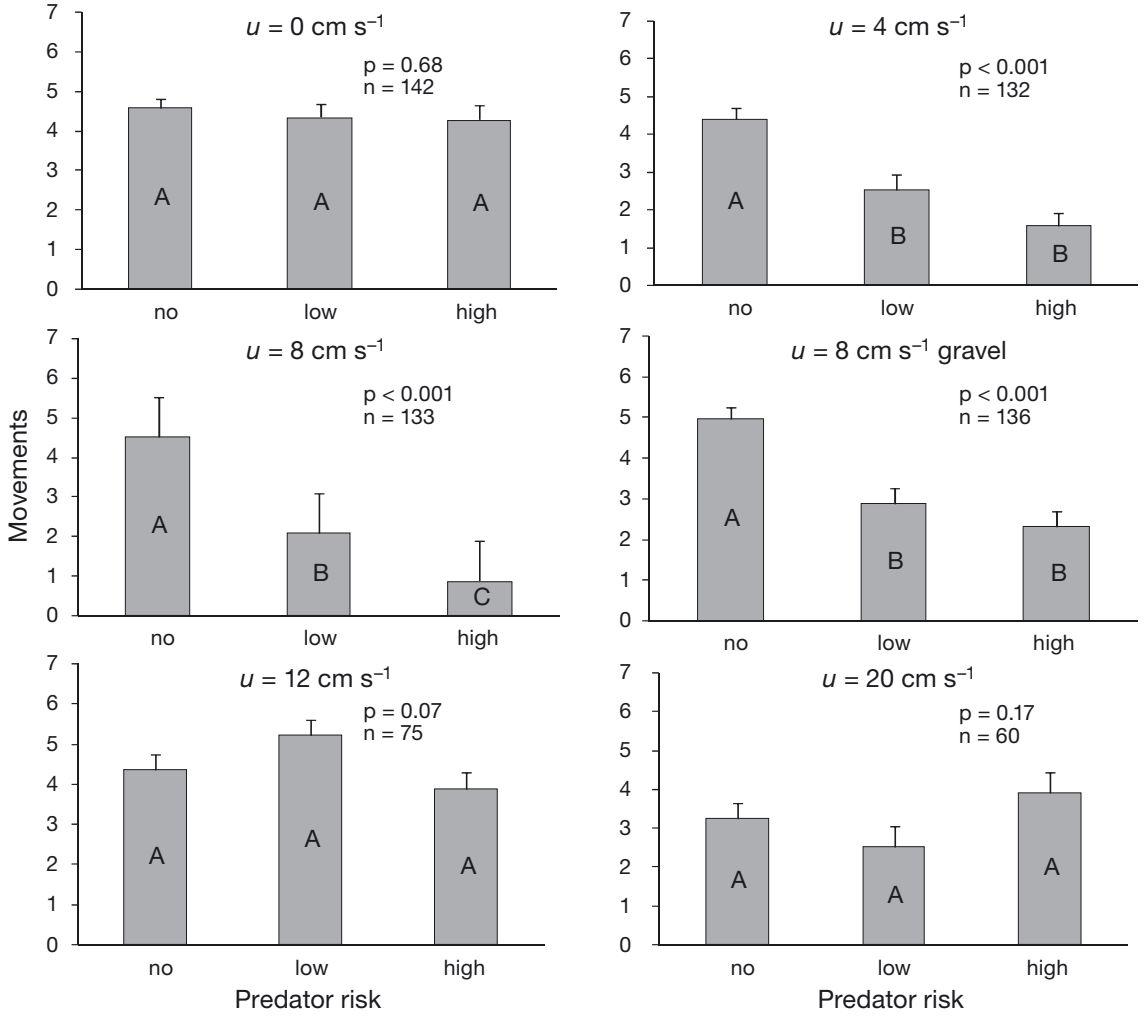

Fig. 4. Number of *Nucella* movements (mean + SE) in response to different risk levels in individual flow treatments (u = flow velocity) . Each flow treatment is labeled and a 1-way ANOVA was used to compare *Nucella*'s responses between risk levels within that flow treatment. All assays were performed on tiled surfaces except where gravel is indicated in the figure title. Sample sizes and p-values are presented with each flow treatment. Letters on the bars denote significant differences between risk levels in that flow treatment based on Tukey-Kramer post hoc tests

DISCUSSION

Within a given system, environmental forces such as flow may play an important role in dictating how organisms detect and respond to risk and may ultimately affect the strength of emergent, indirect predator effects on lower trophic levels (Post et al. 1999, Smee & Weissburg 2006, Peckarsky et al. 2008). Factors such as predator identity (Turner et al. 2000, Bernot & Turner 2001, Relyea 2001, 2004, Schmitz et al. 2004), habitat type (Trussell et al. 2006) and complexity (Grabowski 2004, Grabowski & Kimbro 2005), and hydrodynamic conditions (Smee et al. 2008, Ferner et al. 2009) may influence the magnitude of prey responses. In our model system, we found that flow significantly influenced the response of *Nucella* to predation risk across a relatively small range of flow conditions. Hence, the decision making of intermediate consumers like *Nucella* under predation risk can be significantly influenced by environmental conditions. The relationship between predator avoidance and flow velocity was nonlinear in this study, suggesting complex relationships between nonlethal predator effects and environmental conditions that enhance or attenuate the transmission of cues indicative of risk.

Turbulent flows strongly affect the advection of chemical odor plumes (Webster & Weissburg 2001) and the performance of organisms that use chemical signals to forage, find mates, and avoid predators (Weissburg & Zimmer-Faust 1993, Vickers 2000, Powers & Kittinger 2002, Ferner & Weissburg 2005, Smee & Weissburg 2006, Jackson et al. 2007). Faster, more turbulent flows increase mixing of chemical signals, homogenize odor plumes, increase plume width, and decrease the range of concentration of odor filaments within the plume (Webster & Weissburg 2001, Rahman & Webster 2005, Jackson et al. 2007). By altering chemical signal structure, turbulent flows can affect the chemoreceptive abilities of organisms. For example, turbulence reduces the ability of the blue crab *Callinectes sapidus* to locate prey (Weissburg & Zimmer-Faust 1993, Powers & Kittinger 2002, Jackson et al. 2007). Similarly, green crab predation on *Nucella* declines sharply in fast flows, suggesting that green crabs may have difficulties foraging under these conditions (Leonard et al. 1998). Unlike crustaceans, some gastropods are more successful foragers in fast, turbulent flows (Powers & Kittinger 2002, Ferner & Weissburg 2005). For example, increased turbulence increases the foraging efficiency and success rates of the knobbed whelk *Busycon carica* in the lab and field (Powers & Kittinger 2002, Ferner & Weissburg 2005, Ferner et al. 2009).

In this study, *Nucella* were most responsive to green crabs in intermediate flow velocities and turbulence levels. In the absence of flow, *Nucella* did not show significant behavioral responses to green crabs, presumably because advection of predator cues did not occur. Similarly, blue crabs are also unresponsive to chemical signals in the absence of flow (Weissburg & Zimmer-Faust 1993). The reaction of *Nucella* to green crabs increased with flow until velocity and RMS exceeded 12 and 1.0 cm s^{-1}, respectively (Fig. 4). Previous work has shown that green crab predation on *Nucella* is greatest in regions of slow flow (Leonard et al. 1998) and it was at such flow speeds that we observed a significant reduction in *Nucella* movement in the presence of predators. Because faster flows tend to mix chemical signals, the increased behavioral response to predators at intermediate flows may, at first, seem counterintuitive. However, there are 2 possible mechanisms that may explain this observation. (1) Weissburg proposed that slower moving taxa, such as gastropods, may temporally average odor concentrations from turbulent odor plumes and that their sensory performance may actually increase in turbulent flows that limit faster moving organisms such as crabs. (2) Increased flow velocity and turbulence create a greater transfer of momentum in the form of eddies into the boundary layer. Such increased turbulence may deliver more predator cue to the substrate, which is closer to the primary chemosensory organs of *Nucella*. Regardless of the mechanism, our results suggest that like knobbed whelks, chemosensory performance of *Nucella* is enhanced by moderate increases in turbulence.

When RMS exceeded 1.0 cm s^{-1}, *Nucella* ceased responding to green crabs, and we propose 2 possible mechanisms to explain this finding. First, as turbulence increases, the odor plume mixes such that it becomes undetectable to *Nucella*. Therefore, in the higher flow velocity and turbulence treatments, *Nucella* were not aware of the potential danger upstream. Conversely, green crab predation on *Nucella* declines sharply in fast flows (Leonard et al. 1998), and while *Nucella* may be aware of the danger, they continue to forage because the realized risk posed by these consumers is low in these conditions.

Prey responses to predators are often greater when predatory threats are first detected and may wane over time as prey are forced to accept riskier behavior to acquire sufficient energy for survival (Lima & Bednekoff 1999). The frequency of anti-predator behaviors observed may be greater in short term experiments like ours. Yet, we noted that flow had significant effects on *Nucella* responses to predators. Because we were most likely to observe predator avoidance tactics with our short term behavioral experimental design, we attribute a lack of responses by *Nucella* in more turbulent flows to them being unable to detect chemical cues from potential predators. Additionally, while

predator avoidance tactics are costly for prey, the benefits of surviving a predatory encounter clearly outweigh any short-term reduction in fitness (Dawkins & Krebs 1979, Chivers & Smith 1998, Kats & Dill 1998, Smee & Weissburg 2006). Thus, the failure of *Nucella* to respond to green crabs in faster flows most likely results from an inability to detect predator signals in these flow conditions and not from *Nucella* detecting predators but electing to forage in faster flows. Future experiments will explore which of these mechanisms is responsible for changing the reaction of *Nucella* to predators. Regardless, our results clearly show that hydrodynamics can significantly influence how the intermediate consumer *Nucella* responds to predatory green crabs.

Previous work has shown that prey responses to predators may vary between environments or habitats and be context dependent (Heithaus et al. 2009). For example, predators are much less common on wave-exposed shorelines of New England than in wave-protected habitats. *Nucella* from wave-exposed shorelines are less likely to respond to predatory threats than those from inland populations. Moreover, wave-exposed populations have thinner shells and larger feet that enable them to prevent dislodgement by waves while wave-protected populations of *Nucella* possess thicker shells that help deter predators (Etter 1988, Freeman & Hamer 2009). Similarly, in the Damariscotta River, blue mussels found in low-flow areas where predation pressure is greatest have thicker shells and produce greater numbers of byssal threads than do conspecifics in nearby high-flow habitats where predation pressure is low (Leonard et al. 1998). Like our study, these examples suggest that predator effects on *Nucella* may vary with environmental conditions.

Our results, along with earlier studies by Smee & Weissburg (2006) and Smee et al. (2008) suggest that hydrodynamics can influence prey reactions to consumers. In other systems, environmental factors that differentially affect the transmission of visual, acoustic, or mechanical cues between predators and prey may similarly modify the frequency of prey responses to risk. We propose that measuring how environmental conditions affect the reciprocal responses of predators and prey will be important for understanding how predator effects propagate through natural communities.

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