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Interactions Between Benthic Predators and Zooplanktonic Prey are Affected by Turbulent Waves

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Synopsis Predators capture prey in complex and variable environments. In the ocean, bottom-dwelling (benthic) organisms are subjected to water currents, waves, and turbulent eddies. For benthic predators that feed on small animals carried in the water (zooplankton), flow not only delivers prey, but can also shape predator–prey interactions. Benthic passive suspension feeders collect prey delivered by movement of ambient water onto capture-surfaces, whereas motile benthic predators, such as burrow-dwelling fish, dart out to catch passing zooplankton. How does the flow of ambient water affect these contrasting modes of predation by benthic zooplanktivores? We studied the effects of turbulent, wavy flow on the encounter, capture, and retention of motile zooplanktonic prey (copepods, *Acartia* spp.) by passive benthic suspension feeders (sea anemones, *Anthopleura elegantissima*). Predator–prey interactions were video-recorded in a wave-generating flume under two regimes of oscillating flow with different peak wave velocities and levels of turbulent kinetic energy (“weak” and “strong” waves). Rates of encounter (number of prey passing through a sea anemone’s capture zone per time), capture (prey contacting and sticking to tentacles per time), and retention (prey retained on tentacles, without struggling free or washing off, per time) were measured at both strengths of waves. Strong waves enhanced encounter rates both for dead copepods and for actively swimming copepods, but there was so much variability in the behavior of the live prey that the effect of wave strength on encounter rates was not significant. Trapping efficiency (number of prey retained per number encountered) was the same in both flow regimes because, although fewer prey executed maneuvers to escape capture in strong waves, more of the captured prey was washed off the predators’ tentacles. Although peak water velocities and turbulence of waves did not affect feeding rates of passive suspension-feeding sea anemones, increases in these aspects of flow have been shown to enhance feeding rates and efficiency of motile benthic fish that lunge out of their burrows to catch zooplankton. Faster, more turbulent flow interferes with the ability of prey to detect predators and execute escape maneuvers, and thus enhances capture rates both for passive suspension-feeding predators and for actively swimming predators. However, prey captured in the mouths of fish are not washed away by ambient flow, whereas prey captured on the tentacles of suspension feeders can be swept off before they are ingested. Therefore, the effects of flowing water on predation on zooplankton by benthic animals depend on the feeding mode of the predator.

Introduction

Predators seek food under environmental conditions that can alter the outcome of predator–prey interactions. In the ocean, the motion of water varies due to tides, currents, waves, and turbulent eddies. How does this ambient flow impact feeding by marine organisms? Bottom-dwelling (benthic), predators that feed on small animals in the water column

(zooplankton) are dominant components of many marine communities. They play a key role in transporting material from pelagic systems in the water column down to the ocean floor (reviewed by Gili and Coma 1998). Benthic zooplanktivores use a range of feeding strategies. Visual predators such as burrow-dwelling fish dart out and catch passing plankton, while passive suspension feeders collect

food delivered by ambient currents onto capture-surfaces. This study explores the effects of the flow of ambient water on these two contrasting modes of foraging.

Passive suspension feeders rely on the motion of the surrounding water to transport prey to capture-surfaces, while active suspension feeders generate currents or actively pass a capture-surface through the water. Variations in the strength of the current can affect the amount of prey delivered to benthic suspension feeders and the ability of those predators to hold onto captured food. In response to flow, active suspension feeders can modify their feeding behavior (e.g., Trager et al. 1990; Knott et al. 2004; Shimeta 2009), and passive suspension feeders can passively or actively alter their shape or orientation (e.g., Koehl 1977; Loo et al. 1996; Shimeta 2009), or grow into different configurations (e.g., Wainwright and Dillon 1969; Hunter 1989; Sebens and Johnson 1991; Helmuth and Sebens 1993).

Conditions of flow

In shallow coastal habitats rapidly changing currents, waves, and turbulence (Denny 1988) can impact feeding by benthic organisms. Currents reach maximum velocities shoreward then seaward during flooding and ebbing tides, respectively, and minimum velocities at slack high and slack low tides. As waves approach the shore, the orbital motion of the water in the waves is compressed close to the substratum and oscillates back-and-forth on a scale of seconds (e.g., Bascom 1964). Turbulent eddies of different sizes (due to currents, tides, waves, wind, and water passing over spatially complex substrata) stir the water.

Many benthic zooplanktivores live in shallow coastal habitats where they are exposed to the turbulent reversals of flow associated with waves. Feeding rates by passive suspension feeders in unidirectional flow have been studied both theoretically (Rubenstein and Koehl 1977; Shimeta and Jumars 1991) and experimentally, e.g., in soft corals (Patterson 1984), bryozoans (Okamura 1984), sea pens (Best 1988), and sea anemones (Anthony 1997), but only a few experimental studies have explored the effects of waves and turbulence on rates of suspension feeding (Hunter 1989; Trager et al. 1992).

Effects of flow on different stages of capturing prey

The flow of water around benthic zooplanktivores can affect predator-prey interactions at each successive stage of the feeding process: encounter, capture, retention, and ingestion (Shimeta and Koehl 1997).

The rate of encounters with prey is the number of prey that pass through the capture zone of a predator per time. As water velocity increases, more prey are swept past a benthic predator per time. In contrast, oscillating flow due to waves may lead to a predator resampling the same parcel of water, which could become depleted of prey. However, turbulent eddies of different sizes can stir the water and counteract depletion. Rothschild and Osborn (1988) modeled the role of turbulence in increasing encounter rates between predators and prey by such mixing, but their focus was on pelagic, not benthic, predators. Although it is informative to know how much food is available to a predator, rate of occurrences of encounters do not necessarily predict feeding rates that depend on the proportion of encountered prey that are captured (by contact with a “capture-surface” such as a filter or tentacle), retained (not washed away or lost after contact), and ingested (Shimeta and Jumars 1991; Shimeta and Koehl 1997).

Capture rates describe how frequently prey come in contact with a predator’s capture-surface. As prey pass by a predator, the escape behavior of motile planktonic prey that sense a nearby predator can reduce capture rates (Trager et al. 1994). Waves and turbulence can mask mechanical signals of the predator in the water and can disperse and dilute chemical signals, thereby inhibiting the ability of prey to detect and avoid the predator (Robinson et al. 2007).

Retention is the ability of a predator to hold onto captured prey. Retention of a captured particle or organism depends on the stickiness of the predator, the contact area between the predator and prey, the size and shape of the captured item, and the speed of the water, as well as the ability of the captured prey to struggle and dislodge itself. It has been suggested (Rubenstein and Koehl 1977) and demonstrated in experiments conducted in unidirectional flow (e.g., Patterson 1984; Okamura 1984, 1985; McFadden 1986; Shimeta and Koehl 1997; Allen 1998) that reduced feeding rates by suspension feeders in rapidly moving water are caused by drag forces that wash prey off capture-surfaces, but retention of prey in waves has not been analyzed. Ingestion can only occur if a predator is able to successfully retain prey.

To understand the mechanisms underlying how turbulence affects the feeding rates of benthic predators that eat zooplankton, we must determine how the flow affects encounter rates (which depends on delivery of prey to the capture zone), capture rates (which are affected by escape maneuvers of the prey before contacting the predator), and retention rates

(which can be reduced by the escape behavior of captured prey and by drag on the prey). If feeding rates scale with flow (velocity of water and concentration of prey), rates of encounter, capture, and retention would increase proportionally.

Feeding by a zooplanktivorous fish

Previous studies of benthic zooplanktivorous fish showed that foraging behavior was affected by waves and turbulence (Clarke et al. 2005, 2009; Finelli et al. 2009). Tube blennies (*Acanthemblemaria aspera* and *Acanthemblemaria spinosa*) are small tropical fish that live in burrows within coral heads and actively dart out into the water column to capture passing zooplankton such as calanoid copepods. These suction-feeding fishes use vision to identify potential zooplanktonic prey, and then lunge toward the prey in a “predator approach.” The approach is successful when the fish swallows the prey, or unsuccessful when it misses the prey or the prey escapes and swims away. When exposed to increasing turbulence, the blennies reduced their foraging effort (approaches per minute). When exposed to waves, the blennies only tried to catch prey during the periods of slow flow that occurred as the water in the waves changed direction. However, foraging efficiency (the proportion of prey approached that were eaten) improved with increasing turbulence and stronger waves because the ability of evasive prey to detect and avoid predation declined with turbulent and wavy conditions (Robinson et al. 2007). Although the blennies foraged less frequently, the fish were more successful at capturing prey. For these active zooplanktivores, an increase in turbulence and waves interfered both with the predator’s feeding behavior and prey’s escape behavior, but the net result was an increase in foraging success by the predator. For passive suspension feeders dependent on flowing water to deliver prey, do increases in turbulence and stronger waves similarly impact capture rates and feeding efficiency?

The effects of unidirectional flow on feeding rates of passive suspension-feeders are well-studied (reviewed by Wildish and Kristmanson 1997). By quantifying feeding rates, only the retention or ingestion stage of the feeding process is observed, whereas the impacts of flow on encounter and capture of prey are obscured. Research examining the mechanisms used in passive suspension-feeding to encounter, capture, retain, and ingest prey has been carried out on non-motile “prey” (e.g., beads) and suggests that higher velocities of flow lead to higher rates of encounters and captures (e.g., Shimeta and Koehl 1997). Experiments with corals feeding on motile

planktonic prey demonstrated that evasive swimming behavior by prey reduced capture rates in low flow and in waves (Heidelberg et al. 1997). The research reported here examined how levels of turbulence and speed of waves affected each stage of the feeding process used by benthic suspension feeders eating zooplankton.

The objective of this study was to measure how the trapping of motile zooplanktonic prey by passive benthic suspension feeders is affected by the “strength” (i.e., turbulent kinetic energy and peak water velocities in waves) of ambient flow across the predators. We addressed this question using sea anemones, *Anthopleura elegantissima* (Brandt), which are abundant on intertidal rocky shores (e.g., Dayton 1971), and which eat a variety of zooplankton, including those with strong escape responses such as copepods (Sebens 1981). In this study, we used calanoid copepods (*Acartia* spp.) as model prey organisms because they are an important component of the diets of many benthic suspension-feeding organisms (e.g., Lewis 1992; Clarke 1999; Ribes et al. 1999; Heidelberg et al. 2004), and because their swimming behavior in response to various conditions of flow is well-characterized (e.g., Fields and Yen 1997; Buskey et al. 2002). We examined how the turbulent and wavy flow observed in shallow coastal habitats affect (1) encounter, (2) capture, and (3) retention rates of zooplanktonic prey by a passive suspension-feeding sea anemone. Our goal was to compare the effects of turbulence and waves on predator–prey interactions between passive suspension feeders and actively escaping zooplanktonic prey with the effects of similar ambient flow on interactions between benthic fish and such prey.

Methods

All individuals of *A. elegantissima* were collected from Horseshoe Cove, in the Bodega Marine Reserve along the Sonoma Coast in California (38°18.94' N, 123°04.16' W), during October 2012 and May 2013. Sea anemones from one clone were gently peeled from the rock using a butter knife, and each individual was placed in a separate plastic bag filled with air. The bags were kept in a cooler at 10–15°C and transported to the University of California Berkeley (Berkeley, CA, USA). The anemones were maintained for 10 days in a 19-L aquarium where they were placed on a suspended plastic mesh substratum to prevent attachment to the aquarium walls. In a temperature-controlled cold room kept at 10–15°C, the aquarium had recirculating filtered seawater (FSW; 50 µm filter mesh) with a salinity

of 35%. The sea anemones were exposed to a photoregime of a 12 h dark and 12 h light provided by full-spectrum fluorescent bulbs (Hydroponic 105 W 5500K Perfect Daylight). Sea anemones were fed hatched *Artemia* spp. nauplii once a day, but were not fed 24 h before use in flume experiments. For flume experiments, sea anemones were transported to the University of North Carolina Wilmington (Wilmington, NC, USA) via overnight delivery. Individual sea anemones were placed in plastic bags that were filled with oxygen. The bags were packed into a Styrofoam cooler over a base of ice packs and a middle cushioning layer of newsprint. Upon arrival (<14 h transit time), sea anemones were removed from the plastic bags and housed under aquarium conditions identical to those previously described.

Zooplankton were collected from the Bridge Tender Marina in Wilmington, NC, USA (34°18.27' N, 77°48.80' W), using a plankton net (153 µm mesh). Samples were diluted in seawater, aerated, and used within 12 h of capture. Individual calanoid copepods, *Acartia* spp., were selected using Pasteur pipettes, and held in beakers with bottoms made of Nitex mesh (40 µm) that were submerged in filtered (10 µm) and UV-treated seawater. Before experiments, copepods were dyed red to make the organisms easy to visualize in videos. To dye the plankton, the mesh beaker was submerged in a solution of Neutral Red (10 g L⁻¹ FSW) for 20 min (see Elliott and Tang 2009 for protocol). Copepods were videotaped (Sony HDR cx580v, at 60 frames per second) while swimming in still sea water at 15°C in an aquarium (length and width = 5 cm, height = 10 cm) before and after being stained. The trajectories of the copepods were digitized with ImageJ (version 1.47n), and the behaviors were categorized and measured using Python (version 2.7; with two libraries: numpy 1.7.0 and matplotlib 1.2.0). No change in zooplankton's swimming behavior was observed to result from this treatment. Swimming speed, duration, and direction measured from copepod trajectories in still water were not significantly different between undyed copepods ($n=82$) and dyed copepods ($n=82$; t -test, $P>0.05$, $df=162$). For control experiments that used dead prey, copepods were heat-shocked after treatment with dye.

Flume experiments

Laboratory experiments using an oscillating flume were conducted at the University of North Carolina Wilmington. A motor-controlled piston drove FSW back and forth through a U-shaped flume (21.5 L

with a sealed working section that was 50 cm long, 10 cm wide, and 10 cm tall [see Robinson et al. (2007) and Clarke et al. (2009) for further description of the flume]. Identical arrays of columns at each end of the working section were used to generate eddies in the flow in both directions. The arrays were constructed with a row of larger columns ($n=4$, diameter = 1.2 cm, spacing = 1.5 cm) and a row of smaller columns ($n=8$, diameter = 0.4 cm, spacing = 1.0 cm). Horizontal water velocities parallel (u) and perpendicular (v) to the bidirectional flow, and vertical velocities (w) were measured using an acoustic Doppler velocimeter (Sontek Micro ADV; 25 Hz sampling rate) positioned at the midline of the flume to sample 2 cm above the sea anemones (0.09 cm³ sample volume, 5 cm below probe). Two wave settings ("weak" and "strong") were used in the flume to mimic the range of back-and-forth flow of water as surface waves pass over shallow benthic organisms. The maximum horizontal velocity in the + direction (u) of each wave was measured and the mean of those values for each wave setting was defined as the "peak velocity" for those waves. Turbulent kinetic energy (TKE) was calculated using a modified Reynolds decomposition to separate mean (e.g., \bar{u}) and variance (e.g., u') components of velocity in each direction [u , v , w ; described by Robinson et al. (2007)]. Mean velocity was estimated by a zero-phase displacement running average (*filtfilt* function in MATLAB, version 7.13.0.564, Natick, MA, USA; The MathWorks Inc. 2011). At each measurement of instantaneous velocity, mean velocity was subtracted and TKE was calculated as:

$$TKE = 0.5(\overline{u'u'} + \overline{v'v'} + \overline{w'w'})$$

The peak velocity, wave period, and TKE of each wave setting (Table 1) fell within the range of flow conditions measured using an ADV at a height of 2 cm above *A. elegantissima* at the field site described above (Robinson, unpublished data).

A digital, high-definition video camera (Sony HDR cx580v) was positioned outside the flume to capture a field of view 4 cm wide and 2 cm tall that was parallel to the direction of flow and centered in the working section of the flume (Fig. 1a). A thin volume of light ~1.5 cm thick at the height of the sea anemone illuminated the midline of the working section. Each sea anemone was placed in the flume so its midline was at the back of the light sheet and the half of its crown of tentacles closest to the camera was illuminated (Fig. 1a). The light sheet was produced by covering the lid and floor of the working section with opaque electrical tape, but leaving an

untaped transparent slit (2 mm wide) through which light could pass from two full-spectrum fluorescent light bulbs (Hydroponic 105 W 5500 K Perfect Daylight). These lights were positioned 18 cm above and below the level of the sea anemone. In each experiment, a single *A. elegantissima* was placed in the middle of the flume so the outer tentacles facing the camera were illuminated by the light. The thin volume of light ensured anemones in each experiment were positioned in the same location within the flume, and shone upon prey passing directly over the tentacles of interest. Three hundred *Acartia* spp. (copepod density of 14L^{-1}) were added to the flume and acclimated to flow conditions for 2 min. Videos of the sea anemone feeding were

captured at 60 Hz for 10 min. The duration of the experiments was limited to 12 min total (including both acclimation and the experiment), because copepod responsiveness and escape behavior does not decline due to habituation within this time frame (Hwang et al. 1994). Experiments were replicated six times at each flow setting with new organisms ($n=12$ sea anemones; $n=3600$ copepods). Control experiments using dead copepods as prey were replicated three times at each flow setting ($n=6$ sea anemones; $n=1800$ dead copepods).

Videographic analysis

For each experiment, video records were analyzed frame-by-frame to tally predator-prey interactions between copepods and the sea anemone. Copepods that passed through the field of view but were not in focus nor illuminated by the light sheet were not counted; only copepods passing within a capture zone were included (Fig. 1b). Capture volume (cm^3) was determined by the height of the sea anemone with extended tentacles, and calculated as half of the volume of a cylinder (assuming the sea anemone to be radially symmetrical) because tentacles facing

Table 1 Mean of the peak velocities (positive u), period, and TKE of waves under two conditions of flow in an oscillatory flume (\pm standard deviation).

Flow settings	Mean peak velocity (cm s^{-1})	Wave period (s)	TKE ($\text{cm}^2 \text{s}^{-2}$)
Weak waves	8.24 ± 0.38	8.8 ± 0.55	0.27
Strong waves	27.4 ± 2.3	9.0 ± 0.31	4.5

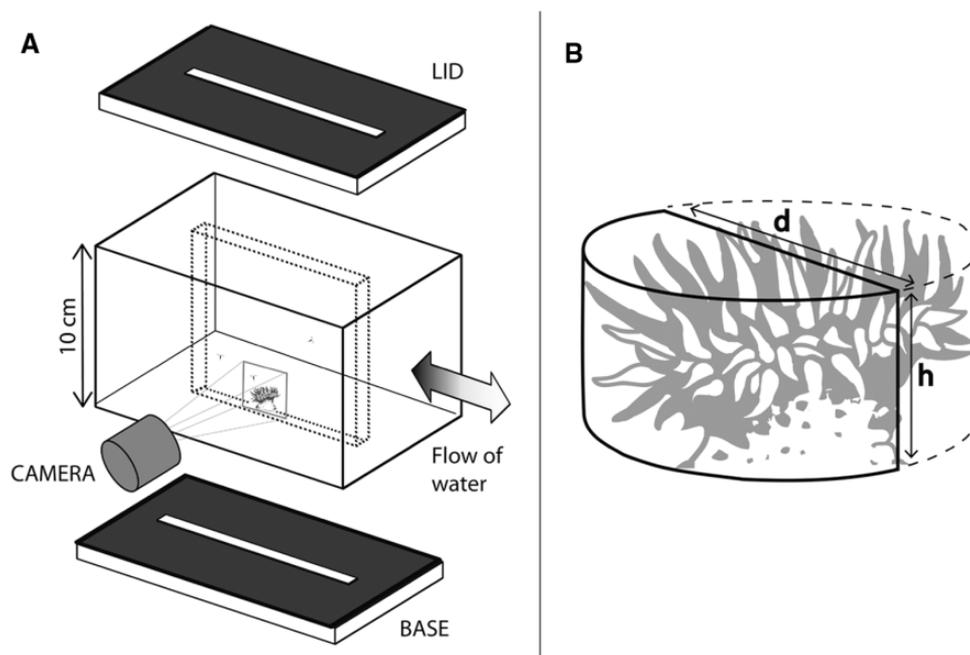


Fig. 1 (a) Diagram of the working section of an oscillating flume, not drawn to scale (the vertical axis has been expanded to show the arrangement of the lid, working section, camera position, and base). The dotted line represents the thin sheet of light in the midline of the flume, formed as light passed through transparent slits in the lid and base to illuminate the camera-side of the sea anemone. (b) Diagram of the capture zone of a sea anemone through which prey were passed as water moved back and forth through the flume. Only half of the total capture volume was visible in recordings made by a video camera positioned parallel to flow, so we counted copepods moving through the visible portion of the capture zone (solid black outline). The volume (V) of the visible capture zone was calculated ($V = \pi d^2 h / 8$) as half of the volume of a cylinder, where d is the diameter of the sea anemone tentacle crown and h is the height of the tallest tentacle relative to the bottom edge of the field of view.

away from the camera were not visible. Therefore, the capture volume observed in these experiments was calculated as:

$$V = \frac{\pi d^2 h}{8}$$

where d is the diameter of the sea anemone tentacle crown, and h is the height of the tallest tentacle relative to the bottom edge of the field of view.

Predator–prey interactions were quantified by calculating rates (events per unit time) and were normalized to the capture volume of each sea anemone. “Encounter rates” were calculated as the total number of copepods that passed through the capture zone per unit time per capture volume (prey encountered per minute per cubic centimeter). “Capture rates” were calculated as the number of copepods that came into direct contact with and stuck to the tentacle of a sea anemone and stuck to a tentacle per unit time per capture volume (prey captured per minute per cubic centimeter). Each of the 12 sea anemones used in these experiments captured prey. Captured copepods were observed to escape from, or to get swept off tentacles, so “retention rates” (prey retained per minute per cubic centimeter) were calculated using only those copepods that remained attached to the sea anemone at the end of each experiment and that had exceeded a threshold retention time of 4 min. This threshold was determined by measuring the duration of attachment to a tentacle for each copepod that was captured and then lost. The maximum retention time measured was 234 s (mean retention time = 48.9 s, standard deviation = 61, $n = 49$ captured copepods).

In some cases, copepods were captured on the far side (facing away from the camera) of the observed tentacles. If a copepod carried in the flow “disappeared” behind an illuminated tentacle and did not re-emerge, we assumed that it was captured. When this occurred, the tentacles were observed carefully in subsequent frames of the video and in every case the captured copepod became visible when the tentacles moved, the copepods fluttered into view during peak velocities, or the copepods were washed off the tentacles. In addition, aerial-view photographs of each sea anemone in still water were taken directly after the experiment and captured copepods were noted. No discrepancies occurred between the total number of captured copepods counted by the end of the experiment and copepods observed on the tentacles once the experiment was complete.

To quantify the vertical distribution of copepods in the water column, and thus the relative availability of prey in the sea anemone’s capture zone, a

“distribution ratio” was calculated for prey in strong and weak wave regimes. The number of copepods per time that passed through the area above a sea anemone (the region from the top of the capture zone, height h , up to a maximum height of $2h$ above the substratum) was counted in each video ($n = 4$ videos of weak waves and $n = 4$ videos of strong waves). The ratio described the rate at which swimming copepods passed above the copepod in the ambient flow, relative to the rate at which swimming copepods were carried through the capture zone. A distribution ratio of one indicates that the rate of prey available in the capture zone is equal to that in the water above the sea anemone (i.e., the prey are evenly distributed vertically). A ratio greater than one indicates that more prey were swimming in the water above the sea anemone than were swimming in the water that passed through the sea anemone’s capture zone.

The rates of predator–prey interactions were used to calculate efficiencies. “Capture efficiency” was defined as the proportion of encountered prey that was captured. “Trapping efficiency” was the proportion of encountered prey that the sea anemone retained. Trapping efficiency was calculated rather than feeding efficiency because the duration of experiments (12 min total) was short relative to the average ingestion times for sea anemones (6–50 min; Hiebner and Bingham 2012), thus most captured and retained prey were not ingested during the videos. The duration of the experiments was chosen to minimize the chances that prey would show a decrease in swimming and escape behaviors (Hwang et al. 1994). Using prey encountered as the denominator when calculating rates for both capture and trapping efficiencies enabled these efficiencies to be compared with published data on feeding efficiency for a zooplanktivorous fish (Clarke et al. 2009). In addition, these efficiencies could be directly related to ecological models that estimate rates of suspension feeding from encounter rates.

All statistical tests were conducted using MATLAB and R (version 3.0.0, The R Foundation for Statistical Computing 2013). Where data were not normally distributed (Shapiro Wilk test, $P < 0.05$), non-parametric tests were used.

Results

There was no difference between the dimensions of the capture zone of sea anemones, *A. elegantissima*, exposed to weak waves and strong waves in our experiments. For each sea anemone, measurements of the volume of the capture zone at the beginning,

midpoint, and end of each experiment showed that this volume did not change significantly with duration of exposure to waves during the experiments [analysis of variance (ANOVA), $P > 0.05$]. Furthermore, there was no significant difference between the volume of the capture zone for *A. elegantissima* exposed to weak waves (3.89 cm^3 , standard deviation = 0.39, $n = 6$ sea anemones, mean area for each) or to strong waves (3.71 cm^3 , standard deviation = 0.56, $n = 6$ sea anemones) (ANOVA, $P > 0.05$).

The strength of the waves affected the vertical distribution of the copepods in the water column and the rates of some of the steps in the predation process. Copepods swam higher in the water column in weak waves (distribution ratio = 2.7, standard deviation = 0.46, $n = 4$), but were more evenly distributed in the water column in strong waves (distribution ratio = 1.1, standard deviation = 0.51, $n = 4$) (one-tailed t -test, $P = 0.004$, $df = 6$). We analyzed a mean number of 177 encounters per sea anemone per 12-min experiment (standard deviation = 128, $n = 6$ sea anemones) in weak waves and a mean number of 197 (standard deviation = 68, $n = 6$ sea anemones) in strong waves. Encounter rates (Fig. 2) were lower in weak waves ($5.6 \text{ prey min}^{-1} \text{ cm}^{-3}$, standard deviation = 3.5, $n = 6$ sea anemones) than in stronger waves ($7.4 \text{ prey min}^{-1} \text{ cm}^{-3}$, standard deviation = 4.4, $n = 6$ sea anemones), although this difference was not statistically significant due to the high variability of encounter rates (one-tailed t -test, $P = 0.458$, $df = 8$). In contrast, in control experiments that used dead copepods as prey, encounter rates were significantly higher in strong waves ($9.3 \text{ prey min}^{-1} \text{ cm}^{-3}$, standard deviation = 4.8, $n = 3$ sea anemones) than in weak waves ($2.6 \text{ prey min}^{-1} \text{ cm}^{-3}$, standard deviation = 2.2, $n = 3$ sea anemones).

Capture rates were a small percentage of the encounter rates (3% of mean encounter rate for weak waves, and 4% in strong waves) and were not significantly different (one-tailed t -test, $P = 0.099$, $df = 8$) between weak waves ($0.16 \text{ prey min}^{-1} \text{ cm}^{-3}$, $SD = 0.11$, $n = 6$ sea anemones) and strong waves ($0.28 \text{ prey min}^{-1} \text{ cm}^{-3}$, standard deviation = 0.18, $n = 6$ sea anemones).

Some captured prey broke free from tentacles or were swept away by water currents, so retention rates were low (0.4% of mean encounter rate for both weak and strong waves). There was no significant difference between the retention rates in weak waves ($0.02 \text{ prey min}^{-1} \text{ cm}^{-3}$, standard deviation = 0.02, $n = 6$ sea anemones) and strong waves ($0.03 \text{ prey min}^{-1} \text{ cm}^{-3}$, standard deviation = 0.06,

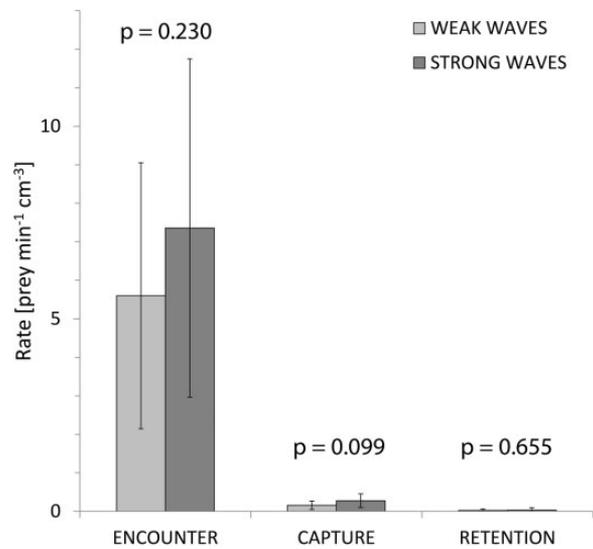


Fig. 2 The rate of encountering prey (number of prey passing through a capture zone per unit time per capture volume), capture (number of prey contacting and sticking to a tentacle per unit time per capture volume), and retention (number of prey held by a tentacle until the end of each experiment per unit time per capture volume) by a sea anemone ($n = 12$) feeding on copepods in the two wave settings described in Table 1. Error bars indicate one standard deviation. Differences between flow regimes were tested with a one-tailed Student's t -test for rates of encounter and capture and a Mann–Whitney U-test for retention rates ($W = 15$).

$n = 6$ sea anemones) (Mann–Whitney U-test, $P = 0.655$, $W = 15$).

“Mean capture efficiency” (number of prey captured per number encountered) and “mean trapping efficiency” (number of prey retained per number encountered) were not significantly different between weak waves and strong waves (Table 2).

Discussion

Effects of flow on feeding

We found that increasing the “strength” of ambient water flow (higher peak velocities in waves and greater TKE) enhanced rates of some steps in the feeding process and decreased others for a passive suspension-feeding predator (the sea anemone, *A. elegantissima*) eating zooplanktonic prey (copepods, *Acartia* spp.) that have strong escape responses.

Encounter rates normalized to capture volume (number of prey passing through the predator's capture zone per unit time per volume) depend on the speed of the water moving through the capture zone, and on the turbulence of the flow that stirs the water carrying new prey into prey-depleted water in the capture zone. Therefore, we expected that higher peak wave velocities and turbulence would enhance

Table 2 Mean capture efficiency and mean trapping efficiency of *A. elegantissima* ($n = 12$ sea anemones) feeding on copepods in each flow setting (\pm standard deviation).

Flow setting	Capture efficiency [prey captured/prey encountered (%)]	Trapping efficiency [prey retained/prey encountered (%)]
Weak waves	4.12 \pm 3.29	1.06 \pm 1.76
Strong waves	3.69 \pm 0.67	0.32 \pm 0.54
Significantly different?	No; $P = 0.761$ ($df = 5$; $\alpha = 0.05$)	No; $P = 0.532$ ($W = 14$)

Differences between flow regimes were tested using a two-tailed Student's *t*-test for capture efficiency (capture efficiency was predicted to be lower in weaker waves due to the prey's escape behavior, but was also predicted to be lower in stronger waves due to reduced contact-time to fire nematocysts into prey), and a Mann–Whitney U-test for trapping efficiency (trapping efficiency was predicted to increase in stronger waves because of higher encounter rates, but was also predicted to decrease in stronger waves due to higher hydrodynamic forces dislodging prey from tentacles).

encounter rates for sea anemones, and this effect was observed for dead copepods. We also found that encounter rates were greater in strong waves than in weak waves for living copepods, but there was high variation in encounter rates for these swimming prey; thus the difference was not statistically significant. If the tentacles of a predator are deformed by hydrodynamic forces, the volume of the capture zone can be reduced as the velocity of ambient water increases (Anthony 1997; Wolcott and Gaylord 2002; Shimeta 2009), thereby reducing the rate of encounters in strong waves. However, such deformation of the capture zone did not occur for *A. elegantissima* in the flow regimes used in our experiments, and all rates were normalized to capture volume. In weak waves more copepods swam above the capture zone of the sea anemone, rather than in it, whereas in strong waves the copepods were evenly distributed vertically within the water column near the sea anemone. We expected that this difference in vertical distribution would further enhance encounter rates in strong waves compared with weak waves. However, our results suggest the variability in the behavior of living copepods plays an important role in shaping encounter rates.

We expected that capture rates would be higher for sea anemones feeding in strong waves than in weak waves. We observed that fewer of the copepods passing through the capture zone executed escape maneuvers that avoided the predators' tentacles in strong waves than in weak waves. Similarly, Heidelberg et al. (1997) found that zooplankton could avoid or escape benthic suspension-feeding corals under conditions of slow flow. Likewise,

Robinson et al. (2007) showed that in weak waves (peak velocities of 7.8 cm s^{-1}), copepods executed escape maneuvers that enabled them to avoid being captured by a siphon that simulated suction feeding by a predatory fish, whereas in strong waves (peak velocities of 24.3 cm s^{-1}), the copepods were unable to detect hydrodynamic cues of the siphon and did not swim to avoid capture. Thus, Robinson et al. (2007) found higher capture rates for their siphon in strong waves than in weak ones. In our study of *A. elegantissima*, we also found that capture rates (number of prey caught on tentacles per unit time) were 75% greater in strong waves than in weak waves, but this difference was not significant due to the high variability of encounter rates and the low capture rates of *A. elegantissima* (Fig. 2).

Retention rates (prey retained on the tentacles per unit time) were the same for both conditions of flow (Fig. 2), and represented $<0.5\%$ of the prey encountered by a sea anemone. In turbulent and wavy flow, hydrodynamic forces can sweep captured prey off the tentacles of the predator (Shimeta and Koehl 1997). In slow flow with low turbulence, fewer prey are encountered and captured per time, but a greater proportion of them are retained by the predator than in faster, more turbulent flow. The net result is that the rate of retention of prey (and hence feeding rates) of a passive suspension-feeding benthic predator did not change as wave peak velocities and turbulence increased.

Nematocysts (stinging cells) on the tentacles of sea anemones adhere to prey that contact the tentacles. The adhesive strength of the nematocysts of *A. elegantissima* was found to be independent of habitat, availability of food, exposure to light, and species of symbiont (Hiebert and Bingham 2012). This suggests that the lower retention of prey by *A. elegantissima* in strong waves was not due to physiological differences in the ability of tentacles to hold onto prey, but rather was due to higher hydrodynamic forces dislodging prey in the more rapid flow.

Feeding by *A. elegantissima*

“Capture efficiency” (number of prey captured per number of prey encountered) and “trapping efficiency” (number of prey retained per number encountered) of *A. elegantissima* were not significantly different between wave regimes (Table 2). The low feeding rates we measured in the flume are similar to those measured in the field for *A. elegantissima* in shallow coastal habitats. Using measurements of mean dry weight for copepods ($10 \mu\text{g}$ per *Acartia* spp. adult, Durbin et al. 1983) and using the feeding

Table 3 Comparison of feeding efficiency for zooplanktivorous fish (*A. aspera* and *A. spinosa*) (Clarke et al. 2009) and passive suspension-feeding sea anemones (*A. elegantissima*) preying on calanoid copepods in different levels of turbulence and waves. Conditions of flow in the two studies are within comparable ranges for both mean peak velocities (centimeter per second) and turbulence (TKE in centimeter squared per second squared).

Benthic zooplanktivores			
Active fish		Passive sea anemone	
Feeding efficiency (prey eaten/prey approached)		Feeding efficiency (prey retained/prey encountered)	
<i>A. aspera</i>	<i>A. spinosa</i>	<i>A. elegantissima</i>	
Change in flow regime:		Change in flow regime:	
Weak waves		Weak waves	
Peak velocity = 11.6		Peak velocity = 8.24	
TKE = 0.077	93%	35%	TKE = 0.27
to	increase	increase	No change
Strong waves		Strong waves	
Peak velocity = 24.6		Peak velocity = 27.4	
TKE = 0.35		TKE = 4.5	

rates measured in our experiments (Fig. 2), we estimated that *A. elegantissima* ingested 0.08–0.14 mg of copepod prey per hour in our flume. Similarly, gut contents of *A. elegantissima* that were collected from intertidal habitats showed that these sea anemones ingested 0.08–0.25 mg of prey per hour (natural prey density and natural assemblage of prey organisms) during 6 h of immersion and feeding (Zamer 1986). Shimeta and Jumars (1991) suggested that suspension feeders could survive with a low feeding efficiency if the predation rate was high enough to meet their metabolic needs. Verde and McCloskey (1996) suggested that the energy from prey eaten by an *A. elegantissima* (3000 μg C per day) can supply more than twice the daily metabolic energy requirement of the sea anemone (1300 μg C per day). *Anthopleura elegantissima* also are supplied with energy from symbiotic algae within their tissues, although estimates of the autotrophic contribution of carbon to the sea anemone vary widely (e.g., Muscatine 1971; Zamer and Shick 1987) and stable isotopic signatures of the sea anemone suggest that *A. elegantissima* relies primarily on heterotrophy (Bergschneider and Muller-Parker 2008).

Comparison of different feeding modes of benthic zooplanktivores

Stronger waves increased feeding efficiency (number of prey ingested per number approached) for benthic zooplanktivorous fish but had no effect on feeding efficiency for a passive suspension-feeding sea anemone (number of prey retained per number encountered) (summarized in Table 3). In both cases, the escape

behavior of zooplanktonic prey in slow flow resulted in lower capture rates than in faster flow. As peak velocities and turbulence increased, fewer of the prey moving through the capture zone were stimulated to execute escape maneuvers in response to either type of predator. Although the fish reduced feeding effort (approaches per minute) and the time spent feeding during a wave cycle, their foraging efficiency improved in stronger waves. These active predators were able to modify their behavior in a way that minimized expenditure of energy for foraging in faster, more turbulent flow, yet their feeding rates increased because fewer of their prey tried to escape capture. In contrast, passive suspension feeders do not swim after their prey and thus probably expend less energy per prey captured than do darting fish. Passive *A. elegantissima* maintained the same trapping efficiency in both weak and strong waves because, although they capture more prey per unit time in stronger waves, they also lose more of the prey that they catch in the faster, more turbulent flow. During capture of prey, a fish merely swallows its food, whereas a passive suspension feeder has to transfer captured food from the capture-surface to the mouth before hydrodynamic forces can wash the prey away.

This study reveals the importance of both the behavior of the prey and the flow of ambient water in determining the predation rates of benthic predators. In slow water feeding rates on non-swimming or weakly swimming zooplanktonic prey might be higher than on prey with strong escape responses. Furthermore, studies of feeding by benthic predators on passive particles (e.g., beads) that have no

swimming behavior might overestimate feeding rates. Likewise, feeding studies of shallow-water benthic predators carried out in flumes with steady-state water flow that does not mimic the waves and turbulence to which such predators are exposed in nature could yield unrealistic feeding rates because: (1) actively swimming prey might be able to avoid predators more readily in steady flow with less turbulence and no back-and-forth flow of waves, and (2) the ability of predators to hold on to captured prey exposed to steady drag forces might be different from their retention abilities when prey are exposed to the pulsatile hydrodynamic forces in turbulent waves.

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