



Hydrodynamic mediation of predator–prey interactions: differential patterns of prey susceptibility and predator success explained by variation in water flow

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Abstract

In most shallow water marine systems, fluid movements vary on scales that may influence local community dynamics both directly, through changes in the abundance of species, and indirectly, by modifying important behaviors of organisms. We examined how differences in current speed affect the outcome of predator–prey interactions for two species of marine benthic predators (knobbed whelks, *Busycon carica*, and blue crabs, *Callinectes sapidus*) foraging on two common prey species (bay scallops, *Argopecten irradians*, and hard clams, *Mercenaria mercenaria*). The predators differ in their foraging strategies and prey in their potential escape responses. Predation by blue crabs, highly mobile predators/scavengers that rely upon chemical odors transported in the water column to locate prey, could be strongly affected by changes in current speed and turbulent mixing because their foraging strategy relies on a high degree of spatial integration of prey odor plumes. Whelks, slow moving, predatory gastropods that often forage with their bodies buried in the sediment, may be less susceptible to flow-induced distortion of prey odor plumes because their sluggish movements result in a high degree of temporal integration of prey odors. Bay scallops, relatively mobile bivalves capable of rapid short-distance swimming burst, and hard clams, sedentary bivalves, have been shown to respond to varying degrees to predator odors that are dispersed in the water column. Flow regime for the predator–prey experiments was manipulated in situ using large channels. Predation by blue crabs on both juvenile hard clams and bay scallops decreased with increases in water flow (0–12 vs. 0–30 cm s⁻¹). Whelk predation on bay scallops increased with increases in water flow, whereas predation by whelks on hard clams did not differ between flow regimes. For blue crabs

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movement decreased at periods of high water flow. Because blue crabs locate prey through chemolocation of water-borne cues, which are diluted rapidly at higher flows, decreases in foraging may result from the inability to successfully detect prey at enhanced flows. Differences in predation by whelks could not be explained by a similar mechanism. Visual observations of foraging whelks revealed no differences in whelk behavior between the two flow regimes. The pattern of higher whelk predation on scallops at enhanced flow is likely to be related to a flow-inhibiting ability of scallops to detect predator approach. Thus, flow enhancement interferes with three of the predator–prey systems but the effect on predator success depends on whether the predator or prey is most affected. © 2002 Elsevier Science B.V. All rights reserved.

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1. Introduction

Variation in predation intensity has the potential to regulate species abundance in space and time in most systems (e.g., Peterson, 1979; Sih et al., 1985; Schmitz et al., 2000). The ability of predators to successfully detect and consume prey is a key factor in determining the potential regulating effect of predators on prey communities. Variation in many physical/chemical variables may affect a predator's ability to locate prey as well as escape or defense responses of prey to an approaching predator. For example, variations in water clarity (e.g., Benfield and Minello, 1996), substrate type (e.g., Quammen, 1984; Reinsel and Rittschof, 1995) and concentration of gases in aquatic systems (e.g., dissolved oxygen: Pihl et al., 1991; Breitburg et al., 1994) all have been shown to modify predator success. For aquatic systems, variation in water movement can also alter the outcome of predator–prey interactions. In both laboratory (Hansen et al., 1991) and field (Hart and Merz, 1998) experiments, predation on black fly larvae by flatworms was shown to decrease with increasing flow as a result of reduced encounter rates (flatworms were less abundant in areas of high flow) and reduced probability of capture following encounters (flatworms are less efficient at capturing prey in higher flows). Similar results demonstrating changes in predation rate in response to differences in water flow have been reported for other freshwater (Peckarsky et al., 1990; De Nicola and McIntire, 1991; Poff and Ward, 1995; Sih and Wooster, 1994) and marine benthic systems (Palmer, 1988).

In most of freshwater studies, increased water flow resulted in decreased predator success. Swifter moving currents generally reduced the ability of predators to successfully capture and consume prey, i.e., hydromechanical predator constraints. In contrast, Palmer (1988) demonstrated that higher current velocities increased erosion of meiofauna into the water column resulting in higher predation upon meiofauna by spot. Weissburg and Zimmer-Faust (1993) found changes in predator success under smaller (i.e., +10 to 15 cm s⁻¹), non-erosive increases in water velocity. In their laboratory flume study, the frequency of successful searches by blue crabs (*Callinectes sapidus*) preying on juvenile hard clams (*Mercenaria mercenaria*) decreased as current velocities increased.

Variation in water flow occurs across a range of spatial scales in marine systems. On small scales (<1 m), topographic changes and/or the presence of structure (e.g., vegetation, animal tubes, reefs, or small rocks) can create areas of reduced and enhanced

water movement (Jokiel, 1978; Eckman et al., 1989; Gambi et al., 1990; Komatsu and Murakami, 1994; France and Holmquist, 1997; Lenihan, 1999). On larger scales (km), the interaction of topographical features with tidal and/or wind-driven circulation patterns create spatial heterogeneity in water flow patterns (e.g., Genin et al., 1986; Xie and Eggleston, 1999; Inoue and Wiseman, 2000). Temporal variation in water flow may result from lunar and meteorological forcing. In many estuarine and marine systems, tidal patterns create predictable periods of high and low water flows. For shallow water systems, episodic increases in wind can result in increased water flow and can also modify the influences of tides. The net result of these factors for marine and estuarine habitats is a dynamic system in which significant temporal and spatial variation exists in water flow and many flow-dependent variables (e.g., sediment grain size, food) on multiple scales.

Here, we investigate how relatively minor alterations in current speeds (± 10 to 15 cm s^{-1}) affect the outcome of predator–prey interactions under field conditions. Given that both predator and prey could be affected by changes in water flow, we examined a suite of predators and prey that differ in foraging strategies and their potential mobility. We hypothesize that species relying on water-borne olfactory cues to locate prey or detect predators will be less effective in these tasks under enhanced water flow. Our study is novel in that it simultaneously assesses both predator and prey responses using direct manipulations of flow in a natural, tidally oscillating system. Previous studies have been conducted in either laboratory flumes with unidirectional flows (e.g., Weissburg and Zimmer-Faust, 1993; Palmer, 1988) or through correlative studies (Leonard et al., 1998). Given that many environmental variables (e.g., sediment grain size, organic content, habitat complexity, larval supply) co-vary with flow (Snelgrove and Butman, 1994), direct in situ manipulations are necessary to examine the effect of water flow on species interactions.

2. Materials and methods

2.1. Water flow manipulations

Water flow was manipulated in situ by use of large plywood channels (Judge et al., 1992; Powers and Peterson, 2000). Conducting flow manipulations at a single field site avoids potential artifacts of site differences common in many comparative studies and avoids the artificiality of the simplified environments of laboratory flumes. By varying the width of the channel opening relative to the width of the working section (the area where the predator–prey interaction is observed), flow over a fine-sand bottom was modified in a repeatable fashion (Judge et al., 1992). Our channels measured 7.5 m in length, 0.8 m in height, and 1.0 m in width in the center working section. Widths of the opening were 2.2 m for the enhanced-flow treatment and 0.4 m for the reduced-flow treatment. The working section of the channel measured 0.75 m (width) by 2.0 m (length). Channel walls were made of five sections of 1.25-cm treated plywood that were hinged together allowing the channels to be configured to either reduce or increase water flow (see Fig. 1 in Powers and Peterson, 2000). Minimizing the angles at the hinged joints along the walls decreased the amount of flow separation at the hinge (Nowell and Jumars, 1987; Judge et al., 1992),

which minimized turbulent mixing within the working area (Powers and Peterson, 2000). Walls of the channels were anchored by 1.5-m long, 5-cm-diameter galvanized fence posts inserted outside the walls to a depth of 0.7 m in the sediments. Each wall was attached to six posts using 5-cm-diameter wall fasteners. Walls were inserted 10 cm into the sediments. To further stabilize the sediments along the channel walls, sandbags (2-m long tubes with a diameter of 25 cm) were completely buried against the outer edges of the walls and along the first section of the inner edges.

In order to retain predators within the working area of the flume, 1-m² PVC-framed panels of stainless-steel mesh screen (40-mm opening) were buried 25 cm deep and attached with cable ties to each end of the working section. Trials (three in the enhanced flow, three in the reduced flow) were conducted in which flow measurements were made at multiple points within the working sections of both mesh enclosed and non-enclosed channels at maximum tidal movement. Minor variations in current velocity (± 1 to 2 cm s^{-1}) with no consistent direction in the differences were found between the mesh enclosed and non-enclosed channels. The *t*-tests between enclosed and non-enclosed channels under each flow revealed no significant difference in current velocities ($n=3$, $p>0.4$ for both tests). Thus, this mesh opening was large enough to prevent any significant blockage in water flow while preventing predator escape.

Experiments were performed in fall 1998 and spring 1999 within the Middle Marsh area of the Rachel Carson National Estuarine Research Reserve, Back Sound, North Carolina (see map in Irlandi and Peterson, 1991). Two sets of channels were constructed on low intertidal sand flats (i.e., flats exposed only at extreme spring low tides) in fall 1998 and again in spring 1999; each channel set contained one enhanced flow channel and one reduced flow channel. Tides are diurnal with depth at the sites ranging from 10 cm at MLLW to 80 cm MHHW. The channels were moved two times in fall 1998 and spring 1999 between experimental trials to prevent differences in sediment grain size from accumulating within the working section.

To quantify the effects of each channel design on water flow, we measured current velocities within the channel and in adjacent unmodified areas during the experiments. Current velocities were measured at nine positions (see Powers and Peterson, 2000) within the working section of both channel designs on four dates during both ebb and flood tides. Measurements were taken every half-hour over each 12-h tidal cycle. Current velocities were measured with a Marsh–McBirney model 201 portable water flow meter. The probe, 3 cm in diameter at its widest point and 6.5 cm long, was attached 5 cm from the bottom of a 1.5-m long PVC pole. Two measurements were taken at heights of 5 cm (measured from the bottom of the probe) above the sediment and 8 cm below the water surface.

2.2. Experimental design

Predator and prey species used in the experiments were chosen to represent a range of mobility and probable response to water-borne odors. Two common epibenthic predators were used in the experiments, the blue crab, *C. sapidus*, and the knobbed whelk, *Busycon carica*, both of which are important predators on bivalves along the Atlantic and Gulf of Mexico Coasts (Virnstein, 1977; Peterson, 1982; Micheli, 1997). The prey searching strategy for blue crabs, a highly mobile predator/scavenger, has been characterized as

odor-conditioned rheotaxis (Weissburg and Zimmer-Faust, 1993; Finelli et al., 2000). Such strategies are characteristic of animals that have a low temporal sampling rate for chemical cues, but have high spatial integration of odor plumes, a result of high mobility in the case of blue crabs (Weissburg, 2000). *Busycon* are slow moving, predatory gastropods that forage with most of their body buried in the sediment. Although there is minimal work examining chemotaxis mechanisms with regard to snail foraging, slow-moving animals (e.g., echinoderms and gastropods) are generally thought to use gradient detection mechanisms that operate over long time scales (Moore and Lepper, 1997; Weissburg, 2000). Unlike the prey search mechanism in blue crabs, whelks may be less prone to flow-induced disruptions in prey searching since this type of chemotaxis operates over long time scales with a high degree of temporal integration. Two common prey species were used for the study, the bay scallop, *Argopecten irradians*, and the hard clam, *M. mercenaria*. Both bay scallops (Ordzie and Garofalo, 1980) and hard clams (Irlandi and Peterson, 1991; Nakaoka, 2000) have been shown to respond to predator odors that are dispersed in the water column. The escape response of each prey species differs greatly in that bay scallops represents one of the more mobile species of bivalves capable of rapid, short-distance swimming bursts (Peterson et al., 1982), whereas hard clams are sedentary bivalves whose only response once a predatory threat is detected is to retract its siphons and close its shell (Irlandi and Peterson, 1991).

With the exception of juvenile hard clams, all organisms were collected from areas within 1 km of the study area. Bay scallops, hard clams (except juveniles), and whelks were collected by hand from these areas. Juvenile hard clams were obtained from a local shellfish nursery. Blue crabs were collected with baited commercial crab pots from Back Sound, North Carolina. All animals were held in seawater tanks at the Institute of Marine Sciences in Morehead City, NC until used in the experiments (no longer than 4 weeks). Predators were fed a diet of fish, scallop and clam meat ad libitum while in the seawater tanks.

Separate experiments were performed on every combination of the two predators and two prey species. Each combination was replicated five times in both the reduced and enhanced flow channels. Sizes of prey items were chosen to reflect natural foraging preferences of both predators. For experiments with whelks, adult bay scallops (shell length, SL=3.9–5.4 cm) or clams (SL=4.5–7.0 cm) were used as prey. Predator experiments with blue crabs used juvenile bay scallops (SL=1.3–2.2 cm) or hard clams (SL=1.3–1.8 cm). For the whelk–hard clam experiments, trials began at low tide by burying six pre-measured and marked hard clams evenly distributed throughout the working section of both channels. No one area received a density greater than 1 clam per 0.25 m² and no prey items were placed within 15 cm of the channel walls. Two whelks (length=13.5–16.5 cm) were then placed 25 cm apart in the center of the working section and allowed to forage within the working section for 36 h. Two whelks were used because foraging by whelks is usually slow and whelks are not known to interfere with each other during feeding. For the whelk–bay scallop experiments, trials began by tethering six bay scallops to metal staples buried throughout the working section of the channel. Bay scallops were tethered with 30-cm lengths of 10-lb test monofilament fishing line. One end of the tether was glued to the posterior portion of the upper valve of the scallop and the other end attached with a swivel to the metal staple. The spatial distribution of bay scallops in the working section matched that of hard clams previously described. Two whelks

(length = 13.7–16.3 cm) were then placed in the working section of the channel and allowed to forage for 36 h.

For the blue crab experiments, six juvenile bay scallops or six juvenile hard clams were tethered to metal staples and the staples buried throughout the working section of the channel and distributed in a similar manner as described for the whelk experiments. For the blue crab–bay scallop experiments, juvenile scallops were tethered with 10-cm lengths of 6-lb test monofilament line and attached to the shells and staples as previously described. One male blue crab (carapace length = 115–145 mm) was allowed to forage within the working section of the channel for 24 h. At the end of the experimental runs, the number of scallops surviving was counted, as well as the number of living scallops with chipped or damaged shells. By initially stocking the experiments with clams or scallops without damaged shells, we assessed the number of unsuccessful attacks by blue crabs on these bivalves by counting the number of living scallops or clams that had damaged shells when the experiment was terminated. The experiments with hard clams as prey items followed the same procedures as those of the blue crab–bay scallop experiments. Controls for each experiment in which prey items were placed in channels without predators also were performed for every combination of predators and prey and replicated five times. In most cases, control runs were paired with the predator inclusion experiments. In the few cases that pairing was not possible, control runs were performed within the same week of the predator inclusion experiments.

Tethering of prey items in the blue crab experiments was necessary to insure recapture and, more importantly, to insure that the prey items remained in the working section of the channel where water flow patterns were characterized. For hard clams, tethering should not interact with flow treatments (*sensu* Peterson and Black, 1994) because these organisms lack any significant escape response (see also tethering effects in Micheli, 1996). In our experiments, we tethered only juvenile clams to guarantee their recapture at the end of the experiment; large clams were not tethered because clams in this size range are easy to find and retrieve. Any artifact introduced as a result of tethering juvenile scallops in the size range used in our blue crab experiment should be minimal because scallops at this stage are generally attached by byssus threads to seagrass (see also tethering effects of crabs feeding on scallops in Barbeau and Scheibling, 1994). Tethering of adult bay scallops, the size range used in the whelk experiments, could reduce the total distance moved by bay scallops in response to predators. The 30-cm tether length allowed an escape flight of 30–60 cm. Powers and Peterson (2000) showed that a normal swimming burst (in response to density manipulations) for bay scallops resulted in displacement distances of up to 50 cm. Given the potential for a tethering artifact, we also performed experiments to compare predation by whelks on tethered and untethered adult scallops. These experiments were restricted to ambient flow regimes (achieved by making the channel sections straight). If untethered scallops were introduced into the reduced or enhanced channels, they could migrate to the walls of the channels where the flow regime was unpredictable because of the boundary layer formed by the presence of the wall. For these experiments, one channel held six tethered scallops and a second channel held six untethered scallops. Two whelks were introduced into the center of each channel. After 48 h, the numbers of living and dead scallops were recorded. Three replicates of this experiment were performed.

Tethering of scallops in the scallop–whelk experiment did not affect adult scallop survival under ambient flow conditions in the channels. Mortality of scallops remaining in the channel averaged 30% in the untethered treatment and 35% in the tethered treatment ($p=0.4$ for paired t -test). However, one to two untethered scallops did escape the caged area where they were retrieved alive, demonstrating the need to use tethers to conduct the experiment.

Observations of whelk and blue crab movements and foraging were performed periodically during the experimental runs. For whelks, four separate 6-h observation periods were established. Two of these began 1 h after the start of the experiments on incoming (flood) tides. The others occurred on falling (ebb) tides. During each observation period, position and direction of movement were recorded every 15 min for both whelks. Because whelks often burrow and move within the sediment, we attached bright, orange ping pong balls to the whelks with 10 lb test monofilament line. One end of the line was tied through a small hole drilled in the whelk shell and the other glued to the Ping Pong ball. A 1-m length of line was sufficient for the Ping Pong ball to be visible on the water surface. Blue crab behavior and movements were observed for 10-min periods nine times in both reduced and enhanced flow during the blue crab experiments. These observations were scattered throughout the tidal cycle such that three 10-min observations were made at slack tide, three at periods of low water flow, and three at periods of high water flow.

2.3. Statistical analyses

Analysis of variance (ANOVA) was used to estimate the difference in water flow between channel designs, whereas t -tests were used to compare the effects of flow regime on predator success and movement patterns of predators. A two-way ANOVA was performed to examine the effect of channel design and tidal stage (standardized hour, 0 to 12 with 0 being the start of the ebb tide) on current speeds. Current speed data were pooled over dates, after date was demonstrated not to be significant at the conservative level of $p>0.25$ (Underwood, 1981). Before we performed the ANOVA, we confirmed homogeneity of variances using Cochran's C -critical test; in no case was transformation necessary. Comparisons of percent of prey missing (assumed to be percent successfully consumed because recovery was virtually 100% in controls) between the flow treatments were performed via two-tailed, paired t -tests. Separate t -tests were performed for those experimental runs that included predators (treatments) and those that did not include predators (controls) for each predator–prey combination. Separate statistical tests for each predator–prey combination were necessary because of differences in prey sizes, duration of experiments, tethering among the various predator–prey combinations and the questions posed. Because it was not always possible to conduct paired control and treatment experiments, separate analysis of controls and treatments were necessary. For the observational data on whelks, we used paired t -tests to determine if there were any differences in the net distance moved over a 6-h period. We also used paired t -tests to determine if the total number of 15-min intervals in which some whelk movement was observed differed between flow treatments.

3. Results

3.1. Water flow treatments

Modification of the channel design was successful in creating flow differences during all non-slack tide periods (ANOVA, $p < 0.01$ for the interaction between channel design and time). While there was no effect of channel design at slack tides (0 and 6 h into ebb and flood tides) when water movement is minimal ($p > 0.05$ for SNK tests), current speeds were significantly greater in the enhanced flow channel at all other times in the tidal cycle (1–5 h into ebb and flood tides, $p < 0.05$ for all SNK post hoc contrasts). Current speeds ranged from 0 to 30 cm s^{-1} in the enhanced flow channel and 0 to 12 cm s^{-1} in the reduced flow channel (Fig. 1). During periods of peak water flow (2–4 h into ebb and flood tides), current speeds were 70–100% higher in the enhanced-flow channel than the reduced-flow channel. Water flow within a channel was fairly uniform; velocities at the nine measurement positions in the working section differed by only 1–2 cm s^{-1} during any one sampling period.

3.2. Blue crab predation

Predation rate by blue crabs on both hard clams and bay scallops differed between the two flow regimes. For hard clams, mortality averaged 49% in the reduced flow channel compared with 21% in the enhanced-flow channel ($p < 0.01$) when blue crabs were present (Fig. 2A). All clams were alive at the end of the trials when blue crabs were absent (Fig. 2B). For bay scallops in the presence of blue crabs, bay scallop mortality averaged 50% in the reduced-flow channel compared with 12% in the enhanced-flow channel ($p < 0.02$;

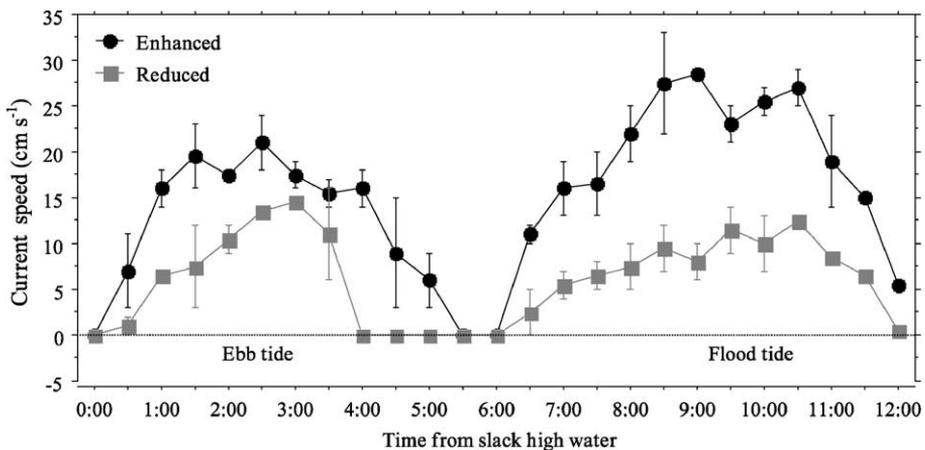


Fig. 1. Current speeds (mean \pm 1 S.E., $n = 4$) in the enhanced and reduced flow channels over a 12-h tidal cycle recorded 5 cm above the sediment surface. If no standard error bar is present on a particular point, then the error associated with the mean was too small to be shown. Current velocities differed at all times except periods of slack tide (i.e., 0 and 6 h; see text for ANOVA results).

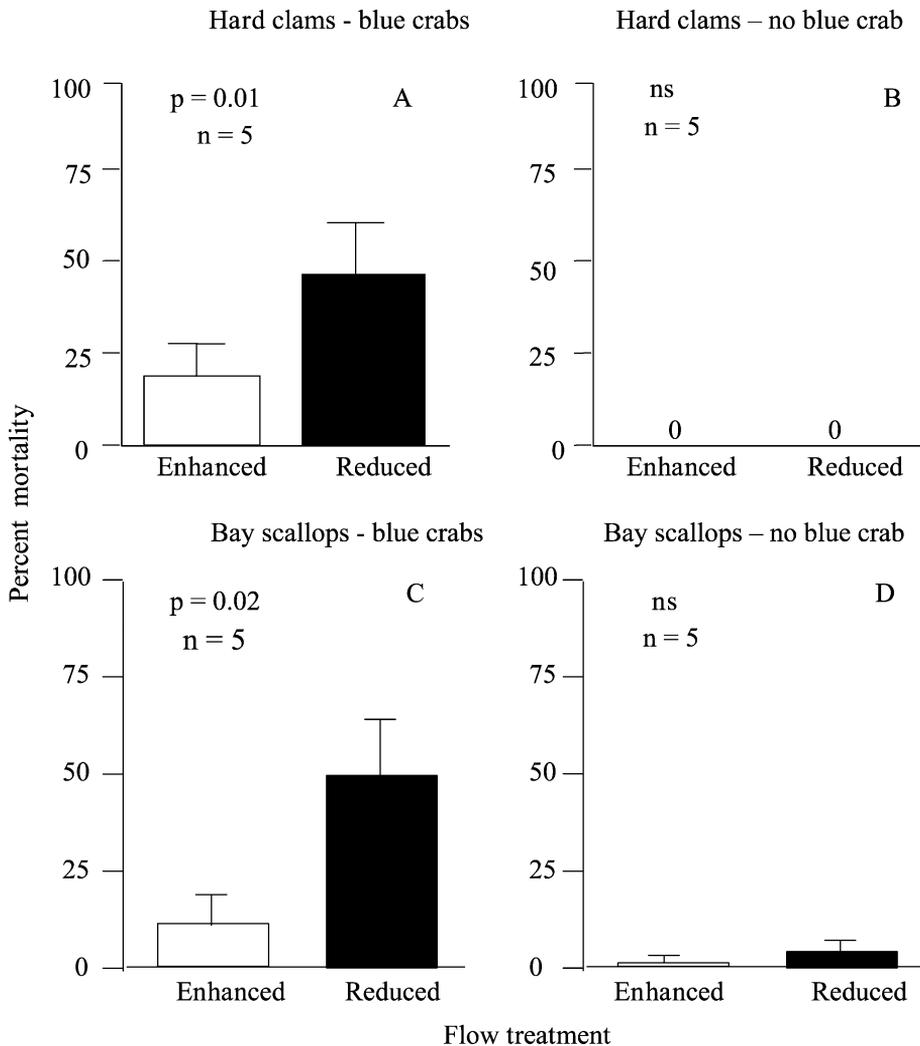


Fig. 2. Mortality (mean + 1 S.E.) of juvenile hard clams and bay scallops in the presence and absence of blue crabs under enhanced and reduced water flow. Results of paired *t*-tests are given in the upper corner of each graph.

Fig. 2C). In the absence of blue crabs (controls), bay scallop mortality was low (4–8%) and did not differ between flow treatments ($p > 0.05$; Fig. 2D). The number of chipped clams or bay scallops was low (< 10% for hard clams in either flow regimes, 0% for bay scallops in both flow regimes) and did not differ between flow treatments ($p > 0.05$ for all tests).

Blue crabs exhibited slightly different behavior when placed in the two different flow treatments. The proportion of observations in which blue crabs were moving at some point during the 10-min period was higher in the reduced than in the enhanced-flow channel (0.67 vs. 0.33, Fig. 3). Blue crabs appeared to be more active at low flows. During periods

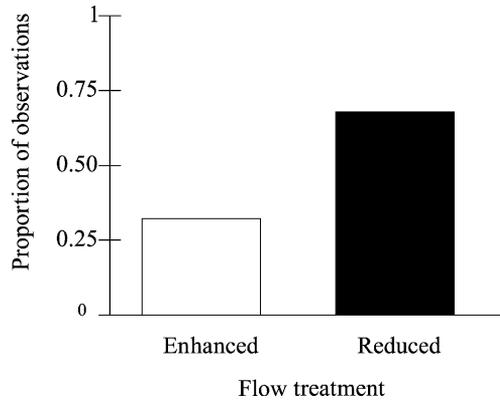


Fig. 3. Proportion of paired observations in which blue crabs were seen moving under two different water-flow regimes.

of low water flow, blue crabs were observed moving in both directions (against and with the current) in the enhanced and reduced flow treatments. However, during periods of high flow blue crabs reduced their activity and often remained motionless.

3.3. *Whelk predation*

The pattern of predation by whelks in the two different flow treatments varied with prey species. Mortality of hard clams did not differ between flow treatments ($p > 0.05$ for t -test), averaging 40% in the enhanced flow and 45% in the reduced flow channels (Fig. 4A). Mortality in the absence of whelks (controls) was low and did not vary between flow treatments (Fig. 4B). For bay scallops, mortality was higher in the enhanced flow channel, averaging 50% compared to 15% in the reduced flow treatment ($p < 0.01$; Fig. 4C). Mortality was low and did not differ between the two flow treatments ($p > 0.05$ for t -test) when whelks were absent (Fig. 4D).

Observations of whelk foraging revealed no detectable difference in the total distance moved over 6 h between whelks placed in the reduced and enhanced flows ($p > 0.05$; Fig. 5A). Similarly, no difference was detected in the number of 15-min intervals in which some movement on the part of the whelks was observed ($p > 0.05$; Fig. 5B). Whelk burrowing and overall movement patterns were similar in both flow regimes.

4. Discussion

We found that the influence of water flow on the outcome of predator–prey interactions depends on the degree to which the predator or prey is most affected by the change. In our experiments, modifications of flow regime resulted in changes in the success of one predator, the blue crab, regardless of prey species, whereas the effect on success of another less mobile predator, the knobbed whelk, depended on the prey species included in the trial.

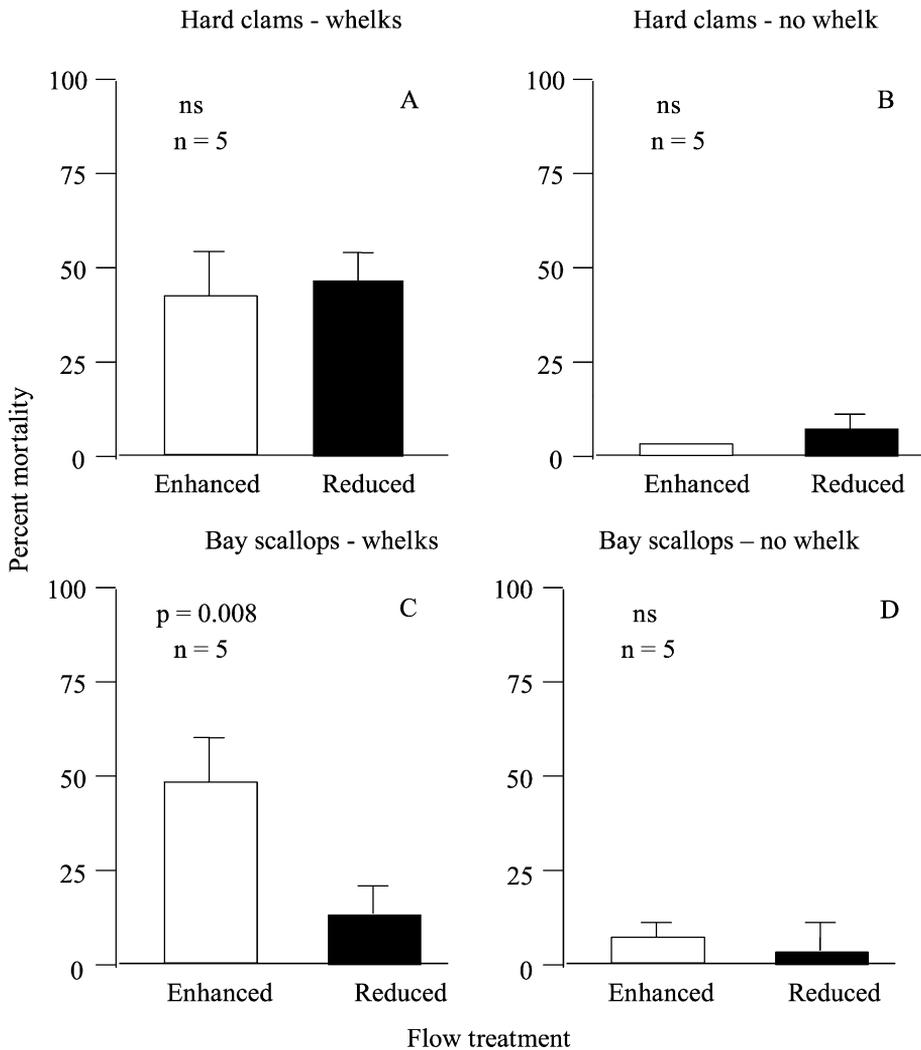


Fig. 4. Mortality (mean \pm 1 S.E.) of adult hard clams and bay scallops in the presence and absence of knobbed whelks under enhanced and reduced water flow: results of paired *t*-tests are given in the upper corner of each graph.

Blue crabs preyed upon a significantly higher number of juvenile hard clams and bay scallops in reduced ($0\text{--}12\text{ cm s}^{-1}$) than in enhanced flows ($0\text{--}30\text{ cm s}^{-1}$). Predation in the reduced flow was double that of the enhanced-flow treatment when blue crabs were present. There are two possible explanations for this pattern: (1) predators can not successfully handle or consume prey at enhanced flow and/or (2) enhanced flows lead to reduced prey encounter rates. Our ability to visualize damage to bivalve shells allows us to assess the first explanation. Given that the percentage of remaining clams or scallops that showed predator-related damage (i.e., chipped shells) did not differ between flow

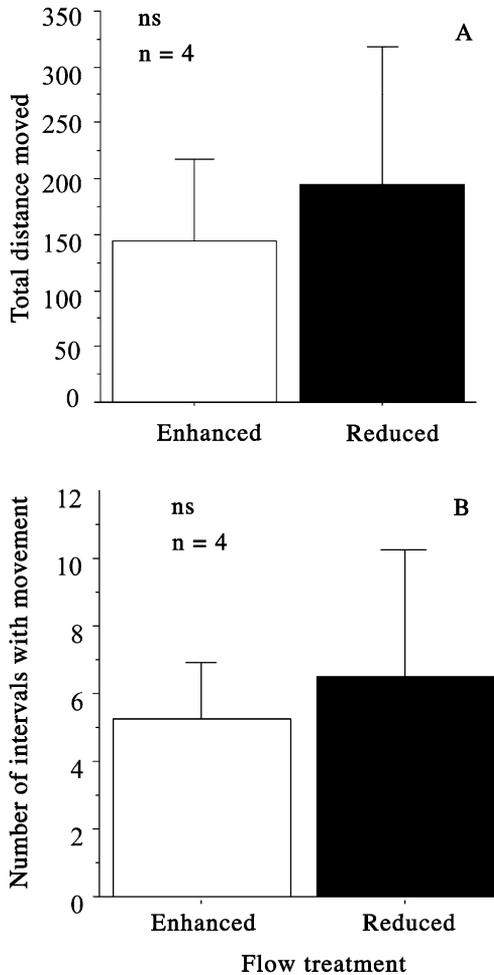


Fig. 5. Comparisons of the total distance moved over 6-h periods (mean + 1 S.E.) between whelks placed in the enhanced flow and the reduced flow channels (A) and the number of 15-min intervals (mean + 1 S.E.) in which some movement was recorded in the enhanced flow and reduced flow channels (B). Results of paired *t*-tests are given in the upper corner of each graph.

treatments, it is unlikely that once captured, consumption of prey items differed between the flow treatments.

For prey with limited mobility, predator encounters with prey may differ among flow regime (our second explanation) as a result of changes in the ability of predators to efficiently locate prey. Search efficiency may be altered because current speeds may be high enough that predators are physically unable to forage (Menge, 1978) or higher flow regimes may interact negatively with the cues predators rely upon to find prey (Weissburg and Zimmer-Faust, 1993). The range of current speeds in our experiments were not erosive to either predator or prey and in no case were organisms swept out of the working section

of the flume. Furthermore, blue crabs are frequently captured in high numbers in unvegetated-subtidal channels that experience current speeds similar to or higher than current speeds of the enhanced flow treatment (Powers, unpublished data). There is convincing evidence to support our contention that enhanced water flows negatively interact with the cues blue crabs use to locate prey. Weissburg and Zimmer-Faust (1993) found that the frequency of successful searches was greatest at low current speeds ($1\text{--}3\text{ cm s}^{-1}$) and decreased with increasing current speed ($12\text{--}15\text{ cm s}^{-1}$). Their findings were best explained by the rapid mixing and dilution of water-borne chemical odors at high current speeds as a result of increases in turbulent mixing. Rapid mixing and dilution of the odors makes it difficult for crabs to follow the odor trail to its point of origin. The pattern of decreased blue crab movement at periods of high flow (Fig. 3) may be a result of the inability of crabs to successfully locate prey items at times of enhanced water flow. Rather than expend energy on unsuccessful attempts to navigate odor plumes, blue crabs may remain sedentary and wait until those periods during the tidal cycle when flow rates are more conducive to locating prey. Although in our tidally oscillating system there were periods of slack or low water movement in both flow regimes, the percentage of time current speeds were within the best range for blue crab to locate clams (1 to approximately 12 cm s^{-1} in the studies of Weissburg and Zimmer-Faust, 1993; Finelli et al., 2000) was much higher in the reduced flow treatment.

Whereas differences in the abilities of blue crabs to successfully locate prey under high and low current speeds leads to a parsimonious explanation of the differences in clam and bay scallop mortality in the blue crab predator experiments, this model fails to explain the whelk predation results. There was no effect of flow regime on mortality of clams in the whelk–hard clam experiment. The percentage of hard clams preyed upon was almost identical in the two flow treatments (Fig. 4C). Furthermore, our analysis of the observational data demonstrated no effect of flow regime on overall frequency of movement or distance moved between the two flow regimes (Fig. 5A,B). These data suggest that the signals that whelks use to locate hard clams are not altered by our changes in current speeds. This conclusion is consistent with the predictions of Weissburg (2000) who speculated that prey odor detection of predatory gastropods like *Busycon* would be largely unaffected by changes in fluid movement because their sluggish movements leads to a high degree of temporal integration of odor trails. Hard clams have been shown to reduce feeding activity in the presence of whelk odors dispersed in the water column (Irlandi and Peterson, 1991; Nakaoka, 2000). Although the ability of clams to detect whelks may be modified in response to changes in current speeds, the limited escape response of clams and the sub-surface foraging strategy of whelks causes any changes in detection ability by clams to be of limited use in escaping whelk predation.

In contrast to the three other predator–prey systems tested, bay scallop mortality was higher in the enhanced flow channel when whelks were present. This pattern, higher mortality of prey items in the enhanced flow, was not evident when hard clams were the prey item for whelks. Given the results of the hard clam–whelk experiment and the fact there were no differences in whelk activity between the flow regimes, we conclude that some difference in the bay scallops' response to the whelks must vary between flow regimes. Bay scallops generally attempt to swim away when a predatory threat is perceived (Peterson et al., 1982; Winter and Hamilton, 1985; Peterson et al., 1989).

Although tethering a scallop limits the distance that it can swim, the length of the tether did allow an immediate response on the spatial scale similar to those that have been observed (Powers and Peterson, 2000). Such short swimming bursts, often involving only 1–7 claps of the shell (Ordzie and Garofalo, 1980) are often effective in escaping predation by *Busycon* whelks (Peterson et al., 1989).

Two possible explanations exist for the pattern of higher mortality of bay scallops at enhanced flows. First, enhanced flows may affect negatively the swimming response of bay scallops. Second, enhanced water flow may reduce the ability of bay scallops to react to a predatory threat. Enhanced flow should result in an energetically more favorable environment for effective swimming than reduced flows (Wildish and Kristmanson, 1997; Vogel, 1997; Powers and Peterson, 2000), consequently, the first explanation is not consistent with our understanding of scallop swimming. The second explanation requires that changes in current speed interact with the mechanism that scallops use to detect a predator. Scallops have been shown to detect predatory threats through both direct physical contact with a predator (Thomas and Gruffydd, 1971; Ordzie and Garofalo, 1980) and prior to contact via water-borne cues associated with predators (Thomas and Gruffydd, 1971). At close proximity, scallop tentacles have been shown to use chemosensory stimuli to differentiate between predatory and non-predatory snails (Ordzie and Garofalo, 1980).

Enhanced water flows could affect both the chemosensory (i.e., water-borne cues) and mechanical stimuli that result in an escape response. Increased current speeds and the consequent increases in turbulent mixing could cause rapid dilution of any water-borne chemicals below the level useful for prey to recognize potential predators (Weissburg and Zimmer-Faust, 1993). At periods of increased water flow, scallops may withdraw their tentacles to avoid damage (Wildish and Kristmanson, 1997) resulting in shorter distances between predator and prey when physical contact is the primary stimulus for flight. Retraction of tentacles would also result in less surface area exposed to the surrounding fluid medium for chemosensory reception of predatory threats. Such hypotheses need to be tested fully before a mechanistic explanation for the pattern of higher scallop predation by whelks at enhanced flows can be established, but it is clear that increased current speed decreased the ability of scallops to detect an approaching whelk. The benefit of more effective detection of whelks in low-flow environments may be one reason why adult bay scallops continue to reside in seagrass meadows, a low-flow habitat, after their detachment from seagrass blades.

Slight advantages in perception can often determine the difference between survival or death for prey and success or failure for predators. As in any battle, the ability to receive and interpret information regarding the location and condition of an enemy or victim is critical and can determine the outcome of an encounter. The location of a particular engagement and/or the environmental conditions at the time of encounter often result in one side having an advantage over the other in the acquisition of information. For many predator–prey systems, information on a victim's or enemy's whereabouts comes through chemosensory reception of cues dispersed through air or water (e.g., Chiszar et al., 1990; Schwenk, 1995; Kessler and Baldwin, 2001). Our study demonstrates how differences in fluid movement can alter this advantage with the direction of change being dependent on who, predator or prey, is affected most by flow related disruptions in signal detection.

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