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The effect of turbulent waves and prey swimming behavior on suspension feeding  
by an intertidal sea anemone

by

Heather Eve Robinson

A dissertation submitted in partial satisfaction of the  
requirements for the degree of  
Doctor of Philosophy

in

Integrative Biology

in the

Graduate Division

of the

University of California, Berkeley

Committee:

Professor Mimi A.R. Koehl, Chair  
Professor Thomas M. Powell  
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Assistant Professor Evan A. Variano

Fall 2013

The effect of turbulent waves and prey swimming behavior on suspension feeding  
by an intertidal sea anemone

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Heather Eve Robinson

## ABSTRACT

The effect of turbulent waves and prey swimming behavior on suspension feeding  
by an intertidal sea anemone

by

Heather Eve Robinson

Doctor of Philosophy in Integrative Biology

University of California, Berkeley

Professor Mimi A.R. Koehl, Chair

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, without actively generating feeding currents. What are the characteristics of flow over benthic suspension feeders and how do these vary over time? How do the environmental fluctuations in flow affect the encounter, capture, and retention of motile zooplanktonic prey (copepods, *Acartia* spp.; nauplii, *Artemia* spp.) by passive benthic suspension feeders (sea anemones, *Anthopleura elegantissima*)? For suspension feeders that can dominate the rocky intertidal, how does the presence of neighbors impact feeding by downstream sea anemones?

In Chapter One, I quantify water flow over sea anemones found in a wave-exposed and a wave-protected site. I measured variations in flow habitat using a high-frequency instrument (an acoustic Doppler velocimeter) deployed at many temporal scales to assess the range of conditions in which benthic suspension feeders live. I compare the flow habitat over sea anemones between sites, between heights above the substratum, between the flood and ebb of a daily tidal cycle, the spring and neap of a monthly tidal phase, and between onshore and offshore measures of flow conditions. I show that temporal variation is not as significant a factor as spatial variation between two sea anemone clones, and that waves dominate the flow environment. I found that microhabitats over benthic organisms were disrupted or eroded by incoming waves, so that the velocity over organisms at the leading edge of a rocky intertidal shelf could be estimated using free-stream flow. And I discuss how the offshore measurements of wave height to estimate average onshore conditions are not suitable for predicting localized flow at scales relevant to benthic organisms.

In Chapter Two, I compare predator-prey interactions between a benthic sea anemone and an active, lunging fish that both suspension feed on zooplankton prey. In an oscillating flume designed to replicate the characteristics of flow measured

over sea anemones *in situ*, I video-recorded and quantified the rates of predator-prey encounter, capture, and retention in flow regimes with “weak” and “strong” waves. I found that increasing flow did not correspond to increases in encounter rate or capture for prey that swim, and retention rates were a small fraction of the number of prey that pass benthic predators. Faster flow interfered with the ability of the prey to detect predators so feeding efficiency of motile fish increased with higher waves. In contrast, strong waves washed prey off the tentacles of a passive suspension feeder, so feeding efficiency did not improve with waves and that the effect of flow on predation by benthic animals depended on the feeding mode of the predator.

In Chapter 3, I examine how zooplankton prey with different swimming behavior affects suspension feeding by solitary predators, and predators with upstream neighbors. The prey used in this study were nauplii (*Artemia* spp.) that swim with no escape response, dead copepods that have no behavior but are subject to drag, and living copepods (*Acartia* spp.) that can escape jump to avoid predators. Strong waves enhanced encounter rates for the passive, dead copepods but not for prey that actively swim. There was much variability in the behavior of the live prey. I found that higher encounter rates for passive prey and for solitary sea anemones did not result in higher capture or retention rates. Instead, the behavior of the prey and the presence of neighbors contradict expectation based upon estimates of feeding that use beads or unidirectional flow.

Dearest.  
With thanks.

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- Robinson, H.E.**, Finelli, C.M., and Buskey, E.J. (2007) The turbulent life of copepods: the effect of flow over a coral reef on their ability to detect and evade predators. *Marine Ecology Progress Series* 349: 171-181
- Voordouw, M.J., **Robinson, H.E.**, and Anholt, B.R. (2005) Paternal inheritance of the primary sex ratio in a copepod. *Journal of Evolutionary Biology* 18: 1304-1314
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*Project Peace East Bay*



# Chapter 1: Measuring wavy flow conditions at scales relevant to benthic suspension feeders

## 1.1 INTRODUCTION

Flow habitat is critical for rocky intertidal organisms that rely on water motion to deliver prey. Benthic suspension feeders are bottom-dwelling organisms that feed on small particles or zooplankton prey. Passive suspension feeders depend on ambient flow to bring food to an extended capture surface as they do not actively generate feeding currents. Suspension-feeding organisms live in a wide range of flow habitats from shallow coasts to abyssal depths, and from polar to tropical latitudes. Animals that use this feeding strategy are important components of benthic communities and play a key role in transporting material from the water column to the ocean floor (e.g. Gili & Coma 1998). How does the fluid environment in which suspension feeders live affect predator-prey interactions?

### *1.1.1 Variation in flow*

It is first necessary to understand how flow conditions fluctuate in habitats where benthic suspension feeders live. On rocky intertidal coasts, variation in flow occurs at a wide range of spatial and temporal scales. Spatial variation can depend on the local topography or bathymetry, fractal geometry of the coast, and the recruitment and distribution of organisms to the community (e.g. Menge & Olson 1990, Denny et al. 2004, O'Donnell & Denny 2008, Sousa 1984). Temporal variation can occur due to small-scale fluctuations in the flow (fractions of a second), waves (seconds), large eddies (minutes), the flood and ebb of a tide (hours), the spring and neap phase of a tide (days and weeks), season (months), and climate patterns (years) (Denny 1988). As a result, rocky intertidal organisms are exposed to rapidly-fluctuating velocity, reversals of flow as waves pass through shallow habitats, hydrodynamic forces imposed by breaking waves, turbulent eddies of different sizes that mix the water, and tides that constantly alter the water level (Denny 1988).

### *1.1.2 Measuring spatial and temporal scales relevant to a suspension feeder*

Quantifying flow conditions at the scale of the organism is important to accurately capture relevant variation (O'Donnell & Denny 2008). The passive suspension feeder used in this study is the aggregating sea anemone, *Anthopleura elegantissima* (Brandt). This sea anemone is abundant across a wide range of rocky intertidal habitats (e.g., Dayton 1971) and feeds on a variety of zooplankton prey (Sebens 1981). The *A. elegantissima* are between <1—10's of centimeters in body

width, while they eat prey that is less than <1 millimeter in length (Sebens 1981). These organisms inhabit environments that are also exposed to large scale variations of flow. Quantifying the range of conditions experienced by sea anemones requires high-frequency, high-resolution measurements spanning spatial and temporal scales from small to large.

Measuring small-scale variations of flow over intertidal habitats at high-frequencies and high-resolution is possible with several instruments and techniques (e.g., particle image velocimetry, laser Doppler anemometry, electromagnetic flow meters). The acoustic Doppler velocimeter (ADV) is suitable for collecting flow data in the intertidal because it can be positioned directly above an organism and takes high-frequency data at a remote sample volume below the probe. The ADV emits sound pulses which reflect off particles in the sample volume. The signal reflected back to receivers is used to calculate velocity in three directions. To capture the range of fluctuations that sea anemones experience in the rocky intertidal, an ADV can collect repeated measures of fine-scale variation in flow between two contrasting sites, over long time periods.

Other common instruments used to quantify flow in the intertidal are not suitable for this study of small-scale predator-prey interactions. For example, dynamometers measure maximum velocity experienced by intertidal organisms (Bell & Denny 1994). Although a fine-scale grid of these instruments can address spatial heterogeneity of peak velocities, temporal variation is reduced to a single peak velocity event averaged over the time the instrument is deployed. Oceanographic instruments that collect high-frequency data over long time scales, such as acoustic Doppler current profilers (ADCP), are unable to take measurements close to the substratum (lowest measurements are ~1m above the ocean floor). The height of the instrument would also exceed the depth of water during much of the tidal cycle. While exposed, it would be unable to record the incoming or outgoing tide.

The purpose of this study was to quantify the flow experienced by a suspension-feeding sea anemone in two habitats (wave-exposed and wave-protected), across a range of small-scale to large-scale temporal variation. We examined: (1) the variations in flow around sea anemones; (2) how the local flow habitats compared to measures of freestream flow, (3) how daily tides and monthly tidal phases affect local flow over sea anemones; and (4) to what extent offshore weather and wave conditions influenced the flow environment around benthic suspension-feeders.

## 1.2 METHODS

Flow was measured over colonies of the sea anemone *Anthopleura elegantissima* at two sites with contrasting exposure to waves (Fig. 1.1a). The 'wave-exposed' site was in Horseshoe Cove, in the Bodega Marine Reserve along the Sonoma Coast in

California, USA (38°18.94' N, 123°04.16' W); the 'wave-protected' site was in Campbell Cove, on the leeward side of Bodega Head (38°18.27' N, 123°03.37' W). At each site, the sea anemones used in this study occupied a relatively flat portion of the rocky shelf, with no obvious upstream obstacles. This species of aggregating sea anemone reproduces asexually by undergoing fission, forming a dense, homogenous bed of genetically identical sea anemones. An acoustic Doppler velocimeter (Sontek ADV) measured water velocity at 25 Hz sampling rate in shoreward ( $u$ ), alongshore ( $v$ ), and vertical ( $w$ ) directions. The ADV was suspended from a horizontal bar of an aluminum sawhorse frame that had supporting legs on either side positioned to avoid interfering with flow (Fig. 1.1b). The legs were secured from slipping by placing them on pegs that were glued into the rocky shelf using epoxy. This also ensured the ADV was positioned in the same place during repeated measurements over the course of a year. The body of the ADV was hose-clamped to a length of speed rail (40cm long) that was able to slide vertically along a fixed piece of matching rail on the aluminum frame. The height of the probe of the ADV was lowered or raised to measure a sample volume (0.09 cm<sup>3</sup> sample volume, 10 cm below probe) at five heights (2, 3, 5, 9, and 17cm) above a bed of sea anemones. The ADV was slid into position (e.g., height at 12 cm above the sea anemones to measure flow at 2 cm), then firmly secured by wing screws. This configuration meant that measurements could be repeated over the same anemone bed, in the same position, and at multiple heights.

The ADV was cabled to a computer that was housed in a watertight box on dry ground. Once the ADV was slid to a particular measurement height, data was recorded for three minutes. Flow was measured at each height for 4 minutes to ensure the complete profile (measurements at all heights) was collected in <30 minutes.

### 1.2.1 Data collection

Data was collected at a wave-exposed site in Horseshoe Bay, and a wave-protected site in Campbell Cove. Measurements were collected over the course of one year (August 2010 – August 2011). The sea anemone clone at each site was positioned on a flat rock shelf with no upstream obstacles to incoming waves. The sea anemones at the exposed site (mean = 1.87 cm, SD = 0.385, n = 58) were larger than the sea anemones at the protected site (mean = 1.35 cm, SD = 0.412, n = 76) (one-way ANOVA  $F(1,132) = 55.3, p < 0.001$ ). Flow data were collected during spring and neap tides, at flood and ebb cycles of the tide, and over the course of a year. Since flow measurements required assembly and manually adjusting the vertical position of the ADV while in the water, safety concerns limited data collection. Collections were not taken during the night, so low tides that occurred during the day or evening were used. This meant that there were not many days sampled during the winter months (Sept – Dec) when the low tides occur mostly at night on the

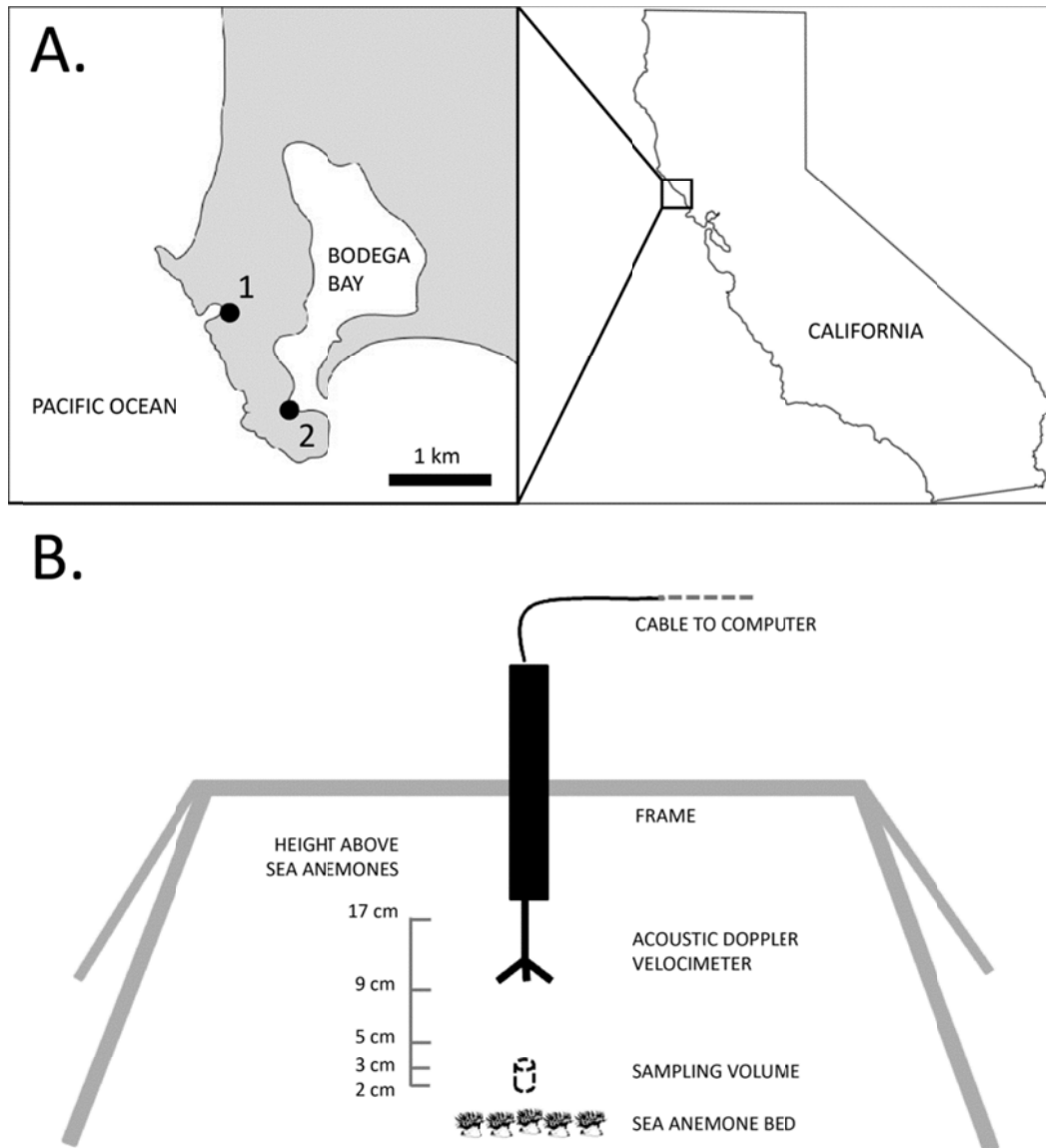


Figure 1.1: A) Map of two site locations in Bodega Bay, California. The ‘exposed’ site (1) was located in Horseshoe Cove along the western shore of Bodega Head, while the ‘protected’ site (2) was semi-sheltered on the eastern shore in Campbell Cove. B) Water velocity was measured over sea anemone populations (*Anthopleura elegantissima*) at both sites, by positioning an acoustic doppler velocimeter (ADV) on a sawhorse frame over the sea anemones. Measurements of flow in the ADV sample volume (located 10 cm below the probe) were made at 2, 3, 5, 9, and 17 cm above the sea anemones. A scale bar for the map insert (A) represents one kilometer; otherwise the illustration is not drawn to scale.

California coast. Measurements of flow at the exposed site were limited to the summer months when waves were less extreme. The frame could not reliably withstand the heavy wave action of storms (pers. obs.)

### 1.2.2 Flow analysis

Raw flow data was post-processed to exclude points when the correlation score (the ADV's internal measure of quality) was below 70%. The unreliable data was replaced with blanks. Since the water flow at both sites was wavy, a mean velocity including both shoreward (+ $u$ ) and seaward (- $u$ ) components of flow would be close to zero. Instead, the maximum horizontal velocity in the shoreward and seaward direction of each wave was measured, so the mean velocity used in this study was defined as the mean of peak velocities ( $n$  = number of waves). Where multiple measurements were taken at the same site and the same height, a mean of the mean peak velocities was used ( $n$  = number of flow records). Turbulence was quantified by calculating the turbulent kinetic energy (TKE). The mean (e.g.  $\bar{u}$ ) and variance (e.g.  $u'$ ) components of velocity in each direction ( $u$ ,  $v$ ,  $w$ ) were separated using a modified Reynolds decomposition (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, Massachusetts; The MathWorks Inc. 2011). For each measure of instantaneous velocity, the running average mean velocity was subtracted. The remaining variance was used to calculate  $TKE = 0.5(\overline{u'u'} + \overline{v'v'} + \overline{w'w'})$ . Turbulence spectra were generated (*pwelch* function in MATLAB) to show how much of the variation in flow velocity was due to fluctuations at different frequencies. For each spectrum, maximal energy was calculated, and peaks were identified (peak energy [ $\text{cm}^2\text{s}^{-2}$ ] and peak frequency [Hz]). Differences between flow characteristics were tested using an analysis of variance (ANOVA).

### 1.2.3 Freestream flow above sea anemones

The mean of shoreward peak velocities were calculated at each height above sea anemone beds. A vertical profile of peak velocity above sea anemones used flow records taken within an hour of each other. Quantification of the profile shape (e.g.,  $u^*$ ) was not possible because the flow measurements at each height were not collected simultaneously. Mean peak velocities between the sea anemone flow microhabitat (2 cm) and freestream flow were compared using paired t-tests. The coefficient of variation ( $C_v$ ) was calculated (standard deviation/mean) to compare relative variance between flow records.

### 1.2.4 Temporal variation

Mean peak velocities (at 2cm) were compared between spring and neap tides at each site, and during flood and ebb cycles of the tide. For flood and ebb tides, flow measurements taken on the same day were compared using a paired t-test. Since

spring and neap tides were a few weeks apart, flow records could not be similarly paired. Instead, the effect of tide on peak shoreward velocity measured at 2 cm above sea anemones at each site was tested using a two-way ANOVA (analysis of variance). This analysis was repeated for all flow characteristics measured: turbulence, maximum energy, and peak frequency.

#### *1.2.5 The effect of weather conditions*

The influence of local wind conditions on flow habitat over sea anemones was tested. Wind speed data was collected by the Bodega Marine Laboratory anemometer, located on top of the lab (approximately 350m from the exposed site, and 2km from the protected site). Data was downloaded from the Bodega Ocean Observing Node (BOON) website (provided by the University of California, Davis, Bodega Marine Laboratory). The wind speed was averaged per hour, for each day that flow measurements were collected. The time of day that flow measurements were taken determined the hourly average wind speed selected. Correlations between ambient wind speeds and mean shoreward peak velocity (and TKE) were tested using Pearson correlation coefficients.

#### *1.2.6 Offshore wave height*

The effect of incoming wave height on the flow microhabitat above sea anemones was tested using wave data from two nearby instruments. Remotely-sensed, high-frequency (HF) radar measurements of wave height were collected from a sensor (CODAR Ocean Sensor SeaSonde HF Radar System, 12 MHz) located at the Bodega Marine Lab (38°19' 2.3" N, 123°4' 20.9" W). Wave height measurements were also collected by a National Oceanic and Atmospheric Administration buoy (NOAA Station 46013) located in 116m of water, 22 km offshore (38°14' 31" N, 123°18' 2" W). Wave height data were averaged per hour for each day flow measurements were collected. Pearson correlation coefficients tested the relationship between the height of incoming waves and flow microhabitat. A linear regression was performed for significant results to determine the percentage of variation explained by the relationship.

All statistical analysis was done in Matlab and IBM SPSS Statistics for Windows (version 21.0.0.0; Armonk, New York; IBM Corp. 2012).

### 1.3 RESULTS

#### *1.3.1 Flow microhabitat*

At both sites, shoreward velocity was greater than seaward velocity (paired t-test  $df = 10$ ,  $p = 0.001$ ). Mean peak shoreward velocities (Fig. 1.2) were higher at the exposed site than at the protected site (Table 1.1). Average wave period was not

significantly different between the exposed site and at the protected (one-way ANOVA  $F(1,20) = 0.610$ ,  $p = 0.444$ ).

Fluctuations in the flow of water were due to waves and turbulence (Fig. 1.3). At the exposed site, much of the energy was concentrated in waves and turbulence followed an approximate  $-5/3$  slope. The protected site had lower energy with multiple peaks that were widely distributed. Between the two flow habitats, the maximum wave energy at the exposed site was an order of magnitude greater than wave energy at the protected site (Table 1). Peak frequencies were lower at the exposed site than at the protected site. At small scales, turbulent kinetic energy was significantly higher at the exposed site than at the protected site.

Table 1.1: Summary of flow measurements at two sites (exposed and protected) for shoreward velocity ( $\text{cm s}^{-1}$ ), seaward velocity ( $\text{cm s}^{-1}$ ), mean peak shoreward velocity ( $\text{cm s}^{-1}$ ), turbulence ( $\text{cm}^2 \text{s}^{-2}$ ), maximum energy ( $\text{cm}^2 \text{s}^{-2}$ ), and peak frequency (Hz). Mean  $\pm$  one standard deviation. Statistical results are in Table 1.2.

Flow Measurements	Sig.?	EXPOSED	PROTECTED
Shoreward velocity [ $\text{cm s}^{-1}$ ]	Yes	$28.2 \pm 9.88$	$5.28 \pm 2.51$
Seaward velocity [ $\text{cm s}^{-1}$ ]	Yes	$24.1 \pm 7.96$	$3.78 \pm 1.84$
Mean peak shoreward velocity [ $\text{cm s}^{-1}$ ]	Yes	$52.3 \pm 22.5$	$7.72 \pm 2.68$
Wave period [s]	No	$6.20 \pm 1.04$	$7.89 \pm 7.13$
Max. wave energy [ $\text{cm}^2 \text{s}^{-1}$ ]	Yes	$3.39 \times 10^4 \pm 1.75 \times 10^4$	$2.29 \times 10^3 \pm 2.38 \times 10^3$
Peak frequency [Hz]	Yes	$0.266 \pm 0.098$	$1.51 \pm 0.100$
TKE [ $\text{cm}^2 \text{s}^{-2}$ ]	Yes	$50.3 \pm 16.6$	$3.72 \pm 2.00$

### 1.3.2 Freestream flow above sea anemones

In this study, flow microhabitats above sea anemones were not significantly different than freestream flow (Fig. 1.4). Freestream velocity was estimated using measurements taken at 9 cm above the sea anemones. Velocity measurements collected higher above the substratum (17 cm), and therefore more likely to represent freestream velocity, were limited. The water depth required to submerge the ADV probe at this height reduced the amount of time available for taking measurements so there were fewer samples with which to compare sea anemone microhabitat. Also, as waves passed by the trough of the wave exposed the ADV probe to air which created intermittent gaps in the data. Peak velocities at 17cm were not significantly different from measurements at 9 cm ( $df = 13$ ,  $p > 0.05$ ,  $n = 14$  pairs), so flow measured at 9cm was used as a metric of freestream velocity.

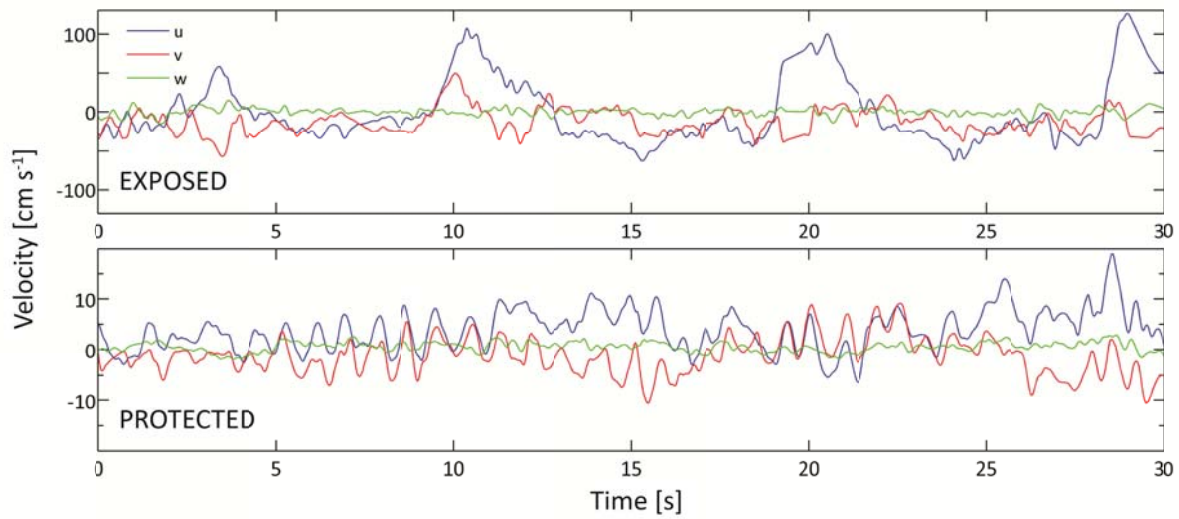


Figure 1.2: Examples of water velocity in  $\text{cm s}^{-1}$  measured by an acoustic doppler velocimeter (ADV) at 2 cm above sea anemones, during the ebb of a spring tide, at two sites (exposed and protected). The three components of velocity are represented by  $u$  (shoreward/seaward direction; in blue),  $v$  (alongshore direction; in red), and  $w$  (vertical direction; in green). Note the different magnitude in y-axes between the exposed and protected sites.

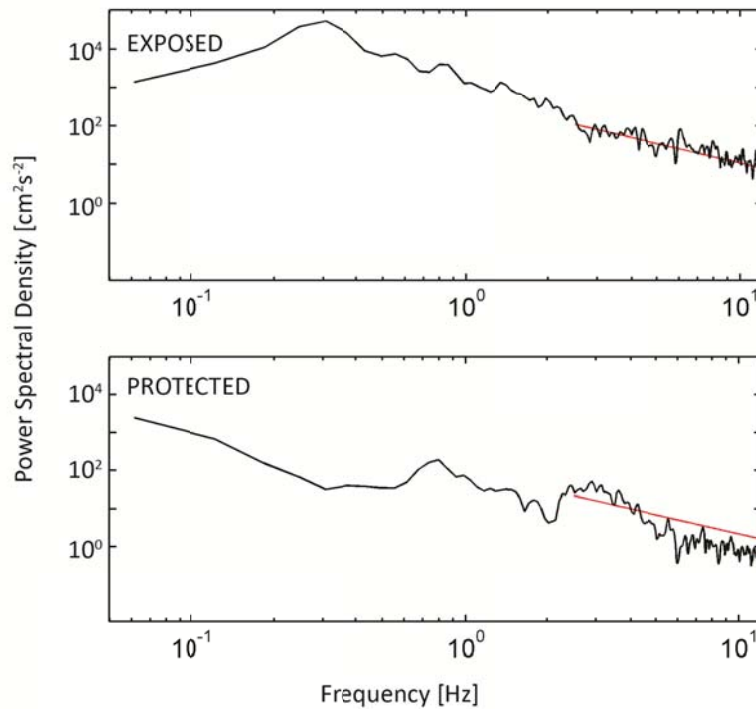


Figure 1.3: Power spectral density ( $\text{cm}^2\text{s}^{-2}$ ) of sample water velocity records (see Fig. 2) measured at 2 cm above sea anemones, during the ebb of a spring tide, at two sites. A  $-5/3$  slope is represented in red.



The mean peak shoreward velocity and TKE measured 2 cm above sea anemones was lower than flow measured at 9cm, although this difference was not statistically significant due to high variation. At the exposed site, mean peak velocity close to the sea anemones (mean = 51.4 cm s<sup>-1</sup>, SD = 28.6, n = 4) and 9 cm above sea anemones (mean = 77.7 cm s<sup>-1</sup>, SD = 19.0, n = 4) was not significantly different (paired t-test, df = 3,  $p = 0.069$ , n = 4 pairs). In three out of four pairs, the coefficient of variation was higher in the freestream flow than in the sea anemone's microhabitat. Similarly, at the protected site the mean peak velocity at 2 cm (mean = 7.16 cm s<sup>-1</sup>, SD = 1.40, n = 10) was lower than at 9 cm above sea anemones (mean = 9.94 cm s<sup>-1</sup>, SD = 5.09, n = 7), but this was not significantly different (paired t-test, df = 6,  $p = 0.673$ , n = 7 pairs). The coefficient of variation was higher in freestream flow compared to variation directly above the sea anemones in six of seven pairs.

There was no significant difference between turbulence in the sea anemone's flow microhabitat (mean = 41.7 cm<sup>2</sup>s<sup>-2</sup>, SD = 25.6, n = 4) and freestream flow (mean = 54.7 cm<sup>2</sup>s<sup>-2</sup>, SD = 11.4, n = 4) at the exposed site (paired t-test, df = 3,  $p = 0.381$ ), nor at the protected site (mean at 2cm = 3.82 cm<sup>2</sup>s<sup>-2</sup>, SD = 1.87; mean at 9cm = 3.24 cm<sup>2</sup>s<sup>-2</sup>, SD = 2.05; n = 10) (paired t-test, df = 6,  $p = 0.223$ ). At each of the heights at which flow was measured above sea anemones, mean peak velocity was greater at the exposed site than at the protected site (e.g., Fig. 1.4).

### 1.3.3 Temporal variation

In this study, variations in the flow conditions over sea anemones were not significantly affected by daily (flood and ebb) or monthly (spring and neap) tidal cycles during 2010-2011 (Fig. 1.5). At the exposed site, water flow during the daily flood of the tide was not significantly different from conditions during the ebb of the tide on the same day (paired t-tests df=1, mean peak velocity  $p=0.506$ , turbulence  $p=0.386$ , n = 2 days). Mean peak velocity and turbulence during flood and ebb tides at the protected site were also not significantly different (paired t-test df = 2, mean peak velocity  $p = 0.106$ , turbulence  $p = 0.219$ , n = 3 days). Tidal phase did not have a significant effect on mean peak shoreward velocity, turbulence, maximum energy, or peak frequency at each site (Table 1.2).

### 1.3.4 The effect of weather

Ambient wind speeds did not predict flow conditions in sea anemone habitats (Fig. 1.6). On the days when flow was measured at the exposed site, average wind speeds were 3.05 m s<sup>-1</sup> (SD = 1.60, n = 9 days). Wind speed did not correlate significantly with mean peak velocity ( $r = 0.152$ ,  $p = 0.656$ , n = 11), nor with turbulence ( $r = 0.156$ ,  $p = 0.648$ , n = 11). Limitations to site access throughout the year narrowed the days of data collection to summer months, when wind speeds were relatively low. However, flow conditions were measured at the protected site over a wide range of windy days, yet there was no correlation between ambient wind speed and

Table 1.2: Summary of two-way Analyses of Variance (ANOVAs) to test the effect of tide (spring, neap, flood, and ebb) and site (exposed and protected) on mean peak shoreward velocity ( $\text{cm s}^{-1}$ ), turbulence ( $\text{cm}^2 \text{s}^{-2}$ ), maximum energy ( $\text{cm}^2 \text{s}^{-2}$ ), and peak frequency (Hz).

ANOVA	Peak Velocity [ $\text{cm s}^{-1}$ ]			Turbulence [ $\text{cm}^2 \text{s}^{-2}$ ]		Max Energy [ $\text{cm}^2 \text{s}^{-2}$ ]		Peak Frequency [Hz]	
	df	<i>F</i>	<i>p</i>	<i>F</i>	<i>p</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>p</i>
Site	1	24.5	<0.001*	70.8	<0.001*	20.7	<0.001*	75.9	<0.001*
Tide	3	1.16	0.359	1.73	0.204	0.197	0.897	1.51	0.255
Site*Tide	2	1.03	0.381	3.31	0.064	0.224	0.802	2.89	0.089
Error	15								
<b>R<sup>2</sup> =</b>			0.773		0.887		0.659		0.885

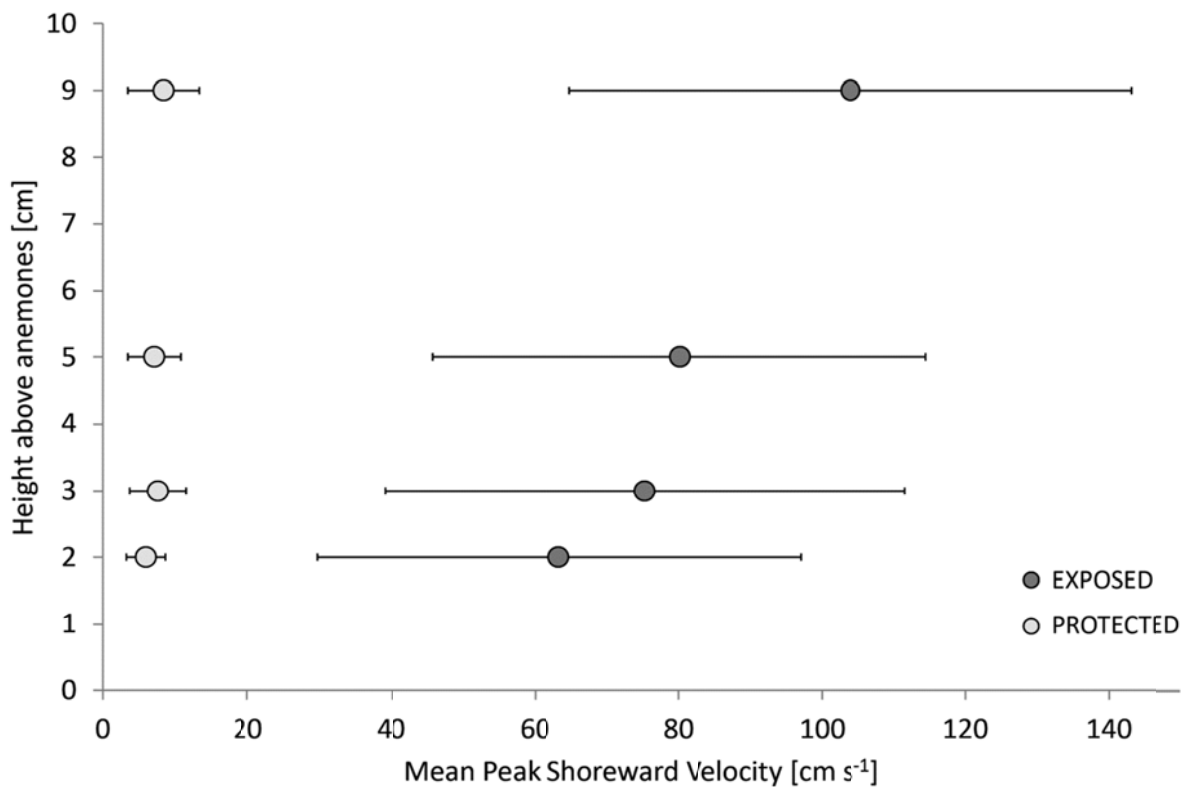


Figure 1.4: Mean peak shoreward velocity ( $\text{cm s}^{-1}$ ) measured at five heights above sea anemones, during the ebb of a spring tide, at two sites. Error bars represent one standard deviation.

flow measurements of mean peak velocity ( $r = 0.127$ ,  $p = 0.709$ ,  $n = 11$ ) or turbulence ( $r = 0.364$ ,  $p = 0.271$ ,  $n = 11$ ). Average wind speeds were higher for days when flow was measured at the protected site (mean =  $5.27 \text{ m s}^{-1}$ , SD =  $3.85$ ,  $n = 10$  days) than sampling days at the exposed site (t-test  $df = 10$ ,  $p = 0.001$ ).

### 1.3.5 Offshore wave height

Oceanic conditions did not consistently correlate to the flow habitat over sea anemones (Fig. 1.7, Table 1.2). Average wave height was  $1.52 \text{ m}$  (HF Radar, SD =  $2.88$ ,  $n = 9$  days) on the days when flow was measured at the exposed site, and did not predict mean peak velocity or turbulence of the microhabitat (Table 1.2,  $p > 0.05$ ). On days when flow was measured at the protected site, mean wave height was significantly higher (mean =  $2.37 \text{ m}$ , SD =  $0.593$ ,  $n = 10$  days) (t-test  $df = 10$ ,  $p < 0.001$ ) and was not significantly correlated with variation in turbulence (Table 2,  $p > 0.05$ ). Wave height measured by the high-frequency radar explained 50% of the mean peak velocity variation ( $p = 0.014$ ), however wave height measured by an offshore buoy did not (Table 1.3).

Table 1.3: Summary of Pearson correlation coefficient ( $r$ ) results that tested the effect of wave height (measured by high-frequency radar and an offshore buoy, both in meters) on microhabitat flow characteristics (mean peak shoreward velocity in  $\text{cm s}^{-1}$ , and turbulence as TKE in  $\text{cm}^2\text{s}^{-2}$ ). Significant values ( $\alpha = 0.05$ ) are indicated with an asterisk; a linear regression equation and associated  $R^2$  are reported below.

MICROHABITAT	WAVES	n	EXPOSED		PROTECTED	
			$r$	$p$	$r$	$p$
Peak Velocity	HF radar	11	0.337	0.311	0.711	0.014*
	NOAA buoy	5	0.076	0.825	0.850	0.068
Turbulence	HF radar	11	0.136	0.690	0.197	0.563
	NOAA buoy	11	0.184	0.587	0.760	0.136

\* significant correlation: peak velocity =  $3.22 \times \text{waves}(\text{HF Radar}) + 0.088$   
 $R^2 = 0.506$

## 1.4 DISCUSSION

The purpose of this study was to quantify the flow experienced by a suspension-feeding sea anemone in two contrasting habitats, across a range of small-scale to large-scale temporal variation.

### 1.4.1 Flow microhabitat

Sea anemones living in intertidal habitats experience fluctuations in velocity and turbulence on the order of seconds. The mean peak shoreward velocities at the exposed site were within the range of values previously observed over sea anemones

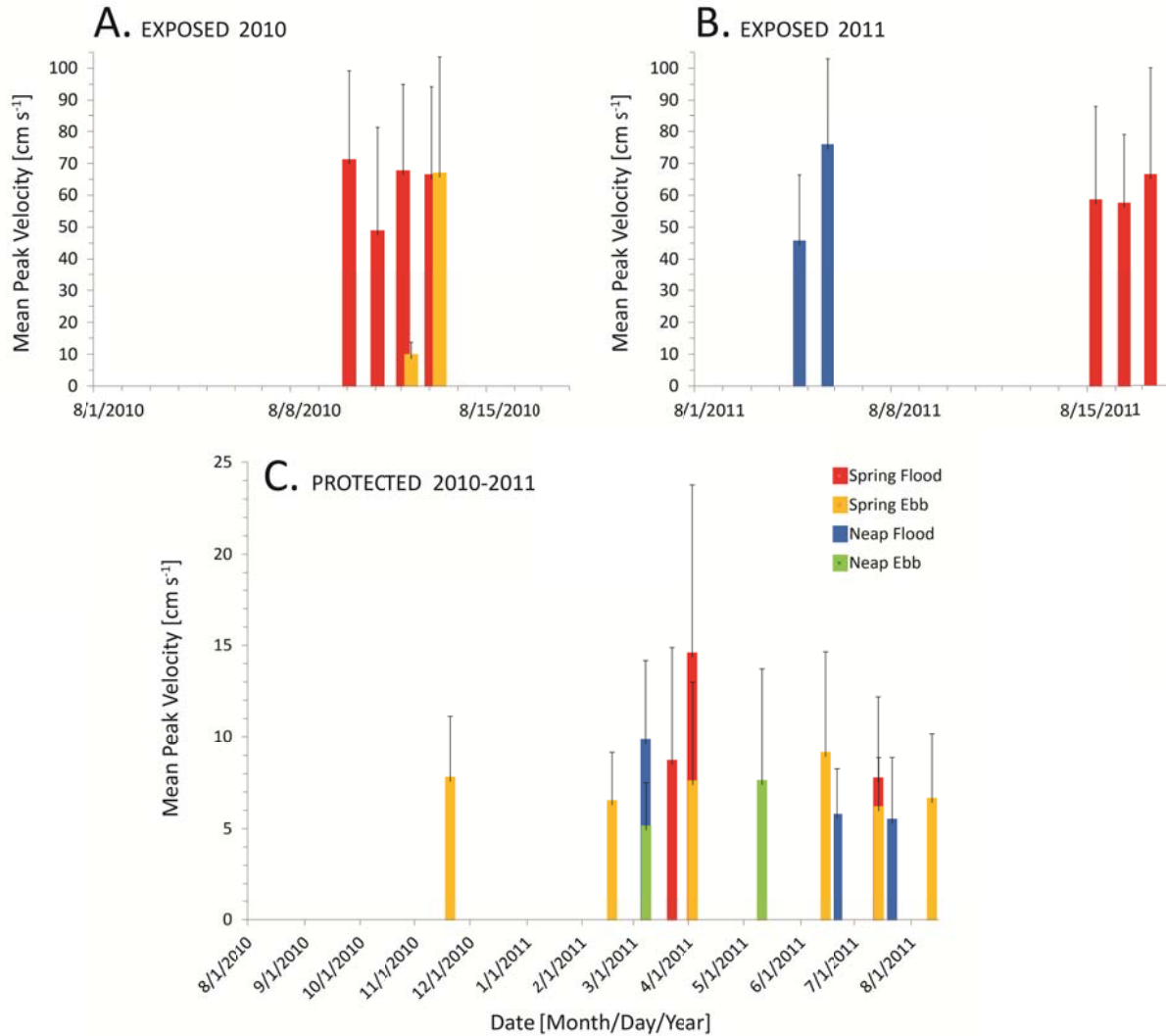


Figure 1.5: Temporal variation in mean peak shoreward velocity ( $\text{cm s}^{-1}$ ) measured at 2 cm above sea anemones at two sites from August 2010—August 2011. The tidal phase (spring and neap) and tidal cycle (flood and ebb) are shown in colors. Measurements were taken at the exposed site during A) August 2010 and B) August 2011 ( $n = 9$  days). C) The protected site was sampled throughout the year ( $n = 11$  days). A two-way analysis of variance tested the effect of tide and site on variation in the flow microhabitat over sea anemones (Table 1). Error bars represent one standard deviation.

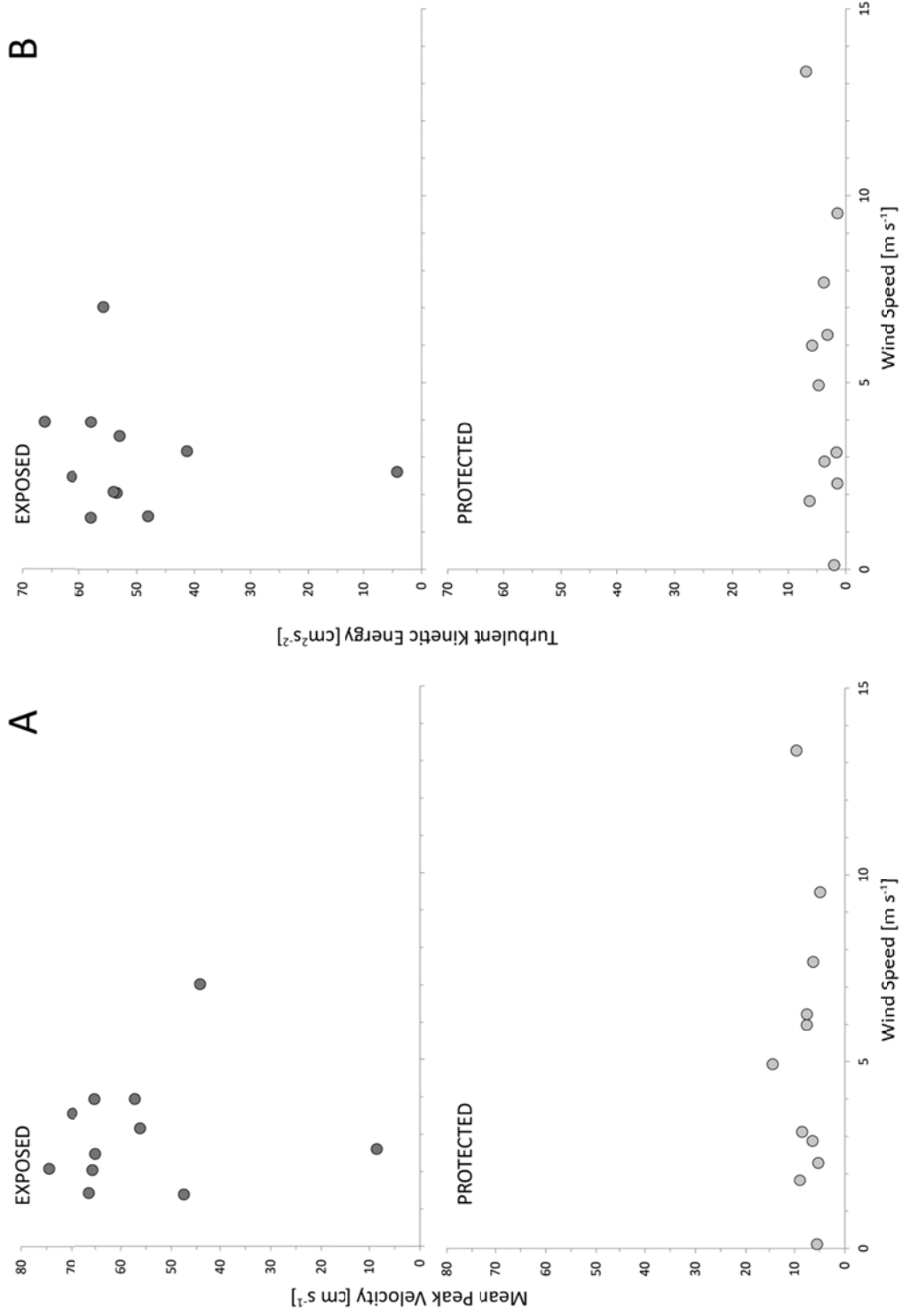


Figure 1.6: Correlation between water flow measured at 2 cm above sea anemones at two sites and average wind speed ( $m s^{-1}$ ) measured by an anemometer at the Bodega Marine Laboratory. The flow microhabitats over sea anemones at exposed and protected sites are quantified by A) mean shoreward peak velocity ( $cm s^{-1}$ ) and B) turbulent kinetic energy ( $cm^2 s^{-2}$ ). Pearson correlation coefficients tested the effect of average wind speed on the flow over sea anemones (Table 2).

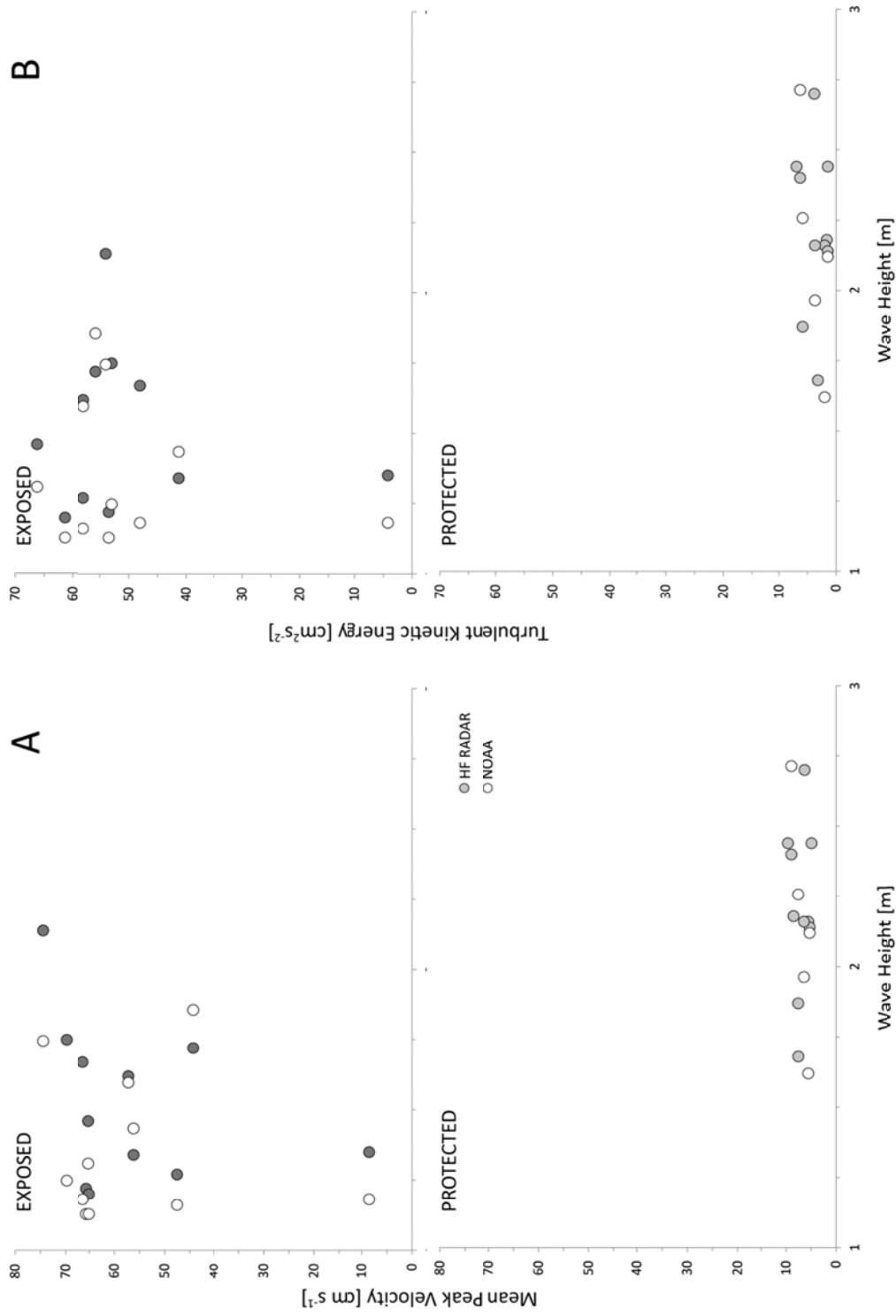


Figure 1.7: Correlation between water flow measured at 2 cm above sea anemones at two sites and wave height (m) measured by a high-frequency radar sensor (CODAR Ocean Sensors SeaSonde, 12MHz; open circles) and an offshore buoy (NOAA Station 46013; shaded circles). The flow microhabitats over sea anemones at exposed and protected sites are quantified by A) mean shoreward peak velocity (cm s<sup>-1</sup>) and B) turbulent kinetic energy (cm<sup>2</sup>s<sup>-2</sup>). Pearson correlation coefficients tested the effect of wave height on the flow over sea anemones (Table 2).

(30-40 cm s<sup>-1</sup> at 2 cm above *A. xanthogrammica*, Koehl 1977; 5-100 cm s<sup>-1</sup> at 10 cm above *Metridium senile*) and also in slower flow regimes at the protected site (5-10 cm s<sup>-1</sup> at 2 cm above *A. elegantissima*, Koehl 1977). Turbulence at the exposed site was higher than measures of TKE over coral reefs (maximum 25 cm<sup>2</sup>s<sup>-2</sup> at 10 cm above a reef, Reidenbach et al 2006)

In low flow habitats (e.g., the protected site in this study), sea anemones experience mean peak velocities under 10 cm s<sup>-1</sup>, with waves at high frequencies, and turbulent kinetic energy under 7 cm<sup>2</sup>s<sup>-2</sup>. In habitats directly exposed to offshore waves, the mean peak velocities, turbulence, and wave energy experienced by sea anemones increase by an order of magnitude. The exposed site in this study does not provide the upper limit for flow over rocky intertidal shores since measurements were only collected during the summer months when wave energy is seasonally low. However, this study demonstrates that sea anemones experience wide fluctuations in flow habitat at small time scales.

#### 1.4.2 Freestream flow above sea anemones

In this study, the fluid environment over sea anemones was similar to freestream flow. The no-slip rule tells us that velocity at the surface of the sea anemone is zero. Since the flow measured 2 cm above the sea anemone matched freestream flow, this suggests a steep velocity gradient in the 2 cm directly above sea anemones on flat rock surfaces. In contrast, Koehl (1977) found that the water velocities encountered by *A. elegantissima* on the bottoms of surge channels were much lower than freestream flow throughout the channel. At the sites used in this study, the sea anemone clone was on a flat rocky shelf. At this leading edge, an incoming wave would not develop a thick boundary layer, and so the anemone microhabitat was similar to freestream flow. The topography at the site plays an important role in the hydrodynamic forces experienced by sea anemones. Measurements of freestream flow in this study could have informed flow conditions at the organism-scale, but this does not remain true for all sites in the rocky intertidal.

#### 1.4.3 Temporal variation

The temporal variation due to the flood and ebb of a tidal cycle, or the spring and neap of a tidal phase, did not affect the flow habitat over sea anemones. Instead, spatial variation between the exposed and protected sites dominated. Although relative terms that describe sites like ‘exposed’ and ‘protected’ are ambiguous (i.e., ‘exposed’ in this study could have flow characteristics similar to a ‘protected’ site in another study), the contrast between the two flow habitats provided an important comparison. The differences between the two sites in this study demonstrated a range of flow environment in which sea anemones live.

#### 1.4.4 Offshore wave height

The use of offshore measurements of waves is not a reliable predictor of the flow over benthic organisms (explained 35-56% of onshore variation, Bell & Denny 1994). Similarly, in this study the offshore wave height measured by a high-frequency radar explained 50% of the variation in water velocity over sea anemones. Again, spatial variation and local topography plays a large role in the flow experienced by benthic organisms in the rocky intertidal so that buoy measurements ought to be used as predictors only once tested.

At the exposed site, measurements over sea anemones were only collected during August. However, measuring throughout the year might not have been necessary to estimate the peak velocities experienced by sea anemones at this site. The wave height was <2.5 m during days when peak velocities were measured at the exposed site. The peak velocities over benthic organisms did not demonstrate a positive trend with wave height, which would have suggested that larger wave might have led to higher flows over sea anemones. Helmuth and Denny (2003) observed no increase in force measured onshore with significant wave height above 2-2.5m, suggesting a microsite-specific maximum force, presumably set by wave breaking.

Knowing the mechanisms that drive flow over a study organism or at a particular site is necessary to determine the spatial and temporal scales relevant to study. Measuring flow can be achieved with a wide range of instruments and variables to describe the fluid environment. The metrics used in a particular study ought to be tailored to answer the research question and be measured at the appropriate frequency and duration. Measures of freestream flow or using offshore wave height data may or may not predict local flow over benthic organisms, depending upon the topography of the shore. Using these measurements as indicators of the flow experienced by benthic organisms must be tested first.

For suspension feeders that are intrinsically linked to the fluid environment, it is necessary to understand how flow conditions fluctuate in habitats where these organisms live. The effect of flow on small-scale interactions between a benthic predator and zooplankton prey are more easily observed in a laboratory flume, where high-speed cameras can capture predator-prey events and prey type and concentration can be controlled. Knowing the flow environment in which these animals live can be used to recreate realistic flow conditions in a flume by matching the characteristics of flow observed over the organisms.



# Chapter 2: Interactions between benthic predators and zooplanktonic prey are affected by turbulent waves\*

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## 2.1 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 & 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 & Dillon 1969; Hunter 1989; Sebens & Johnson 1991; Helmuth & Sebens 1993).

### 2.1.1 Conditions of flow

In shallow coastal habitats rapidly-changing currents, waves, and turbulence (Denny 1988) can impact feeding by benthic organisms. Currents reach maximum

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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 & Koehl 1977; Shimeta & 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).

### *2.1.2 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 & 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 & Jumars 1991; Shimeta & 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 & Koehl 1977) and demonstrated in experiments conducted in unidirectional flow (e.g. Patterson 1984; Okamura 1984, 1985; McFadden 1986; Shimeta & 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 depend 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.

### 2.1.3 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; Finelli et al. 2009; Clarke et al. 2009). Tube blennies (*Acanthemblemaria aspera* and *A. 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 towards 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 foraging effort (approaches  $\text{min}^{-1}$ ). 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 & Kristmanson 1997). By quantifying feeding rates, only the retention or ingestion stage of the feeding process is observed, while 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 & 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 & 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.

## 2.2 METHODS

All individuals of *Anthopleura 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, California, USA). The anemones were maintained for ten days in a 19-liter 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 hours dark and 12 hours 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 hours before use in flume experiments. For flume experiments, sea anemones were transported to the University of North Carolina Wilmington (Wilmington, North Carolina, 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 (less than 14 hours 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, North Carolina (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 hours 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<sup>-1</sup> FSW) for 20 minutes (see Elliott & 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 = 5cm, 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 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 the dye treatment.

### 2.2.1 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 = 0.4cm, 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 cm<sup>3</sup> 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, Massachusetts; 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 turbulent kinetic energy (TKE) of each wave setting (Table 2.1) 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 (see Chapter 1).

Table 2.1: Mean of the peak velocities (positive  $u$ ), period, and turbulent kinetic energy of waves under two conditions of flow in an oscillatory flume ( $\pm$  standard deviation).

Flow settings	Mean peak velocity [cm s <sup>-1</sup> ]	Wave period [s]	TKE [cm <sup>2</sup> s <sup>-2</sup> ]
Weak waves	8.24 $\pm$ 0.38	8.8 $\pm$ 0.55	0.27
Strong waves	27.4 $\pm$ 2.3	9.0 $\pm$ 0.31	4.5

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. 2.1a). A thin volume of light approximately 1.5cm 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. 2.1a). 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 (2mm wide) through which light could

pass from two full-spectrum fluorescent light bulbs (Hydroponic 105 W 5500K 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  $14 \text{ L}^{-1}$ ) were added to the flume and acclimated to flow conditions for two minutes.

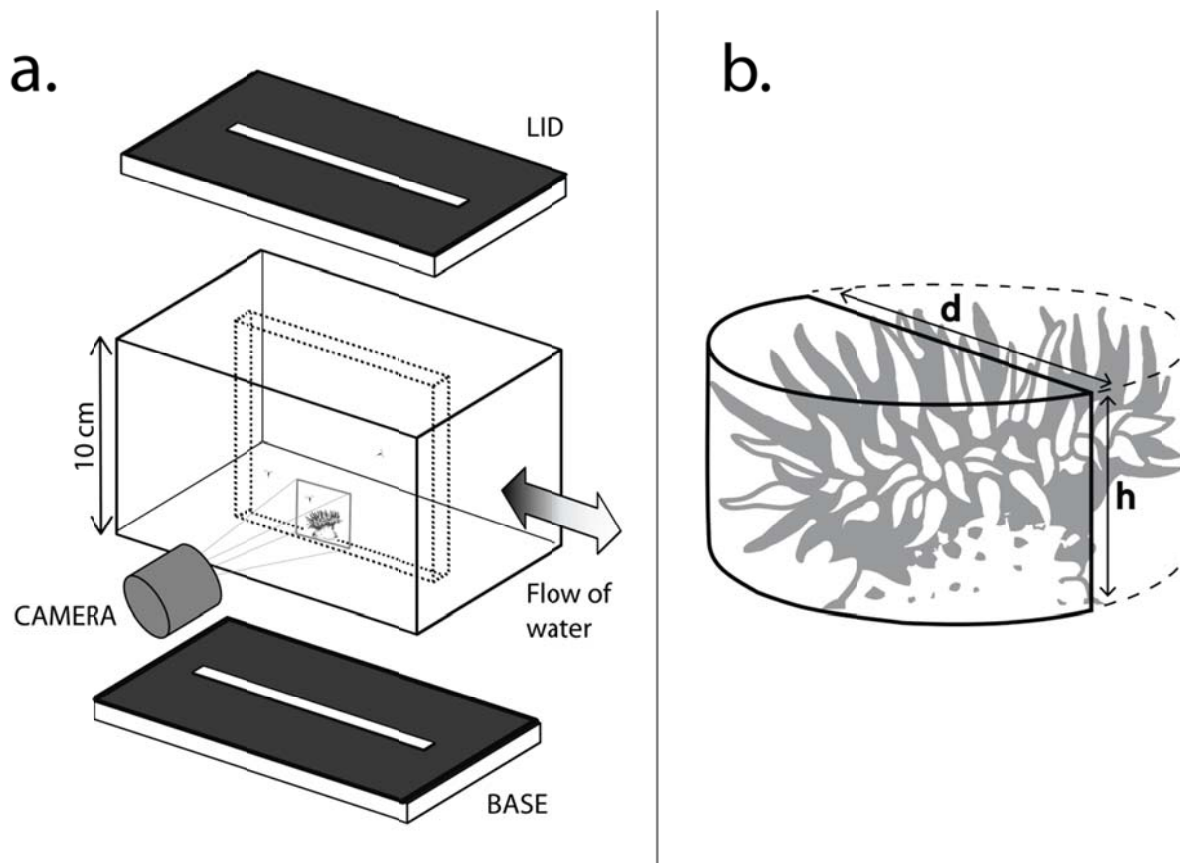


Figure 2.1: (a) Diagram of the working section of an oscillating flume, not drawn to scale (the vertical axis has been expanded to show the arrangement of the lid, working section, camera position, and base). The dotted line represents the thin sheet of light in the midline of the flume, formed as light 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.

Videos of the sea anemone feeding were captured at 60 Hz for 10 minutes. The duration of the experiments was limited to 12 minutes total (including both acclimation and the experiment), since 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).

### 2.2.2 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. 2.1b). Capture volume (cm<sup>3</sup>) 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 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 min<sup>-1</sup> cm<sup>-3</sup>). *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 min<sup>-1</sup> cm<sup>-3</sup>). 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 min<sup>-1</sup> cm<sup>-3</sup>) 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 four minutes. 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 seconds (mean retention time = 48.9 s, SD = 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 washed off the tentacles. In addition, aerial-view photos 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 value 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.; Hiebert & 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 & Strickler 1994). Using prey encountered as the denominator when calculating rates for both capture and trapping efficiencies enabled these efficiencies to be compared with published feeding efficiency data for a zooplanktivorous fish (Clarke et al. 2009). In addition, these efficiencies could be directly related to ecological models that estimate suspension feeding rates from encounter rates.

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

## 2.3 RESULTS

There was no difference between the dimensions of the capture zone of sea anemones, *Anthopleura 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 (ANOVA,  $p > 0.05$ ). Furthermore, there was no significant difference between the volume of the capture zone for *A. elegantissima* exposed to weak waves ( $3.89 \text{ cm}^3$ ,  $SD = 0.39$ ,  $n = 6$  sea anemones, mean area for each) or to strong waves ( $3.71 \text{ cm}^3$ ,  $SD = 0.56$ ,  $n = 6$  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,  $SD = 0.46$ ,  $n = 4$ ), but were more evenly distributed in the water column in strong waves (distribution ratio = 1.1,  $SD = 0.51$ ,  $n = 4$ ) (one-tailed t-test,  $p = 0.004$ ,  $df = 6$ ). We analyzed a mean number of 177 encounters per sea anemone per 12-minute experiment ( $SD = 128$ ,  $n = 6$  sea anemones) in weak waves and a mean number of 197 ( $SD = 68$ ,  $n = 6$  sea anemones) in strong waves. Encounter rates (Fig. 2.2) were lower in weak waves ( $5.6 \text{ prey min}^{-1} \text{ cm}^{-3}$ ,  $SD = 3.5$ ,  $n = 6$  sea anemones) than in stronger waves ( $7.4 \text{ prey min}^{-1} \text{ cm}^{-3}$ ,  $SD = 4.4$ ,  $n = 6$  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 ( $9.3 \text{ prey min}^{-1} \text{ cm}^{-3}$ ,  $SD = 4.8$ ,  $n = 3$  sea anemones) than in weak waves ( $2.6 \text{ prey min}^{-1} \text{ cm}^{-3}$ ,  $SD = 2.2$ ,  $n = 3$  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 ( $0.28 \text{ prey min}^{-1} \text{ cm}^{-3}$ ,  $SD = 0.18$ ,  $n = 6$  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 ( $0.02 \text{ prey min}^{-1} \text{ cm}^{-3}$ ,  $SD = 0.02$ ,  $n = 6$  sea anemones) and strong

waves ( $0.03 \text{ prey min}^{-1} \text{ cm}^{-3}$ ,  $\text{SD} = 0.06$ ,  $n = 6$  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 2.2).

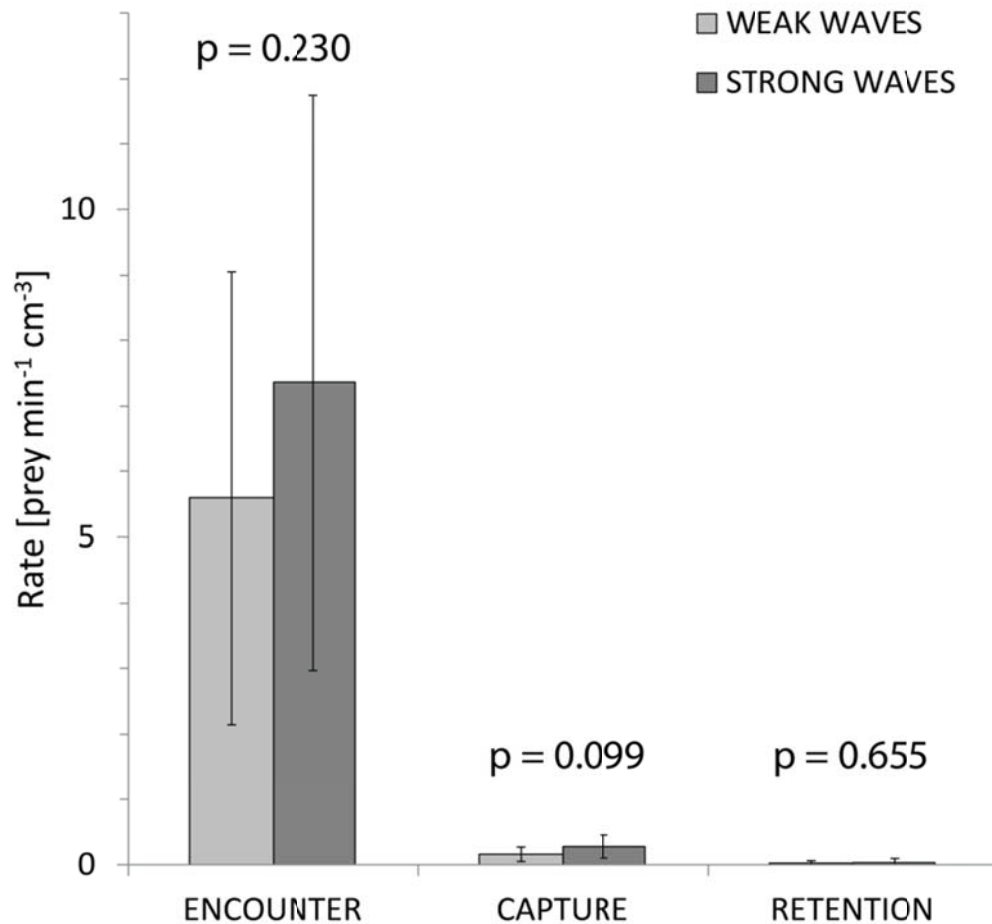


Figure 2.2: The rate of encountering prey (number of prey passing through a capture zone per unit time per capture volume), capture (number of prey contacting and sticking to a tentacle per unit time per capture volume), and retention (number of prey held by a tentacle until the end of each experiment per unit time per capture volume) by a sea anemone ( $n = 12$ ) feeding on copepods in the two wave settings described in Table 2.1. 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 ( $W = 15$ ).

Table 2.2: Mean capture efficiency and mean trapping efficiency of *Anthopleura elegantissima* (n = 12 sea anemones) feeding on copepods in each flow setting ( $\pm$  standard deviation). 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).

<b>Flow setting</b>	<b>Capture Efficiency</b> [% prey captured/ prey encountered]	<b>Trapping Efficiency</b> [% 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)

## 2.4 DISCUSSION

### 2.4.1 Effects of flow on feeding

We found that increasing the "strength" of ambient water flow (higher peak velocities in waves and greater turbulent kinetic energy) enhanced rates of some steps in the feeding process and decreased others for a passive suspension-feeding predator (the sea anemone, *Anthopleura 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 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 & 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 rather

than in the capture zone of the sea anemone, 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  $7.8 \text{ cm s}^{-1}$ ), 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  $24.3 \text{ cm s}^{-1}$ ), 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. 2.2).

Retention rates (prey retained on the tentacles per unit time) were the same for both conditions of flow (Fig. 2.2), and represented less than 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 & 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 & 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.

### 2.4.2 Feeding by *Anthopleura 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 2.2). 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 rates measured in our experiments (Fig. 2.2), we estimated that *A. elegantissima* ingested 0.08 to 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 to 0.25 mg of prey per hour (natural prey density and natural assemblage of prey organisms) during six hours 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  $\mu\text{g C day}^{-1}$ ) can supply more than twice the daily metabolic energy requirement of the sea anemone (1300  $\mu\text{g C day}^{-1}$ ). *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 & Shick, 1987) and stable isotopic signatures of the sea anemone suggest that *A. elegantissima* relies primarily on heterotrophy (Bergschneider & Muller-Parker, 2008).

### 2.4.3 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 2.3). 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  $\text{min}^{-1}$ ) 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.

Table 2.3: Comparison of feeding efficiency for zooplanktivorous fish (*Acanthemblemaria aspera* and *A. spinosa*) (Clarke et al. 2009) and passive suspension-feeding sea anemones (*Anthopleura 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 ( $\text{cm s}^{-1}$ ) and turbulence (TKE in  $\text{cm}^2\text{s}^{-2}$ ).

BENTHIC ZOOPLANKTIVORES			
<u>Active fish</u>		<u>Passive sea anemone</u>	
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:	
<u>Weak waves</u>		<u>Weak waves</u>	
Peak velocity = 11.6		Peak velocity = 8.24	
TKE = 0.077		TKE = 0.27	
	93%	No change	
to	increase		
<u>Strong waves</u>		<u>Strong waves</u>	
Peak velocity = 24.6		Peak velocity = 27.4	
TKE = 0.35		TKE = 4.5	

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.

# Chapter 3: Effects of ambient water flow, prey swimming behavior, and neighbors on suspension feeding by sea anemones

## 3.1 INTRODUCTION

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 carried by ambient water onto capture surfaces. Turbulent flow can stir the fluid environment, enhance prey delivery (Rothschild & Osborn 1988), reduce the ability of the prey to detect and avoid predation (Robinson et al. 2007), or wash prey off capture surfaces (Shimeta & Koehl 1997). How does flow impact predator-prey interactions between a benthic suspension feeder and zooplanktonic prey?

Studies of passive suspension feeding have been done experimentally in unidirectional flow for corals (e.g. Patterson 1984), bryozoans (Okamura 1985), sea pens (Best 1988), and sea anemones (Anthony 1997), but few studies have examined the effects of waves and turbulence on suspension feeding (e.g., Clarke et al. 2009, Hunter 1989, Trager et al 1994; Robinson et al 2013). Experiments have generally focused on the consumption of non-motile prey, yet actively swimming zooplankton can contribute significantly to the diet of passive suspension feeders (Sebens & Koehl 1984; Berschneider & Muller-Parker 2008). Brine shrimp (*Artemia* spp.) neutrally-buoyant cysts, or hatched nauplii have been used as live prey (e.g. Leversee 1976). A small number of studies of benthic suspension-feeding predators that used zooplankton prey (e.g., Hunter 1989, Heidelberg et al 1997; Robinson et al 2013) suggest prey swimming and escape responses might impact capture rates. Although *Artemia* spp. nauplii can swim, they do not exhibit escape behavior. Suspension feeders are important components of many marine communities. Previous research on this ubiquitous feeding strategy (reviewed in Wildish & Kristmanson 1997) has been useful in estimating how much suspension feeding can contribute to ecological links between pelagic and benthic communities. A common measure of interactions between predator and prey are encounter rates (number of prey passing through a predator's capture zone per unit time). For sedentary predators that rely on ambient water to deliver food, encounter rates are dependent on the ambient flow and prey behavior. Humphries (2009) suggested the efficiency of particle capture might be higher than estimated for filter feeders in low flow. Chapter 2 suggests that retention (number of prey successfully held on to) is not



100% as is often assumed, and can be a small fraction of the initial encounter rate (Robinson et al 2013).

The presence of neighbors affects flow around benthic suspension feeders. Okamura (1985) found that the feeding rate of an encrusting bryozoan colony was enhanced in the presence of a neighboring colony. The feeding current from the upstream colony drew currents closer to the substratum so that downstream zooids captured more prey. Passive suspension feeders do not generate their own feeding current. However, ambient flow over a bumpy surface of organisms can generate eddies from which extended tentacles can capture prey from turbulent wakes (Sebens & Johnson 1991).

The objective of this study was to measure how ambient water flow, prey swimming behavior, and the presence of neighbors affect predation by benthic passive suspension feeders. I addressed this question using sea anemones, *Anthopleura elegantissima* (Brandt), which live in wave-dominated flow habitats (chapter 1), feed on a variety of zooplankton that exhibit different swimming behaviors, and live in dense colonies surrounded by conspecifics (e.g., Sebens 1981). In this study we used prey with different swimming behaviors: 1) the calanoid copepod *Acartia* spp., which has a well-characterized escape response (Chapter 2), 2) heat-killed *Acartia* spp., which are non-swimming prey with the same size, shape, and drag as living *Acartia* spp., and 3) nauplius larvae of *Artemia* spp., which are swimming prey with no escape behavior. We examined the effects on feeding of (1) the peak water velocities and turbulent kinetic energy of the wavy ambient water flow, (2) prey swimming and escape maneuvers, and (3) upstream and downstream neighbors. Understanding how zooplankton swimming and the effect of neighboring suspension feeders in realistic flow conditions can contribute to predictions about the link between pelagic and benthic communities based upon flow and prey type.

### 3.2 METHODS

All sea anemones, *Anthopleura elegantissima*, were collected in October 2012 and May 2013 from Horseshoe Cove, in the Bodega Marine Reserve along the Sonoma Coast in California (38°18.94' N, 123°04.16' W). The clone from which sea anemones were selected was the same bed over which flow measurements were collected (Chapter 1). Sea anemones that were next to one another and positioned away from the edges of the clone (surrounded on all sides by conspecifics) were selected. Since *A. elegantissima* forms genetically identical polyps by binary fission, adjacent sea anemones were likely from the same clone though genetic testing was not performed. Sea anemones were gently peeled from the rock, and each individual was placed in an air-filled plastic bag. The bags were transported to the University of California Berkeley (Berkeley, California, USA) in a cooler kept at 10-15°C. The anemones were housed in a 19-L aquarium filled with recirculating filtered

seawater (FSW; 50  $\mu\text{m}$  filter mesh) with a salinity of 35‰. The aquarium was kept in a temperature-controlled cold room at 10-15 °C and exposed to a photoregime with 12 hours dark and 12 hours light provided by full-spectrum fluorescent bulbs (Hydroponic 105 W 5500K Perfect Daylight). The sea anemones were placed on a suspended plastic mesh substratum to prevent attachment to the aquarium walls, and were fed hatched *Artemia* spp. nauplii once a day, but were not fed 24 hours before use in flume experiments. For flume experiments, sea anemones were transported to the University of North Carolina Wilmington (Wilmington, North Carolina, 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 (less than 14 hours 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, North Carolina (34°18.27' N, 77°48.80' W), using a plankton net (153  $\mu\text{m}$  mesh). Samples were diluted in whole seawater, aerated, and used within 12 hours of collection. Under a dissecting microscope, individual calanoid copepods (*Acartia* spp.) were selected using Pasteur pipettes and placed in beakers with bottoms made of Nitex mesh (40  $\mu\text{m}$ ) that were submerged in filtered (10  $\mu\text{m}$ ) 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<sup>-1</sup> FSW) for 20 minutes (see Elliott & Tang 2009 for protocol). No change in copepod swimming behavior was observed to result from this treatment (Chapter 2). To test the effect of copepod shape and drag without swimming behavior, dead copepods were used as prey. The copepods were selected and dyed as described above, then heat-shocked. To compare copepod swimming behavior with a smaller prey that does not escape, nauplii of *Artemia* spp. were hatched from frozen cysts by placing cysts in aerated, filtered seawater. Nauplii between 2-3 days old were selected using Pasteur pipettes, were housed in mesh-bottomed beakers, and underwent the same dye treatment as the copepods.

### 3.2.1 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) to mimic the range of back and forth flow of water as surface waves pass over shallow benthic organisms (see Chapter 2 for flume description). 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

cm<sup>3</sup> sample volume, 5 cm below probe). Two wave settings (“weak” and “strong”) were used in the flume (see Table 2.1). The maximum horizontal velocity in the positive direction ( $u$ ) of each wave was measured and the mean of those values for each wave setting was defined as the peak shoreward 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 ( $u, v, w$ ). Mean velocity was estimated by a zero-phase displacement running average (*filtfilt* function in MATLAB, version 7.13.0.564, Natick, Massachusetts; 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 turbulent kinetic energy (TKE) of each wave setting (Table 2.1) matched flow conditions measured using an ADV at a height of 2 cm above *A. elegantissima* at the field site described above (see Chapter 1).

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. 2.1a). A thin volume of light approximately 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. 2.1a). 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 (2mm wide) through which light could pass from two full-spectrum fluorescent light bulbs (Hydroponic 105 W 5500K Perfect Daylight). These lights were positioned 18 cm above and below the level of the sea anemone. For experiments with solitary sea anemones, 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. For experiments testing the effect of neighboring sea anemones, a centered sea anemone (positioned in the same way described above) was surrounded by six sea anemones, so there was always one sea anemone upstream in any direction. For the camera to see the centered sea anemone, a small gap was left between two surrounding sea anemones closest to the camera. Otherwise, this community of sea anemones was positioned closely together and filled the working section. For feeding experiments, three hundred *Artemia* spp. nauplii, or dead *Acartia* spp., or live *Acartia* spp. (prey density of 14 L<sup>-1</sup>) were added to the flume and acclimated to flow conditions for two minutes.

Videos of the sea anemone feeding were captured at 60 Hz for 10 minutes. The duration of the experiments was limited to 12 minutes total (including both

acclimation and the experiment), since live copepod responsiveness and escape behavior does not decline due to habituation within this time frame (Hwang et al 1994). Experiments were replicated at each flow setting with new organisms (Table 3.1).

Table 3.1: Number of sea anemone predators and zooplanktonic prey used in predator-prey interaction experiments in three flow regimes. Sample size of the sea anemone is provided outside of parentheses, and the number of prey is in parentheses.

Prey Type	<u>Solitary Sea Anemones</u>			<u>Downstream Sea Anemones</u>	
	Still Water	Weak Waves	Strong Waves	Weak Waves	Strong Waves
Nauplii		3 (900)	3 (900)		
Dead Copepods		3 (900)	3 (900)		
Copepods	3 (900)	6 (1800)	6 (1800)	3 (900)	3 (900)

### 2.2.2 Videographic analysis

For each experiment, video records were analyzed frame-by-frame to tally predator-prey interactions between planktonic prey and the sea anemone. Prey that passed through the field of view but were not in focus nor illuminated by the light sheet were not counted; only prey passing within a capture zone were included (Fig. 2.1b). Capture volume ( $\text{cm}^3$ ) 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 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 prey that passed through the capture zone per unit time per capture volume (prey encountered  $\text{min}^{-1} \text{cm}^{-3}$ ). “Capture rates” were calculated as the number of prey that came into direct contact with and stuck to the tentacle of a sea anemone per unit time per capture volume (prey captured  $\text{min}^{-1} \text{cm}^{-3}$ ). Each of the sea anemones used in these experiments captured prey. Captured zooplankton were observed to escape from, or to get swept off tentacles, so “retention rates” (prey retained  $\text{min}^{-1} \text{cm}^{-3}$ ) were calculated using only those prey that remained attached to the sea anemone at the end of each experiment and that had exceeded a threshold retention time of four minutes. 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 seconds (mean retention time = 48.9 s, SD =61, n = 49 captured copepods).

In some cases prey were captured on the far side (facing away from the camera) of the observed tentacles. If a prey 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 plankton became visible when the tentacles moved, the prey fluttered into view during peak velocities, or the prey washed off the tentacles. In addition, aerial-view photos of each sea anemone in still water were taken directly after the experiment and captured plankton were noted. No discrepancies occurred between the total number of captured prey counted by the end of the experiment and prey observed on the tentacles once the experiment was complete.

Predator-prey interactions were identified by the behavior of the prey (Fig. 3.1). “Pass” described when prey passively swept by the anemone within the capture zone. “Avoid” described when a copepod actively changed trajectory with an escape jump to avoid contact with the predator (the *Artemia* spp. nauplii do not perform escape jumps; the dead copepods have no active swimming behavior). A “bump” described when prey passively bumped into a tentacle but continued without a capture or escape. “Escape” described when a copepod bumped into a tentacle then actively swam off (nauplii were not observed to actively swim off the tentacle). “Capture” described when prey bumped into a tentacle and was held by the anemone. Importantly, captured prey did not always lead to retention (and subsequent ingestion), so a final term “loss” was used to describe when prey would dislodge from the tentacle. The interactions “bump” and “escape” do not result in a capture so “loss” only refers to prey removed after a capture.

The rates of predator-prey interactions were used to calculate efficiency. In Chapter 2, capture and trapping efficiency were calculated based on the proportion of encountered prey so that these values could be compared between predators with different feeding modes. In this Chapter, “retention efficiency” is defined as the proportion of captured prey that was retained so that we could compare the ability of the predator to hold onto prey that have different swimming behaviors. Since the duration of experiments (12 min. total) was short relative to the average ingestion times for sea anemones (6-50 min.; Hiebert & Bingham 2012), most captured and retained prey were not ingested during the videos. Therefore, the retention efficiency for sea anemones feeding on different prey alludes to feeding success but is not a confirmed measure of how much the predators consumed.

All statistical tests were conducted using MATLAB, R (version 3.0.0, The R Foundation for Statistical Computing 2013), and IBM SPSS Statistics for Windows (version 21.0.0.0; Armonk, New York; IBM Corp. 2012). When data were not normally distributed (Shapiro Wilk test,  $p > 0.05$ ), non-parametric tests were used.

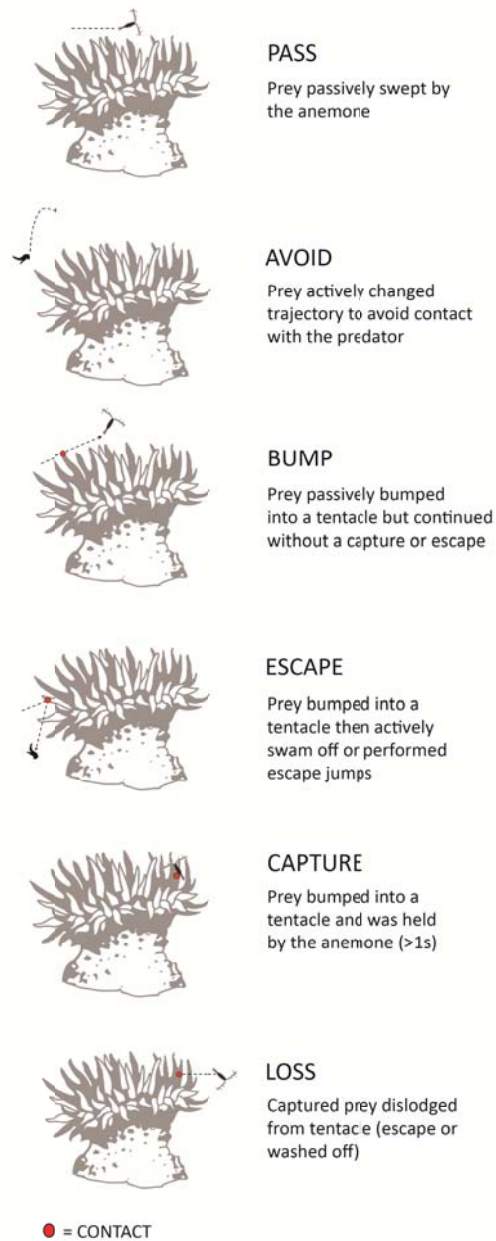


Figure 3.1: Categories of predator-prey interactions between a sea anemone predator and zooplanktonic prey.

### 3.3 RESULTS

The capture volume of the sea anemones, *A. elegantissima*, did not significantly change during the course of experiments, nor was volume significantly different between sea anemones exposed to weak waves and strong waves. Measurements of the capture volume at the beginning, midpoint, and end of the experiment showed that the capture volume for each individual did not change (Repeated Measures ANOVA,  $F_{(7,22)} = 0.94$ ,  $p = 0.521$ ,  $n = 30$  sea anemones). There was no significant difference between the volume of the capture zone for sea anemones exposed to weak waves (mean = 3.97 cm<sup>3</sup>, SD = 2.28,  $n = 15$  sea anemones) or to strong waves (mean = 3.32 cm<sup>3</sup>, SD = 2.23,  $n = 15$  sea anemones) (ANOVA,  $df = 29$ ,  $p = 0.433$ ).

#### 3.3.1 The effect of flow on the predation of zooplanktonic prey by a solitary sea anemone

For most prey types used in this study, encounter rates increased in strong waves (Fig. 3.2a; Table 3.2; two-way ANOVA, significant effect of flow  $F_{(1, 18)} = 8.30$ ,  $p < 0.001$ ). Although the sea anemones encountered more nauplii prey in strong waves than in weak waves, though this difference was not significant (Mann-Whitney U,  $p = 0.127$ ). In addition, encounter rates with living copepods was not affected by the strength of waves (ANOVA,  $df = 11$ ,  $p = 0.458$ ), although encounter rates with non-swimming, dead copepod prey were significantly higher in strong waves (Mann-Whitney U,  $p = 0.05$ ).

Table 3.2: Summary of statistical comparisons between the rate (number of prey per minute per capture volume) of encounter, capture, and retention of three prey types in weak and strong waves (mean  $\pm$  standard deviation). Significance determined by ANOVA,  $p \leq 0.05$ .

Prey	Waves	Mean Rate [prey min <sup>-1</sup> cm <sup>-3</sup> ]		
		<u>Encounter</u>	<u>Capture</u>	<u>Retention</u>
Nauplii	Weak	1.60 $\pm$ 0.843	0.160 $\pm$ 0.123	0.033 $\pm$ 0.0577
	Strong	6.99 $\pm$ 4.04	0.353 $\pm$ 0.120	0.0133 $\pm$ 0.0231
	Significant?	No	No	No
Dead Copepods	Weak	2.64 $\pm$ 2.22	0.217 $\pm$ 0.237	0.133 $\pm$ 0.167
	Strong	9.29 $\pm$ 4.76	0.383 $\pm$ 0.104	0
	Significant?	Yes	No	No
Copepods	Weak	5.60 $\pm$ 3.45	0.160 $\pm$ 0.111	0.0177 $\pm$ 0.0203
	Strong	7.35 $\pm$ 4.39	0.275 $\pm$ 0.175	0.0297 $\pm$ 0.0620
	Significant?	No	No	No

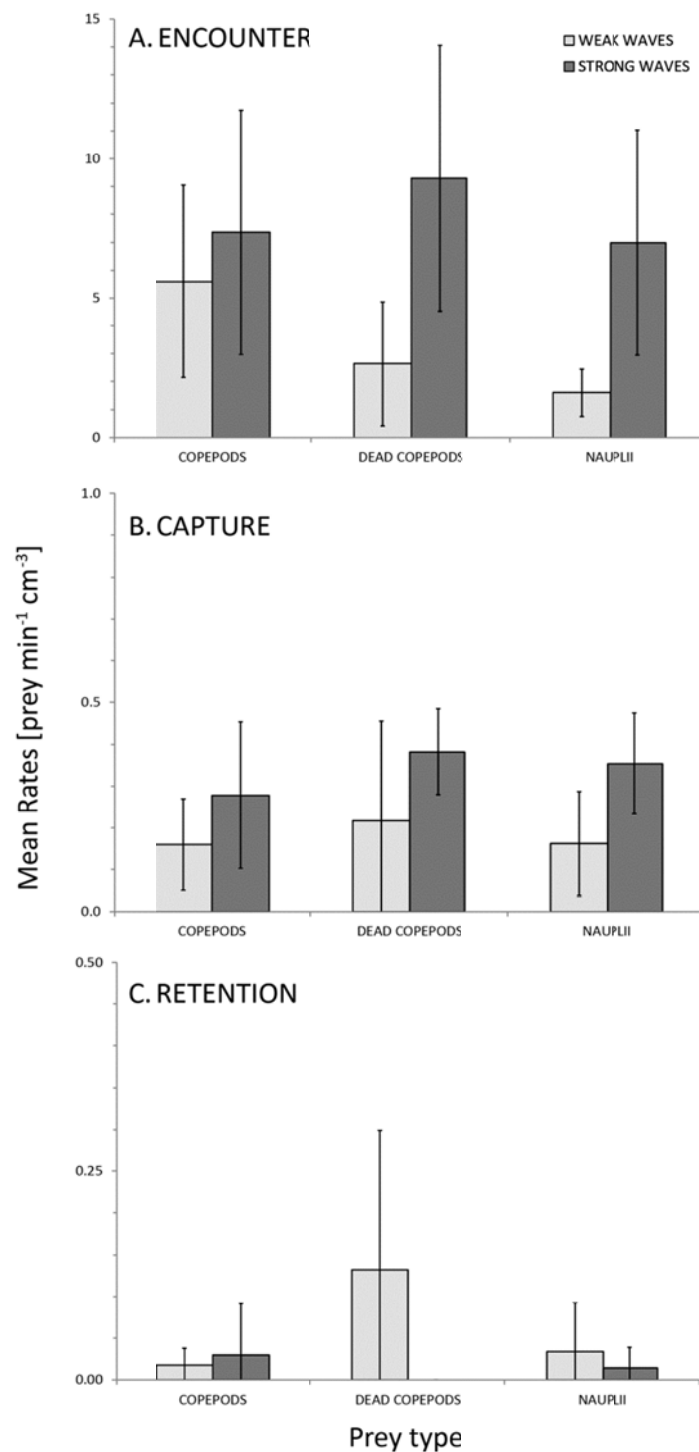


Figure 3.2: Mean rates of encounter (number of prey that passed through the capture zone of a sea anemone predator), capture (number of prey that came into direct contact with the predator and stuck), and retention (number of prey retained) for three prey types. Rates were normalized to capture volume of the predator. Error bars indicate one standard deviation.



Capture rates were an order of magnitude smaller than encounter rates (Fig. 3.2b; Table 3.2). Capture rates were generally higher in stronger waves for all types of prey (two-way ANOVA, significant effect of flow  $F_{(1, 18)} = 5.98$ ,  $p = 0.025$ ). Although the mean capture rates of nauplii prey in weak waves was doubled in strong waves, this difference was not statistically significant (ANOVA,  $df = 5$ ,  $p = 0.123$ ). Similarly, capture of dead copepods was not significantly different between flow regimes (ANOVA,  $df = 5$ ,  $p = 0.327$ ), even though predators encountered the dead copepods at a greater rate in strong waves than in weak waves. For live copepod prey, capture rates of living copepods and nauplii were similar in weak waves even though sea anemones encountered nauplii at a lower rate than they encountered living copepods. The capture rates of copepods did not significantly vary as wave strength increased (ANOVA,  $df = 11$ ,  $p = 0.204$ ).

Prey retention rates by *A. elegantissima* were less than 5% of the rates of prey encountered (Fig. 3.2c; Table 3.2). There were a few replicate experiments in which no prey were retained, which resulted in very high variability in retention rates measured. Therefore, differences in retention rates between weak and strong waves were not significantly different (tested with a Mann-Whitney U) for nauplii ( $U = 4$ ,  $p = 0.796$ ), dead copepods ( $U = 1.5$ ,  $p = 0.121$ ), or live copepods ( $U = 15$ ,  $p = 0.591$ ). However, the increase of wave strength on prey retention depended on the prey type. Nauplii were retained more in weak waves than in and strong waves. Similarly, dead copepods were retained at the highest observed rate in weak waves, while in strong waves, no dead copepods were retained by a predator. In contrast, the retention rates of living copepods increased in strong waves.

### 3.3.2 *The effect of flow on predator-prey interactions between zooplankton and a solitary sea anemone*

Most of the zooplankton prey passed through the capture zone of a sea anemone without contacting the predator (i.e., “pass”; Fig. 3.3; Table 3.3). In weak waves, prey passively bumped into the predator, although live copepods came into brief contact with a sea anemone less than nauplii or dead copepods. In strong waves, the proportion of “bump” interactions increased for all prey types. Living copepods were able to avoid or escape the predator more in weak waves than in strong waves, but this difference was not significant. Nauplii and dead copepods do not actively avoid or escape from predators. Yet the proportion of predator-prey interactions that resulted in capture did not vary with exposure to stronger waves.

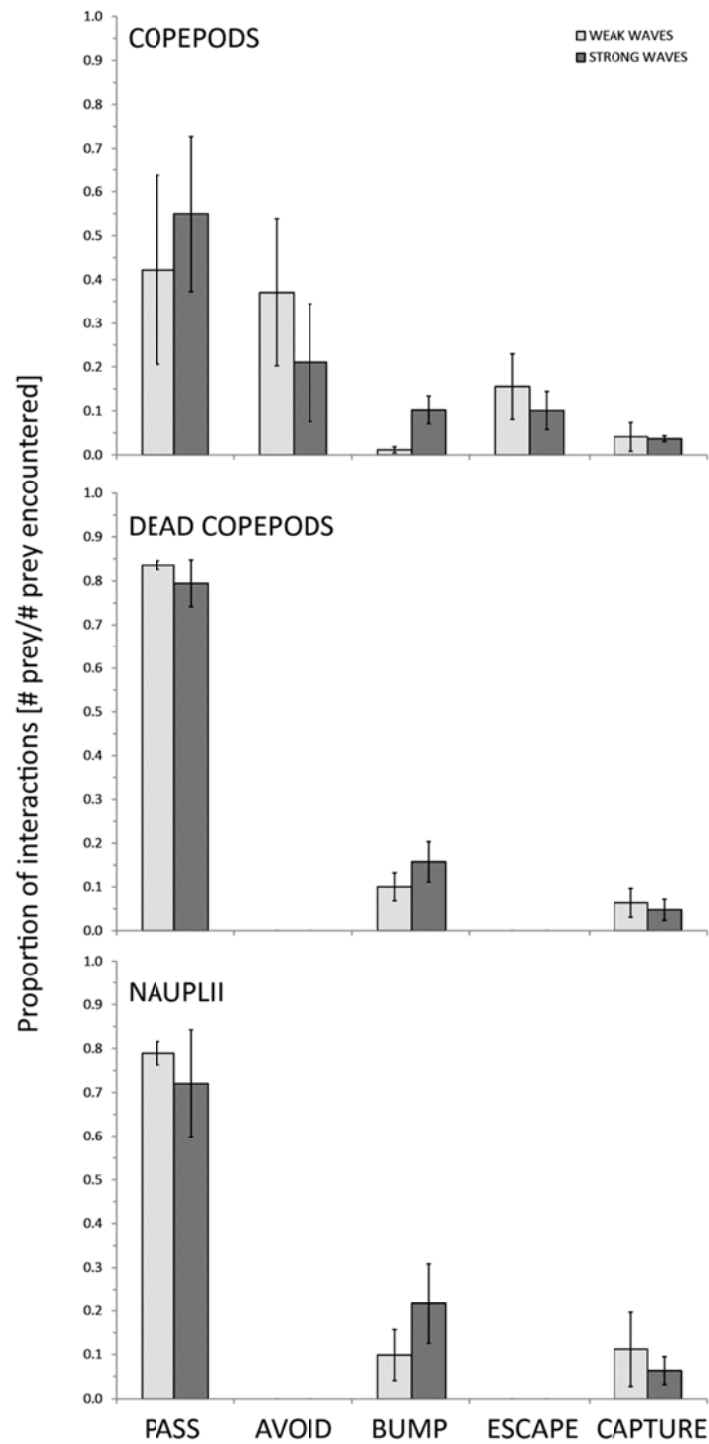


Figure 3.3: Predator-prey interactions between a sea anemone predator and three types of zooplanktonic prey, in weak and strong waves. Error bars indicate one standard deviation.

Table 3.3: Summary of statistical comparisons between the proportion of predator-prey interactions (pass, avoid, bump, escape, and capture) for three prey types in weak and strong waves (mean  $\pm$  standard deviation). Significance determined by ANOVA,  $p \leq 0.05$ .

Prey	Waves	Proportion of interactions [# prey/ # encountered (%)]				
		<u>PASS</u>	<u>AVOID</u>	<u>BUMP</u>	<u>ESCAPE</u>	<u>CAPTURE</u>
Nauplii	Weak	79 $\pm$ 2.6		9.7 $\pm$ 6.1		11 $\pm$ 8.9
	Strong	72 $\pm$ 13		22 $\pm$ 9.0		6.3 $\pm$ 3.2
	Significant?	No		No		No
Dead Copepods	Weak	84 $\pm$ 1.0		10 $\pm$ 3.6		6.3 $\pm$ 3.5
	Strong	79 $\pm$ 5.5		16 $\pm$ 4.9		4.7 $\pm$ 2.5
	Significant?	No		No		No
Copepods	Weak	42 $\pm$ 22	37 $\pm$ 17	1.2 $\pm$ 1.0	16 $\pm$ 7.3	4.2 $\pm$ 3.3
	Strong	55 $\pm$ 18	21 $\pm$ 13	10 $\pm$ 2.9	9.8 $\pm$ 4.4	3.8 $\pm$ 1.0
	Significant?	No	No	Yes	No	No

### 3.3.3 Suspension feeding by a downstream sea anemone

Downstream sea anemones encountered fewer copepod prey than solitary sea anemones (Fig. 3.4; Table 3.4). However, solitary sea anemones did not capture or retain significantly more prey per time. In weak waves, retention rates of copepods were similar between solitary and downstream sea anemones, whereas in strong waves, retention rates of copepods by solitary sea anemones were more variable than in weak waves. There was no significant effect of flow on the encounter, capture, and retention rates for downstream sea anemones between weak and strong waves.

Table 3.4: Summary of statistical comparisons between the rate (number of prey per minute per capture volume) of encounter, capture, and retention of copepods by solitary and downstream sea anemones in weak and strong waves (mean  $\pm$  standard deviation). Significance determined by ANOVA,  $p \leq 0.05$ .

Prey	Waves	Mean Rate [prey min <sup>-1</sup> cm <sup>-3</sup> ]		
		<u>Encounter</u>	<u>Capture</u>	<u>Retention</u>
Solitary Copepods	Weak	5.60 $\pm$ 3.45	0.160 $\pm$ 0.111	0.0177 $\pm$ 0.0203
	Strong	7.35 $\pm$ 4.39	0.275 $\pm$ 0.175	0.0297 $\pm$ 0.0620
	Significant?	No	No	No
Downstream Copepods	Weak	0.974 $\pm$ 0.329	0.0892 $\pm$ 0.0911	0.0184 $\pm$ 0.0319
	Strong	1.58 $\pm$ 0.619	0.102 $\pm$ 0.0759	0.0168 $\pm$ 0.0156
	Significant?	No	No	No

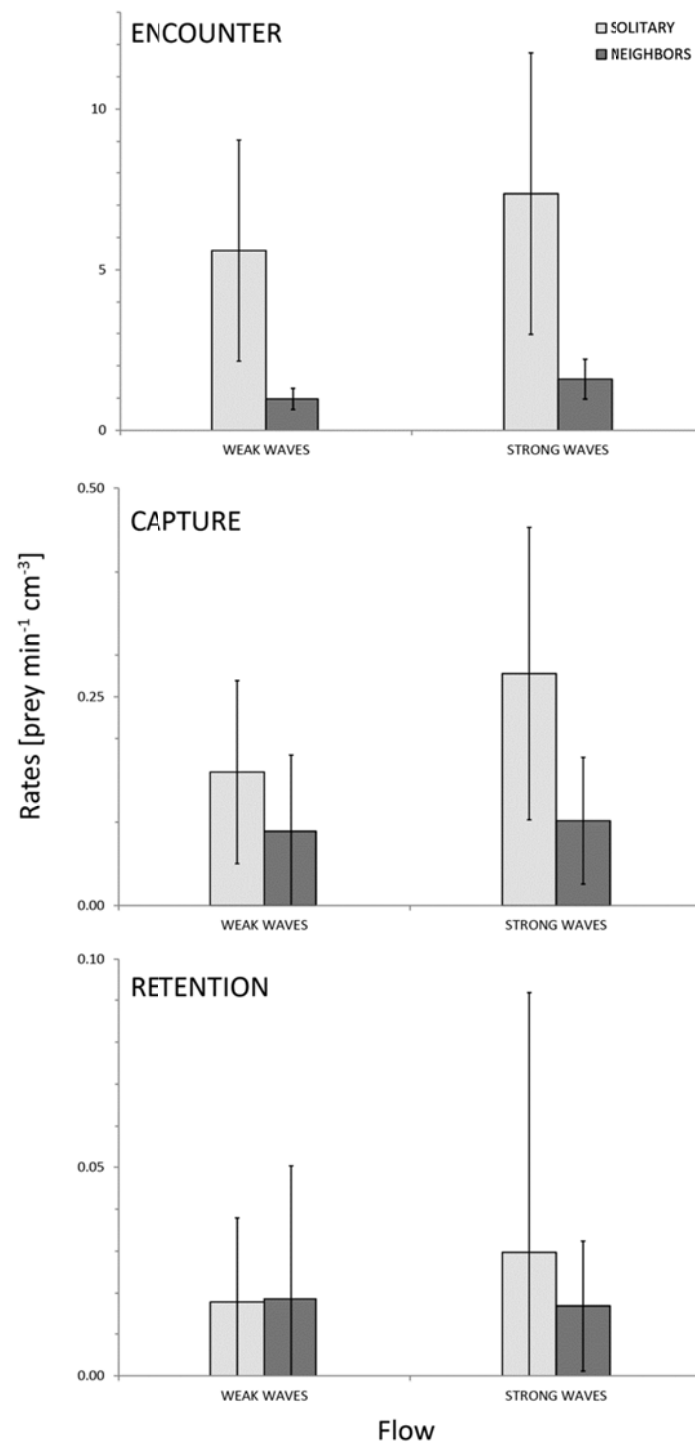


Figure 3.4: The mean rates of encounter (number of prey that passed through the capture zone of a sea anemone predator), capture (number of prey that came into direct contact with the predator and stuck), and retention (number of prey retained) for a solitary predator, or predator surrounded by neighbors in two flow regimes. Living copepods were the prey. Rates were normalized to capture volume of the predator. Error bars indicate one standard deviation.

### 3.3.4 The effect of flow on predator-prey interactions by downstream sea anemones

The largest proportion of prey pass near the sea anemone without reacting (Fig. 3.5). When solitary sea anemones preyed upon copepods, the prey avoided or escaped the predator more in weak waves than in strong waves. With a downstream predator, prey avoidance and escape swimming occurred less than in the same flow over solitary sea anemones, and increased in stronger waves, though not significantly (Table 3.5). Predator-prey interactions between copepods and solitary sea anemones in still water were included to compare whether the differences in behavior over downstream sea anemones was due to slower flow conditions. In still water, the proportion of prey avoidance and escape responses were also low and increased as flow increased (still water to weak waves). The proportion of prey captured is not significantly different between solitary or downstream copepods, nor is it affected by increases in flow.

Table 3.5: Summary of statistical comparisons between the proportion of predator-prey interactions (pass, avoid, bump, escape, and capture) between copepods and solitary or downstream sea anemones in weak and strong waves (mean  $\pm$  standard deviation). Significance determined by ANOVA,  $p \leq 0.05$ .

Anemone	Waves	Proportion of interactions [# prey/ # encountered (%)]				
		<u>PASS</u>	<u>AVOID</u>	<u>BUMP</u>	<u>ESCAPE</u>	<u>CAPTURE</u>
Solitary	Still Water	73 $\pm$ 25	11 $\pm$ 10		9.9 $\pm$ 7.9	5.4 $\pm$ 7.3
	Weak	42 $\pm$ 22	37 $\pm$ 17	1.2 $\pm$ 1.0	16 $\pm$ 7.3	4.2 $\pm$ 3.3
	Strong	55 $\pm$ 18	21 $\pm$ 13	10 $\pm$ 2.9	9.8 $\pm$ 4.4	3.8 $\pm$ 1.0
	Significant?	No	No	Yes	No	No
Downstream	Weak	66 $\pm$ 18	12 $\pm$ 6.6	8.2 $\pm$ 2.9	5.2 $\pm$ 4.6	8.2 $\pm$ 6.0
	Strong	49 $\pm$ 8.6	17 $\pm$ 5.3	14 $\pm$ 5.3	15 $\pm$ 7.3	5.9 $\pm$ 4.1
	Significant?	No	No	No	No	No

Table 3.6: The effect of flow (weak and strong waves) and the presence of neighbors on zooplankton prey capture by a benthic sea anemone (mean  $\pm$  standard deviation). Significance determined by ANOVA,  $p \leq 0.05$ .

Predator	Prey	Retention Efficiency [prey retained / prey captured (%)]	
		<u>Weak Waves</u>	<u>Strong Waves</u>
Solitary Anemones	Copepods	15 $\pm$ 19	8.3 $\pm$ 14
	Dead Copepods	39 $\pm$ 35	0
	Nauplii	11 $\pm$ 19	3.0 $\pm$ 5.3
Downstream Anemones	Copepods	10 $\pm$ 16	11 $\pm$ 10

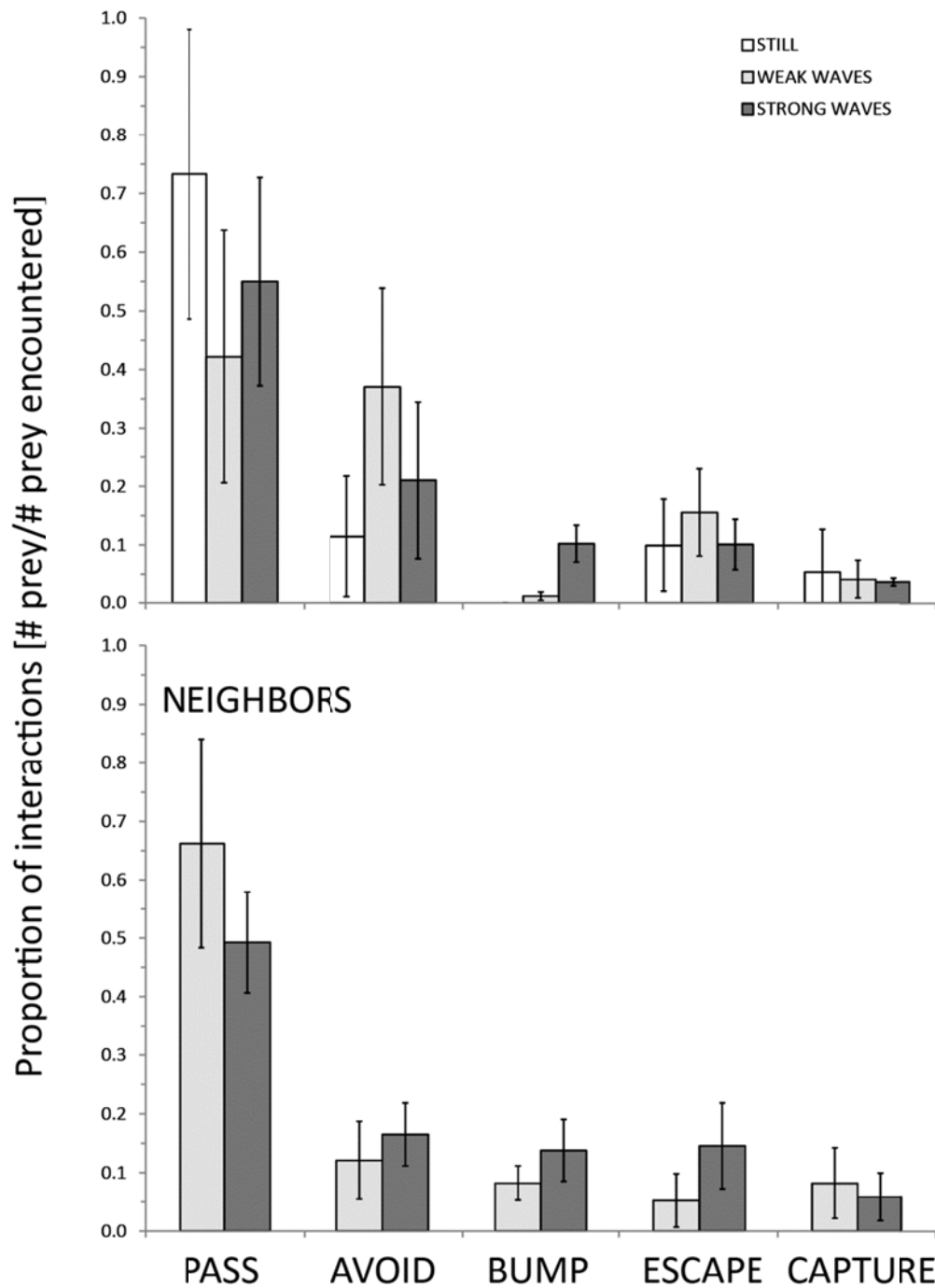


Figure 3.5: Predator-prey interactions between a solitary sea anemone predator and a downstream sea anemone, and copepods *Acartia* spp., in weak and strong waves. Error bars indicate one standard deviation

### 3.3.5 Retention efficiency of sea anemones feeding on zooplanktonic prey in wavy flow

Retention efficiency (Table 3.6) describes the proportion of prey that a predator has retained out of the number of prey captured. In this study, the passive prey were retained with the greatest efficiency in weak waves. The effect of waves reduced feeding efficiency of most prey except by downstream anemones.

## 3.4 DISCUSSION

We examined the effects on suspension feeding of (1) the peak water velocities and turbulent kinetic energy of the wavy ambient water flow, (2) prey swimming and escape maneuvers, and (3) upstream and downstream neighbors.

### 3.4.1 The effect of flow on predation

Many studies of benthic suspension feeders test the effect of flow on feeding rate by animals in unidirectional flow with passive and uniform prey (e.g., Shimeta, 2009). Encounter rates (the number of prey passing through the predator's capture zone) increase with water velocity, which leads to higher ingestion rates. In this study, stronger waves led to increased encounter rates only for passive particles, such as dead copepods (Fig. 3.2). For prey that swim and perform escape maneuvers, stronger waves did not significantly enhance encounter rates. In weak waves, sea anemones encountered copepod prey at higher rates than nauplii and dead copepods, which suggests prey swimming behavior affects variability of encounter rates.

The differences in how flow affected encounter rates for three prey types were not mirrored in capture or retention rates. For passive prey, more encounter rates with a benthic predator did not result in greater rates of capture. Copepods in weak waves encountered a predator at a higher rate than nauplii, but capture rates were similar, which indicates that the capture and subsequent retention (or ingestion) of prey does not scale equally from encounter rates for prey with different behavior. Importantly, retention rates were low for both nauplii and copepods in both weak and strong flow regimes. Dead copepods represented the extreme range of retention rates since these prey were retained at high rates in weak waves, but were not retained at all in strong waves.

### 3.4.2 The effect of prey swimming behavior on predation

The comparisons between rates of encounter and capture for prey with different swimming behavior suggests the importance of evasive responses in avoiding contact with a predator, reducing passive bumps into predators, and jumping free after getting captured. The proportion of predator-prey interactions between nauplii and dead copepods were similar (Fig. 3.3). Copepod avoidance might have reduced

passive bumping into predators in weak waves, but the proportion of capture remained the same in weak and strong waves.

### *3.4.3 The effect of upstream neighbors on suspension feeding in wavy flow*

Downstream sea anemones encountered fewer prey than solitary sea anemones. Upstream neighbors can deplete water of prey as flow passes over the clone. The encounter, capture, or retention of prey by downstream sea anemones was independent of flow. Although these predators encountered fewer prey than solitary sea anemones, they retained approximately the same rate of prey.

For benthic suspension feeders, turbulent and wavy flow enhanced encounter rates for passive prey but not for prey with active swimming behavior. Higher encounter rates of passive prey did not result in higher capture or retention rates. Similarly, feeding in the presence of neighbors lowers encounter rates but retention efficiency remains the same in weak and strong wakes. This study highlights the use of realistic flow conditions, prey with swimming behavior, and in the presence of neighbors to examine passive suspension feeding in benthic organisms.



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