# ORIENTATION BEHAVIOR AND FEEDING ECOLOGY OF THE SCYPHOMEDUSA *CHRYSAORA FUSCESCENS*

by

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THESIS ABSTRACT

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Title: Orientation Behavior and Feeding Ecology of the Scyphomedusa *Chrysaora fuscescens*

*Chrysaora fuscescens* is a cnidarian scyphomedusa that occurs in the northern California Current. In this upwelling system, medusae are seasonally abundant, and individuals can ingest 10-60% of the standing stock of vulnerable zooplankton taxa per day. Yet little is known about this medusa's feeding ecology. Using laboratory pseudokreisels, *C. fuscescens* feeding rates and behavior were quantified in the presence of a controlled flow field. *C. fuscescens* collected aboard research cruises were dissected, and prey items were counted in order to calculate feeding rates and prey selectivity. In the lab, *C. fuscescens* feeding rates were not affected by shear flow, and medusa maintained position by swimming counter-current. Field work demonstrates high feeding rates and positive prey selection for nonmotile taxa. For the first time, high clearance rates of ichthyoplankton have been documented. An understanding of jellyfish behavior can help explain jellyfish distributions and trophic impacts in a productive upwelling system.

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I would like to dedicate this work to my grandmother, Ella Mae Zeman, and all of my friends who never let me forget the important things in life.

TABLE OF CONTENTS

LIST OF FIGURES

Figure Page

LIST OF TABLES

Table Page

# CHAPTER I
# GENERAL INTRODUCTION

Cnidarian jellyfish consume a variety of plankton taxa and are potential keystone predators (Arai 1997, Pauly et al. 2009). Despite their simple nervous and muscular systems, jellyfish are effective at clearing the water of potential prey (Acuna et al. 2011), can compete with pelagic fish for food resources and can restructure marine ecosystems in heavily exploited areas (Lyman et al. 2006, Purcell 2009). Review articles and food web models demonstrate the importance of jellyfish as key parts of the trophic structure in marine ecosystems (Kremer and Sullivan 2011, Brodeur et al. 2011).

Top-down control of zooplankton populations by jellyfish is demonstrated in a variety of coastal ecosystems (Matsakis and Conover 1991, Purcell 1992, Brodeur et al. 2002). Prey selection indices have shown that certain zooplankton groups are more susceptible to predation by certain types of jellyfish. For example, larvaceans and ichthyoplankton (fish eggs and larvae) can be preferentially selected over more abundant prey items (Purcell 2003, Purcell 1997). These selection pressures are important because they highlight key trophic connections and indicate which prey items may be more vulnerable. Prey selection, feeding rate data, and food web models also reveal competitive overlap with fish species (Purcell and Sturdevant 2001, Brodeur et al. 2014).

Medusae can form large aggregations of individuals at distinct physical features such as fronts or pcynoclines (Graham et al. 2003). Complex flow patterns within frontal zones accumulate buoyant particulate matter to create regions of high plankton biomass (Flint et al. 2002). This phenomenon of dense aggregations is not uncommon and is a characteristic of the spatial and temporal variability of marine plankton (McManus and Woodson, 2012). Non-random orientation at physical boundaries has been noted in mesoplankton at upwelling and downwelling fronts and in Scyphozoan medusae at tidal currents and frontal systems (Genin et al. 2005, Morris 2006, Fossette et al. 2015). Active swimming by plankton at flows associated with physical features can maintain their position in an aggregation with possible benefits including enhanced feeding, reproduction and defense (Folt and Burns 1999, Genin et al. 2005, Graham et al. 2003).

*Chrysaora fuscescens* is a large scyphomedusa in the northern California Current (NCC) system which can be found from the Gulf of Alaska to Mexico (Suchman et al. 2008, Carlton 2007). Medusae occur in large numbers off the western coast of the United States with abundances reaching 1800 L medusae per $10^5$ $m^3$ in the summer months (Shenker 1984). On smaller spatial scales, *C. fuscescens* have been shown to aggregate at fronts within the California Current (Graham 1994, Morris 2006). Diet and isotope work demonstrate the predation impact of these large jellyfish on crustacean and gelatinous zooplankton populations; adult medusae have the ability to remove 60% $d^{-1}$ of the standing stock of vulnerable taxa, and potential trophic overlap with forage fish species (Suchman et al. 2008, Brodeur et al. 2008).

*C. fuscescens* is a cruising predator: contraction and relaxation of the bell creates a characteristic flow field and vortices that bring fluid and potential prey in contact with tentacles and oral arms. The full pulsation cycle allows fluid to be brought into the subumbrellar region during contraction and subsequent relaxation entrains a large volume of water near feeding structures (Ford et al. 1997, Dabiri et al. 2005). The relationship between the rowing pulsations and prey capture has been studied in still water. However, flows that are characteristic of the natural environment likely influence prey capture by altering fluid motions around the bell and oral arms but these effects are not well-studied (Katiji et al. 2011, Hamlet and Miller 2012). For instance, *Aurelia* sp., a large Scyphozoan, will pulse asymmetrically in response to shear flow. This asymmetry between the two sides of the bell leads to stronger contractions on one side of the bell which may increase marginal bell velocities and entrain more fluid (Rakow and Graham 2006).

Laboratory experiments and field work were used to answer the following questions: (1) Does *C. fuscescens* have an increased clearance rate in shear flow, if so, (2) Are enhanced clearance rates driven by prey concentration, increased encounter in flow or a combination of the two?, (3) Does swimming in shear affect the orientation behavior of *C. fuscescens*? and, (4) What are the *in situ* feeding rates and prey selectivity of *C. fuscescens* in the northern California Current? A more complete picture of jellyfish trophic dynamics and orientation behavior is crucial especially considering increases in gelatinous zooplankton abundance in some regions due to invasions, fishing activities,

euthrophication and other anthropogenic forcings (Graham et al. 2003, Purcell et al. 2007, Richardson et al. 2009). The NCC may not represent a region of atypical jellyfish biomass, but studying *Chyrsaora* can provide baseline data for distribution patterns and important trophic relationships in a dynamic upwelling system.

# CHAPTER II
# LABORATORY CLEARANCE RATES

## INTRODUCTION

Scyphozoan medusae are ubiquitous members of the marine zooplankton and laboratory research has expanded on the importance of predator-prey interactions on feedings rates (Purcell 1997, Hansson and Kiørboe 2006b, Kremer and Sullivan 2011). Laboratory experiments reveal high feeding potential of jellyfish on a variety of zooplankton prey assemblages (Purcell 1997, Suchman and Sullivan 2000, Purcell 2009). Jellyfish feeding is highly coupled to swimming behavior. As a medusa contracts and relaxes its bell, it produces defined vortices that bring prey in contact with stinging cells on the oral arms and tentacles. Particle imaging techniques, using neutrally buoyant particles and videography, allows researchers to visualize and quantify the fluid velocities around the bell margin (Ford et al. 1997, Colin and Costello 2002). However, much of this work has been done in still water which does not take into account the turbulent environment that jellyfish inhabit. For instance, interactions between currents and jellyfish swimming have been shown to play a role in jellyfish aggregations (Rakow and Graham 2006, Fossette et al. 2015).

Medusae may be concentrated by advective flow patterns at large scale hydrographic features, such as convergent fronts. At sites of downwelling currents, strong swimming medusae may actively swim in counter-current direction in order to maintain position and not become dispersed. Accumulation would also occur if medusae swam parallel to the front as they would be entrained again by downwelling velocities. This scenario could explain the observation of *Chrysaora fuscescens* swimming in non-random directions at frontal zones (Graham 1994). Directed swimming likely maintains jellyfish in regions of fluid flow and velocity gradients. Jellyfish have exhibited asymmetrical pulsing to maintain their heading into vertical shear (Rakow and Graham 2006). Asymmetric pulsing, and the interaction of fluid flow along feeding appendages, could disrupt or enhance fluid vortices and therefore alter the feeding potential of jellyfish.

Clearance rates, or the ability of a predator to clear prey from the fluid, are useful calculations to compare feeding rates using the same prey items. Laboratory feeding studies have been conducted in either still water or flow, but the possible effects of these separate conditions on feeding rates have not been quantified (Suchman and Sullivan 2000, Titelman and Hansson 2006). In this study, I examined the effect of velocity shear and prey concentrations on the clearance potential of *C. fuscescens*. If there is a change in clearance rates, is it driven by prey concentration, fluid movement, or an interaction between the two variables?

## METHODS

### Experimental Tank and Velocity Measurements

A 120 L (70 × 38 × 76 cm) pseudokreisel was used as the experimental tank designed after Hamner (1989) (Figure 2.1). Circular flow was created by pumping water into a head tank that dispensed water through a thin layer of plastic punctured with square holes to create laminar flow at the inlet. The tank was supplied with seawater with the use of a submersible utility pump (Danner Manufacturing Inc., model 18B) that rested in a 10 gallon sump. Water was returned to the pump via an outlet flow that emptied back into the sump (Figure 2.1). Seawater was filtered through a 10 µm filter bag while the tank was filled. During still water experiments, a plug was placed in the outlet hole of the pseudokreisel to keep the tank volumes equivalent for all treatments.

For all treatments, the volume of the tank was approximately 118 L. A 100 µm mesh, located before the outlet flow, was used to contain prey in the body of the tank. Water velocities were measured in three dimensions with a Nortek Acoustic Doppler Velocimeter (ADV). The down-looking ADV probe (beam frequency: 25 Hz , sampling rate: 200 Hz) was used to take measurements in a 50 × 30 cm window located in the center of the tank where the ADV was not constrained by the tank design (Figure 2.2). In a pseudokreisel, the highest flow and shear are generated near the tank walls; therefore, this measurement window represents a region of high velocity and shear (Figure 2.3, Figure 2.4). Average velocities were measured at 4 cm intervals along nodes marked on a 1 $cm^2$ grid situated behind the pseudokreisel. Velocity measurements were processed using ExploreV 1.59 (programmer Alexander Sukhodlov, Nortek) and vector maps were

plotted in Matlab (Mathworks, R2007a). High-flow treatments were characterized by maximum flow velocity of 8.54 cm $s^{-1}$ and mid-flow treatments were characterized by maximum velocity of 4.17 cm $s^{-1}$. (Figure 2.3, Figure 2.4). Maximum flow velocities were constrained by the minimum and maximum flow rates that the medusae could withstand and still exhibit 'normal' behavior. These flow conditions are also within the range of velocities encountered in the California Current system (Woodson et al. 2009; McClatchie et al. 2012). Vertical shear (S) was calculated from ADV measurements as,

$$S = \delta w / \delta x$$

where w is water velocity in z-axis direction and x is distance on the x-axis. Average shear rate was 0.30 $s^{-1}$ in high flow (max: 8.54 cm $s^{-1}$) and 0.16 $s^{-1}$ in mid-flow (max: 4.14 cm $s^{-1}$) conditions (Figure 2.3, Figure 2.4).

Subsampling Prey Items

Experimental prey items, 2-day old *Artemia* nauplii, were subsampled from a 1 L beaker with a 1 mL disposable pipette. *Artemia* are not natural prey items, but are often used in feeding studies because of their ease to culture and similarity to crustacean prey (Clifford and Cargo 1978). A bubbler was placed in the 1 L beaker to maintain a homogenous prey distribution. Upon removal of the air stone, a 1 mL subsample was pipetted from the middle of the beaker and nauplii were counted. This subsampling technique was repeated 10 times for each treatment and for both high (506 *Artemia* $L^{-1}$) and low (57 *Artemia* $L^{-1}$) prey concentrations. Lower prey concentrations represent a realistic range of prey concentrations in the field and the high prey concentration accounts for high satiation potential of coelenterates (Clifford and Cargo 1978, Hansson and Kiørboe 2006).

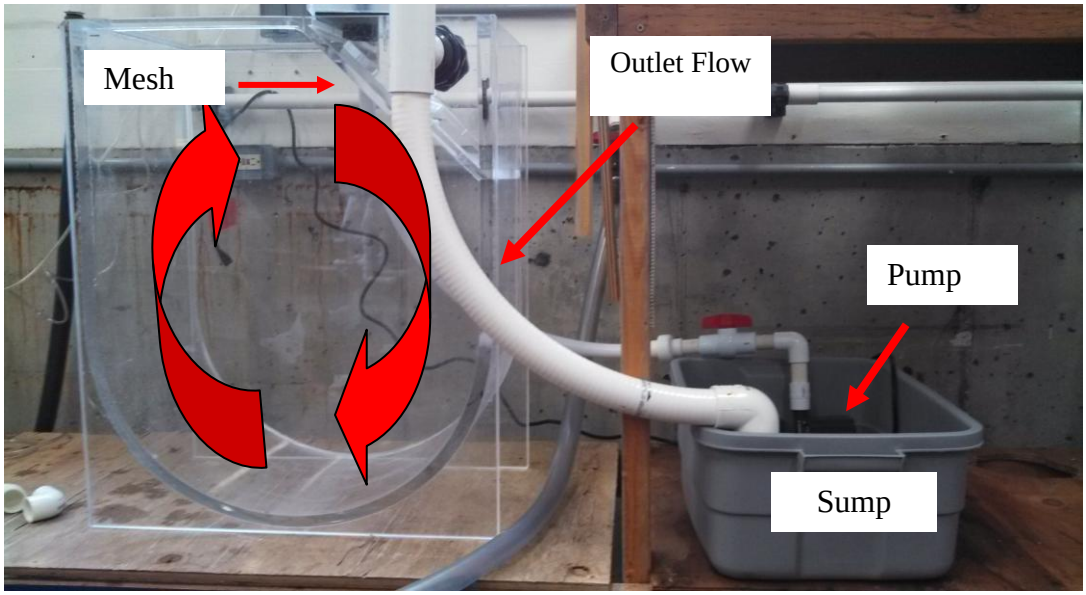


Figure 2.1. Layout of 120 L pseudokreisel used for *C. fuscescens* orientation and feeding experiments. Red arrows represent general flow patterns in the tank created by pumping water into the head tank and through plastic material punctured with square holes.

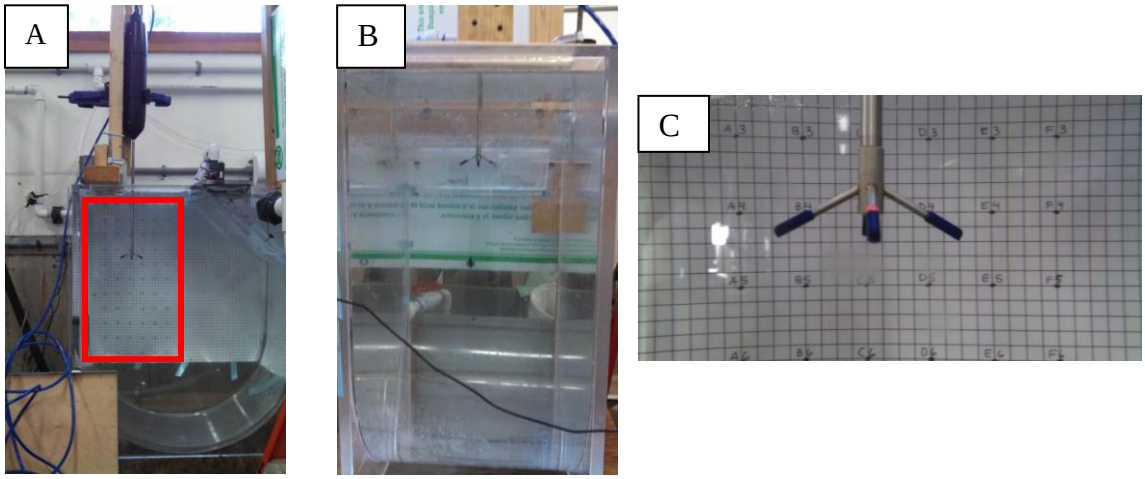


Figure 2.2. (A) Set-up of ADV measurements in experimental pseudokreisel with (B) a view from the side of the tank showing placement of ADV probe-head and (C) an up-close view of probe and 1 $cm^2$ grid. The red rectangle represents the approximate location of the 50 × 30 cm measurement area where ADV measurements were taken.

Maintaining Medusae

Wild caught *Chrysaora fuscescens* were housed in large aquaria at the Oregon Coast Aquarium in Newport, Oregon. Jellies were starved for 16-22 hours before feeding experiments. Thirteen medusae, which ranged in size from 6 to 9 cm, were used in the feeding experiments.

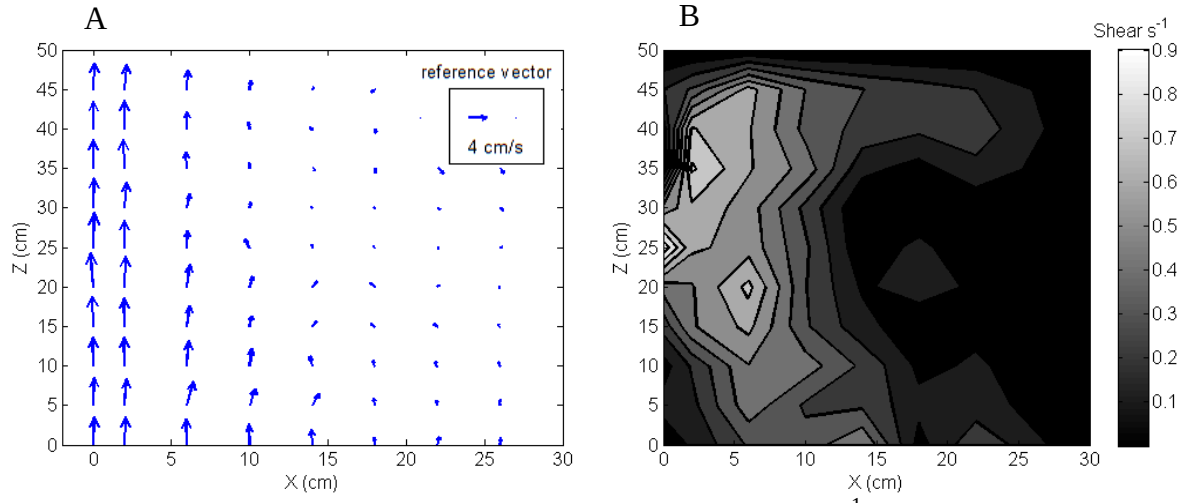


Figure 2.3. Velocity vector map (A) in high-flow (max: 8.84 cm $s^{-1}$) using the 50 × 30 cm measurement window as working section of the tank. Contour map of shear stress (B) calculated from velocity measurements.

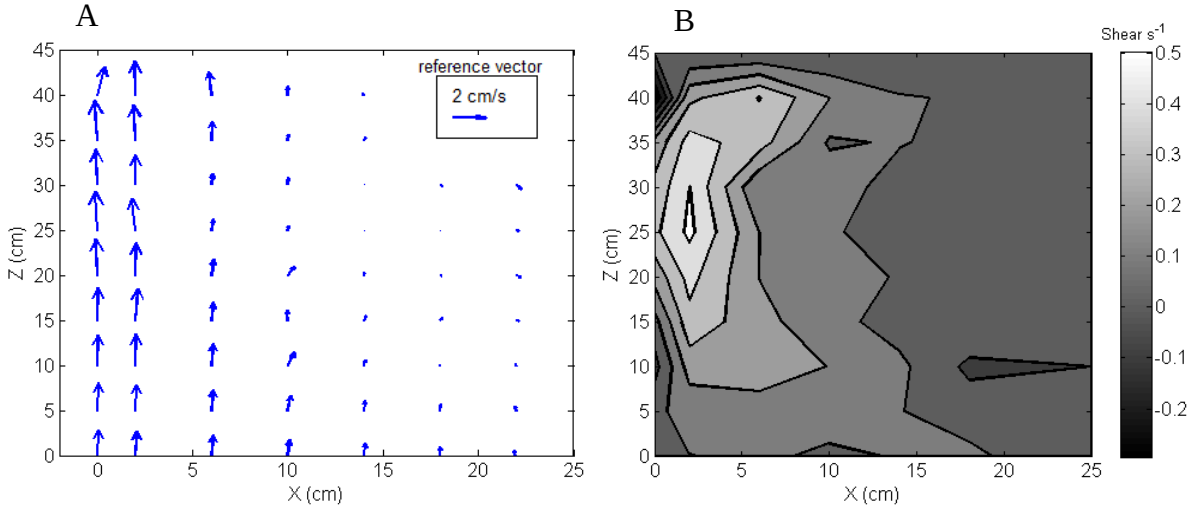


Figure 2.4. Velocity vector map (A) in medium-flow (max: 4.14 cm $s^{-1}$) using the 50 × 30 cm measurement window as working section of the tank. Contour map of shear stress (B) calculated from velocity measurements.

Clearance Rate Experiments

Studies by Suchman and Sullivan (2000), Titelman and Hansson (2006), and Clifford and Cargo (1978) were used as guides for experimental design and analysis. Clearance rate experiments were conducted at the Oregon Coast Aquarium in winter 2014. Five treatments, with two prey and three flow regimes, were used to assess the effect of flow and prey concentration on feeding rates (Table 2.1). Prior to the start of each experiment, an individual medusa was placed in the tank and monitored for 5 min to allow the animal to acclimate to the tank. If the medusa was actively pulsing, *Artemia* were placed into the tank and black, plastic bags were wrapped around the tank to keep out ambient light. In control experiments, prey distributions were examined by eye to ensure that *Artemia* were evenly distributed in the tank.

The medusa was allowed to feed for one hour and was observed every 10 min to check if on behavior of jelly. The behavior of the medusa was observed to ensure that individuals were swimming and not remaining motionless in the tank. After one hour, the plastic was removed and the medusa was quickly dipped from the surface a 2 L container. Upon removal, the medusa was rinsed with fresh seawater to remove prey items adhering to the outside of the medusa; these prey items were then returned to the experimental tank. The medusa was returned to holding tanks and used for subsequent treatments. The water in the pseudokreisel and sump was then siphoned through a 63 µm sieve. In the high-flow treatments, prey escaped through the 100 µm mesh and were lodged in a 10 µm filter bag that was also rinsed and cleaned. The uneaten prey were transferred to a 1 L beaker for subsequent subsampling. Controls were conducted for each treatment to determine that 98% of nauplii were retained using experimental protocol. Each medusa was observed under multiple conditions. A repeated measure design was implemented so that 13 medusae were used in each of the five treatments (Davis, 2002).
Ingestion rate (I) was calculated as,

$$I = C_{in} - C_{out} / t$$

where $C_{out}$ is prey concentration ($L^{-1}$) at end of the experiment, $C_{in}$ is prey concentration ($L^{-1}$) at beginning of experiment, and t is incubation time (h). A linear model was employed since food reduction was less than 50% (Båmstedt et al. 2000).

Clearance rate (F) was determined with the following equation:

$$F = V/t \times \ln(C_{in}/C_{out})$$

where V (L) is volume of tank, $C_{out}$ is prey concentrations ($L^{-1}$) at end of experiment, $C_{in}$ is prey concentration ($L^{-1}$) at beginning of experiment, and t is incubation time (h) (Titelman and Hansson 2006).

Table 2.1. Summary of velocity measurements, shear rates, prey concentrations and number of medusae used for feeding rate experiments.

| Maximum Flow (cm $s^{-1}$) | Maximum Shear ($s^{-1}$) | Mean *Artemia* concentration ($L^{-1}$) | Total medusa used in experiment |
|---|---|---|---|
| Still Water | na | 55 | 9 |
| Still Water | na | 502 | 13 |
| 4.14 | 0.37 | 509 | 5 |
| 8.54 | 0.97 | 60 | 10 |
| 8.54 | 0.97 | 508 | 13 |

Statistics

Using R 2.15 (R Core Team 2013), multivariate repeated measures analysis of variance (MANOVA) was used to evaluate the effect of flow and prey concentration on clearance rate. Simple linear regression models were employed to highlight patterns in clearance and ingestion rates with regard to prey density and bell diameter.

## RESULTS

Medusae 3, 4, 5, and 6 were not used in all of the treatments, either because they died during the course of the experiments, or they were exhibiting poor health. Medium flow (max: 4.14 cm $s^{-1}$) treatments were suspended because medusae were dying and I decided to maximize data points for the two extreme flow regimes (still water and high flow). There was large variability in clearances rates with a minimum of 12 L $h^{-1}$ and a maximum of 114 L $h^{-1}$ (Figure 2.5). During periodic checks, medusae were actively pulsing in the tank. Medusae were not dissected to calculate feeding rates, but *Artemia* were visible inside the guts and in patches on oral arms, demonstrating that ingestion was occurring.

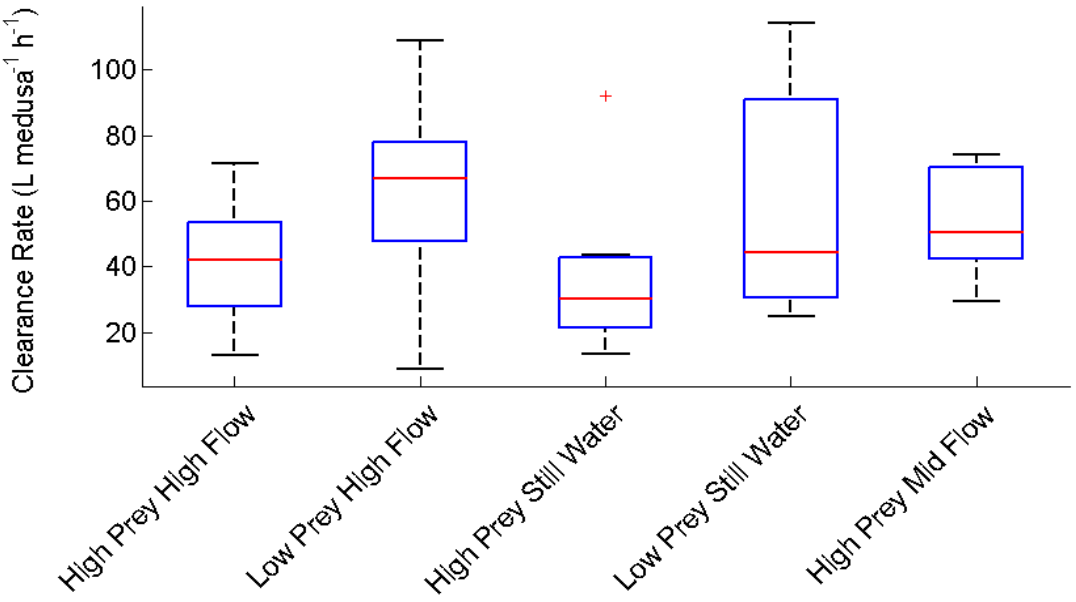


Figure 2.5. Box plots of measured clearance rates of *C. fuscescens*. The red line represents the median and whiskers represent the maximum and minimums. The top and bottom of the blue box are 25% and 75% percentiles, respectively. Outliers are represented as individual points.

Since the data violated the assumption of sphericity (p=0.006), a multivariate model was used to analyze effects of prey concentration and flow velocity on clearance rate. Clearance rates in low prey concentrations were significantly higher than in high prey concentrations ($F_{1,8}$=5.5; $p$=<0.05) which could be attributed to prey saturation (low prey, high-flow: mean=64; high prey, still water: mean=35; high prey, high-flow: mean= 42). There was no significant main effect of flow ($F_{1,8}$=1.57; $p$=0.25) or an interaction between flow and prey ($F$=0.42$_{1,8}$; $p$=0.53) (Figure 2.6, Table 2.2). Ingestion rate data were pooled to determine that ingestion rate increased linearly with prey density (I = 28.838 *Artemia*/L + 1173.9, $R^2$ = 0.68, $p$<0.001, df=43 ). There was no significant linear relationship between clearance rates and bell diameter (F=4.8; df=11, $p$=0.6).

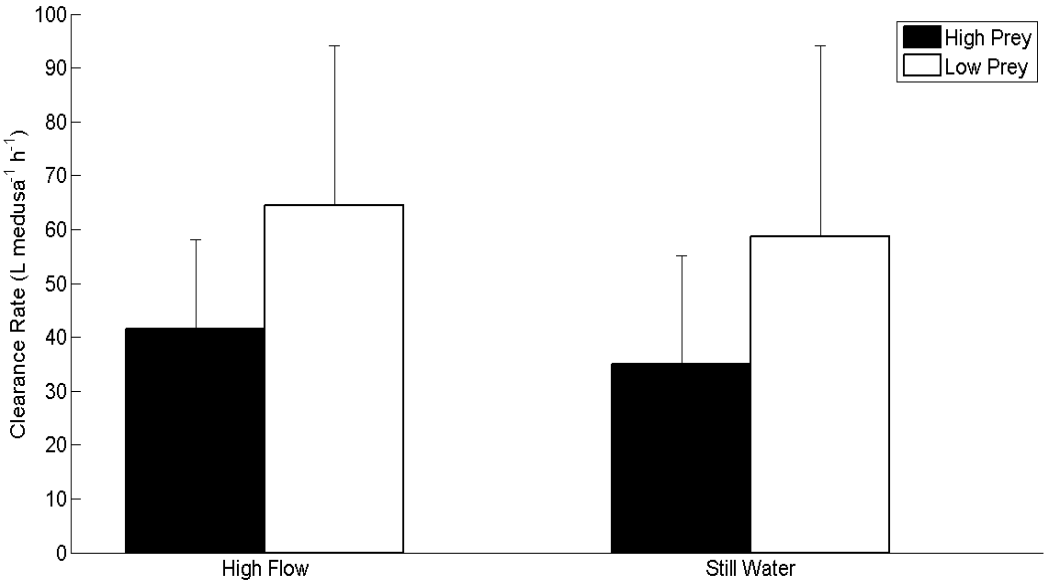


Figure 2.6. Average clearance rates from four experimental trials with high-flow (max: 8.84 cm s$^{-1}$) and still water and high prey (mean = 505 *Artemia* L$^{-1}$) and low prey (mean= 58 *Artemia* L$^{-1}$) concentrations (N=9). Error bars represent standard deviation.

Table 2.2. Results of Type III Repeated Measures MANOVA.

| | *F* stat. | df | *p* value |
|---|---|---|---|
| Flow Rate | 1.57 | 8 | 0.25 |
| Prey Concentration* | 5.50 | 8 | 0.05 |
| Flow × Prey | 0.42 | 8 | 0.54 |

*represents significant effect

## DISCUSSION

These results represent the first calculated feeding rates for *C. fuscescens* under laboratory conditions. In previous studies with scyphomedusae, the average clearance rates on *Artemia* range from 60 L $cm^{-1}$ $day^{-1}$ for *Chrysaora quinquecirrha* (Feigenbaum et al. 1982) and 41 L $cm^{-1}$ $day^{-1}$ for *Pelgia noctiluca* (Morand et al. 1987). Even though feeding rate variability was common, these previous studies present lower clearance rates than *C. fuscescens* (mean=120 L $cm^{-1}$ $day^{-1}$). These high clearance rates for *C. fuscescens* could be explained by a variety of factors: tank volume, experimental design, and capture dynamics between predator and prey. The volume of the incubation tank is an important consideration because *Chrysaora* are cruising, tentaculate predators that need large, unobstructed volumes of water in order to display natural behaviors. Calculations suggest that using an experimental tank that is 15,000 times the biovolume of the study organism would produce reliable results (Toonen and Chia 1993, Hansson 2006). A 4-cm *Chrysaora*, with approximate biovolume of 165 mL, would need an appropriate volume tank >2000 L (Purcell 1992). The larger tank volume (120 L) in this study could explain the increase in clearance rates as compared to previous studies that used 20-25 L tanks (Feigenbaum et al. 1982). Counting prey items also adds uncertainty to calculated feeding rates because of the inherent error in sub-sampling (van Guelpen et al. 1982). Also, starved jellyfish in high prey environments will exhibit elevated clearance rates (Hansson and Kiørboe 2006a).

The third factor is tied to the ability of the predator to encounter and capture prey. Medusae were not continually observed in this study so it is difficult to address differences in behavior. For example, *C. fuscescens* may exhibit higher feeding rates because of a phenotypic trait that increases flux of fluid into subumbreller region or more efficient handling of prey during capture events (Ford et al. 1997, Hansson and Kiørboe 2006b). Jellyfish generate flow patterns that depend on moving a large volume of water to maximize prey encounter. Therefore, altering pulsations could decrease or increase the encounter radius. It may also constrain the selectivity of prey as the fluid velocity generated by pulsing will place a limit on prey that have fast or slow escape responses (Suchman & Sullivan 1998, Hansson & Kiorbøe 2006). It is apparent that *C. fuscescens* can clear large volumes of crustacean plankton. These baseline feeding rates are also useful as part of larger datasets used to create predictive models of feeding rates (Purcell 2009).

In pseudokreisel experiments, medusae are encountering velocity gradients that could interrupt eddies around the bell margin and feeding appendages. Results show that feeding in this flow has no effect on clearance rates of *C. fuscescens*. Experiments in Chapter III demonstrate the counter-current orientation behavior of *C. fuscescens* in pseudokreisels. Assuming this behavior in clearance rate experiments, medusae are maintaining their position and consistently encountering volumes of fluid containing non-depleted prey items. The artificial nature of the pseudokreisel creates a homogenous prey distribution, in an enclosed volume, which could allow for high encounter rates that are similar in flow and still water. Clearance rates were significantly decreased in high prey concentrations which could be attributed to prey saturation (Hansson et al. 2005) or the possibility of prey-dependent changes in swimming at different prey concentrations. *Chrysaora quinquecirrha* decreased pulsation rate and increased velocities in response to prey, which demonstrates that feeding rates are likely altered in presence of prey but does not explain if prey concentrations were a factor (Matoanoski et al. 2001).

# CHAPTER III
# ORIENTATION BEHAVIOR

## INTRODUCTION

Jellyfish aggregations are defined as an accumulation of individuals due to passive current drifting, behavioral modification on part of the medusa, or an interaction of these two factors. Large scale hydrographic features, such as upwelling fronts or eddies, can retain and concentrate planktonic organisms. Aggregations are a common phenomena and seen in many gelatinous clades (Lucas and Dawson 2014). Scyphomedusae are often observed in dense aggregations and studies suggest that swimming in a non-random direction may contribute to maintenance of these aggregations. Medusae in aggregations have been shown to orient to a variety of physical factors including sun position (Hamner et al. 1994) circulation patterns (Zavodnik 1987, Purcell et al. 2000, Fossette et al. 2015), Langmuir cells (Hamner and Schneider 1986, Larson 1992), haloclines (Graham et.al. 2003), wind-driven waves (Shanks and Graham 1987) and fronts (Graham 1994).

*Chrysaora fuscescens* is known to form large aggregations of individuals at frontal features (Graham et al. 2001). Fronts are classified as boundaries between two water masses that differ in hydrographic properties such as temperature or salinity. The formation and evolution of fronts is spatially and temporally complex and can be associated with upwelling events, topography, river plumes, etc. The associated convergence and divergence of fluid flow can entrain particulate and animals creating regions of enhanced plankton biomass (Cromwell and Reid 1955, Federov 1986, Olson et al. 1994). *In situ* studies of *C. fuscescens* in the California Current system demonstrate active directional swimming at convergent fronts. At upwelling shadows in Monterey Bay, CA, *C. fuscescens* occurs in dense patches that can be explained by physical forcing and swimming behavior of the medusae. In this scenario, medusae remain concentrated at convergent zones because of active vertical swimming matching downwelling velocities of frontal flow (Graham 1994). ROV video transects at convergent fronts support directed swimming behavior; medusae are seen orienting northward on the southern side

of the front and orienting southward on the northern side of the front. The medusae swim perpendicular to the greatest flow which counteracts dispersive currents and maintains aggregations along the front (Morris 2006). The importance of physical processes should not be understated and on a local scale zooplankton behavior plays a key role in maintaining these aggregations (Hamner 2001).

Laboratory studies with *Aurelia* sp. orienting into shear flow supports orientation behavior in the field. Shear stress across the bell surface initiated asymmetric pulsing behavior. Asymmetric pulsing allowed the medusa to maintain position in the flow field and this behavior may be common in other Scyphozoans (Rakow and Graham 2006, Purcell et al. 2000). Further inquiry into the role of velocity shear as a possible cue to orient to flow is a logical step as velocity gradients are a fundamental physical characteristic of frontal convergences (Cromwell and Reid 1956). Exploring *C. fuscescens* interactions with flow fields will lead to a greater understanding of jellyfish distribution patterns. This is worthwhile as *Chrysaora* inhabit a highly productive upwelling system, overlap in time and space with lucrative commercial fisheries and we are only recently gaining insights into their ecology and behavior (Suchman et al. 2008, Suchman et al. 2012, Brodeur et al. 2014, Conley and Sutherland 2015). *Chrysaora* in the NCC may not be demonstrating irregular population trends, but understanding how jellyfish interact with fluid flow can identify possible areas of increased jellyfish biomass. These behaviors may translate to other Scyphozoan populations and be useful to consider when discussing the potential increase in jellyfish biomass in heavily exploited marine ecosystems (Purcell et al. 2007, Condon et al. 2012, Purcell 2012).

Few studies demonstrate how scyphomedusae behaviorally orient at small scales in response to a controlled environmental cue. I used flow generated in a laboratory pseudokreisel as a cue for the orientation behavior of individual *C. fuscescens.* Does *C.fuscescens* swim in a non-random direction in response to shear flow, if so, is this swimming orientation different than in still water?

## METHODS

Experimental Tank and Velocity Measurements

Behavior trials were conducted in a 120 L (70 × 38 × 76 cm) pseudokreisel based on the design of Hamner (1989). Pseudokreisels offer unique tank designs for delicate gelatinous taxa by creating continuous circular flow and minimizing contact with walls and outflow (Raskoff et al. 2003, Chapter II: Figure 2.1).Orientation behavior of *C. fuscescens* to current flow was assessed in three different flow treatments: still water, medium flow (max.:4.14 cm $s^{-1}$), and high flow (max.:8.84 cm $s^{-1}$). Flow levels are comparable to horizontal frontal velocities from the field (McClathchie et al. 2012, Graham and Largier 1997). The average shear rates were 0.16 $s^{-1}$ for medium flow and 0.30 $s^{-1}$ for high flow. Flow velocities were measured with an Acoustic Doppler Velocimeter (ADV) in a 50 × 30 cm rectangular located in the middle of the pseudokreisel (Chapter II: Figure 2.2). The measurement window became the working section of the tank and was representative of flow in the pseudokreisel. Flow in the pseudokreisel created high velocity and shear along the walls and minimal flow in the center of tank (Chapter II: Figure 2.3). Refer to Chapter II for methodology details. Behavior was recorded at 30 frames per second with a digital video camera (Sony HDR-CX560V Handycam) that was mounted in front of the pseudokreisel. A 1-$cm^2$ grid placed behind the tank provided a spatial scale for video analysis. Individual medusae were placed in the pseudokreisel with a fixed concentration of prey (10 *Artemia* $L^{-1}$) to stimulate pulsing behavior (Bailey and Batty 1983). *Artemia* are not natural prey items, but are often used to quantify feeding rates in the laboratory (Clifford and Cargo 1978). Each medusa was videotaped for 10 minutes at each flow regime (still water, medium flow: 4.14 cm $s^{-1}$, high flow: 8.54 cm $s^{-1)}$. Prior to commencing video recording, medusae were observed in no flow to ensure that they were pulsing normally. Medusae were removed from the tank for 5 minutes between flow treatments to allow flow levels to reach a steady state and to allow any air bubbles to escape.

## Angle Measurements

Swimming angles were measured from each 10-minute video in Image J (U. S. National Institutes of Health, USA). Angles were imposed on a circular plot with a reference vertical axis running from bottom of tank (270°) to top of tank (90°). For flow treatments, angles were only measured when the bell was in the 50 × 30 cm window in which ADV velocity measurements were collected. Refer to methodology in Chapter II. This measurement window represents an area of high velocity and high shear created by the circular flow in the tank (Chapter II: Figure 2.3). During flow treatments, medusae were not always swimming in the working section of the tank. To maximize data points, measurements were taken every one second (30 frames). To maintain consistent frame numbers for analysis, medusae in still water treatments were monitored throughout the entire tank and angle measurements were taken every three seconds (90 frames). Measurements were not collected in frames when the medusa was not swimming in a vertical plane or touching the walls of the pseudokreisel.

## Statistics

Because of the directional nature of the data, circular statistics (Batschelet 1981) were employed to describe the data and compare treatments. Uniformity of angle direction was analyzed for each treatment using Rao's spacing test, as provided in Matlab CircStat toolbox (Berens 2009). Based on our preliminary observations of medusae swimming in pseudokreisels, we predicted that medusae would show a preference for swimming vertically with aboral surface oriented either directly upward or downward. Under this assumption, the predicted distribution was bimodal and therefore, the method of doubling the angles was applied to transform data into a unimodal sample (Batschelet 1981). Watson's $U^2$ test was then used to test for differences in swimming direction between treatments.

## RESULTS

### Randomness and Swimming Angles

Assuming a bimodal sample, the distribution of swimming means were non-random in still water (N=6, $U$=242°, $U_{0.05}$=180°). There was no significant difference in mean orientation between high flow and medium flow samples ($U^2_{0.05,6,6}$=0.0396); therefore, data from the medium and high flow treatments were pooled. Medusae were non-randomly distributed in flow (N=12, $U$=212°, $U_{0.05}$ = 180°, Table 3.1). There was a significant difference in swimming orientation between flow and still treatments ($U^2_{0.05,12,6}$=0.3607, mean still water = 75°, mean flow=263°, Table 3.2).

Table 3.1. Results from Rao's spacing test to determine randomness of distribution. If $U>U_{crit}$, then $H_0$ can be rejected.

| Treatment | N | U stat. | $U_{crit}$ |
|---|---|---|---|
| Still Water* | 6 | 242° | 180° |
| Flow* | 12 | 212° | 180° |

*indicates significance at α=0.05

Table 3.2. Results for Watson's $U^2$ test to determine difference in swimming direction. If $U^2 > U_{crit}$, then $H_0$ can be rejected.

| Treatments | Watson's $U^2$ | $U_{0.05,n1,n2}$ |
|---|---|---|
| Medium Flow vs. High-Flow | $U^2$=0.04 | $U_{crit}$ = 0.21 |
| Flow vs. Still Water* | $U^2$ = 0.36 | $U_{crit}$ = 0.28 |

*indicates significant difference

### Medusae Behavior

During flow treatments, medusae swam consistently in a vertical orientation either with or against bulk flow. This behavior maintained a medusa's position near regions of the tank with maximum velocity and shear. Though medusae periodically

swam horizontally through the center of the tank where flow velocities were minimal, as they approached the walls, they shifted to a vertical orientation due to active swimming against the flow. Swimming direction was between 180° and 360° in 86% of the analyzed frames. Individual medusae were filmed swimming in vertical positions at 90° and 270°. Other angle measurements, away from the vertical (90° and 270°), occurred when medusae were shifting position. In flow treatments, medusae spent the majority of the time pulsing nearly vertically downward (mean=263°, Figure 3.1). On the other side of the tank, medusae demonstrated the same orientation behavior by swimming upward against the bulk flow.

In still water, medusae swam vertically at the top or bottom of the tank and seldom swam though the center of the tank. This behavior created a bimodal distribution of swimming angles (Figure 3.1). Medusae rarely changed position once they achieved a certain heading. Often, individuals in still water swam in horizontal circular paths at the bottom of the tank and these angles were not analyzed. Medusae in still water maintained a vertical heading at the water's surface (Figure 3.1).

## DISCUSSION

In laboratory experiments, *C. fuscescens* are able to actively orient and maintain position in flow velocities that they would encounter in the California Current system (Woodson et al. 2009). Swimming direction in flow was significantly different then medusae swimming in still water. Even when the medusae were not in the 50 × 30 cm measurement grid, they were pulsing parallel to water flow in another section of the tank. Medusae were generally swimming counter-current and maintaining a nearly vertical heading, even at the highest flow velocity (Figure 3.2). In still water, *C. fuscescens* frequented either the bottom or the top of the tank, creating a non-random distribution in the pseudokreisel. This behavior has been noted in other scyphozoans in laboratory tanks and shallow waters (Zavodnik 1987, Matanoski et al. 2001). This suggests that *C. fuscescens* may favor swimming with aboral surface in a vertical position. However, the artificial nature of the pseudokreisel, e.g. wall effects and minimal fluid flow, may have influenced medusae behavior in the still water experiments.

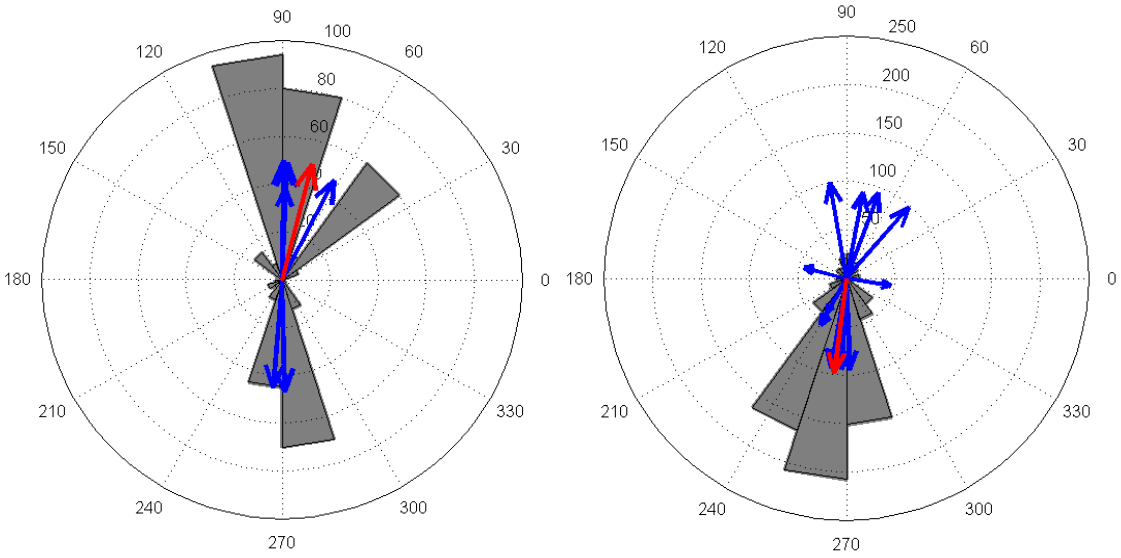


Figure 3.1. Circular plots of *C. fuscscens* swimming angles in A) still water and B) flow treatments. Vertical swimming upward and downward is indicated by 90° and 270°, respectively. Instantaneous swimming angles from all individuals are plotted in gray. Labels on the dashed circular lines indicate the number of angles measured. Blue vector arrows represent the mean directions of each individual. Longer vectors indicate less dispersion around the mean for each individual medusa in still water (N=6) and flow (N=12). The red vector is the grand mean direction and grand mean vector length based on all individuals.

These findings complement previous field work that measured current direction and compass headings of large scyphozoans *in situ*. Medusae were distributed non-randomly and swam countercurrent in response to tidal currents (Fossette et al. 2015). This orientation behavior observed in laboratory pseudokreisels could explain how medusae are orienting at fronts in response to downwelling currents. As medusae are passively entrained by convergent flow at a frontal system, they may counter the downwelling velocities by swimming vertically upward. If the medusa's swimming speed is strong enough to counter the plunging velocities, this behavior could accumulate and

maintain medusae in a band near the surface. The importance of active swimming in aggregation maintenance is inferred from previous studies (Graham 1994) and model scenarios (Fossette et al. 2015, Franks 1992).

Rheotaxis, or behavioral orientation to flow, is a well-studied occurrence in taxonomically diverse aquatic organisms demonstrating its importance for maintaining individuals in flow. Researchers speculate that rheotaxtic behavior could be a response to current shear as demonstrated in orientation studies with copepods, fish, and sea turtles (Montgomery et al. 1997, Genin et al. 2005, Kobayashi et al. 2014). Shear mediated behavior is seen in *Aurelia* sp. as it maintains position in shear flow by pulsing asymmetrically. This righting behavior has not been studied in *Chrysaora*, but they could employ a similar strategy as Scyphozoans share similar sensory organs. *C. fuscescens* has eight rhopalia arranged along the bell margin with statocysts and 'plates' of sensory cells that allow medusae to detect and change orientation with respect to gravity (Sotje et al. 2011). The neuronal bases for these behaviors are not fully understood but future work could explain mechanisms as the complexity of jellyfish nervous systems become more appreciated (Satterlie 2010, Katsuki and Greenspan 2013). For instance, discoveries with the large nudibranch, *Tritonia tetraquetra*, show pedal neurons that are directly sensing and mediating orientation into flow (Murray and Willows 1995).

Aggregations of medusae are mostly limited to the class Scyphozoa and potential aggregators can be predicted based on phenotypic traits; such as alteration of generations and prey preference (Hamner and Dawson 2009). This suggests a possible benefit for jellyfish to occur en masse. Feeding and reproduction are two essential activities for species survival. These medusae inhabit an environment where resources, including prey and conspecifics, are patchy (Mackas et al. 1985). Medusae would benefit from accumulating in areas of high prey concentrations, which is an often-cited property of convergent zones (Franks 1992). Aggregations could be beneficial for feeding on temporary time scales but jellyfish also have high satiation and clearance rates (Chapter II, Acuna et al. 2011) which could deplete zooplankton stocks. For example, sampling at large *Aurelia* blooms showed decreased zooplankton concentrations within the bloom versus background ocean conditions (Uye et al. 2003). Aggregations could also be

advantageous for reproduction as *Chrysaora* is a broadcast spawner that benefits from large accumulations of conspecifics (Uye et al. 2003, Widmer 2008).

t=0 t=2 t=4

Figure 3.2. Sequence of frames showing *C. fuscescens* orienting into high flow (max: 8.84 cm $s^{1}$).

# CHAPTER IV

# *IN SITU* FEEDING ECOLOGY OF *CHRYSAORA FUSCESCENS*

## INTRODUCTION

The ecological role of gelatinous zooplankton as predators and competitors in marine ecosystems has become a significant field of study in recent years (Purcell 1997, Sullivan and Kremer 2011). *In situ* gut content analysis is a standard technique used to resolve diet compositions of pelagic cnidarians (Purcell 1997, Suchman et al. 2008). More importantly, data from the field can be used to look for trends and patterns in trophic relationships. Documented predation impacts of cruising gelatinous predators on zooplankton populations vary between and within prey taxa of interest. Predation work on large Scyphozoans in coastal ecosystems illustrates their potential to remove up to 25% $day^{-1}$ of mesozooplankton biomass (Purcell 1992, Olesen 1995, Uye and Shimauchi 2005). On the other hand, lower predation rates of < 1% $day^{-1}$ are documented on copepod stocks in Prince William Sound and the North Sea (Purcell 2003, Hansson et al. 2005). Notably, predation potential on fish early life stages can be as high as 30% $day^{-1}$ but lower rates are also frequent (0-3% $h^{-1}$) (Purcell et al. 1994, Purcell et al. 2014). Variability in calculated feeding rates is not uncommon, but there are distinct trends toward high clearance rates for soft-bodied taxa and lower clearance rates of larger, more abundant zooplankton such as copepods (Purcell 2003).

Prey selectivity occurs when prey are ingested in different proportions than the background plankton (Pearre 1982). Prey selection can be attributed to active pursuit by the predator or to differential prey vulnerability based on direct encounter or capture events (Greene 1986). In gelatinous species, encounter and capture events can be constrained by several factors: direct handling, marginal bell velocities, nematocyst type, chemical cues, and prey escape responses (Purcell 1997). Even as non-visual predators, large Scyphozoans preferentially ingest prey taxa in different proportions than the ambient prey field (Suchman and Sullivan 1998, Purcell and Sturdevant 2001, Grahman and Kroutil 2001). Understanding prey selectivity is essential for recognizing vulnerable taxa and the potential for cascading effects on marine food web structure.

*Chrysaora fuscescens* is the most abundant cnidarian scyphomedusa in the northern California Current and has the potential to deplete 1-12% $day^{-1}$ of zooplankton standing stocks and can consume up to 60% $day^{-1}$ of euphuasiid eggs standing stock (Suchman and Brodeur 2005, Suchman et al. 2005). These studies document high potential for direct predation on zooplankton prey and the possibility of competition, especially with planktivorous fish species. As such a ubiquitous jellyfish in the summer months, previous work only represents a small sample size (N=31) spread over 2 years. The observed results are intriguing, making it worthwhile to continue to monitor and sample these medusae in this productive upwelling center. In this study, we opportunistically sampled *C. fuscescens* medusae in the Northeast Pacific during summer 2014. Gut content analysis was performed to calculate clearance and ingestion rates in conjunction with prey electivity and carbon ingestion calculations.

## METHODS

### Medusae and Plankton Collection

*Chrysaora fuscescens* medusae used for gut content analysis were dip-netted at 13 survey stations from Brookings, Oregon to Queets River, Washington during June, July, and September 2014 (Table 4.1; Figure 4.1). Captured medusae were immediately placed in 2 L containers with 5% buffered formalin solution. Prey were enumerated with a Nikon SMZ1000 stereoscope by dissecting medusae and identifying prey in oral arms, tentacles, gastric pouches, and regurgitated in formalin. Depending on sampling constraints, horizontal or vertical plankton tows were used to quantify the ambient zooplankton abundance at each station. Zooplankton prey were categorized into taxonomic groups based on class or order. At stations 1-3, plankton assemblages were collected with 100-um mesh ring net towed horizontally at the surface for approximately 5 min. At all other stations (4-12), vertical tows with a 202 µm mesh were taken from 5 m off the bottom to the surface. A calibrated TSK Flowmeter was used for vertical tows to calculate the volume filtered. Zooplankton samples were preserved in 5% buffered formalin. Plankton samples were subsampled using a Hensen-Stempel pipette to obtain at

least two 1-mL subsamples to quantify zooplankton abundance. Prey were counted and identified to the same taxonomic groupings as medusae guts.

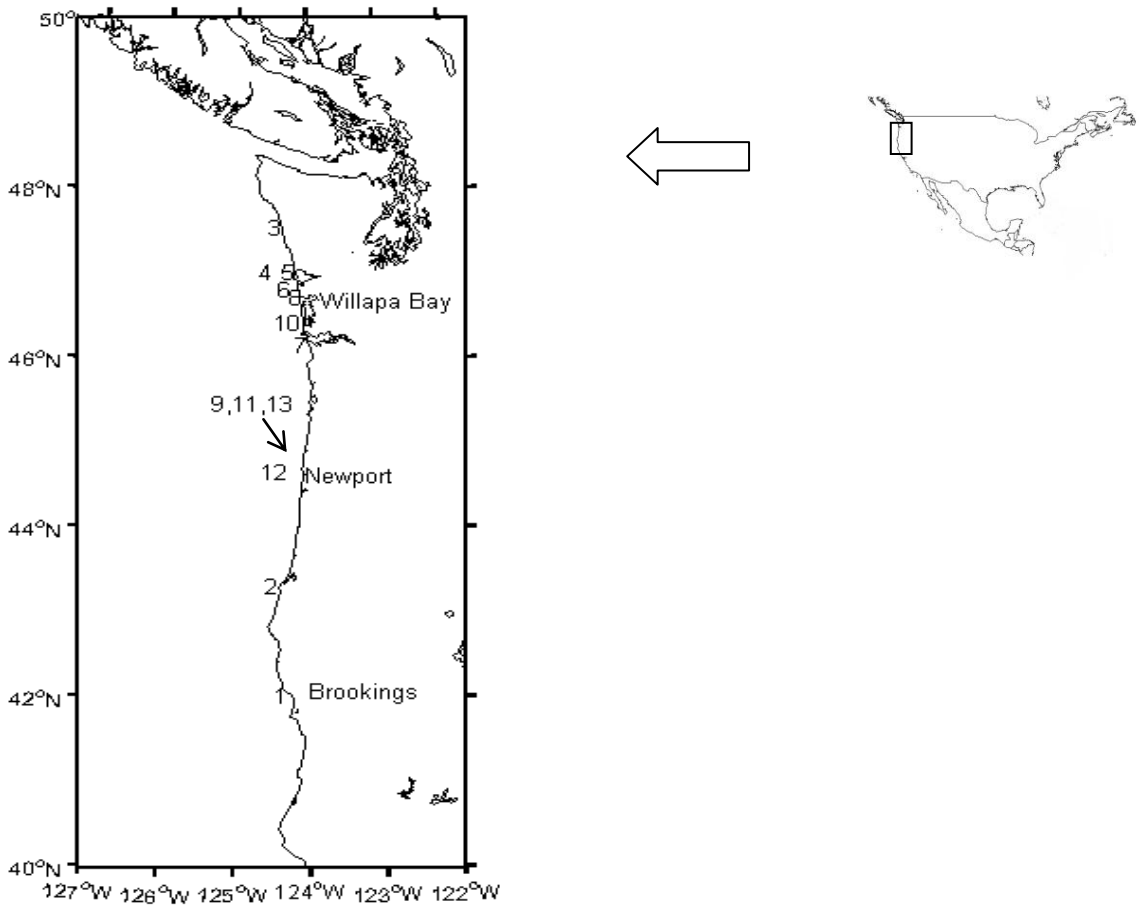


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Figure 4.1. Map of study site with stations marked by numbers where *C. fuscescens* andplankton tows were collected in June, July and September 2014. Refer to Table 4.1 for a summary of each station.

Table 4.1 Summary of *C. fuscescens* collection data from 13 sample stations in June, July, and September 2014. Refer to Figure 4.1 for map of study site. na corresponds to plankton tows with no corresponding flowmeter data.

| Station. | Location | Collection Date | Surface Temp. (°C) | N | Bell Diameter (cm ± SD) | Prey Ingested (N ± SD) | Zooplankton Density ($m^{-3}$ ± SD) |
|---|---|---|---|---|---|---|---|
| 1 | 42.00° N, 124.39° W | June 19 | 10.8 | 1 | 17 | 10 | na |
| 2 | 43.29° N, 124.17° W | June 21 | 10.5 | 1 | 15 | 30 | na |
| 3 | 47.53° N, 124.42° W | June 22 | 13.4 | 3 | 8 ± 1 | 355 ± 297 | 9000 ± 1000 |
| 4 | 47.00° N, 124.56° W | June 23 | 13.4 | 1 | 16 | 20 | 4000 ± 300 |
| 5 | 47.00° N, 124.24° W | June 23 | 13.1 | 1 | 15 | 7025 | 4000 ± 300 |
| 6 | 46.68° N, 124.29° W | June 24 | 15.1 | 5 | 15 ± 3 | 12 ± 4 | 3000 ± 200 |
| 7 | 46.14° N, 124.07° W | June 25 | 12.5 | 3 | 14 ± 2 | 502 ± 180 | 11000 ± 2000 |
| 8 | 46.64° N, 124.19° W | June 24 | 12.1 | 1 | 7 | 20 | 13000 ±800 |
| 9 | 44.65° N, 124.19° W | June 27 | 11.6 | 1 | 23 | 7251 | 5000 ± 400 |
| 10 | 46.45° N, 124.29° W | July 1 | 16.9 | 5 | 17 ± 3 | 102 ± 57 | na |
| 11 | 44.65° N, 124.18° W | July 22 | 11.1 | 3 | 24 ± 4 | 36 ± 5 | 2000 ± 100 |
| 12 | 44.65° N, 124.30° W | July 22 | 15.6 | 1 | 14 | 18 | 3000 ± 600 |
| 13 | 44.39° N, 124.06° W | Sept. 30 | 15.4 | 11 | 25 ± 9 | 58 ± 47 | 4000 ± 900 |
| | | | | N=37 | | | |

Selection Index

Pearre's *C* tests were used to quantify prey selection patterns by individual *C. fuscescens*. Pearre's *C* uses a 2 X 2 contingency table to compare prey groups in medusa guts to prey present in the plankton (Pearre 1982) (Table 4.2).

A Chi-square was used to test whether there was a significant difference between zooplankton prey in the guts compared to background prey:

$$\chi^2 = (a_d b_e - b_d a_e)^2 \times n / a \times b \times d \times e$$

The values of *C* range from -1 to 1, with 0 indicating neutral selection. Negative values represent negative selection for prey type (occurrence is low in guts vs. plankton) and positive values represent positive selection for prey type (occurrence is high in guts vs. plankton).

Table 4.2. Contingency table used to calculate Pearre's *C* using proportions of prey in medusa gut and background prey field.

| | Prey Type | | |
|---|---|---|---|
| | A | Others | Total |
| Diet | $a_d$ | $b_d$ | $a_d + b_d = d$ |
| Environment | $a_e$ | $b_e$ | $a_e + b_e = e$ |
| Total | $a_d + a_e = a$ | $b_d + b_e = b$ | $a_d + a_e + b_d + b_e = n$ |

$$C = \pm [( \left| a_d b_e - b_d a_e \right| - n/2)^2 / a \times b \times d \times e]\text{^}1/2$$

## Feeding Rates

Two common metrics used to express feeding rates are ingestion (prey consumed predator$^{-1}$ day$^{-1}$) and clearance rate (L cleared predator$^{-1}$ day$^{-1}$). Clearance rate is useful to compare *C. fuscescens* prey removal efficiency on similar prey items, but cannot be used to compare different prey types (Purcell, 1997). Ingestion rates can be used to estimate daily ration and detect trends in feeding rates. Ingestion rate (I) for a specific prey type was calculated as:

$$I = (G/D) \times 24$$

where G = prey count in gut, D = prey digestion time (h),

Gut content analysis was used to quantify prey specific clearance rate (F) -- the liters cleared of a specific prey type by medusa per day-- using the following equation:

$$F = (G/ D \times C) \times 24$$

where C = ambient plankton concentration (# L$^{-1}$).

Digestion times for prey types were obtained from previous studies with *C. fuscescens* or related scyphomedusae (Purcell et al. 1994, Suchman et al. 2008). In order to compare to other studies, ingestion rate and clearance rate were standardized by wet weight. Simple linear regression models were used to quantify ingestion rate patterns by medusa diameter and prey density. A non-parametric Kruskal-Wallis test was used to test if sampling month, depth, and location had an effect on fish egg ingestion rates.

## Carbon Conversions

Using biometric equations (Shenker 1984), live bell diameters were converted to wet weight and carbon content (0.280% of WW). Hand-dipped medusae were not measured prior to being preserved in formalin in order to minimize prey loss via handling. Therefore, bell diameters of live medusae were estimated using previously derived measurements of *C. fuscescens* shrinking rates (Suchman et al. 2008). Carbon contents for each zooplankton grouping were obtained from the literature (Ross 1982,

Martinussen and Bamstedt 1995, Berggreen et al. 2002, Desai and Anil 2004, Espinoza et al. 2009). Amount of carbon ingested per prey grouping was calculated by:

$$I \text{ (prey consumed medusa}^{-1}\ h^{-1}) \times \text{carbon content of prey (mg C)} \times 24$$

Total carbon ingested per day was calculated by adding all prey types. Average daily ration was expressed as mg of carbon ingested per day, as percentage of medusa carbon content. Daily carbon ration values were not normally distributed, so a non-parametric Mann-Whitney test was used to compare carbon daily ration between medusae at stations containing anchovy eggs and stations without anchovy eggs. Simple linear regression was used to look for relationship between medusae size and daily carbon ingestion.

## RESULTS

### Diet Analysis

Zooplankton in medusae guts and plankton tows were split into the following taxonomic groupings: 1) cladocerans, 2) copepods 3) early stage euphausiids (meta/nauplius, calyptopes, and furcilia), 4) gelatinous taxa, 5) ichthyoplankton, 6) invertebrate eggs, 7) molluscs, 8) other crustaceans, and 9) 'other'. Cladocerans were all *Podon* and *Evadne* spp. Copepods included Calanoid copepods in the genera *Pseudocalanus, Acartia,* and *Centrophages.* Cyclopoids were more rare also and mostly consisted of *Oithona* sp. Gelatinous taxa were mostly larvaceans but also included hydromedusae, ctenophores, siphonophores and doliolids. When ichthyoplankton (eggs > 600 µm and fish larvae) were present in large numbers, the dominant stage was *Engraulis mordax* (northern anchovy) eggs. Other eggs and fish larvae were not identified. Invertebrate eggs were mostly euphausiid eggs (400 µm) and for feeding rate calculations, invertebrate eggs were further divided into euphausiid eggs and 'other' invertebrate eggs. Other crustaceans were a mixture of barnacle larvae (nauplii and cyprids) and copepod nauplii. The mollucs grouping contained larval gastropods, pteropods and bivalves. Gut content analysis also included symbionts classified as non-prey: *Cancer* megalopae, hyperiid amphipods, and larval amphipods (Buecher et al. 2001, Wrobel and Mills 1998). Larval amphipods are included as a non-prey since

amphipods are known to colonize and use medusae as reproductive habitat and larvae were observed embedded in bell tissue (Fleming et al. 2014).

Though the total amount of prey items counted in medusae guts varied by orders of magnitude between stations (Table 4.1), there were consistencies in general feeding patterns between stations and individuals (Figure 4.2). At most stations, the dominant taxa ingested were copepods (17% - 92%) or cladocerans (30% - 77%). At station 1, the medusa's gut contained only 10 prey items and was dominated by barnacle larvae (52%). At stations 8 and 13, gelatinous taxa were the dominant prey items (>30%). At stations 1 and 7, ichthyoplankton were dominant secondary prey taxa. Euphausiid eggs (400 µm) were 20% of the diet at station 6. Notably, at stations 7 and 10, ichthyoplankton in medusae guts were dominated by northern anchovy eggs (*Engraulis mordax*) (Figure 4.2).

At all stations, medusae ingested prey in different proportions from background plankton (Figure 4.4, Figure 4.5). Copepods were the dominant background zooplankton group (30%-70%) at most stations, excluding station 1, where euphausiid eggs comprised the majority of the zooplankton (65%) (Figure 4.3). At most stations, copepods were ingested at low rates relative to the proportion that was available in the plankton (Figure 4.4). Cladocerans, gelatinous taxa and invertebrate eggs were usually ingested in greater relative proportions while early stage euphausiids, molluscs, and 'others' were more variable. At station 1, which was dominated by euphausiid eggs (65%), there were no eggs counted in the gut.

Prey proportions at station 13 (N=11) illustrate the variability within individual medusae (Figure 4.6). Gelatinous taxa made up the primary prey ingested (20-50%), but secondary taxa varied widely. Spatial variability was also apparent at the Newport transect line. Medusae were collected on the same day, 9 km apart, with comparable numbers of prey items but different proportions of prey taxa. Also, at Station 13, medusae were collected at a large aggregation site. Approximate abundances, using photographs with a known scale, were 8 individuals per $m^2$. The highest prey proportions were larvaceans and 'other crustaceans' (mostly barnacle cyprids) (Figure 4.6, Figure 4.7)

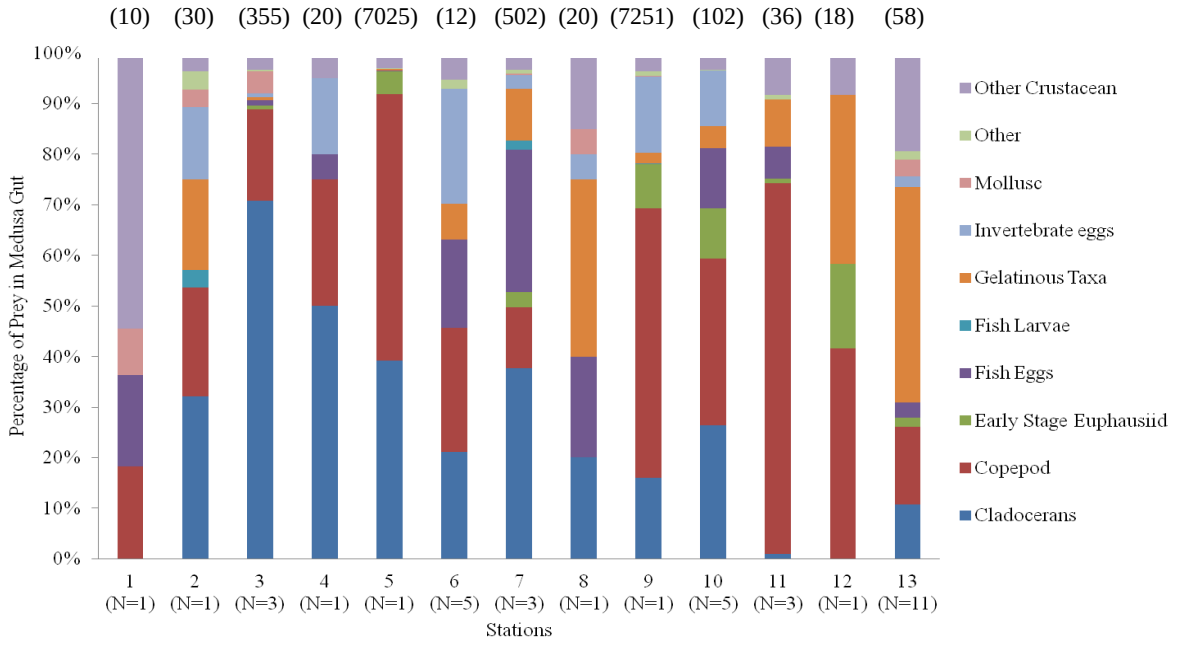


Figure 4.2. Relative proportions of zooplankton taxa in *C. fuscscens* guts collected at each station during summer 2014. Table 4.1 and Figure 4.1 contain relavent information related to station numbers. N is the number of meduase dissected and parenthesis above bar plots are the average number of prey items counted at each station

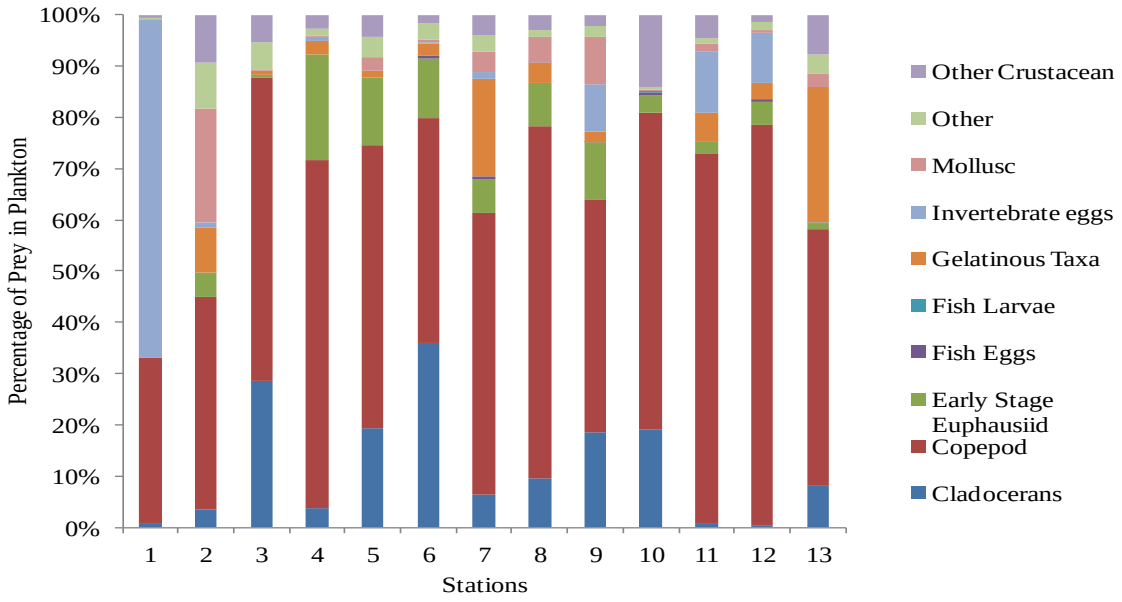


Figure 4.3. Relative proportions of background zoopankton taxa in plankton net tows from 13 sampling stations during summer 2014. Refer to Table 4.1 for relavent station information.

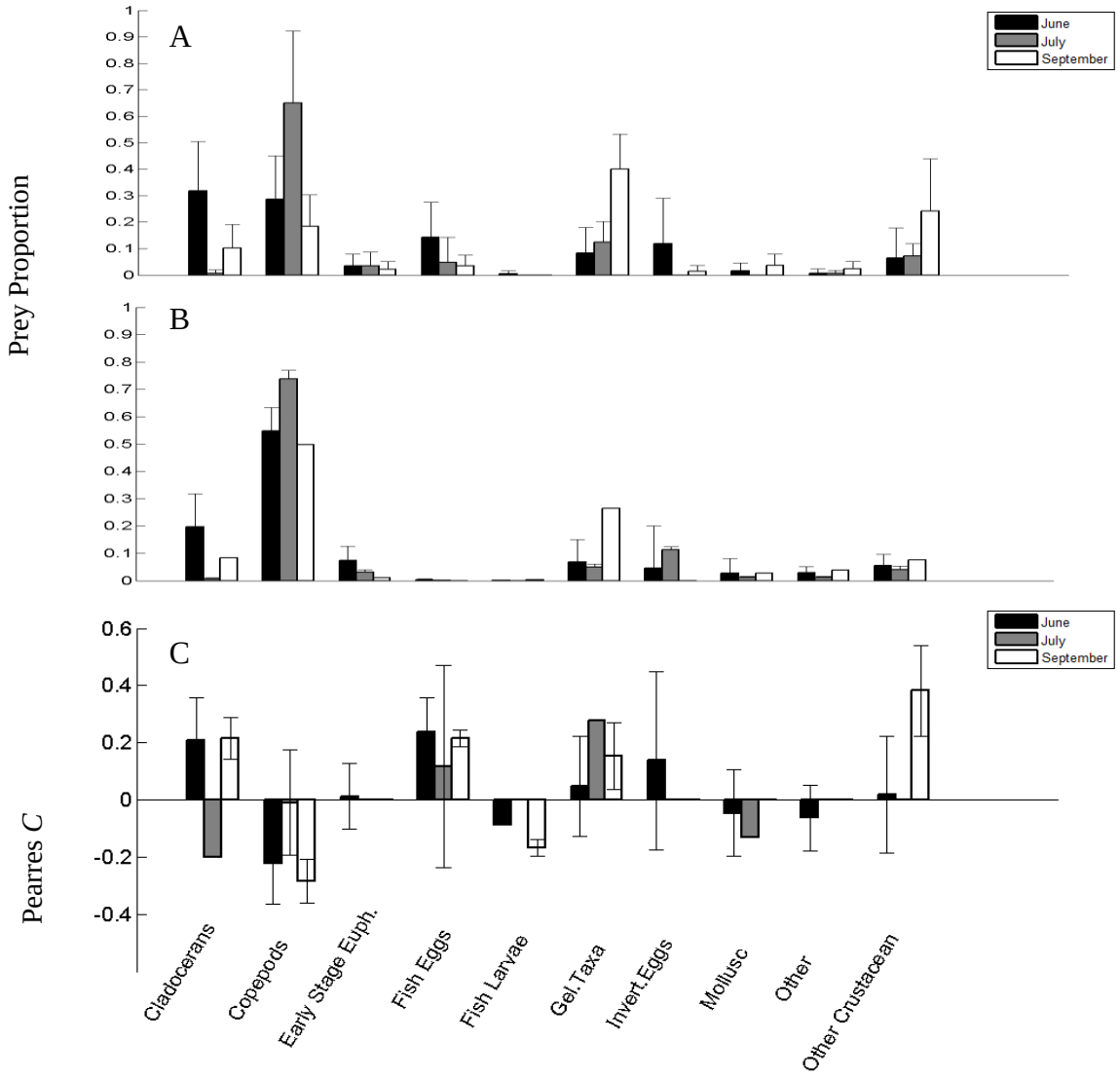


Figure 4.4. Relative proportions of prey groupings organized by collection month in A) medusae guts and B) background zooplankton. C) Selection summarized by averaging significant *C* values for each sampling month and prey taxa. Error bars represent standard deviation.

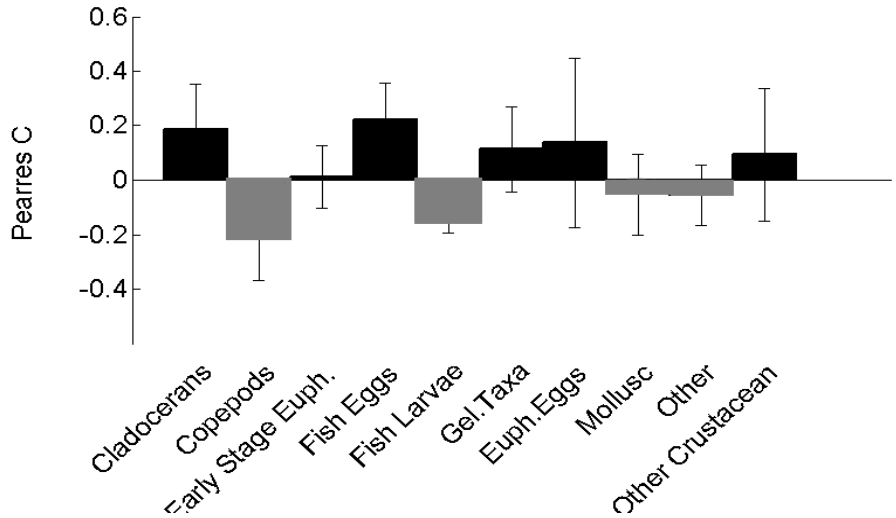


Figure 4.5. Pearre's *C* electivity index as a measure of prey selection by averaging significant *C* values. 1 represents strong positive selection for prey group and -1 represents strong negative selection. Error bars represent standard deviation.

Selection Index

General feeding patterns can also be examined with electivity values (Figure 4.4, Figure 4.5). Copepods dominated the background prey field at most stations, but were consistently negatively selected. The two exceptions were stations 9 and 11, where copepod selection was positive ($C$ = 0.15 and $C$=0.04, respectively) and copepods were >50% of prey ingested. Fish larvae were also negatively selected at all stations when they were present in the gut. Cladocerans, fish eggs, and invertebrate eggs were preferentially selected while gelatinous taxa and molluscs were also positively selected, but less strongly. The highest selection for fish eggs was seen in June (Figure 4.4). The prey grouping 'other crustacean' had the highest selection in medusae collected in September which were all collected at an aggregation site. Gelatinous taxa were consistently positively selected.

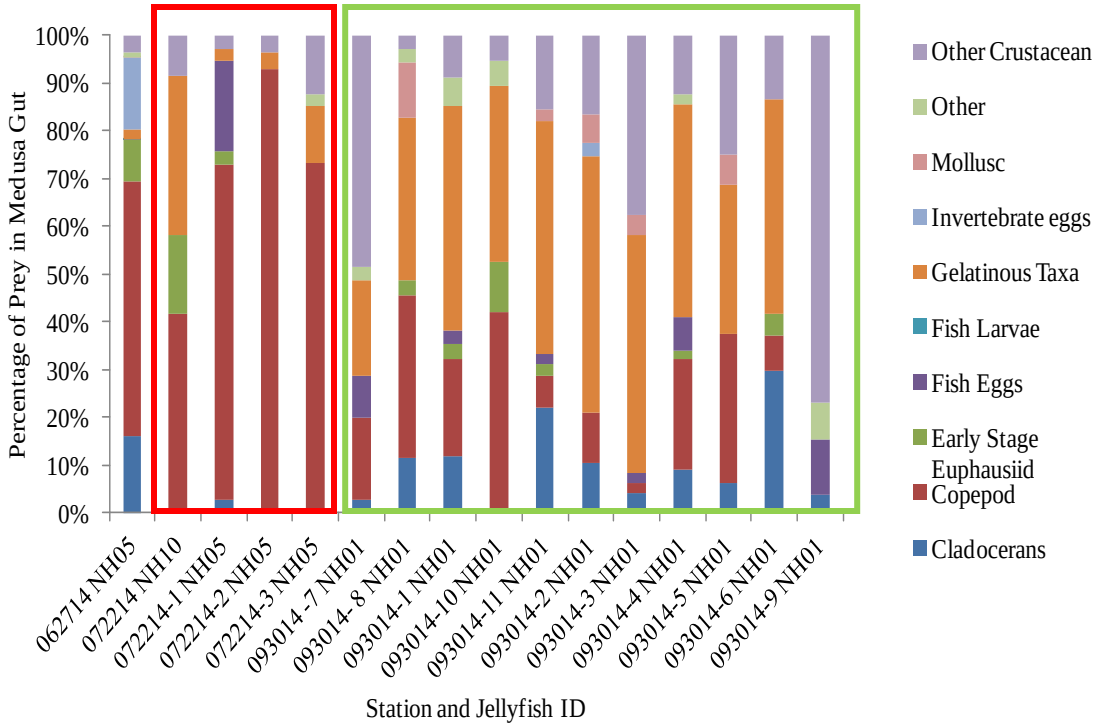


Figure 4.6. Relative proportions of prey groupings for individual *C. fuscescens* at survey stations along the Newport transect line. Labels are organized by date (month/day/year) and station (NH= Newport ; 01,05,10 = 1,5, and 10 nautical miles from shore). Number after date is the medusa ID number. Stacked bar plots within the green box are 11 individuals collected at large aggregation site. Stacked bar plots in red box are 3 individuals collected at NH05 (Sta. 11) and 1 medusa collected at NH10 (Sta. 12) on the same date but 5 nautical miles apart.

Figure 4.7: Photograph of *C. fuscescens* aggregation site from station 13. The net in the bottom right corner is approximately 0.70 m.

Feeding Rates and Daily Carbon Rations

Clearance rates can be a useful metric of the efficiency of prey removal. Averaged clearance rates varied considerably, even within prey taxa (Appendix A). Across stations, clearance rate potential ranged from 6 to 7,353 L $day^{-1}$. On average, gelatinous taxa and fish eggs were cleared at higher rates than the more commonly ingested prey such as copepods (gelatinous taxa: mean=1,472 L $day^{-1}$; fish eggs: mean=5,327 L $day^{-1}$ ; copepods= 487 L $day^{-1}$). Ingestion rates also varied across stations; for example, individual ingestion rates of copepods ranged from 4 – 15,508 copepods $day^{-1}$. The highest ingestion rates of nonmotile prey, fish and invertebrate eggs, reached 1,095 fish eggs $day^{-1}$ and 2,515 euphausiid eggs $day^{-1}$ (Appendix B). Medusae diameter was not a significant predictor of feeding rate but, for more vulnerable prey, taxon density in the background plankton predicted ingestion rates in medusae (Table 4.3). Unidentified factors are more important for explaining ingestion rates in copepods and cladocerans. Samples collected near the Columbia River (Sta. 6, 7, and 10) had significantly higher fish egg ingestion rates than other sampling stations ($\chi^2 = 15.5$, d.f.=6, $p$=0.02).

Table 4.3. Results of simple linear regression of medusae ingestion rates for different prey groups by prey density. I= ingestion rate of single medusa per day and D=density of prey grouping per $m^3$. Euph.=euphausiid.

| Prey Group | p-value | Model Equation | $R^2$ |
|---|---|---|---|
| Euph. Eggs | <.0001 | I=4.6(D)-(-117) | 0.34 |
| Fish Eggs | <.0001 | I=13.1(D)-(-21.9) | 0.62 |
| Gelatinous Taxa | 0.03 | I=0.29(D)- 120 | 0.11 |
| Cladocerans | 0.37 | Average Ingestion=589 | na |
| Copepods | 0.96 | Average Ingestion = 897 | na |

The average daily carbon rations varied between stations (Table 4.4). There was no significant relationship between size of medusa and carbon ingestion (F=0.134, *p*=0.72). Carbon ingestion rates were highest at stations 5, 7, and 9, exceeding 10% medusa body carbon. Stations 5 and 9 had large prey ingestion rates, exceeding 7,000 prey items, and station 7 had relative gut proportions of ichthyoplankton >20%. Carbon daily ration was significantly different at stations where anchovy eggs were present (anchovy: 1 ± 2 % body C $day^{-1}$; no anchovy: 0.8 ± 3 % body C $day^{-1}$; Mann-Whitney: W=144, *p*=0.02).

## DISCUSSION

### Diet Analysis and Prey Selection

Gut content analysis work during summer 2014 reveals high variability in prey selection and feeding rates of *C. fuscescens*. Proportions of prey in medusae guts varied between stations, months, and individuals. Despite this variability, medusae regularly ingested prey at different proportions than the background prey field. *C. fuscescens* positively selects for nonmotile prey and negatively selects for copepods and fish larvae. This suggests that fish eggs, invertebrate eggs, and larvaceans are more vulnerable to predation by *C. fuscescens.* These results mostly contradict prey selection trends of other large scyphozoans. *Aurelia* sp. demonstrates positive selection for small copepods and cladocerans and negative selection for larvaceans in Prince William Sound (Purcell and

Sturdevant 2001). Graham and Kroutil (2001) also noted positive selections of small copepods in *Aurelia aurita* and negative selection of large copepods. Field studies with *Chrysaora quinquecirrha* document positive selection of copepods and negative selection of copepod nauplii stages, larvaceans and polycheate larvae (Purcell 1992). *C.quinquecirrha* in laboratory experiments shows negative selection for copepod nauplli and positive selection for adult copepods (Suchman and Sullivan 1998). A strong positive selection for ichthyoplankton (fish eggs and larvae) has also been noted (Purcell et al. 1994, Purcell 2001). Interestingly, positive selection for larger copepods is noted in most prey selectivity studies. Comparing selection indices between species is not advisable as sampling design and spatial and temporal trends in ambient prey fields or predators could be affecting selection criteria (Shiplett 2011). For instance, results from this study demonstrate variation in electivity indices over different months. Selection results substantiate *C. fuscescens* selection trends in previous field work; negative selection for copepods and positive selection for euphausiid eggs (Suchman et al. 2008).

Medusae prey selection exemplifies the complexity of predator-prey dynamics in marine systems. Medusae are not actively pursuing prey; instead prey selection is connected to direct encounter and capture events (Greene 1968). *Chrysaora* have long, trailing tentacles and oral arms that can extend meters beyond the bell margin (Morandini and Marques 2010). These numerous appendages can widen the encounter zone and increase prey encounter rates (Madin 1988). As a cruising predator, *Chrysaora* swims continuously, creating complicated velocity and vortex fields. Ford et al. (1997) calculated marginal bell velocities for *Chrysaora quinquecirrha* to explain predation on zooplankton prey with different swimming velocities. In the present study, most medusae analyzed were large enough (mean = 19 ± 8) to produce marginal bell velocities that would overwhelm the fastest prey item which would suggest that escape responses are insignificant factors. Still, the medusa is producing a complex hydrodynamic signal that could be recognized by quick swimming prey (e.g. copepods) who can then escape (Allan 1976, Alldredge 1982, Fisher et al. 2000, Buskey and Hartline 2003, Dabiri et al. 2005). The importance of prey behavior (i.e. swimming) has been noted in laboratory feeding experiments (Suchman and Sullivan 1998, Fitzgeorge-Balfour et al. 2013).

Table 4.4. Daily carbon rations by station. Stations 3 and 8 were not included in calculations because bell diameters did not fit the model provided in Shenker (1984).

| Station | mg C medusae$^{-1}$ (± SD) | mg C ingested day$^{-1}$ (± SD) | % C day$^{-1}$ (±SD) |
|---|---|---|---|
| 1 | 913 | 0.25 | 0.03 |
| 2 | 570 | 0.45 | 0.08 |
| 4 | 772 | 0.25 | 0.03 |
| 5 | 671 | 75 | 11.2 |
| 6* | 548 ± 527 | 0.24 ± 0.1 | 0.04 ± 0.02 |
| 7* | 366 ± 143 | 18 ± 10.2 | 4.45 ± 2 |
| 9 | 1985 | 84 | 4.2 |
| 10* | 853 ± 544 | 1.8 ± 1.5 | 0.41 ± 0.1 |
| 11 | 2053 ± 860 | 0.8 ± 0.5 | 0.06 ± 0.1 |
| 12 | 469 | 0.26 | 0.05 |
| 13 | 2743 ± 1048 | 0.88 ± 0.4 | 0.04 ± 0.02 |
| | | All medusae | 0.9 ± 2.4 |

*represents stations with medusae ingesting northern anchovy eggs

Feeding Rates and Daily Carbon Rations

*C. fuscescens* exhibit potential for high clearance and ingestion rates of nonmotile and gelatinous taxa. Fluctuating trends in feeding rates are noted in several gut analysis studies (Purcell 1992, Purcell 2003). Previous diet analysis work in the California Current with *C. fuscescens* points to high ingestion of euphausiid eggs and gelatinous taxa over copepods (Suchman et al. 2008). At certain stations, ingestion rates of copepods can be substantial, so it is unwise to overlook predation effects on these abundant zooplankton that are important trophic links in marine food webs (Turner 2004). The standardized feeding rates on copepods from this study (mean=3.3 copepods g WW$^{-1}$ day$^{-1}$) were comparable to other Scyphozoans (typically under 10 copepods g WW$^{-1}$ day$^{-1}$) (Purcell 1992, Purcell 2003).

In this study, euphausiid eggs were a dominant prey item in individual medusae but overall were not selected over copepods. High feeding rates of northern anchovy eggs

are notable, but no surprise, as high spatial overlap with important forage fish species has been proposed (Brodeur 2014). The medusae with the highest anchovy egg feeding rates were collected in late June at stations near the Columbia River plume which overlaps in time and space with regions of high anchovy spawning biomass (Parnel et al. 2008). High clearance rates of fish eggs could have negative effects as predation on early life stages may affect recruitment (Bailey and Houde 1989). It is difficult to quantify predation potential without a thorough knowledge of *Chrysaora* and fish egg abundances in the NCC. Northern anchovy spawn multiple times in a season, between February and June, and are sensitive to environmental shifts (Brodeur et al. 2006). Fisheries scientists recognize that northern anchovy are the most abundant forage fish in the California Current system with egg densities as high as 5,600 per $m^2$ (Emmett 1997). This study substantiates that *Chrysaora* is able to exploit pulses of fish eggs.

Carbon daily rations (mean=0.9 % C $day^{-1}$) are comparable to 1.3% C $day^{1}$ calculated for *C. fuscescens* and 2.1% C $day^{-1}$ for *Aurelia* sp. (Suchman et al. 2008, Ishii and Tanaka 2001). These studies put forward that medusae are food limited since rates <2% are low for carbon requirements (Malej 1989). It has been suggested that these numbers are low because gut content work does not take into account night-time feeding (D'ambra et al. 2013). In this instance, most medusae were collected in the day-time. Variable carbon ingestion rates could also be attributed to the unique lifestyle of a jellyfish. The jellyfish body plan, constituted by low-carbon content, water-laden tissues and energetically efficient propulsion allow for low energy demands and high growth rates (Pitt et al. 2013, Gemmell et al. 2013). These traits are especially desirable in an environment where prey items are patchy and exploitation of prey pulses is essential. When medusae were collected at sea, they were previously feeding in an unknown volume of the water column (Moriarty et al. 2012). High daily carbon rates may represent medusae that encountered prey patches which are not evident in plankton tow samples.

High carbon ingestion rates at stations 5, 7 and 9 occurred where medusae were ingesting an abundance of high quality, carbon-rich food (copepods and ichthyoplankton) (Espinoza et al. 2009). At station 7, fish eggs made up >20% of the gut contents and the average prey count was more than ten times lower than at stations 5 and 9. This demonstrates the importance of fish eggs as dense, nutrient-rich packets of food that

allow for rapid growth (Larson 1986). Abundance data shows that *C. fuscescens* maximum growth rates occur in the late spring and early summer months which coincide with predicted spawning events of northern anchovy (Suchman et al. 2012, Parnel et al. 2008). These snapshots in time show that *C. fuscescens* is preying on fish eggs at a vital time in their lifecycle. This also drives home the importance of sampling over an entire season as to 'catch' seasonal events.

This large variability in feeding rates and newly documented anchovy egg predation calls out for more systematic sampling of medusae in the NCC. This study represents the first time that ichthyoplankton feeding rates are encountered in *C. fuscescens*, but these results are not surprising considering the noted overlap in time and space with northern anchovies. Continuing to quantify these trophic interactions is necessary to show the impact of large medusae directly impacting zooplankton stocks, re-routing carbon pathways, and preying on early life stages of fish. Medusae gut work should be done in concert with other large scale sampling of ichthyoplankton, as the tangible effects of this predation are hard to tease apart without knowledge of jellyfish and prey abundance and distribution. These feeding results are also data points for the creation of ecosystem models in the NCC. These models can be useful tools for understanding trophic pathways and predicting responses to environmental changes (Ruzicka et al, 2012).

# CHAPTER V

# GENERAL CONCLUSIONS AND FUTURE DIRECTIONS

The goals of this project were aimed at understanding jellyfish behavior in flow and the feeding ecology of *C. fuscescens in situ*. These novel results are part of a larger field of research focused on examining the role of jellyfish populations in marine systems.

## Chapter II

Experiments in pseudokreisels show that *C. fuscescens* have high clearance rates on *Artemia* prey and these feeding rates are not affected by flow. This work represents the first time that fluid flow was examined as a possible factor affecting feeding rate efficiency. Future work in laboratory studies could continue to examine predator-prey interactions using natural prey assemblages. Laboratory and field work would also benefit from particle imaging techniques by relating the fluid structure created by a swimming medusa to actual ingestion rates.

## Chapter III

*C. fuscescens* maintains its position by swimming counter-current to flow fields created in pseudokreisels. This behavioral trait explains how *C. fuscescens* may maintain aggregations at frontal convergences by interaction with complex downwelling currents. These data represent another taxonomic grouping using rheotaxic behavior as an adaptive advantage. Orientation behavior may help explain the long and rich evolutionary history of cnidarian jellyfish. Future studies addressing the exact behavior mechanism (pulsation symmetry) will solidify these results and identify important aggregator traits..

**Chapter IV**

What are *C. fuscescens* eating and how much? This seemingly simple question will only be answered with systematic and focused gut analysis work. The results of *C. fuscescens* gut analysis work show that these large medusae ingest a variety of zooplankton taxa and feeding rates vary by station, month, and individual. This variability demonstrates the need for multi-year, mesoscale sampling in the NCC. A glimpse into the feeding ecology of *C. fuscescens* clarifies vulnerable prey and reports the first sighting of fish eggs as a sizeable component of *Chrysaora* diets. Continued monitoring of gelatinous zooplankton abundances and predation rates will become important components of ecosystem models and long-term gelatinous zooplankton studies.

APPENDIX A

CLEARANCE RATES

Table A.1. *C. fuscescens* clearance rates calculated from gut contents by prey taxa and station. Digestion times used for copepods , other crustacean , and early stage eupahusiids was 6 h, 1.5 h for gelatinous taxa, 4.9 h for eupahusiid eggs, 3.9 h for fish eggs, and 1 h for fish larvae. na represents stations with no taxa in background plankton. Clad= cladocerans, Euph = euphausiid, Gel= gelatinous, Crust=crustacean

| Clearance Rate (L cleared medusa$^{-1}$ day$^{-1}$) ± SD | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Station | Clad. | Copepod | Early Stage Euph. | Fish Eggs | Fish Larvae | Gel. Taxa | Euph. Eggs | Mollusc | Other Crust. |
| 3 | 399 ± 468 | 49 ± 36 | 166 ± 190 | na | na | 598 ± 518 | na | 1,910 ± 1,433 | 101 ± 56 |
| 4 | 242 | 7 | 0 | na | 0 | 0 | 475 | 0 | 34 |
| 5 | 15,659 | 7,353 | 2655 | 0 | na | 10626 | 0 | 41 | 5,638 |
| 6 | 7 ± 5 | 6 ±4 | 0 | 607 ± 480 | na | 132 ± 215 | 1,209 | 0 | 16 ± 23 |
| 7 | 1,132 ± 641 | 42 ± 8 | 86 ± 86 | 14,362 ± 9,130 | na | 409 ± 153 | 564 ± 666 | 16 ± 5 | 190 ± 77 |
| 8 | 13 | 0 | 0 | na | 0 | 219 | na | 6 | 31 |
| 9 | 4,876 | 6,602 | 4478 | na | 11187 | 24,395 | 11,447 | 68 | 9,081 ± 1,553 |
| 11 | 65 ± 112 | 62 ± 4 | 22 ± 37 | na | na | 395 ± 255 | 0 | 0 | 109 ± 84 |

Table A.1. (continued).

| Station | Clad. | Copepod | Early Stage Euph. | Fish Eggs | Fish Larvae | Gel. Taxa | Euph. Eggs | Mollusc | Other Crust. |
|---|---|---|---|---|---|---|---|---|---|
| 12 | 0 | 9 | 62 | 0 | na | 759 | 0 | 0 | 11,200 |
| 13 | 80 ± 93 | 19 ± 11 | 76 ± 88 | na | 0 | 397 ± 218 | na | 68 ± 79 | 183 |
| Mean (± SD) | 883 ± 2,944 | 487 ± 1767 | 295 ± 925 | 5,327 ± 8601 | 699 ± 2797 | 1,472 ± 4,728 | 1,097 ± 3,137 | 214 ± 688 | 1,057 ± 2,708 |
| L cleared g $WW^{-1}$ $day^{-1}$ | 1 ± 5 | 0.6 ± 2 | 0.3 ± 0.9 | 10 ± 18 | 0.4 ± 1.5 | 1 ± 4 | 0.9 ± 2 | 0.02 ± 0.03 | 2 ±5 |

APPENDIX B

INGESTION RATES

Table B.1. *C. fuscescens* ingestion rates calculated from gut contents by prey taxa and station. Digestion times used for copepods, other crustacean, and early stage euphausiids were 6 h, 1.5 h for gelatinous taxa, 4.9 h for euphausiid eggs, 3.9 h for fish eggs, and 1 h for fish larvae. na represents stations with no taxa in background plankton. Clad= cladocerans, Euph = euphausiid, Gel= gelatinous, Crust=crustacean.

| Ingestion Rate (prey consumed medusa$^{-1}$ day$^{-1}$) ± SD | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| Station | Clad. | Copepod | Early Stage Euph. | Fish Eggs | Fish Larvae | Gel. Taxa | Euph. Eggs | Mollusc | Other Crust. |
| 1 | 0 | 8 | 0 | 12 | 0 | 0 | 0 | 4 | 24 |
| 2 | 36 | 24 | 0 | 12 | 24 | 80 | 0 | 4 | 4 |
| 3 | 975 ± 1,142 | 240 ± 185 | 11 ± 12 | 21 ± 9 | 0 | 32 ± 28 | 12 ± 4 | 61 ± 46 | 45 ± 27 |
| 4 | 40 | 20 | 0 | 6 | 0 | 0 | 15 | 0 | 4 |
| 5 | 11,016 | 14,804 | 1,288 | 0 | 0 | 464 | 0 | 4 | 848 |
| 6 | 10 ± 7 | 11 ± 7 | 0 | 12 ± 10 | 0 | 13 ± 21 | 5 | 0 | 3 ± 4 |
| 7 | 757 ± 429 | 227 ± 49 | 60 ± 60 | 911 ± 565 | 216 ± 72 | 821 ± 355 | 86 ± 100 | 7 ± 2 | 57 ± 38 |
| 8 | 16 | 0 | 0 | 25 | 0 | 112 | 0 | 4 | 12 |
| 9 | 4,644 | 15,508 | 2,536 | 25 | 72 | 2,512 | 5,378 | 32 | 1,052 |
| 10 | 114 ± 75 | 149 ±110 | 42 ± 34 | 79 ± 73 | 0 | 58 ± 61 | 0 | 0 | 14 ± 7 |

Table B.1. (continued).

| Station | Clad. | Copepod | Early Stage Euph. | Fish Eggs | Fish Larvae | Gel. Taxa | Euph. Eggs | Mollusc | Other Crust. |
|---|---|---|---|---|---|---|---|---|---|
| 11 | 1 ± 2 | 109 ± 9 | 4 ± 2 | 14 ± 25 | 0 | 112 ± 115 | 0 | 0 | 9 ± 9 |
| 12 | 0 | 20 | 8 | 0 | 0 | 64 | 0 | 0 | 4 |
| 13 | 20 ± 23 | 24 ± 16 | 3 ± 4 | 7 ± 9 | 0 | 267 ± 184 | 0 | 6 ± 6 | 37 ± 27 |
| Average | 589 ± 1,956 | 897 ± 3458 | 282 ± 703 | 169 ± 390 | 132 ± 115 | 349 ± 547 | 1,115 ± 2,838 | 10 ± 9 | 92 ± 246 |
| Prey consumed g $WW^{-1}$ $day^{-1}$ | 3 ± 9 | 3.3 ± 12 | 0.7 ± 2 | 0.9 ± 2 | 0.6 ± 0.8 | 0.8 ± 1 | 2 ± 8 | 0.02 ± 0.01 | 0.2 ± 0.7 |

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