ABSTRACT

Title of dissertation: THE BEHAVIOR OF THE SCYPHOMEDUSAE *CHRYSAORA QUINQUECIRRHA* AND *AURELIA AURITA* AND ITS ECOLOGICAL IMPORTANCE

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Scyphomedusae are important components in trophic and community structures of marine and estuarine systems worldwide. Behavior likely has a significant influence on medusa population dynamics and growing evidence points to the disproportionate effect individual behavior has on population responses, yet there are few quantitative studies of medusa behavior and no method for quantifying the behavior of individual pelagic organisms. A numerical model of medusa swimming behavior would be an important tool for assessing its effect on spatial patterns and foraging efficiency.

An approach was developed that uses a suite of statistical techniques to quantitatively describe time-dependent changes in behavior of pelagic organisms and tested on the swimming behavior of *Aurelia aurita* and the foraging behavior of

Chrysaora quinquecirrha. An individual-based model of medusa swimming behavior was formulated as a correlated random walk of velocity vectors in three dimensions.

Each *A. aurita* medusa exhibited a unique swimming behavior, including varying swimming bell pulsations, speed, and turning at characteristic frequencies. *C. quinquecirrha* swam in mostly linear trajectories that alternated between periods of slow and fast swimming while searching for prey, but swam at a constant moderate rate with increased anisotropic turning while feeding. Foraging behavior by medusa groups depended on interindividual and intraindividual variability in medusa behavior, including deterministic changes in swimming pulsation strength and turning.

Empirical and model results showed that variability of behavior among medusae and by individual medusae over time are integral components determining the aggregated population response. Medusa foraging behavior appears adapted for patchily distributed prey. Alternating between slow and fast swimming while searching for prey may minimize energy expended while periodically generating prey-entraining currents. Increased turning in the presence of prey increases the likelihood of remaining in prey patches. Anisotropic turning created vertically spiraling paths, well suited to horizontally compressed prey patches. Model results demonstrated that medusae tend to swim toward and accumulate at the surface, avoid direct contact with the bottom, orient search patterns to long-range stimuli (e.g. gravity) and feeding patterns to local stimuli (e.g. prey contact), and exhibit periodicities of velocity outside prey patches and turning within patches that result from deterministic behavior.

THE BEHAVIOR OF THE SCYPHOMEDUSAE *CHRYSAORA QUINQUECIRRHA* AND *AURELIA AURITA* AND ITS ECOLOGICAL IMPORTANCE

by

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Dedicated to my mother.

For all that I am I owe to her.

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CHAPTER 1

Introduction

Scyphozoa are ubiquitous in marine and estuarine systems worldwide. Although previously regarded as trophic "dead ends", they are increasingly recognized as having an important, and sometimes controlling, influence on the population and trophic dynamics of systems in which they are found (Möller 1980; Feigenbaum and Kelly 1984; Baird and Ulanowicz 1989; Båmstedt et al. 1994; Schneider and Behrends 1998).

Scyphomedusae most often influence trophodynamics as predators although this may be as much a consequence of how little we know of their role as prey as any difference between the trophic functions they serve. A generalized predator-prey model indicates an inverse relationship between medusae and their zooplankton prey (Legović 1987), and this same pattern has been observed in situ (Feigenbaum and Kelly 1984; Behrends and Schneider 1995). In the Kiel Bight, *Aurelia aurita* controls the abundance of zooplankton stocks generally, those stocks being lower in years when *Aurelia aurita* is abundant. But, it selectively preys on some copepod species, thus also influencing zooplankton community composition (Behrends and Schneider 1995). Often, medusae impact the food web in several ways. *Cyanea capillata* controls the structure of the pelagic community in coastal waters of western Norway by preying on zooplankton groups and by consuming both fish and gelatinous competitors (Båmstedt et al. 1994). Similarly, *Chrysaora quinquecirrha* medusae affect zooplankton populations in Chesapeake Bay and its tributaries directly by preying on copepods and indirectly by consuming the ctenophore *Mnemiopsis leidyi*, itself a voracious copepod predator (Feigenbaum and Kelly 1984; Purcell 1992). In fact, in an ecosystem model, it was estimated that *C. quinquecirrha* is the top predator in Chesapeake Bay because it feeds on eggs and larvae of piscivorous fish (Baird and Ulanowicz 1989).

Most scyphomedusae are generalist feeders preying on copepods, fish eggs and larvae, chaetognaths, protozoa, gastropod veligers, polychaete larvae, and other gelatinous species (reviewed in Purcell 1997). Medusa feeding rates can be extremely high, causing significant reductions in prey species (Möller 1984; Purcell 1992; Behrends and Schneider 1995; Olesen 1995). One factor amplifying their effect on prey populations is that medusa feeding does not appear to saturate at normall observed in situ prey concentrations enabling them to exploit prey patches and variable food supplies (Kerstan 1977 as cited by Behrends and Schneider 1995; Garcia and Durbin 1993; Båmstedt et al. 1994). *Aurelia aurita* medusae can consume as much as two-thirds of the copepod community in the western Baltic daily (Schneider and Behrends 1994) and has the potential to clear the entire volume of some systems several times per day (Olesen 1995). In Chesapeake Bay, *Chrysaora quinquecirrha* medusae remove up to 40% of bay anchovy eggs (Cowan and Houde 1993; Purcell et al. 1994) and 94% of the standing stock of copepods in tributaries per day (Purcell 1992). Although there is no comprehensive evidence that they are competitors with fish, scyphomedusae often feed on the same prey as zooplanktivorous fish and fish larvae (Purcell and Arai 2001). Moreover, medusae sometimes feed high on the food chain (Baird and Ulanowicz 1989; Malej et al. 1993), and where their feeding rates are high, it is likely they reduce prey stocks sufficiently to cause decreases in fish (Möller 1980; Fossa 1992).

Alternatively, medusae may be prey for fish and gelatinous predators (reviewed in Purcell 1997 and Purcell and Arai 2001). Quantitative estimates of the specific role of scyphomedusae as prey for fish is lacking due to the rapid digestion of gelatinous tissue in fish stomachs (Arai 1988). However, jellyfish generally form some portion of the diet of many more fish species, including commercially important ones, than previously thought (Purcell and Arai 2001). As prey, medusae are an intervening step in the trophic transfers between mesozooplankton and planktivorous fish and may reduce the trophic flows between the two and thus total production of fish (Arai 1988).

Scyphomedusae play a unique role in some systems because their physiology makes them tolerant of harsh environmental conditions (e.g. hypoxia), which exclude other organisms (Gatz et al. 1973; Thuesen and Childress 1994; Condon et al. 2001). In this way, medusae can use otherwise unexploited resources, increasing their abundance (Breitburg et al. 1997; Keister et al. 2000). In addition, the nutrients gained from these resources are subsequently released to the rest of the biota through excretion or when medusae are predated (Hamner and Hauri 1981; Schneider 1990; Thuesen and Childress 1994).

Medusa feeding is highly variable both spatially and temporally largely as a result of differences in medusa and prey abundance (reviewed in Arai 1997). The daily predation rates of *Chrysaora quinquecirrha* medusae on copepods in Chesapeake Bay was estimated over two successive years and at various locations throughout the system and ranged from 1-94% of the standing stock (Purcell 1992). In a two-week study in the same system, medusae accounted for 3 - >50% of daily mortality of fish eggs (Purcell et al. 1994). Malej (1989) noted that predation rates on copepods increased 50-fold within aggregations of swarming medusae. *Aurelia aurita* is estimated to consume up to two-thirds of the secondary production by mesozooplankton daily in the Kiel Bight, but the amount at any given time depends on medusa abundance, which varies interannually, as well as the timing of their annual appearance in the system (Schneider and Behrends 1994).

Medusa feeding rates are controlled by various biotic and abiotic factors. Feeding rates depend on the size and concentration of medusae and their prey and on physical factors that affect medusa metabolic rates (e.g. temperature) (Bailey and Batty 1983; Larson 1986; Cowan and Houde 1992; Purcell 1992; Båmstedt et al. 1994). In addition, medusa feeding is affected by the size and deployment of tentacles, the perceptive field of the medusa and its prey and, because many medusae are cruising predators, on swimming rate and pattern (Madin 1988; Costello and Colin 1994, 1995; Ford et al. 1997; Purcell 1997).

Behavior affects both the encounter and capture of food, but, little is known about its role in medusa feeding, specifically, to what extent the variability of medusa feeding rates can be explained by behavior. Medusa swimming behavior can increase the probability of encountering prey (Bailey and Batty 1983; Cowan and Houde 1992). On a large scale, daily vertical migration by medusae (Mackie et al. 1981; Hamner et al. 1982; Fossa 1992) may be in response to similar patterns by their zooplankton prey (Longhurst 1976; Bollens et al. 1992) and increase their co-occurrence. Medusae also form aggregations that create localized zones of intense predation (Malej 1989; Purcell et al. 2000).

Small-scale foraging behaviors involving search strategies and feeding tactics also increase the overlap of medusa and prey. For example, *Phacellophora camtschatica* swims primarily vertically increasing the encounter rate with its horizontally distributed prey (Strand and Hamner 1988). Similarly, *Aurelia aurita* increases the probability of encountering food by beginning vertical excursions after contacting their first prey (Bailey and Batty 1983). Medusae can also swim in patterns that deploy their tentacles in a manner to maximize the size of the encounter zone (Madin 1988). When moving vertically, *Phacellophora camtschatica* spirals upward to deploy tentacles over a large cylindrical volume (Strand and Hamner 1988). However, when swimming horizontally, medusae change their behavior, swimming linearly, retracting tentacles and reversing course occasionally, to create long narrow lines of horizontally deployed tentacles.

Therefore, one way to improve our understanding of the effect of scyphomedusae on ecosystems is to gain better knowledge of their behavior. Behavior is often the key determinant of an animal's effect on its community because behavior modulates the response of an animal to its environment (Lehner 1996). Behavior systems comprise sensory receptors that receive stimuli (internal or external), an appropriately responsive effector system, and, usually, a regulatory feedback mechanism (op. cit.; Slater 1999). For example, touch (an external stimulus) is perceived and elicits a response (move away) that reduces the stimulus and modifies the response (stop moving).

There are many behaviors that influence the effect a species has on its community including foraging, spawning, aggregating, and predator avoidance (reviewed in Manning and Dawkins 1998). In this dissertation, I have focused on the effect of behavior on foraging. Herein, I define foraging as comprising two parts: searching, the detection and location of food; and feeding, the capture and consumption of food.

Given its importance to animal growth and survival, there is strong selective pressure to evolve stable patterns of behavior that maximize efficiency in locating and consuming food, and considerable attention has been focused on describing them (Dixon 1959; Smith 1974; Kareiva and Shigesada 1983; Grunbaum 1998). Optimal searching strategies increase the net energy gained from the search for food by minimizing the time spent between patches (Schoener 1971; Stephens and Charnov 1982). Optimal feeding strategies maximize the time spent in the proximity of a patch of food, while allowing for abandoning a patch if the energetic return falls below the expected gain from searching further (i.e. patch fidelity). Both strategies increase energetic returns, growth, reproduction and ultimately the fitness of an organism. An example of both behaviors may be found in ladybird beetles. When they encounter a plant, beetles climb to the outermost tip of the top leaves on the plant, those areas that are usually favored by their aphid prey and where the probability of encountering them is highest (Dixon 1959). Their movement before encountering prey is relatively fast and linear. When a first aphid is caught, beetles reduce speed and increase turning creating an area-restricted search pattern and increasing the likelihood of encountering more aphids, which tend to aggregate. Beetles continue searching their way down the plant to progressively older leaves and abandon the plant if energetic returns are less than those that might be expected from searching a new location.

Much of what we know about the importance of animal behavior is derived from studies of groups. However, behavioral processes fundamentally work through the individual. Individuals receive stimuli from their local environment and respond appropriately in ways adaptively selected to maximize fitness (Lehner 1996; Manning and Dawkins 1998; Slater 1999). Thus, individual behavior also provides a framework for understanding population dynamics because natural selection, working through individual fitness, will maintain behaviors that increase a population's survival and growth (Sutherland 1996; Caro 1998; Fryxell and Lundberg 1998).

How a particular animal will behave depends on endogenous variability (e.g. size) and heterogeneities in its local environment. Many physical and biological heterogeneities (e.g. turbulence, patchiness) occur on a scale relevant to the individual (cm to m)(Haury et al. 1978; Davis et al. 1991; Mann and Lazier 1991). Moreover, these individual responses are amplified by feedback mechanisms until they affect population-level processes and variability (Levin 1992). Therefore, it is necessary to consider individual behavioral responses to environmental conditions to understand population-level processes. For example, models indicate that the survival rate of populations of juvenile salmon depends on the behavior (i.e. aggressive or passive) of the few predators in the immediate vicinity of each juvenile, and each predator's response, in turn, is determined by its hunger level (DeAngelis and Petersen 2001).

Because behavior is fundamentally an individual-level process, studies directed at this level are necessary if one is to answer mechanistic questions (the "how") and adaptive questions (the "why") concerning behavior. For example, the cohesion of schooling fish results from each individual responding to the proximity of its neighbor and maintaining a constant distance (Parrish et al. 2002). The adaptive function, however, is the reduced likelihood that an individual fish will be eaten.

Research on scyphomedusae dates back nearly a century (e.g. Hargitt and Hargitt 1910). In general, it has progressed from studies of medusa physiology to population-level processes (e.g. feeding rates) and, most recently, to ecosystem-level research (e.g. trophodynamics). This dissertation brings the research full circle by quantifying individual behavior and linking it to effects on population-level processes such as feeding rates and making predictions about ecosystem-level effects by medusae. The dissertation includes the introduction, three freestanding chapters, and a concluding chapter that synergistically interprets the results of the dissertation.

Chapter 2 presents a new approach to statistically differentiate between the behaviors of individuals. The research addresses two questions:

(1) Can a method be developed to quantify statistical differences in behavior between individuals?

(2) Are there quantifiable differences in swimming behavior between individual medusae?

A method for quantifying differences between individuals is needed because behavior is fundamentally an individual-level process and aggregated measures may lose important details of behavior. Individual differences, as measured by variability, are proving to be vital to predictions of population-level processes (Rice et al. 1993; Letcher et al. 1996; Scheibe and Richmond 2002). In my research, I quantified the swimming behavior of four individual medusae of the scyphozoan *Aurelia aurita*. At the outset, I presumed that swimming patterns were responses to stimuli and, consequently, manifestations of behavior (Lehner 1996; Slater 1999). I decomposed the patterns into the time-dependent change in four characteristics of movement: (1) swimming bell pulsations, (2) velocity, (3) acceleration, and (4) depth. I differentiated between them by simultaneously applying several statistical techniques and demonstrated that each medusa exhibits unique swimming behavior including characteristic cycles of changes in velocity and acceleration.

Chapter 3 reports on studies that quantify the foraging behavior of the scyphomedusa *Chrysaora quinquecirrha* in mesocosms and the implications for its feeding efficiency in situ. The research addresses three questions:

(1) What is the effect of a variable food resource on the foraging behavior of a scyphomedusa?

(2) What behaviors of scyphomedusae have evolved that might increase their feeding efficiency?

(3) What is the effect of foraging behavior on the movement and distribution of a scyphomedusa?

Feeding rates of *Chrysaora quinquecirrha* medusae are highly variable spatially and temporally (Purcell 1992). It is likely that behavior affects the magnitude and variability of these rates as well as the spatial distributions of *C. quinquecirrha* because of the link between swimming and feeding (Ford et al. 1997).

Chrysaora quinquecirrha medusae searching and feeding patterns were consistent with well-documented foraging strategies for a patchy resource that maximize the likelihood of encountering prey and remaining in a patch once located (Smith 1974). However, there were notable differences between medusa foraging strategies and those observed in other animal groups and these may be related to the biomechanics of prey capture and detection by medusae. Taken together, the foraging behavior of *C.*

quinquecirrha medusae would increase efficiency in locating and capturing prey and could be responsible for their high predation rates and in situ spatial distributions.

Chapter 4 develops and describes the development of an individual-based model of scyphomedusa swimming behavior. The research addresses four questions:

(1) Can an individual-based model of medusa swimming behavior be developed?

(2) How can a model of medusa swimming behavior enhance predictions of their ecological effect?

(3) What are the mechanisms that underlie some behaviors exhibited by scyphomedusae in situ?

(4) Can a new quantitative, iterative process be applied to the development of individual-based models that relies on comparisons of empirical and modeled data at the individual level to improve the accuracy of the model?

There are numerous reports of complex behavior by scyphomedusae (reviewed in Arai 1997). Undoubtedly, many influence their ecological role, and most involve movement, yet no model exists of medusa swimming. The model described in this dissertation simulates medusa swimming behavior and how it influences foraging and medusa distributions.

I used an individual-based, correlated random walk of velocity vectors to simulate medusa movement. I found that medusae searching for food alternated between two behaviors that control swimming bell pulsation strength. Timing of the switches was variable, with the result that some medusae swim slowly, others rapidly, and some mix both slow and fast swimming. By contrast, feeding medusae swim at a constant moderate velocity but with more looping than searching medusae. Looping behavior is distinctly anisotropic. Medusa vertical distributions are a result of swimming directed toward the surface in a shallow system as well as avoidance of the bottom. The model confirmed that medusa swimming is driven by deterministic changes in swimming characteristics and that the frequency of these cycles is similar in several members of the population. I developed the model using a novel iterative process in which the model output of a single individual was quantitatively compared to empirical observations to determine the accuracy of the model in simulating individual behavior and to inform changes in the model prior to the next step in development.

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CHAPTER 2

Patterns in swimming by a scyphomedusa: a novel approach to quantifying behavior in individuals[1]

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ABSTRACT

Behavior is commonly studied at the group level using several individuals, but there is increasing evidence that the behavior of a few individuals often has a disproportionate effect on the response of a population to its environment. The present study used a suite of statistical techniques, random series analysis, analysis of variance, spectral analysis, and goodness-of-fit tests of frequency histograms, to quantitatively describe the time-dependent changes in individual behavior. Each technique reveals a different facet of the behavior and, when simultaneously applied to the data, distinguishes significant differences among the behaviors of several individuals. The approach was developed and tested on the swimming behavior of four specimens of the scyphomedusa *Aurelia aurita* (Linnaeus 1758), which were observed for nineteen days beginning 16 January 1998 and videotaped under identical environmental conditions during that period. The analyses showed that each medusa swam in a unique pattern, varying swimming at characteristic frequencies. Application of the approach to individual-based numerical modeling, to the role of endogenous stimuli in the behavioral repertoire, and to in situ studies of animal behavior is discussed.

INTRODUCTION

Behavior modulates the response of an organism to its environment and controls basic life functions such as feeding, reproducing, avoiding predation, and locating and remaining in a suitable environment. Stimuli are continuously received by the sensory systems of an organism and are translated through behavioral responses into actions increasing survival and contributing to the adaptive change of a species (see review by Manning and Dawkins 1998).

Although most behavioral studies focus on the response of a group to environmental stimuli, in fact, all behavior begins with the individual (Lehner 1996; Slater 1999). Indeed, the behavior of individuals can exhibit unique characteristics when compared to the population (Karieva and Odell 1987; Romey 1996; South 1999; Parrish et al. 2002). For example, Hamner et al. (1994) found that the swarming behavior of *Aurelia aurita* in Saanich Inlet, British Columbia, was caused by hundreds of individual medusae orienting swimming to the sun. Mechanistic studies of such emergent behavior in a population require consideration of the next lower scale of behavior, that is, at the individual level (Levin 1992; Romey 1996).

It is also becoming increasingly clear that inter-individual variability in behavior affects survival rates of the population (Rice et al. 1993; Letcher et al. 1996). Rose and Cowan (1993) found that the average survival rate of a group of age-0 striped bass was dependent on the feeding success of only a small proportion of the individuals. Thus, individual behavior provides a theoretical framework for understanding population ecology, namely, that changes in the species at the population level are dependent on the responses of individuals (Sutherland 1996; Caro 1998; Fryxell and Lundberg 1998).

Despite the importance of individuals, the study of behavior in marine species is commonly conducted at the population level using the mean values of a behavioral attribute of a group (e.g., Hamner and Hauri 1981; Forward 1985; Larson 1992; Essler and Kotrschal 1994; Buskey et al. 1995). This reliance on group attributes is in part a consequence of a lack of methods for studying the correlated data of individual behavior, and of difficulties documenting the movement of individuals (see review in Martin 2003).

There are techniques for comparing differences in individual behavior, but they have limited applications to marine species. Considerable attention has been focused on appropriate methods for comparing home range use by individuals (see review in Kenward et al. 2001), but these techniques are restricted to data of time-dependent spatial use. Alternatively, Markov chains can be used to analyze sequences of individual behavior, however, this method requires that behavioral events be easily differentiated (e.g. swimming, resting, feeding) so that behavioral sequences can be distinguished (Cane 1978; Lehner 1996). Therefore, Markov chains are of limited use if behavioral transitions over time are more subtle (e.g. variations in swimming velocity).

In the present study, I describe the development and application of a new approach to statistically characterize the swimming behavior of individual scyphomedusae *Aurelia aurita*. Specifically, I simultaneously applied four statistical techniques, random series analysis, analysis of variance (ANOVA), goodness-of-fit tests of frequency histograms, and spectral analysis, to the time-dependent change in swimming of four medusae. Each technique reveals a different facet of the data, and together the techniques statistically distinguish among the behaviors of individual medusae. Medusae of approximately the same size were cultured and videotaped singly under identical environmental conditions to eliminate all but endogenous factors controlling their behavior. I conducted six pairwise comparisons of the behavior of individuals using the four medusae, testing the null hypothesis that their swimming patterns were identical.

MATERIALS AND METHODS

Experimental medusae

I obtained several specimens of *Aurelia aurita* (Linnaeus 1758), which were raised from polyp cultures at the National Aquarium in Baltimore. The medusae were observed for nineteen days beginning 16 January 1998, and were maintained in the laboratory in an identical manner in order to avoid any differences in environmental factors that might affect behavior. Four medusae of similar swimming bell diameter (8-10 cm) were selected (designated A3, A9, A10, and A11) allowing six pairwise comparisons of individual behavior.

Each medusa was kept in a separate 20-l polypropylene container filled with unfiltered seawater (salinity 30). During the 3 wk of observations, a 12 h light: 12 h dark cycle was maintained and 25% of the water in the containers was exchanged daily with fresh seawater. Temperatures ranged from 19 to 21°C and salinity from 30 to 33 during the study. Freshly hatched *Artemia* sp. nauplii were fed to the medusae daily just prior to the beginning of the dark cycle in amounts sufficient to maintain a constant bell diameter during the experiment.

Experimental conditions

Swimming behavior was observed under identical environmental conditions. Videotaping was conducted in a 180 cm x 60 cm x 70 cm rectangular glass aquarium filled with 756 liters of unfiltered seawater (salinity 30). Temperature was unregulated and remained at the ambient temperature of the laboratory (range 19 to 20°C). When no medusa was in the tank, the water was aerated. Light was supplied by a bank of four 40-W fluorescent light bulbs suspended above the aquarium.

Scyphomedusae are more active in the presence of prey (Bailey and Batty 1983; Arai 1991; Matanoski et al. 2001). To stimulate the swimming behavior of *Aurelia aurita*, I added *Artemia* sp. nauplii to the filming tank (final concentration 4692 ± 1005 m^{-3}) 2 h prior to filming. Circulation of the water caused by aeration dispersed them. Immediately prior to videotaping, aeration stopped and one medusa was gently transferred to the tank. It was allowed to acclimate to its surroundings until it was neutrally buoyant as indicated by its ability to swim throughout the water column. Each medusa was filmed during the 12 h light period of one day, however the duration of filming varied depending on the time needed to obtain sufficient footage for analysis.

Videography and video analysis

Videotaping was conducted using two cameras, a SONY CCD TR400 Hi8 variable focus (5.4-64.8 mm, which remained fixed throughout the experiments) video camera recorder, and a Pulinix monochrome CCD video camera with a Tamron 25-mm lens, recording to a Sony EV-C200 Hi8 video cassette recorder. Cameras were placed on two sides of the tank so that their fields of view were perpendicular and overlapped throughout most of the aquarium volume. I synchronized the video records of both cameras by simultaneously initiating recording in each at the start of each filming session, obtaining the position of the medusae in three dimensions.

Swimming patterns of each medusa were divided into sequences determined by the actions of each individual. A sequence began when the medusa appeared in the view of both cameras and ended when it moved out of the view of either of the two cameras. Nine sequences were videotaped of medusa A3, seven of medusa A10, two of medusa A9, and eleven of medusa A11. Sequences were from 2-35 min duration. To avoid boundary effects, sequences in which the medusa contacted the sides and bottom of the tank or water surface were disregarded. Thus, each sequence was an independent random sample of the swimming pattern of that medusa away from the boundaries of the tank. Sequences were subdivided into segments by reviewing the videotape in 5-s intervals, which was the shortest duration that allowed for precise observations of swimming bell pulsation frequency of the slowest pulsing medusa (i.e. A3, 0.25 pulsations s^{-1}) and changes in medusa position given the resolution of the video system. The mean pulsation rate, velocity and acceleration were calculated (described below) over each 5-s segment and the depth recorded at the beginning of each segment. The result was four time series for each sequence of swimming, one each of the mean pulsation rate, velocity, and acceleration during each 5-s segment and one of the depth of the medusa at 5-s intervals.

For each sequence, the position of the center of the exumbrella of the medusa at the beginning of every 5-s segment was plotted using a VP110 motion analyzer and digitized using an ATT 6386SX/EL WGS personal computer running ExpertVision software (MotionAnalysis Corporation, Santa Rosa, CA). When the contrast of the image with the background was inadequate to allow the motion analyzer to accurately plot the center of the medusa, the swimming path was plotted manually using the pixel grid of the motion analyzer, which ensured continuity of the data. The total number of swimming bell pulsations during each 5-s segment was also counted and recorded.

The distance traveled in each dimension during each 5-s segment was determined by subtracting the initial position of the medusa in one segment from that of the segment immediately following. The apparent distance traveled, however, varied depending on the distance of the medusa from the camera. To compensate for this, a relationship between the size of an object and the lens-to-subject distance for the Sony TR400 video camera recorder was determined by inserting a meter stick into the field of view and linearly regressing the known distances in cm to the apparent distances in pixels. The conversion was

$$X = X_a(0.2457 + [0.0005346 \times D_s])$$

where X was the actual distance in the x direction in cm, X_a the apparent distance in the x direction in pixels, and D_s the lens-to-subject distance for the SONY CCD TR400 video camera recorder. Distances in the Z direction were calculated in an identical manner.

For distances measured by the Pulinix CCD camera (e.g. in the Y direction), the equation for converting between apparent and known distances was

$$Y = Y_a(0.3974 - [0.0003440 \times D_p])$$

where Y was the actual distance in the y direction in cm, Y_a the apparent distance in the y direction in pixels, and D_p the lens-to-subject distance.

Velocity in the x direction was calculated using the distance traversed by the medusa in that direction in cm in 5 s. Velocities in the y and z directions were calculated in an identical manner.

I determined the instantaneous acceleration of each segment in the x direction as

$$A_X = \frac{(V_{X_{i+1}} - V_{X_i})}{(t_{i+1} - t_i)},$$

where V_{X_i} and t_i were the velocity and time at the start of the video segment, respectively, and $V_{X_{i+1}}$ and t_{i+1} the velocity and time at the end of the video segment. Instantaneous acceleration in the y and z directions was calculated in an identical manner.

The magnitude of the instantaneous velocity for each segment was calculated as

$$\text{velocity} = \sqrt{V_x{}^2 + V_y{}^2 + V_z{}^2}\ .$$

Similarly, the magnitude of the acceleration was calculated as

$$\text{acceleration} = \sqrt{A_x{}^2 + A_y{}^2 + A_z{}^2}\ .$$

Preliminary analysis

I first assessed the stationarity of each plotted time series by examining them for obvious changes in mean (i.e. trend) or in the magnitude of variability over time. In addition, I created a covariance matrix for each time series to assess whether the variance function of the behavioral data was constant throughout the observation period.

All time series used in this study were weakly stationary (i.e. constant mean and variance), indicating that swimming behavior was constant over the videotaping sessions. Thus, the results of the statistical analyses did not depend on when during the period of observation the sequences were videotaped.

Random series analysis

To determine whether the variability in swimming characteristics (i.e. pulsation rate, velocity, acceleration, and depth) was the result of behavior, I tested the null hypothesis that the order of values for each characteristic was random using random series analysis. In a runs test, the data are hypothesized to be controlled by a first order Markov process in which the value in a given period is dependent on the value in the preceding period. If the value in the preceding period has no effect, the process is random with respect to time. For velocity, acceleration, and depth, where the data were continuous, I tested the swimming sequences using a runs up or down test (Neter et al. 1982). The time series of pulsation rate, however, consisted of numerous tied observations. So I used a runs test for nominal scale data (Neter et al. 1982, Zar 1984) converting the data to dichotomous, nominal data by defining two categories, 1) resting, in which the medusa did not pulse for 10 s, and 2) active, which consisted of one or more pulsations during any 10-s period. While a medusa is swimming there is a latency period between contractions during which the swimming bell recoils to its relaxed state. The maximum duration of this recoil was 3 s. Thus, I have defined resting as a period without pulsations that is > 3 fold the recoil period, eliminating the possibility of confusing the latency period between pulsations for resting. For all random sequence analysis, I used an experimentwise error rate of 0.05 (Sokal and Rohlf 1995).

Means comparisons

In most instances when inferential statistical techniques (e.g. ANOVA) are applied to data garnered from a population, the experimental unit of interest is an individual. Since I was interested in the differences among individuals and not populations, I had to choose an experimental unit that was a subset of the swimming behavior of a single individual. The obvious choice were the 5-s segments of swimming of an individual observed during the video analysis. This was the shortest duration that allowed for precise resolution of changes in medusa position given the video analysis system. However, neighboring values in a time series are generally correlated, violating one of the assumptions (independence of observations) of ANOVA. Therefore, it was necessary to determine a long enough interval between observations to eliminate autocorrelation thereby allowing the use of ANOVA.

I used the autocorrelation coefficient, r, to determine the dependence between values in a time series. The autocorrelation coefficient is defined as

$$r = \frac{1}{n-k} \frac{\sum_{i=1}^{n-k} (x_i - \bar{x})(x_{i+k} - \bar{x})}{\sum_{i=1}^{n} (x_i - \bar{x})^2},$$

where n is the number of observations in the time series, k the lag between values in the series, x_i the ith value in the series, x_{i+k} the ith $+k$ value in the series, and $\bar{x}$ the mean of the series. Note that r is normalized to the variance of the series. The autocorrelation of acceleration values of a sequence of medusa A10 and velocity values of medusa A11 were typical of the many analyses (Fig. 2.1). The correlation between values rapidly declined toward zero as the lag between them increased. Analyses of all the swimming sequences revealed that values separated by a maximum of 15 s were independent.

I ensured that observations separated by 15 s were statistically independent in all of the time series analyzed in this study using a test for serial independence (data not shown). This test compares the time-independent measure of variability, variance, to an analogous measure of variability that depends on the order of the observations, the mean successive difference,

$$\delta^2 = \frac{\sum_{i=1}^{n-1} (x_{i+k} - x_i)^2}{n-1}$$

(von Neumann 1941; von Neumann et al. 1941). I compared the variance for each swimming characteristic to the mean successive difference at increasing interval length, k, between successive samples. The mean successive difference depends explicitly on the order in which the samples were collected and I found that observations of swimming characteristics separated by 15 s did not depend on the order in which they were sampled. I had, for example, 62 independent observations of the velocity of medusa A10 (from seven videotaped swimming sequences) which were suitable for comparisons of the swimming behavior of the medusa.

I conducted a two-factor, Model I (fixed effects) ANOVA and used the nonparametric Kruskal-Wallis test of ranks because the data did not conform to assumptions of normality. Because I was interested in the differences among the endogenous behavior of individuals, I used the Tukey test for six pairwise comparisons among the four medusae. The level of significance for all tests was 0.05 (Zar 1984).

Distribution of observations

The distribution of values of swimming characteristics can provide important insight into the variability and patterns of movement. I quantified the frequency distributions of observations of these characteristics using a measure of skewness, the third central moment about the sample mean,

$$g_1 = \frac{n\sum_{i=1}^{n} y_i^3}{(n-1)(n-2)s^3}$$

where n is the sample size, y_i the i th measurement of the sample, and s the sample standard deviation (Zar 1984; Sokal and Rohlf 1995). Pairwise comparisons of frequency distributions were conducted using the log-likelihood goodness-of-fit test for the discretely defined pulsation rate (i.e. 0, 1, 2, 3, or 4 pulsations 5 s^{-1} interval) and the Kolmogorov-Smirnov goodness-of-fit test for the continuous data of velocity and acceleration observations. In all cases the appropriate pairwise error rate was determined using the Dunn-Šidák method to yield an experimentwise error rate of 0.05 (Sokal and Rohlf 1995).

Spectral analysis

Spectral analysis was used to determine the frequencies at which the medusae varied their swimming and is demonstrated for the depth changes of medusa A10. First, the time series of observations of depth (Fig. 2.2a) was processed by detrending the data, centering at zero, and passing the data through a low pass filter with an upper limit of twice the frequency of sampling (i.e. 100 mHz), the Nyquist frequency. This frequency is the theoretical upper limit of detectable cycles given the sampling interval (Jenkins and Watts 1968). Another limitation of spectral analysis is that truncation of the time series at less than integer multiples of the component cycles in the series leads to poorly defined peaks at those associated frequencies in the spectrum (i.e. smearing) (Masters 1995). To correct for this phenomenon, I applied the Hanning data window function of IDL (version 5.1, Research Systems, Inc.), whereby each element, k, of the time series of length, N, is multiplied by a corrective algorithm of the form

$$w(k) = \frac{1}{2}\left(1 - \cos\left(\frac{2\pi k}{N-1}\right)\right) .$$

The resulting series was decomposed into its discrete cyclical components using a fast Fourier transform and the power spectrum calculated and plotted versus frequency (Fig. 2.2b) (Proakis and Manolakis 1996). Cyclical variations in the time series (Fig. 2.2a, peaks marked A) were reflected in increased power at the corresponding frequency (Fig. 2.2b, peak A). In this example, changes in direction from upward to downward and the attendant changes in depth were obvious as was the cyclical recurrence of these changes. Spectral analysis, however, also detected more subtle cyclical patterns in swimming where, for example, up and down were not represented by changes in direction, but in the magnitude of the swimming characteristic. For example, a less obvious cyclical pattern in the velocity of medusa A11 (Fig. 2.2c, peaks marked B) was prominently reflected in the power spectrum (Fig. 2.2d, peak B).

I derived a smoothed estimate of the power spectrum using Bartlett’s smoothing procedure (Jenkins and Watts 1968). Briefly, this procedure consists of truncating the time series in shorter subseries (Fig. 2.3a), applying the fast Fourier transformation to obtain a power spectrum for each subseries (Fig. 2.3b), and constructing a smoothed spectral estimate for the time series by averaging the power at each frequency of the several subseries (Fig. 2.3c). The resulting smoothed estimate of the power spectrum is distributed as a chi square with $df = 3\left(\frac{T}{M}\right)$, where T is the length of the original time series and M, the length of the subseries.

I used the several sequences of swimming for each medusa as the basis for Bartlett's smoothing procedure. For spectral analysis, all time series of a single medusa were truncated at the length of the shortest videotaped swimming sequence. Bartlett's smoothing procedure was then used to construct an average spectrum. To ascertain whether any of the peaks in the average power spectrum departed from random white noise, I determined 95% confidence intervals around the mean of the smoothed (average) estimate of the spectrum using the spectrum mean and variance as the best estimate of the population parameters (Jenkins and Watts 1968).

RESULTS AND DISCUSSION

Swimming paths

I observed two swimming patterns during the study (Fig. 2.4). Medusae A3 and A10 swam primarily in tight circles (average diameter ~ 10 cm), but frequently stopped swimming and drifted in a linear path tangential to the last circle. By contrast, medusae A9 and A11 swam primarily in a linear pattern and occasional curved portions of the path were much broader (average diameter ~ 40 cm) than the tight circles of medusae A3 and A10. The swimming pattern of medusae A3 and A10 also included frequent periods of inactivity totaling 25-50% of the time. During these periods, swimming bell pulsation rates averaged $\leq 0.1 \text{ s}^{-1}$. By contrast, medusae A9 and A11 swam > 90% of the time and rest periods were brief (≤ 10 s). These two patterns were visually very distinct. In addition, each medusa consistently used the same pattern during the time of observation. Thus, I differentiated two pairs of medusae, medusae A3 and A10 that swam in the "circle-rest pattern" and medusae A9 and A11 that swam in the "continuous linear pattern".

Random series analysis

I analyzed the swimming paths to determine if they were non-random before deconstructing these patterns quantitatively. Changes in pulsation rate, velocity, acceleration, and depth were not random, and because there was no current in the filming tank, the changes resulted from endogenous behaviors of the medusae (Table 2.1). The only exceptions were the random changes in velocity and acceleration of medusa A9, possibly a result of the shorter duration of videotaping for this medusa when compared to the others. It is likely that longer sequences of videotaped swimming would have been non-random. Although this result indicates that the swimming pattern of medusa A9 was not the result of a behavioral response, I included the swimming data for this medusa in the analysis for the purpose of validating the approach. I consider random series analysis an important first step in any investigation of behavior because randomness implies that a behavioral process does not underlie the data. To my knowledge, this type of analysis has not been undertaken in previous studies of animal behavior.

Means comparisons

I compared the differences in swimming characteristics (pulsation rate, velocity, and acceleration) among individuals using ANOVA. I found significant differences in pulsation rate and velocity among individuals (Table 2.2). Furthermore, pairwise comparisons yielded the same pairings of medusae determined by observing the patterns, that is, medusae A3 and A10 swam more slowly and pulsed less (circle-rest pattern) than medusae A9 and A11 (linear pattern) (Table 2.3; Tukey test, $\alpha = 0.05$).

Interestingly, there were no significant differences in acceleration among medusae (Table 2.2). This was surprising considering the defining features of the patterns. I expected medusae A3 and A10 to have higher acceleration rates due to the more frequent turns and pauses in their “circle-rest pattern,” which would increase their angular and linear acceleration, respectively. However, the long rest periods of their pattern, when acceleration was effectively zero, reduced their average acceleration rate and eliminated the difference between the two groups of medusae. This result also highlights the need to use multiple techniques to differentiate among individuals because any single test may be insensitive to subtle differences in behavior.

I included the length of time the medusae were in the filming tank as a second factor in the ANOVA because it was possible that medusa swimming behavior changed over time (Table 2.2). Time in the filming tank differed among medusae and was dependent on the time necessary to obtain sufficient footage for analysis. However, there was no effect of time in the tank on swimming pattern indicating that behavior was constant during videotaping. Nor was there any interaction between time in the tank and the individual medusae.

Distribution of observations

I used the distribution of observations of the swimming characteristics to examine comprehensive features of swimming patterns. Comparisons of the frequency distributions of the velocities among the four medusae yielded results similar to ANOVA (Table 2.4), namely there was no significant difference between the slower swimming medusae, A3 and A10, and none between the faster swimming medusae, A9 and A11, but a significant difference between the pairs. In addition, there was no difference among the four medusae in the patterns of acceleration. However, whereas there was only a small and non-significant difference in the mean pulsation rate of medusae A3 and A10, the patterns contributing to these means were sufficiently distinct to create significant differences in the frequency histograms. The tendency for A10 to be pulsing at moderate rates (0.4-0.6 s^{-1}) more frequently than A3 (Fig. 2.5a, peak A) was balanced by its tendency to be observed at rest (0.0 s-1) twice as often (Fig. 2.5a, peak

B). This resulted in similar mean pulsation rates in the two medusae, but significant differences in the frequency distributions. Even when differences in swimming patterns were reflected in the mean values of swimming characteristics, examination of the frequency histograms revealed more subtle differences. For example, while medusae A9 and A11 swam faster (i.e. had a higher mean velocity) than medusae A3 and A10, this was not a result of swimming faster all the time. Medusae A9 and A11 spent only 25% less time swimming at slow speeds (≤ 0.6 cm s^{-1}) than A3 and A10 (Fig. 2.5b, peak C), but swam very fast (≥ 1.8 cm s^{-1}) twice as often (Fig. 2.5b, peak D). Therefore, the higher mean velocity of medusae A9 and A11 was due to periods of very rapid swimming and not to continuous, moderately-paced swimming.

Spectral analysis

Spectral analysis of the time series of swimming characteristics provided the first opportunity among the techniques thus far described to decompose the behavior of the four medusae into individual behavior quantitatively and demonstrated the usefulness of applying several techniques simultaneously to reveal subtle individual differences. For example, although spectral analysis revealed that each medusa varied its acceleration rate at a unique frequency, the ANOVA and comparisons of frequency distributions did not distinguish statistically significant differences in acceleration among the medusae. The mean acceleration rates of medusae A3 and A9 were the same, and the two could not be differentiated on this basis. However, changes in A3’s acceleration rate occurred nearly three times as frequently (60 mHz) (Fig. 2.6, peak A) as those in A9 (22 mHz) (Fig. 2.7, peak B). The difference in frequency was a result of the two broad patterns of the medusae. The circular swimming pattern of medusa A3 was caused by more numerous changes in angular velocity (i.e. turns) than the linear pattern of medusa A9. However, while I could not distinguish these differences in the total amount of turning by the mean acceleration rates, spectral analysis distinguished the two patterns based on the variability of these rates, that is, the frequency of turns.

Spectral analysis of the swimming of the medusae also revealed commonalities in their patterns, specifically, low frequency changes in depth. The medusae altered their vertical position less frequently, as indicated by the power spectra of depth, than their horizontal swimming pattern, as indicated by higher frequency changes in velocity and acceleration (Figs. 2.6, 2.7). All four medusae swam primarily horizontally with only occasional changes in depth, a pattern observed by Bailey and Batty (1983) for *Aurelia aurita* in large tanks and by Hamner et al. (1994) in situ.

Applications

Quantification of the differences among individuals is directly applicable to several areas of behavior, including the use of individual-based models (IBM's) (Huston et al. 1988; Lomnicki 1992). This requires quantification of readily measured individual attributes. Paradoxically, IBM's are often parameterized by modeling the individual using a group average and constructing a distribution, usually normally distributed and centered on this value. However, I have observed that the distribution of swimming characteristics of an individual scyphomedusa may be far from the normal and, at any given time, the individual is far more likely to be observed at a value other than the average. Furthermore, medusae change their behavior cyclically at characteristic frequencies. If this pattern of individual differences in behavior is general, it would require further attention to intra-individual variability in behavior when constructing IBM's.

Including measures of individual variability increases the ability of IBM's to reproduce phenomena observed in natural populations (Rice et al. 1993; Rose and Cowan 1993; Letcher et al. 1996). In addition, my approach will enable modelers to differentiate statistically among observations on individuals (such as those summarized in Table 2.5), to parameterize IBM's with measures of central tendency of individuals (e.g. means) as well as measures of the variability of individuals (e.g. skewness and frequency of variations in behavioral measures) and, as computational power increases, to include larger numbers of individuals in models (Huston et al. 1988). my approach will also assess the ability of a model to realistically simulate members of natural populations by comparing behavior characteristics derived from a modeled individual to those of an empirically observed one.

Because this approach can differentiate among individuals, it is relevant for studying endogenous behavior. Little is known regarding the endogenous behavior of planktonic species, and this limits understanding the influence of environmental conditions on populations (Daly and Smith 1993). For instance, one of the most obvious examples of endogenous behavior is biological rhythmicity which, in marine systems, is often manifested as diel or circatidal vertical migrations (see reviews in Ringleberg 1995 and Palmer 1995). Where a biological process (circatidal migration) interacts with a physical process (tidal circulation), the effect can be horizontal transport and retention of a planktonic organism in an estuary or coastal embayment (e.g. Hill 1991). The mechanism underlying this transport only becomes apparent if endogenous circatidal migratory behavior is considered.

The contribution of individual cycles to these biological rhythms has not been studied previously. I found that the frequencies at which individuals changed their swimming varied significantly (Table 2.5). Medusa A10, for example, varied its depth twice as frequently as the other medusae, a difference that would have been lost in the mean frequency of the group.

Until recently, following the movement of a individual pelagic marine animals in situ has been difficult and costly. Advancements in telemetry, electronic tagging, and remote videography now allow simultaneous tracking of numerous individual fish (Cote et al. 1998), crustaceans (Friere and Gonzalez-Gurriaran 1998), marine mammals (Davis et al. 1999), and jellyfish (Purcell et al. 2000). The combination of my approach, which permits direct comparison of the behavior of individuals, and technological innovations would allow, for example, the foraging patterns of individual marine organisms to be differentiated or the behavior of individual schooling fish to be associated with the telemetered data of the position of each individual within the school. In addition, my approach was developed specifically for the swimming of a pelagic organism in three dimensions. Earlier methods for analyzing the movement of marine organisms have often been limited to two dimensions, a significant drawback for studies of pelagic organisms, which move in a three dimensional environment.

CONCLUSION

Despite its importance, the behavior of individuals has historically received scant attention in marine species. I have used several techniques simultaneously to analyze time series of behavioral data. Each technique quantitatively describes a different aspect of individual behavior. By describing sufficient aspects, subtle differences in behavior patterns among individuals can be distinguished. Specifically, (1) random series analysis tests whether actions represent directed non-random changes in the behavioral attribute; (2) ANOVA differentiates between average values among individuals; (3) comparisons of the dispersion of observations provides insight into how patterns of behavior differ among individuals; (4) spectral analysis quantifies periodic variations in behavior over time. To be analyzed using my approach, a behavior must (1) vary over a time scale short enough when compared to the duration of the study so that a time series of sufficient duration can be obtained, (2) be suitable for frequent, easily obtained measurement, and (3) be measured non-destructively. This approach is broadly applicable because most animals continually respond to a variety of stimuli. It can be used to provide information for individual-based models, studies of endogenous behavior and, given recent improvements in methods for tracking free-swimming organisms, for in situ studies of a variety of pelagic marine species.

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TABLES

Table 2.1 *Aurelia aurita*. Random series analysis of swimming characteristics for four medusae using a runs test. Number of swimming sequences used for each medusa indicated by n. C indicates a clustered, nonrandom sequence in the time series, a result of behavior (experimentwise error rate, p = 0.05). R indicates sequence of data was random.

Medusa	n	Pulsation rate	Velocity	Acceleration	Depth
A3	9	C	C	C	C
A11	17	C	C	C	C
A10	8	C	C	C	C
A9	2	C	R	R	C

Table 2.2 *Aurelia aurita*. Differences among four medusae in three swimming characteristics using two-way analysis of variance (ANOVA). There were four levels of the factor medusa, one for each individual (A3, A9, A10, and A11) testing whether there were differences in swimming patterns among the four; two levels for the time the medusa was in the filming tank, <5 h or ≥ 5 h. There were no significant interactive effects between the two factors medusa and time in tank at the 0.05 significance level.

Swimming characteristic	Factor	F	p
Pulsation rate	Medusa	12.18	0.01
	Time in tank	0.10	0.76
Velocity	Medusa	5.20	0.04
	Time in tank	0.56	0.48
Acceleration	Medusa	1.82	0.23
	Time in tank	0.003	0.96

Table 2.3 *Aurelia aurita*. Means ± SE (*n* in parentheses) of swimming characteristics for individual medusae. Within columns, different superscript letters indicate statistically significant differences among individuals and identical superscripts indicate no significant difference (Tukey test, $\alpha = 0.05$).

Medusa	Bell diam. (cm)	Pulsation rate (pulsations s^{-1})	Velocity (cm s^{-1})	Acceleration (cm s^{-2})
A3	9.5	0.26 ± 0.01 (254) ^{a}	0.86 ± 0.04 (177) ^{a}	0.19 ± 0.01 (172) ^{a}
A10	10.0	0.30 ± 0.01 (97) ^{a}	0.89 ± 0.05 (62) ^{a}	0.14 ± 0.02 (59) ^{a}
A9	8.5	0.38 ± 0.02 (50) ^{b}	1.09 ± 0.17 (16) $^{a, b}$	0.19 ± 0.04 (15) ^{a}
A11	8.0	0.40 ± 0.01 (249) ^{b}	1.15 ± 0.07 (185) ^{b}	0.17 ± 0.01 (177) ^{a}

Table 2.4 *Aurelia aurita*. Comparison of frequency distributions of observations of swimming characteristics of medusae. g_1 is the third central moment about the mean, a measure of skewness of the distribution. Within columns, different superscript letters indicate statistically significant differences among distributions and identical superscripts indicate no significant difference (experimentwise error rate = 0.05).

	g_1		
Medusa	Pulsation rate	Velocity	Acceleration
A3	0.22^{a}	1.44^{a}	2.31^{a}
A10	0.01^{b}	0.61^{a}	3.18^{a}
A11	-0.28^{c}	0.31^{b}	1.85^{a}
A9	-0.34^{d}	0.14^{b}	1.22^{a}

Table 2.5 *Aurelia aurita*. Summary of characteristics of swimming patterns of medusae. Spectral signal is the most prominent frequency at which the swimming characteristic varies cyclically.

	Means (s^{-1}, cm s^{-1}, cm s^{-2})				g_1				Spectral signal (mHz)			
	A3	A10	A11	A9	A3	A10	A11	A9	A3	A10	A11	A9
Pulsation rate	0.26	0.29	0.40	0.38	0.22	0.03	-0.28	-0.34	24	52	15	24
Velocity	0.86	0.88	1.15	1.09	1.44	0.62	0.31	0.14	29	40	15	21
Acceleration	0.19	0.15	0.17	0.19	2.31	3.12	1.85	1.22	60	41	31	22
Depth	-	-	-	-	-	-	-	-	7	13	8	10

FIGURES

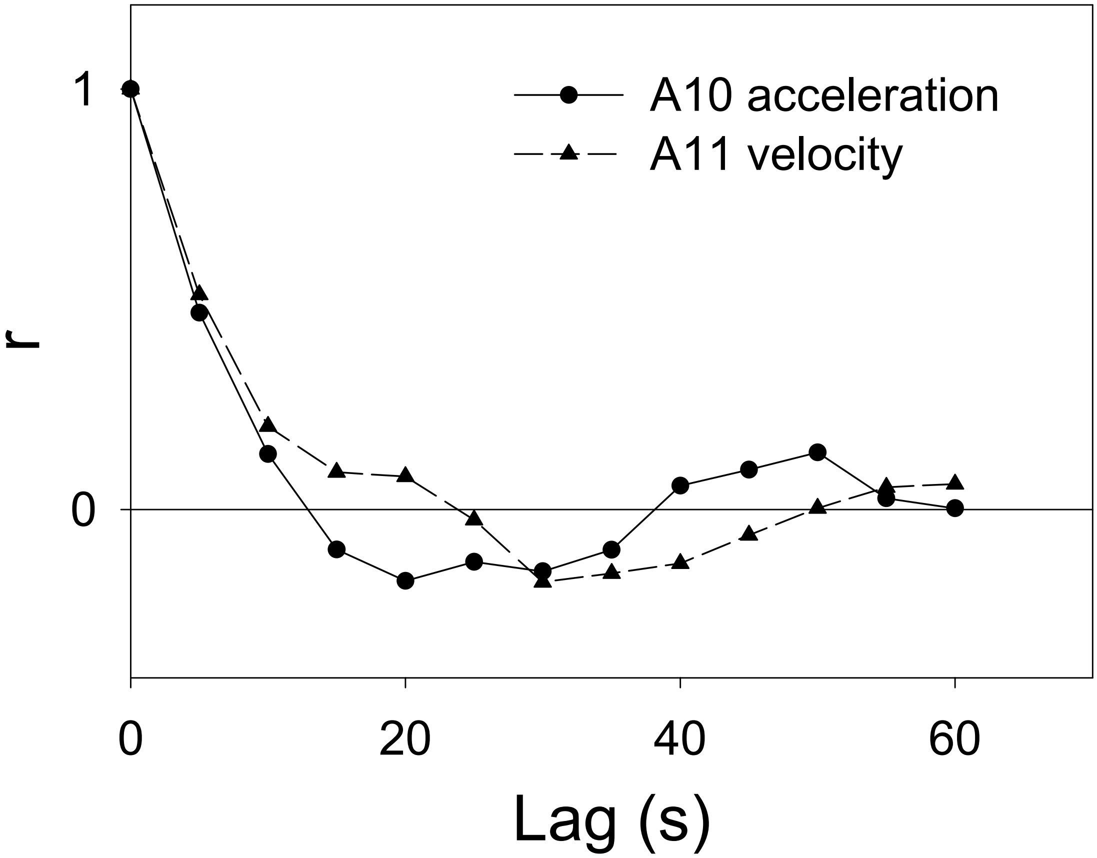

Figure 2.1 *Aurelia aurita*. Autocorrelation between values in the time series of acceleration of medusa A10 and velocity of medusa A11.

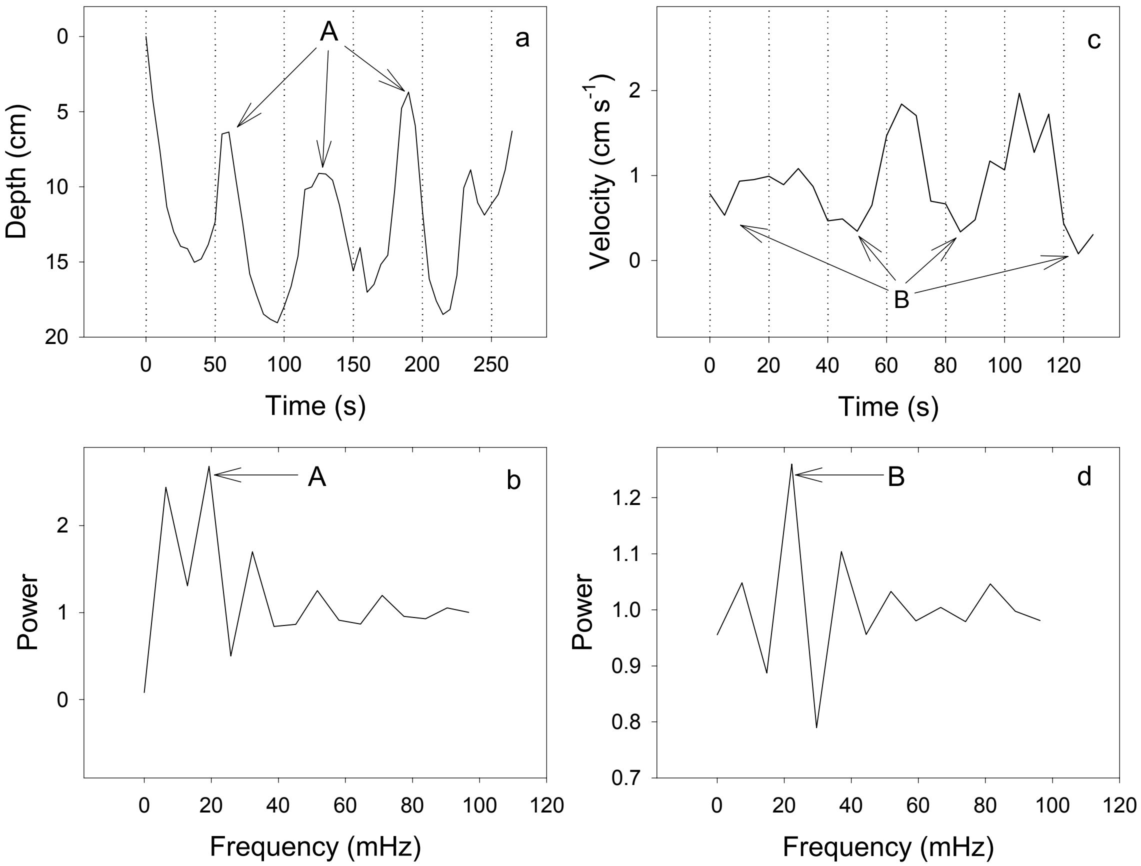

Figure 2.2 *Aurelia aurita*. Time series of depth for a swimming sequence of medusa A10 (a) and velocity of a swimming sequence of medusa A11 (c), and the power spectrum of each (b and d, respectively). Cyclical peaks and troughs in the time series and the corresponding peak in the power spectrum are highlighted by lettered arrows.

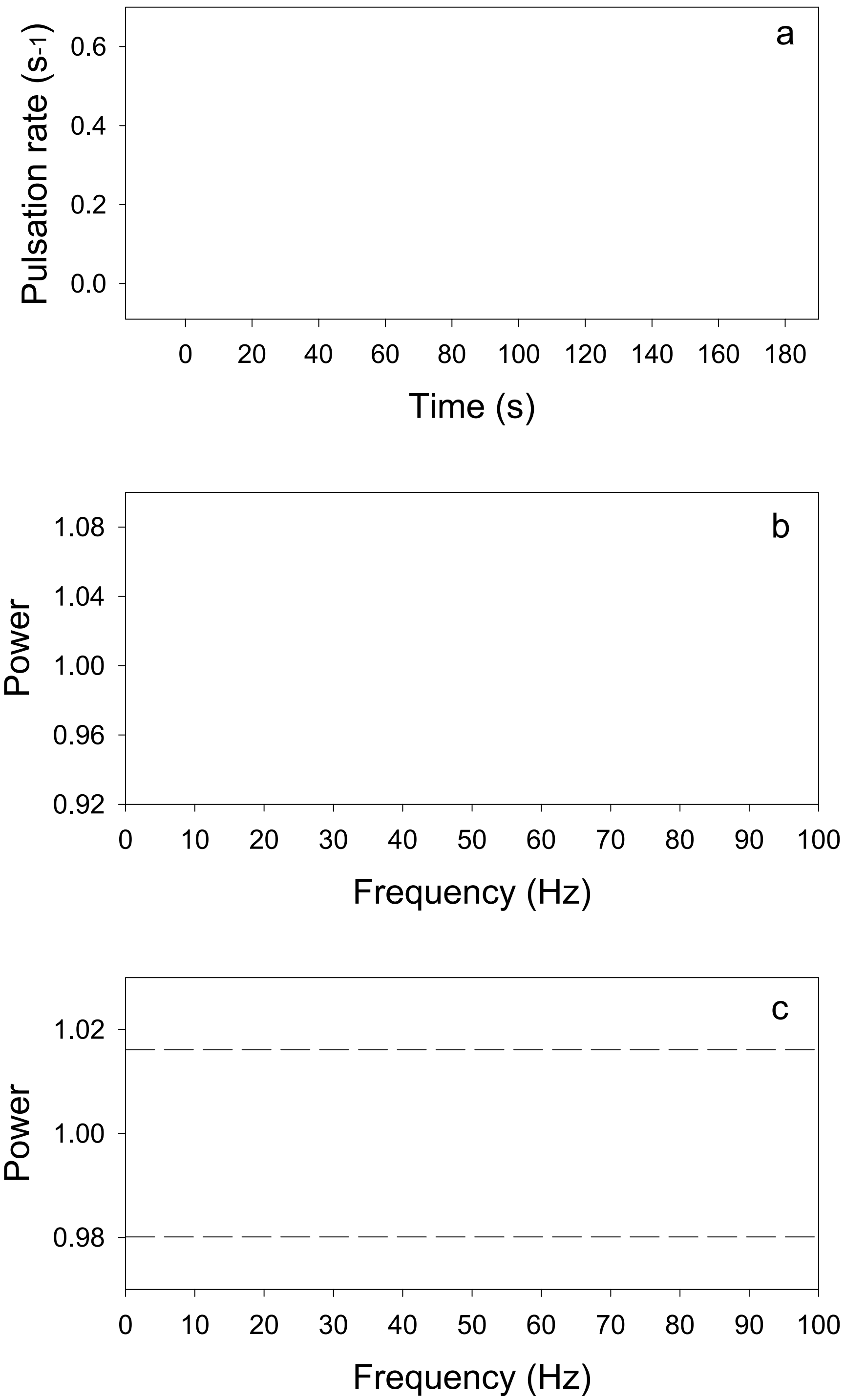

Figure 2.3 *Aurelia aurita*. Pulsation rate of medusa A3 for four sequences of video footage as time series (a), power spectra (b), and the average power spectrum for the sequences (c). Horizontal dashed lines are 95% confidence limits for the average power spectrum.

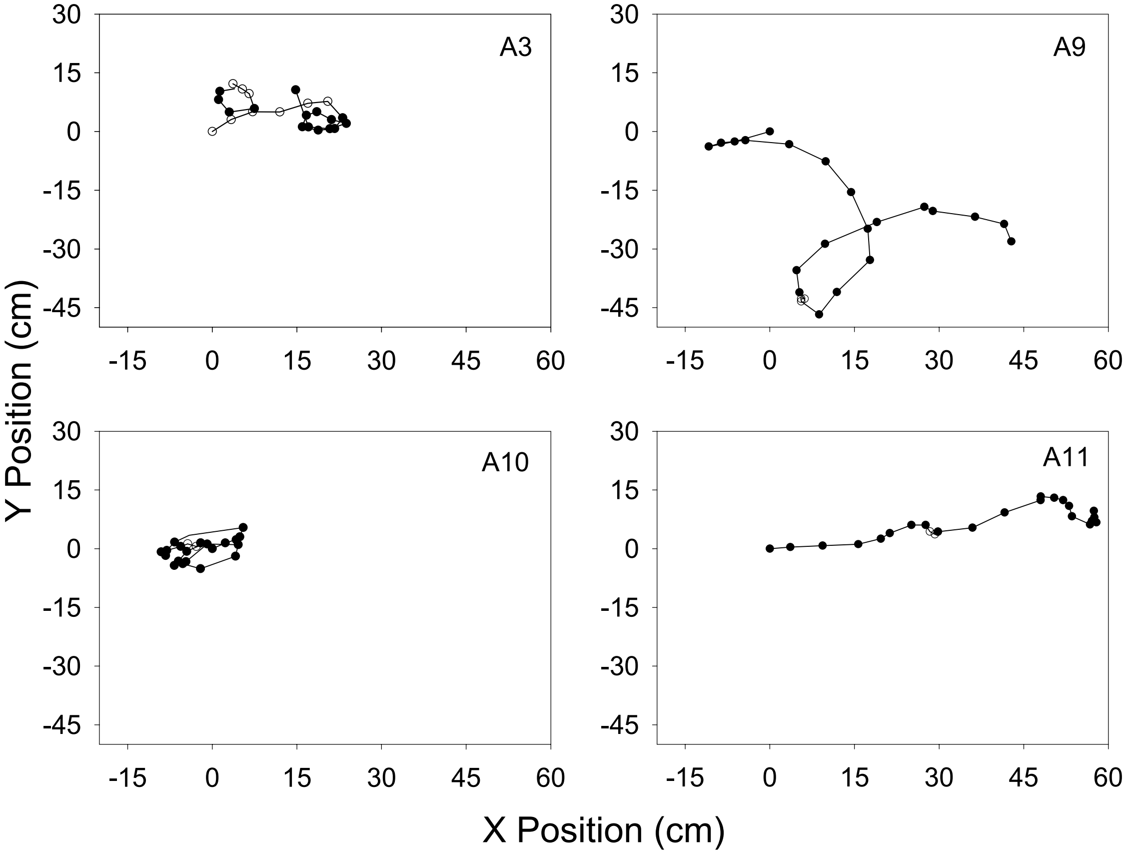

Figure 2.4 *Aurelia aurita*. Typical swimming sequences in two horizontal dimensions for 4 medusae, A3, A9, A10, and A11 when pulsing (filled circles) and resting (open circles). Position refers to the medusa within the filming tank and the starting point of each sequence was arbitrarily set at the origin. Symbols represent the location of the medusa every 5 s, and the duration of each sequence is 2 min.

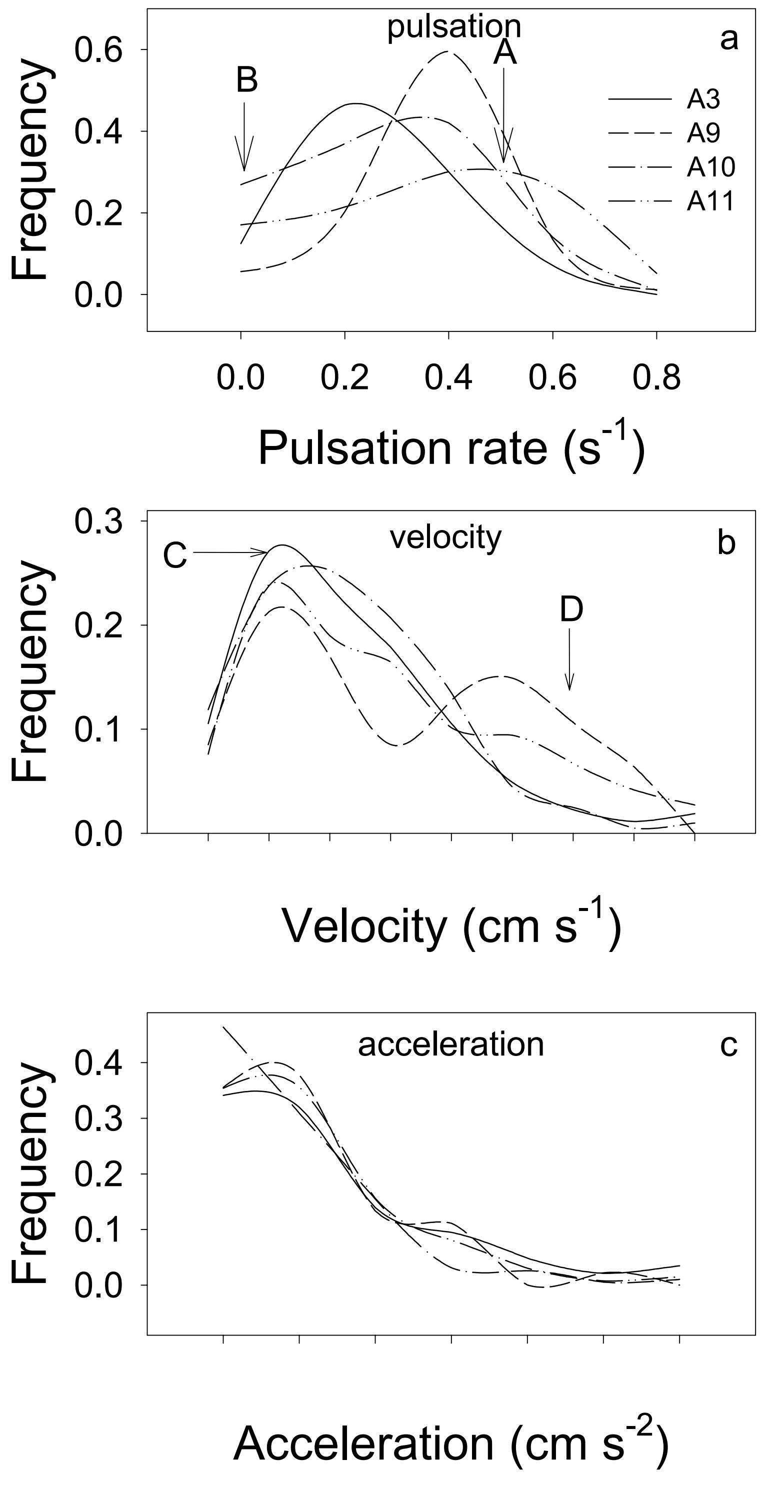

Figure 2.5 *Aurelia aurita*. Frequency histograms for observations of swimming bell pulsation rate, velocity, and acceleration of medusae A3, A9, A10, and A11.

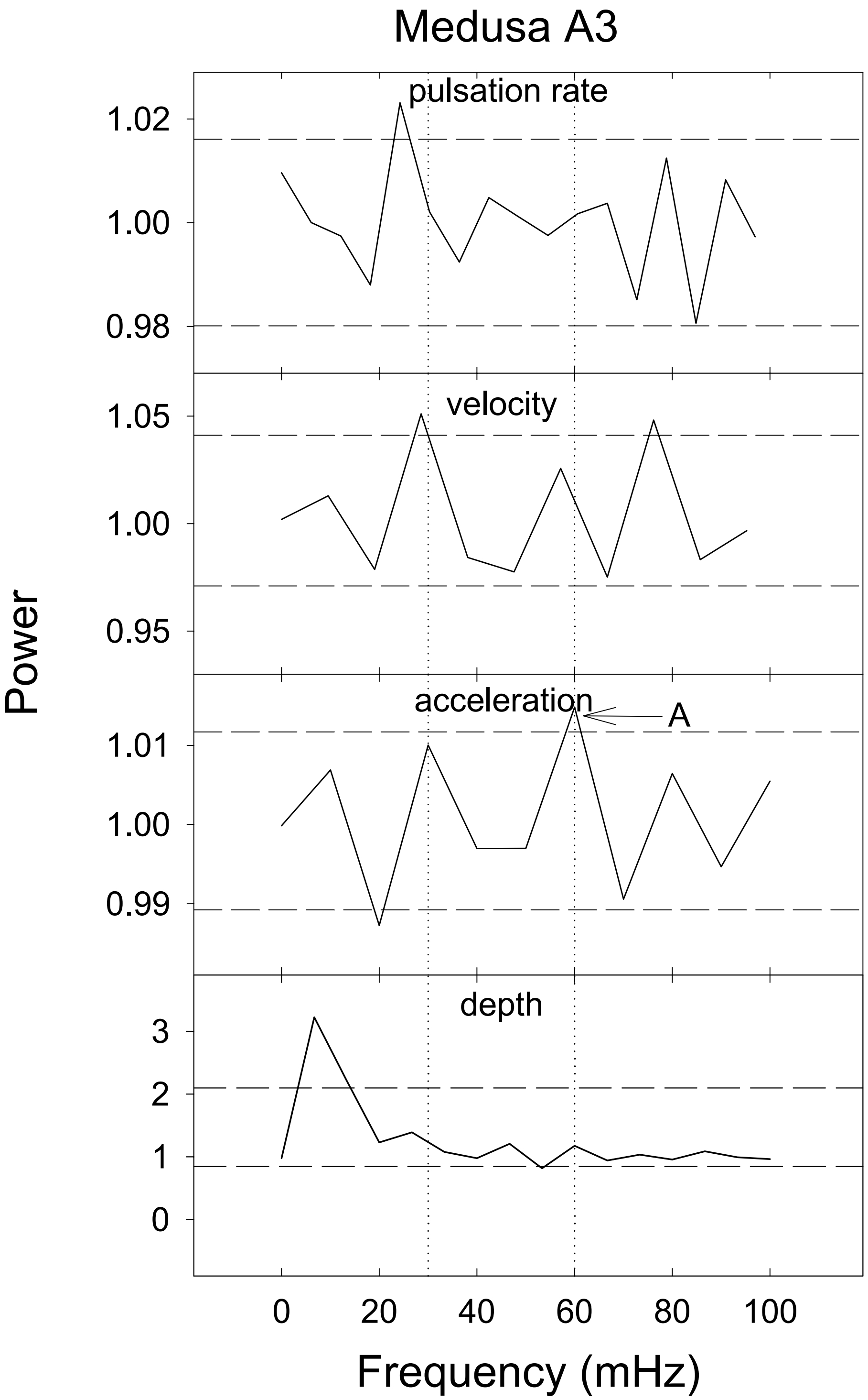

Figure 2.6 *Aurelia aurita*. Average power spectra for pulsation rate, velocity, acceleration, and depth for medusa A3 for all swimming sequences with 95% confidence intervals (dashed line). Dotted, vertical lines represent divisions between frequency ranges, low, middle, and high. Highest peak in power spectrum of pulsation rate is indicated by lettered arrow (see text).

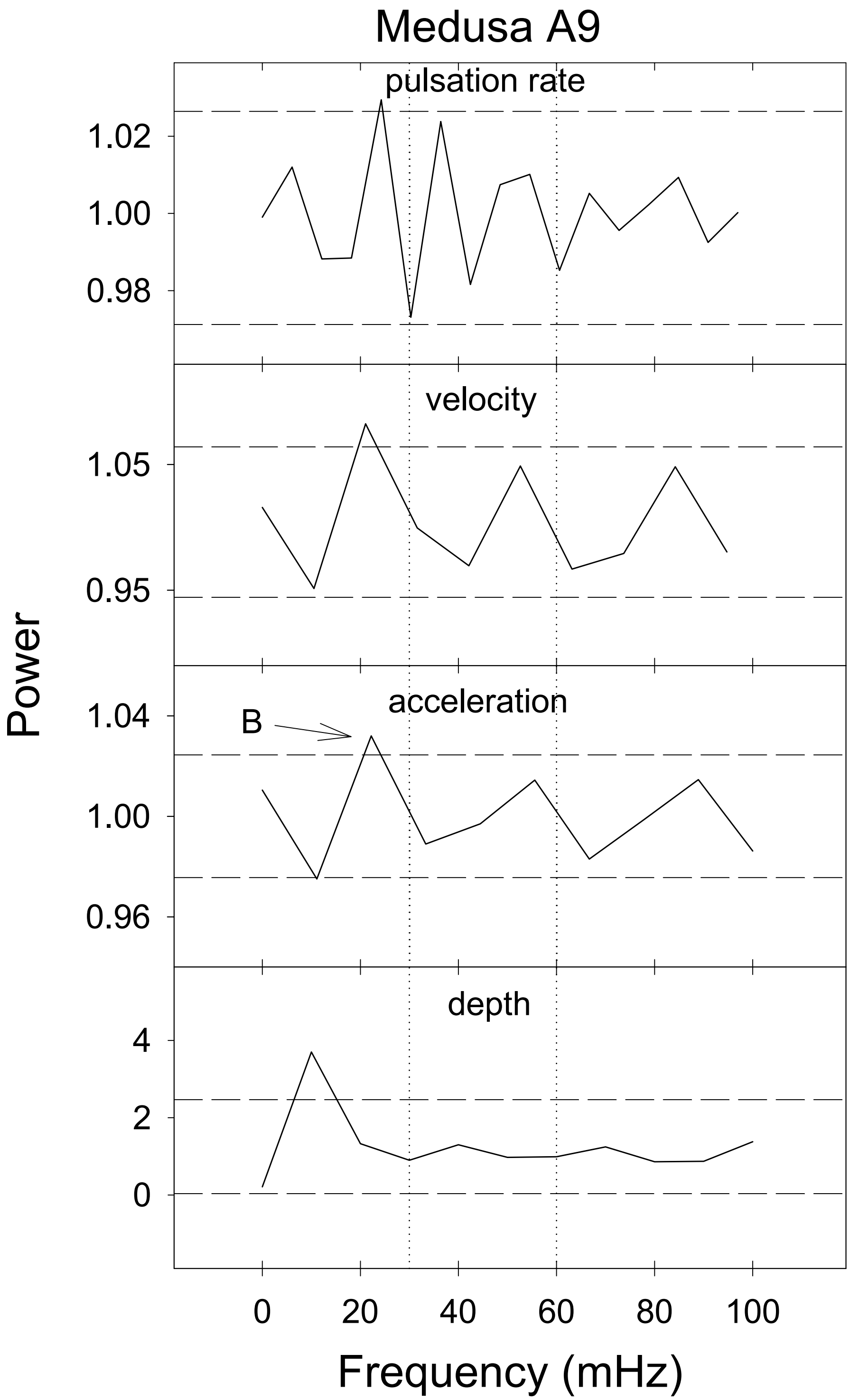

Figure 2.7 *Aurelia aurita*. Same as figure 2.6, but for medusa A9.

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CHAPTER 3

Characterizing the effects of prey on the swimming of the scyphozoan *Chrysaora quinquecirrha* and implications for feeding efficiency[1]

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[1] Matanoski JC, Hood RR, Purcell JE (2001) Characterizing the effects of prey on the swimming of the scyphozoan *Chrysaora quinquecirrha* and implications for feeding efficiency. Mar Biol 139: 191-200

ABSTRACT

The scyphomedusa *Chrysaora quinquecirrha* (Desor, 1848) is an important predator in many coastal and estuarine systems of the eastern USA, but, little is known of its swimming or feeding behavior. Medusae were collected from two tributaries of Chesapeake Bay, USA in August-October 1998 and videotaped in three dimensions in a 10,000-l tank (diam. = 2.4 m, depth = 2.3 m). Their swimming patterns were dependent on the presence of prey. When prey were present, medusae decreased their pulsation rate by 17%, and increased their velocity and acceleration by 87% and 78%, respectively, as compared to when prey were absent. In addition, cyclical variations in each of these characteristics were prey dependent. When prey were absent, medusae altered their pulsation rate and velocity cyclically every 50-100 s. By contrast, when prey were available, pulsation rate and velocity varied every 18 s, and acceleration varied every 37 s. Medusae often were near the surface or bottom of the tanks regardless of the availability of prey, but swimming between these two locations was more frequent when prey were available. I attribute these prey-dependent changes in swimming to feeding behavior that minimizes energy expended while searching for and capturing prey in habitats where prey is heterogeneously distributed.

INTRODUCTION

The scyphomedusa, *Chrysaora quinquecirrha*, is an abundant predator in many coastal and estuarine systems of the eastern United States and consumes a wide variety of zooplankton and ichthyoplankton (Purcell 1992; Purcell et al. 1994). Baird and Ulanowicz (1989) found that *C. quinquecirrha* is the key predator controlling the planktonic community in Chesapeake Bay and thus has an important role in carbon cycling. In situ daily predation rates can range as high as 94% of copepod standing stocks, 17% of fish eggs, and 55% of fish larvae (Purcell 1992; Purcell et al. 1994). In addition, *C. quinquecirrha* may release top down control of secondary productivity by consuming another gelatinous zooplanktivore, the ctenophore *Mnemiopsis leidyi* (Feigenbaum and Kelly 1984; Purcell and Cowan 1995).

Despite the ramifications of predation by *Chrysaora quinquecirrha* medusae on the food chain, little is known regarding their feeding efficiency, although it is clear that factors influencing predatory efficiency will affect the impact of this species on its community (Schoener 1971; Gerritsen and Strickler 1977). For example, predatory behavior that increases the probability that predator and prey populations overlap increases the effectiveness of the predator (Dixon 1959; Smith 1974; Beddingfield and McClintock 1993). Thus, feeding behavior that ensures that distributions of *C. quinquecirrha* and prey overlap in time or space can increase their predatory effects.

I examined swimming patterns in *Chrysaora quinquecirrha* because they are a key component of feeding behavior in scyphomedusae (e.g., Ford et al. 1997). *C. quinquecirrha* uses a combination of swimming and its oblate shape to create a high velocity flow over the exumbrella margin, which creates eddies that entrain zooplankton prey and deliver them to the tentacles and oral arms where they may be captured.

Contact with prey has been shown to affect the swimming behavior of scyphomedusae in a few studies. *Aurelia aurita* medusae increase encounters with herring larvae by swimming faster after capturing the first prey (Bailey and Batty 1983). After initial contact with a prey organism, *Phacellophora camtschatica* moves toward the prey bringing more tentacles into the capture process (Strand and Hamner 1988). Similarly, *Chrysaora quinquecirrha* medusae will turn toward the point of contact with a ctenophore prey, *Mnemiopsis leidyi* (Kreps et al. 1997).

Elucidation of the feeding behavior of *Chrysaora quinquecirrha* medusae will lead to a better understanding of its feeding efficiency and more accurate predictions about its role in the ecosystem. I tested the null hypothesis that the presence of prey has no effect on the behavior of medusae by videotaping the swimming of *C. quinquecirrha* medusae in large laboratory tanks. I then examined the swimming patterns for changes that were dependent on the availability of prey.

MATERIALS AND METHODS

Tank conditions

Experiments were conducted in a 10,000-l, cylindrical fiberglass tank 2.3 m in depth and 2.4 m in diameter, filled with water from Choptank River, Maryland, USA, that had been filtered using a 0.5 μm spun cotton filter to remove ambient prey items and improve water clarity. When no medusa was in the tank (i.e. between videotaping sessions), lights remained off, and a hose bubbling air was placed on the bottom. This maintained O_2 levels and circulated the water. Throughout the experiments, salinity and temperature were monitored with a YSI 33 salinity and temperature meter (Yellow Springs, Ohio), and dissolved O_2 (dO) levels with a YSI 55 dissolved oxygen meter. Tank water was changed after each experiment involving prey, so conditions in the tank closely matched those in the river where medusae were collected. Light was supplied by fluorescent light banks suspended above the tank. Depth profiles of illumination were recorded using a LiCor 1000 datalogger.

Experimental organisms and protocol

Chrysaora quinquecirrha (Desor, 1848) medusae were collected from August to October 1998 from the Choptank and Little Choptank rivers, tributaries of Chesapeake Bay, and transported in river water to the laboratory. Medusae ranged from 3 to 10 cm in bell diameter. For statistical analyses, I classified medusae with swimming bells ≤ 6 cm diameter as small and ≥ 7 cm diameter as large. For experiments requiring prey, natural zooplankton was collected from the Choptank River immediately prior to use with a 202 μm mesh net. The prey were transferred to a 20-l bucket containing ambient river water and transported to the lab. For each experiment, a zooplankton sample was preserved in buffered formalin and organisms counted and identified. Mean prey density in the tank was 5061 ± 3465 m^{-3}, and samples were composed mainly of copepods (87% ± 12%).

Medusae were always videotaped singly within 48 h of capture, and, usually, the total time between collection and the end of filming was < 8 h. Immediately prior to videotaping, the air line was removed from the tank, and a single medusa was transferred to the tank using a fine mesh dip net. The medusa was allowed to acclimate to the tank until it appeared to be neutrally buoyant as indicated by its ability to swim throughout the water column. The lights were turned on immediately prior to the start of videotaping and remained on until the videotaping session was completed. At the completion of videotaping, the medusa was removed from the tank, the air line was reinserted, and the lights turned off until the next filming session. The interval between filming sessions was never < 2 h in order to allow the water in the tank to become homogenized.

The procedure for filming medusae in the presence of prey was identical, except that two hours prior to videotaping, prey were added, lights remained off, and air was bubbled to distribute zooplankton evenly throughout the tank. After each experiment involving prey, the tank was drained completely, rinsed with fresh water, and refilled as above.

In all, 19 individuals were videotaped, 10 in the absence, and 9 in the presence, of prey. In addition, three of the 19 were videotaped in the absence and presence of prey. After videotaping each of these medusae without prey, the medusa was transferred to a 20-l bucket of water from the tank. Prey were added to the filming tank, and air was bubbled for two hours before returning the medusa to the tank and videotaping again in the presence of prey.

Videography

I synchronized the video records of two cameras to obtain the position of a medusa in three dimensions. A SONY CCD TR400 Hi8 video camera recorder with a variable focus lens (5.4-64.8 mm) was mounted 1 m above the center of the tank. The angle of view was adjusted so that it encompassed as much of the volume of the tank as possible and remained fixed throughout the experiments. A Pulinix monochrome CCD video camera with a Computar 3.8 mm fish eye lens connected to a Panasonic TR124MA video monitor and recording to a Sony EV-C200 Hi8 video cassette recorder, was secured in a watertight housing (Subtechnique, Inc., Alexandria, VA), attached to a pole, and suspended 15 cm from the side of the tank. If swimming carried a medusa out of the field of view of this camera, the depth was quickly adjusted to place the specimen back in the center of the field. The camera was again held stationary, the new depth noted, and videotaping continued uninterrupted. During each filming session, the depth of the medusa was recorded each minute to the nearest 0.1 m.

Videotape of the swimming of each medusa was divided into segments beginning when the jellyfish appeared in the view of both cameras and ending when the jellyfish moved out of view of either camera. The result was several sequences of footage for each medusa. The sequences varied in length from one to 9 min ($\bar{x} = 2.5$ min).

Due to the superstructure above the filming tank, I was constrained in the placement of the overhead camera, and, thus, was unable to film specimens throughout all areas of the tank. By maximizing the angle of view, I was able to film most, but not all, of the volume of the tank. Since my method is predicated on subsampling the swimming patterns of test subjects, I recognize that a bias was introduced into the results, specifically, that swimming patterns that led to a jellyfish being in the field of view were preferentially sampled from all patterns the jellyfish might exhibit. Therefore, because my sample from each of the treatment groups (e.g. with prey versus without) shared a common characteristic, behavior that kept them in the field of view, they would tend to be more alike than different. Because this bias would underestimate true differences between sample groups, the variance attributable to the treatment was reduced, and results would be conservative for discovering differences between treatments (Sokal and Rohlf 1995).

Video analysis

Video footage was analyzed by reviewing each sequence in 5-s segments. During each 5-s interval, the total number of pulsations was counted. In addition, the initial position of the center of the exumbrella was digitized using the coordinate grid from a VP110 motion analyzer (MotionAnalysis Corporation, Santa Rosa, CA). Differences in initial position were calculated as a change in pixels on the coordinate grid and converted to distance (cm). The conversion was dependent on the distance of the medusae from the camera, and this relationship was determined by normalizing the grid positions to a meter stick in the field of view of both cameras. The factor required to convert distances on the coordinate grid to known distances obtained from the meter stick was then linearly regressed on the grid positions. For the depth of the medusae as seen in the submerged camera, the conversion was dependent on the x, y, and z position of the specimen. The conversion value was determined as

$$Z_{conv} = 0.7235 + (X \times 0.001049) + (Y \times 0.001881) + (Z \times 0.0002473)$$

where Z_{conv} is the conversion value and X, Y, and Z are the x, y, and z positions of the medusa on the grid. The depth change in pixels over each 5-s interval was determined from the video image, multiplied by the conversion value to obtain the depth change in cm, and a cumulative total of these changes yielded the depth at any given point in the video record. The X position of the medusae was determined from the overhead camera and the conversion factor was dependent on depth. The conversion was determined as

$$X_{conv} = 0.2978 + (0.001641 \times Z_T)$$

where X_{conv} is the conversion value and Z_T is depth (cm). The Y position was calculated in an identical manner. Velocity was calculated as the first derivative of the change in position with respect to time, and acceleration as the first derivative of the change in velocity with respect to time.

Random series analysis

Because observations were taken of pulsation rate, velocity, acceleration, and depth at the end of each 5-s interval, the data formed a time series. I analyzed these series to determine if values were arranged randomly or whether like values were clustered together. For continuous data (i.e. velocity, acceleration, and depth), I used a runs up or down test (Neter 1982). For pulsation rate, which consisted of numerous tied observations, data were converted to a nominal, dichotomous scale by defining two categories, swimming, which consisted of one or more pulsations in a 10-s interval, and resting, in which the jellyfish did not pulse in a 10-s sequence. I then applied a runs test for nominal scale data (Zar 1984).

Activity level

There was an obvious increase in activity of medusae in the presence of prey versus those observed without prey. To test whether these differences were significant, I developed a measure of activity level. Medusae were defined as active if their average velocity was > 0.5 cm s^{-1} for 5 min (index = 1), or inactive if their average velocity was ≤ 0.5 cm s^{-1} over the same interval (index = 0).

Means comparisons

I compared mean values of pulsation rate, velocity, and acceleration with regard to the absence or presence of prey, exumbrella diameter, and time in the filming tank using a three-way 2x2x2 analysis of variance (ANOVA). The interval between placing an individual in the filming tank and videotaping a swimming sequence varied and was dependent on the time for an individual to become neutrally buoyant. I could not be certain whether prey ingested before capture and still in the gut of the jellyfish affected behavior. Digestion time of copepods by *Chrysaora quinquecirrha* at the experimental temperature would have been ~ 3.5 h (Purcell 1992). Because some individuals were filmed before this period had elapsed, I included the length of time in the filming tank as one factor in the ANOVA. All other comparisons were made using Mann-Whitney Rank Sum tests or t-tests. Probability values of < 0.05 were considered significant.

I conducted comparisons of the swimming characteristics of three medusae filmed in the absence and presence of prey. In order to compare multiple observations from the same individual in statistical tests, I used methods of Matanoski et al. (2004). Briefly, the independence of observations from a time series of a single individual was ensured using a test of serial independence (von Neumann et al. 1941). These observations were then subjected to standard inferential statistical tests (e.g., t-tests).

Dispersion of observations

One method for understanding patterns is to compare the dispersion of observations forming different patterns. Statistical comparisons of dispersions (e.g. Bartlett's test) are valid only for normally distributed observations, a condition the data did not meet (Zar 1984). In lieu of this, I made visual comparisons of the frequency histograms of pulsation rate, velocity, acceleration, and depth. To further quantify the differences between histograms, I compared quantiles of the observations of each swimming characteristic.

Spectral analysis

The digital signal generated by the swimming characteristics of each medusa was processed by detrending the data and centering at zero (Masters 1995). Each signal was then subjected to the Fast Fourier Transformation function of IDL (version 5.1, Research Systems, Inc.), and the power spectrum for each was calculated and plotted versus frequency (Masters 1995; Proakis and Manolakis 1996). I calculated 95% confidence limits for the average spectrum of each swimming characteristic by considering the multiple observations (equal to the number of medusae in the group) at a given frequency as a sample of the total population of power observations for the group at all frequencies (Daniel Denman, pers. comm.). The standard normal deviation for the population mean was calculated for the 0.05 significance level (Zar 1984; Sokal and Rohlf 1995).

RESULTS

Experimental conditions

Temperature, salinity, and dO were homogeneously distributed. Mean salinity was 11.2, range 10.7-12.0 and mean dO was 6.0 mg l^{-1}, range 5.7-6.3 mg l^{-1}, and both were homogenous throughout the tank. Mean temperature was 23.7°C (range 22-26°C), and was homogenous except for a 1°C decline in temperature within 10 cm of the surface. Illumination averaged 75.1 ± 1.6 µE m^{-2} s^{-1} at the surface to 18.3 ± 0.3 µE m^{-2} s^{-1} at 2 m (n = 5) in the tank. In situ illumination values for Choptank River during sunny conditions ranged from 1628 µE m^{-2} s^{-1} at the surface and declined rapidly to 90 µE m^{-2} s^{-1} at 1.5 m. Average solar irradiance for September 1998 was recorded at the Horn Point Laboratory (HPL) weather station and yielded values for three representative conditions: partly cloudy = 1250 µE m^{-2} s^{-1}, overcast = 835 µE m^{-2} s^{-1}, and dawn or dusk = 136 µE m^{-2} s^{-1}).

Random series analysis

The swimming of the medusae occurred in distinct patterns and was not the result of random movement. Random series analysis indicated that medusae altered their depth and pulsation rate non-randomly in 100% of the sequences analyzed. In addition, velocity varied non-randomly in 80%, and acceleration in 50% of the sequences. In the zero current conditions of the filming tank, these patterns of movement were indicative of a behavioral response by the medusae.

Activity level

Medusa activity levels were higher when prey were present than when they were absent. The average activity level index increased from 0.6 in the absence of prey to 0.9 when prey were present (Mann-Whitney Rank Sum Test, $p<0.05$, $n = 10$ without prey, $n = 14$ with prey). While the difference in activity levels was obvious between the two prey treatments, there was considerable variation in the activity levels among individuals without prey, as illustrated by their depth profiles (Fig. 3.1). Five of 9 medusae without prey were inactive and swam slowly at a constant depth over the 2 min swimming segment shown. Some individuals, however, were as active as those in the prey treatment. One third of medusae without prey varied their depth as much as 76 cm. Another was inactive for the initial 40 s of the sequence before beginning an oscillatory motion over a 10-cm depth range. By contrast, all medusae swimming in the presence of prey oscillated their depth over a range as great as 153 cm, reflecting the higher level of activity in this group.

Means comparisons

The presence of prey caused the medusae to alter their swimming patterns and these changes were reflected in the means of their pulsation rate, velocity, and acceleration. A three-way ANOVA revealed significant differences in swimming characteristics; medusae swam faster ($F = 12.57$, $p < 0.01$), turned more ($F = 5.98$, $p < 0.04$), and pulsed less ($F = 6.34$, $p < 0.04$) in the presence of prey than without prey (Fig. 3.2). In contrast to the effect of prey on swimming patterns, swimming bell diameter and the length of time medusae were in the tank had no significant effect on pulsation rate, velocity, or acceleration ($p>0.05$; three-way ANOVA). There also were no interactive effects among swimming bell diameter, length of time in the tank, and availability of prey. It is important to note that all medusae were videotaped singly to avoid the confounding effects of interactions between individuals.

In addition to the comparisons of medusae videotaped either with or without prey, I made intra-individual comparisons of three medusae, C15, C16, and C18, videotaped in the absence of prey and then after the addition of prey (Fig. 3.2). Similar to the changes observed in swimming patterns of medusae grouped together based on treatment (prey present or absent), individual medusae swam faster and turned more with prey than without (Fig. 3.3). For C15, C16, and C18, pulsation rates declined and velocity and acceleration increased when prey were present versus when they were absent.

I also observed a different swimming pattern in two medusae, C4 and C5. Most of the time C4 and C5 swam normally (i.e. resting periods were few and of short duration). Occasionally, however, these medusae stopped swimming and sank, slowly passing through their own tentacles. These resting periods averaged 88 s (range 9-142 s) for C4 and 136 s (range 54-510 s) for C5 and were 13 % and 34% of the time budgets of C4 and C5, respectively. Other medusae occasionally stopped pulsing, but, these periods were usually brief (<5 s) and resulted in a vertical displacement of the medusa of only a few centimeters. By contrast, C4 and C5 rested for as much as 6 min and sank up to 0.5 m.

Dispersion of observations

Medusae without prey pulsed at a higher rate more frequently than those with prey, specifically, there was a greater frequency of observations at 0.6 and 0.8 pulsations s^{-1} (Fig. 3.4a). This result is not unexpected given the higher mean pulsation rate in medusae without prey, however, there was also a small number of observations at 0.0 and 0.2 pulsations s^{-1} in these medusae reflecting the more frequent rest periods of two members, C4 and C5.

The velocity observations in medusae without prey were highly positively skewed indicating that most of the time these medusae were swimming slowly (Fig. 3.4b). The observations did not tail off smoothly, however (see, for example, the frequency of observations at 2.1 and 2.7 cm s^{-1}), and there were more observations of very high velocity (2.7-3.6 cm s^{-1}) for the medusae without prey (i.e. the slower swimming medusae overall) than for the medusae with prey. Indeed, most of the individuals (78%) without prey swam as fast as individuals with prey for brief periods (e.g. 10% of the time). In other words, while on the whole, medusae swam more slowly when prey were absent, at times they swam at speeds equivalent to those for individuals with prey. Similarly, accelerations in medusae without prey were highly positively skewed, indicative of a linear swimming pattern of constant velocity (Fig. 3.4c). By contrast, the medusae with prey exhibited more curvilinear swimming (e.g. there were more observations at 0.12-0.36 cm s^{-2}), and they were five times more likely to be accelerating at a very high rate, > 0.44 cm s^{-2} (i.e. making sharp turns) than medusae without prey.

Spectral analysis

Pulsation rate, velocity, and acceleration of *Chrysaora quinquecirrha* increased and decreased in a cyclical manner, and the period of these cycles depended on the absence or presence of prey. For example, in the absence of prey, medusae increased their pulsation rate in two cycles (Fig. 3.5), a shorter period cycle of 17-22 s (peak B) superimposed on another, longer cycle with a period of 110 s (peak A). By contrast, when prey were available, the low frequency variations in pulsation rate disappeared, leaving only the high frequency components of the swimming pattern. Similarly, the low frequency variations in velocity (peak C) were replaced by high frequency variations (peak D) when prey were present (Fig. 3.6). There were also cyclical variations in acceleration indicative of increased turning every 37 s (peak E) in the presence of prey, which were not evident in the absence of prey (Fig. 3.7).

Depth regulation

Medusae increased their average depth from 0.8 m to 1.1 m when prey were present and were twice as likely to be found near the bottom of the tank as indicated by observations of depth each minute throughout the duration of each filming session (Fig. 3.8). The dispersion of the observations indicated that there was a shift of a cohort of the population from the surface to the bottom of the tank (2.1 m), and few individuals swam at mid-depths. Individuals at middle depths were only in transit between the surface and the bottom. Near the surface or bottom, medusae continued to swim horizontally for a significant portion of the time.

Changes in depth occurred cyclically (Fig. 3.9). In the absence of prey, medusae made excursions to depth every 30 min (peak F). When prey were present, however, this low frequency component of changes in depth disappeared, and only cycles with periods of 10 and 6 min (peaks G and H, respectively) remained.

DISCUSSION AND CONCLUSIONS

The oblate swimming bell of *Chrysaora quinquecirrha*, with its attendant high drag coefficient, seems ill-suited to a cruising predator that spends 98% of its time swimming (Ford et al. 1997; Costello et al. 1998). Furthermore, it begs the question of how this unlikely pairing of morphology and feeding strategy could combine so effectively to create a top predator capable of controlling its community structure (Baird and Ulanowicz 1989). The answer may lie in the prey-dependent swimming patterns I observed. Each swimming pattern consisted of unique behavior accomplishing two goals: (1) to locate prey efficiently and (2) to maintain the medusa's position within aggregations of prey.

Searching behavior

It appears that, in the absence of prey, *Chrysaora quinquecirrha* medusae engaged in strategic searching behavior (Smith 1974) consisting of low velocity, primarily straight-lined motion (Fig. 3.3). Nevertheless, most of the medusae (78%) swam at speeds equivalent to those achieved in the presence of prey at least 10% of the time (Fig. 3.4b). In addition, these higher velocities occurred about every 50 s (Fig. 3.6). The reason for this complex pattern may lie in the methods for prey detection in *C. quinquecirrha* and the heterogeneous nature of their prey. *C. quinquecirrha* are tactile predators not known to possess any ability to detect prey remotely. Thus, prey detection probably requires prey contact. Many of their prey are copepods with well-developed escape responses (Purcell 1992; Buskey 1994; Suchman and Sullivan 1998). Ninety percent of the time medusae swam too slowly to generate the flow velocities at the margins of the swimming bell that exceeded the escape velocities of their prey (Ford et al. 1997). While swimming at these speeds, a medusa's encounter rate would be low (Gerritsen and Strickler 1977), and it would get little information about the availability of prey. When a medusa increases its velocity to a rate sufficient to capture prey, the encounter zone expands to include the volume occupied by the tentacles, umbrella, and the entrained fluid around the medusa (Madin 1988). The medusa may, in effect, be "sampling" the surrounding water in an attempt to detect prey. By swimming at these higher velocities only briefly, a medusa can reduce total energy expended by 68% when compared to the higher "feeding" velocity (Klyashtorin and Yarzhombek 1973).

The periodic nature of this "sampling" behavior would be selectively advantageous in a marine habitat where prey are heterogeneously distributed (Haury et al. 1978; Hamner and Carleton 1979; Mackas et al. 1985). Furthermore, given the average velocity for medusae engaged in this pattern (0.78 cm s^{-1}) and the periodic increase in velocity every 50 s, the maximum distance traveled by the medusae between these sampling episodes was approximately 0.4 m. Thus, no patch > 0.4 m in diameter would fail to be sampled by the medusae, a size well-suited to the "microscale" patches in the marine habitat (Haury et al. 1978).

Cruising predators such as *Chrysaora quinquecirrha* are favored in an environment where prey is heterogeneously distributed (Schoener 1971; Huey and Pianka 1981). In this type of habitat, predators can maximize their efficiency by minimizing the time spent between patches (Gerritsen and Strickler 1977). For *C. quinquecirrha*, however, patches of prey are spatially variable, ephemeral, and impossible to detect remotely, thus, it would be impossible for them to minimize the time spent between patches. I propose an alternative strategy whereby *C. quinquecirrha* reduces energy expended, rather than time spent, between patches of prey. By increasing velocity only when prey patches are encountered and higher energy returns are possible, medusae can maximize the energy available for growth and reproduction (Gerritsen and Strickler 1977).

Feeding behavior

I observed a second, distinct behavior in medusae exposed to prey. Under these conditions, medusae swam nearly twice as fast (1.46 cm s^{-1}) as in the absence of prey, generating marginal flow velocities of 2.5-6.8 cm s^{-1}, high enough to capture a variety of fast moving prey (Ford et al. 1997). Swimming faster increases the encounter rate between medusae and their prey by: (1) increasing the relative velocity of predator to prey (first order relationship) and (2) increasing the encounter radius of the medusa (second order relationship) by entraining water in larger diameter eddies generated by the higher marginal flow across the swimming bell (Gerritsen and Strickler 1977; Madin 1988).

In addition to swimming faster in the presence of prey, medusae turned more when prey were available than when it was absent. This response to prey has been observed in other species (Mikheev et al. 1992; Beddingfield and McClintock 1993). Such adaptive behavior is selectively advantageous for organisms whose prey is heterogeneously distributed because it allows the predator to remain within patches of food for longer periods (Smith 1974).

In the presence of prey, these episodes of turning recurred every 37 s, indicative of a pattern of nearly straight-lined motion, followed by a turn before returning to a straight-lined path. Because I did not videotape medusae swimming near the walls of the tank, these turning events were not an artifact of confinement in the tank, and it is interesting to note that the straight-lined portion of *Chrysaora quinquecirrha*'s feeding pattern would be approximately 0.5 m given their increased velocity in the presence of prey (1.46 cm s^{-1}) and a period of 37 s. This distance, like that between "sampling" areas is well suited to "microscale" prey patches ranging from 0.01-1.0 m in diameter (Haury et al. 1978; Mackas et al. 1985).

One of the prominent features of the marine zooplankton community is the heterogeneous distribution of individuals (Haury et al. 1978; Hamner and Carleton 1979; Mackas et al. 1985). At the same time, the predatory effect of *Chrysaora quinquecirrha* is dependent on its location overlapping with these patches of prey (Purcell 1992; Cowan and Houde 1993). Both the sampling behavior and the increased turning I witnessed may increase the likelihood that *C. quinquecirrha* will co-occur with their prey, and, once located, augment the time they will be in proximity to each other. Thus, these behaviors may increase the encounter rate of medusae and their prey and *C. quinquecirrha*'s influence on its ecosystem structure.

Pulsation rate

Pulsation rates were lower in medusae exposed to prey than in those without prey (Fig. 3.2). I attribute this to the need of the medusae to generate higher velocities for prey capture. *Chrysaora quinquecirrha* swims by contracting the muscles of the umbrella, forcing a propulsive jet of water from the subumbrellar cavity (Ford et al. 1997). The recovery stroke involves relaxation of the umbrellar muscles and re-expansion of the subumbrellar cavity. I suspect that, in the presence of prey, *C. quinquecirrha* contracted its bell more deeply, creating a larger propulsive force, thereby requiring a longer recovery period and a slower pulsation rate.

I was surprised that the pulsation rate was not lower in medusae with larger swimming bells. Decreases in the frequency of repetitive motions with increasing size has been shown in *Chrysaora quinquecirrha* as well as other species (Alexander 1971; Gatz et al. 1973). I attribute the lack of size dependency in the study to the fact that I could not videotape very small medusae that were indistinguishable from the background. For example, the pulsation rate of one very small (bell diameter 1 cm) medusa was 1.1 pulsations s^{-1}, in agreement with that predicted by the regression equation of Gatz et al. (1973).

Depth regulation

Most of the time *Chrysaora quinquecirrha* swam horizontally with only occasional periods of vertical swimming, a pattern that was also seen in the scyphomedusa *Aurelia aurita* in laboratory tanks (Bailey and Batty 1983). Episodes of vertical swimming in *C. quinquecirrha* occurred periodically and became more frequent when prey were present (Fig. 3.9).

Medusae positioned themselves either at the surface or the bottom, and a similar distribution has been noted in other gelatinous species (Mills 1983; Zavodnik 1987). Long periods (e.g. > 30 s) of horizontal swimming only occurred near the surface or bottom, and individuals at middle depths were in transit between these locations. It is unlikely that this behavior results from the restricted depth in the tank because *Chrysaora quinquecirrha* is frequently found in shallow waters (e.g. estuarine systems). For example, the mean depth in Chesapeake Bay is only 6.5 m, and considerably less in the tributaries (Schubel and Pritchard 1987), where medusae are most abundant (Purcell 1992).

Position in the tank may have been affected by lighting. Lights were turned on just prior to videotaping, which may have simulated sunrise when *Chrysaora quinquecirrha* and other species aggregate at the surface to spawn (Mills 1983; Purcell, unpub. data). Whatever the cause of the bimodal distribution, it is clear that when prey were present, *C. quinquecirrha* swam at the bottom more often. This shift in distribution may have resulted from the medusae remaining in areas where prey were concentrated, however, I lacked data on fine scale distribution of prey. It is also possible that the shift in distribution may have resulted from the increased frequency of vertical swimming with prey present, which would more evenly distribute the medusae between the top and bottom of the tank.

This depth regulation behavior may alter the horizontal distribution of *Chrysaora quinquecirrha* exposed to conditions of vertical shear common to the coastal and estuarine systems they inhabit (Kullenberg 1978; Okubo 1978; Mackas 1985). Numerous estuarine species migrate vertically exploiting such conditions to effect horizontal transport (e.g. Hough and Naylor 1992; Olmi 1994; Rowe and Epifanio 1994). *C. quinquecirrha* swam vertically more frequently when prey were present. In situ, this behavior would create differences in horizontal as well as vertical distribution, and I expect system-wide surveys of the distribution of *C. quinquecirrha* to reflect these non-random, behavioral processes.

I observed two medusae engaging in an unusual behavior in which they stopped swimming and sank slowly, a pattern that was similar to that described for another scyphomedusan *Phacellophora camtschatica* (Strand and Hamner 1988). Two other medusae collected on the same day and from the same location never exhibited this swimming pattern, so it is unlikely that these two medusae represented a unique geographical or temporal cohort of the population of *Chrysaora quinquecirrha*. The duration of the rest periods was highly variable, and they occurred 7-17 times more than for the average medusa (Schuyler and Sullivan 1997; Costello et al. 1998). The slow sinking of the medusa created a large entangling web of tentacles aligned vertically in the water column, a tentacle placement that is best suited for capturing fast moving prey (e.g. fish larvae) that are horizontally distributed (Gerritsen and Strickler 1977; Greene 1985), and has the added benefit of decreasing energy expenditures (Klyashtorin and Yarzhombek 1973). The sinking pattern, therefore, may favor different prey than the cruising swimming pattern and may be a behavioral response by some individuals to extreme conditions (e.g. starvation).

Price et al. (1988) noted that little is known, "about how energy is partitioned on a behavioral level or about the role of energetic costs in determining when and if certain behaviors will occur." I observed several examples of behaviors adaptive to conditions common to many scyphozoans (e.g. heterogeneously distributed prey, oblate shape) and that reduce the energy expended in searching for and capturing prey. Furthermore, depth regulation by medusae occurred at regular and predictable frequencies and could contribute to their horizontal movement in environments of vertical shear, a common condition in many systems in which *Chrysaora quinquecirrha* is found. I expect that other members of this class exhibit analogous behavior uniquely suited to each species' habitat and morphology, and that studies of these behaviors will increase our understanding of their importance in ecosystems.

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FIGURES

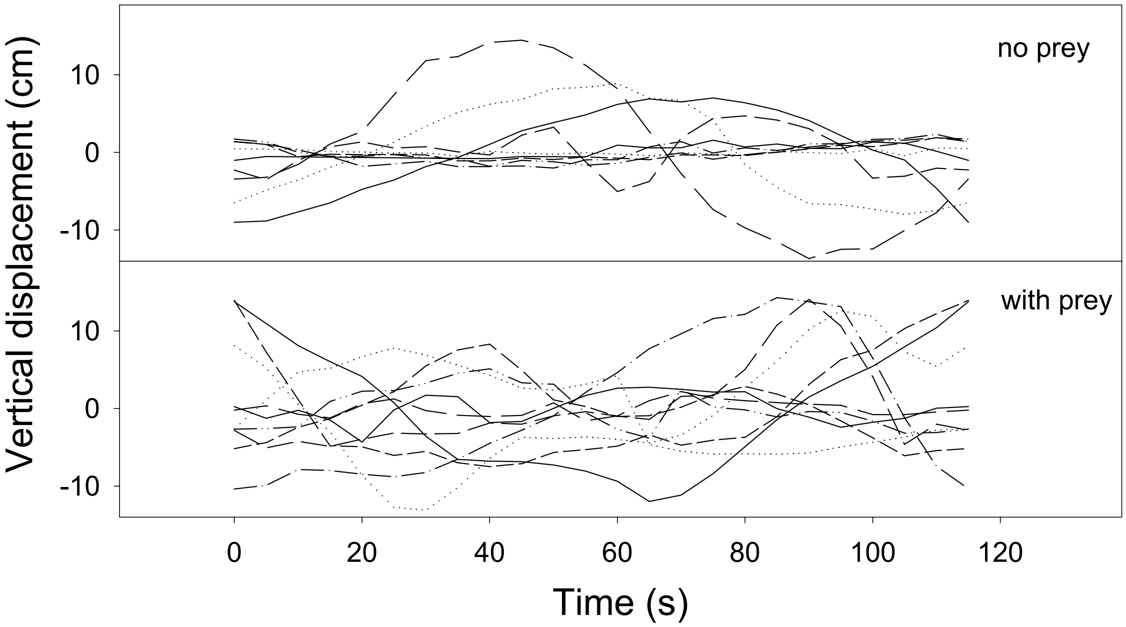

Figure 3.1 *Chrysaora quinquecirrha*. Depth profiles in the absence (n = 9) and in the presence (n = 10) of prey. Each line represents profile of a single medusa. Profiles have been detrended and centered at zero to aid in comparisons.

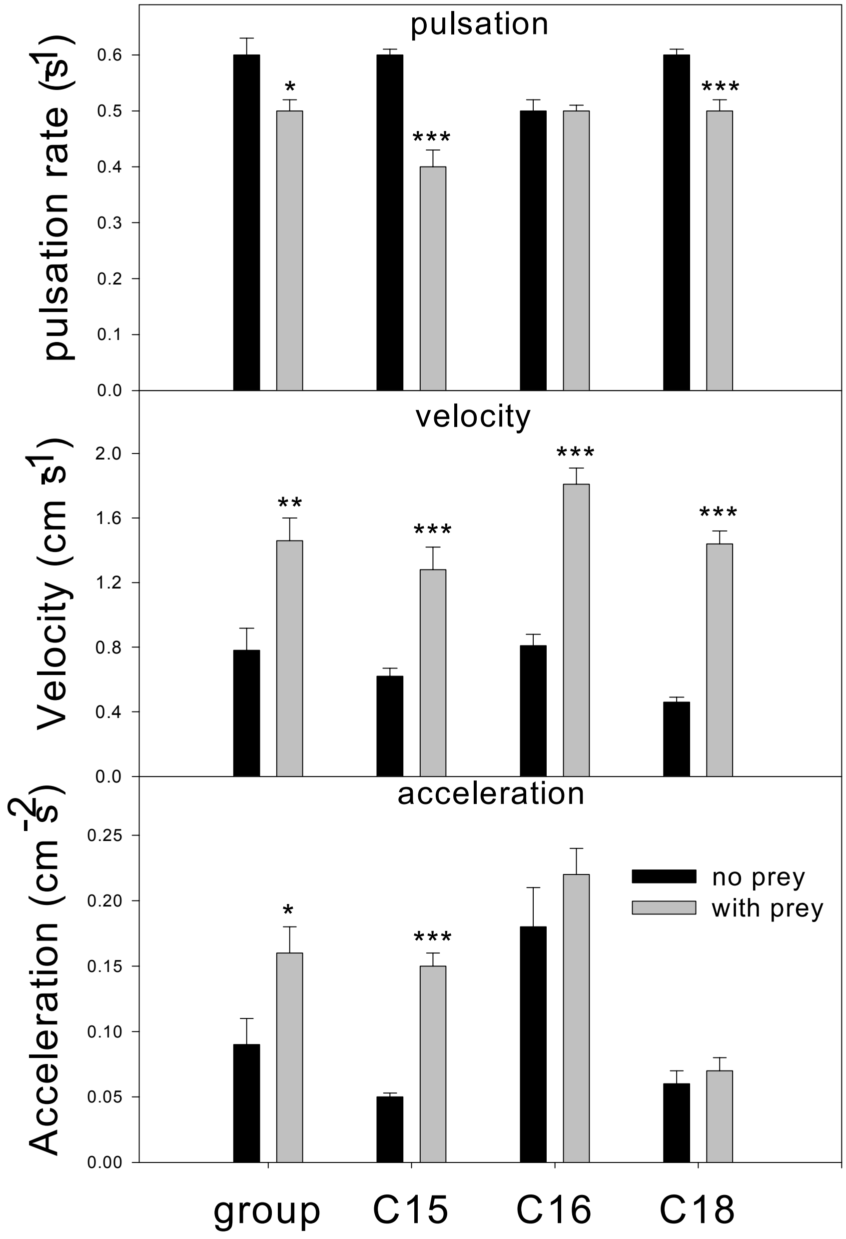

Figure 3.2 *Chrysaora quinquecirrha*. Average pulsation rate, velocity, and acceleration for grouped individuals (n = 9 in each; * $p<0.05$, ** $p<0.01$, three-way ANOVA) and three individuals, C15, C16, and C18 (swimming bell diameter 8, 10, and 7 cm respectively; *** $p<0.001$, Mann-Whitney Rank Sum tests) videotaped in the absence and presence of prey. "Group" data refers to medusae videotaped singly with data grouped according to the absence or presence of prey. Water temperature during videotaping of medusae with and without prey was 22-26°C, and for individuals C15, C16, and C18 with and without prey was 26, 26 and 24°C, respectively. Values are means of each swimming characteristic ± SE.

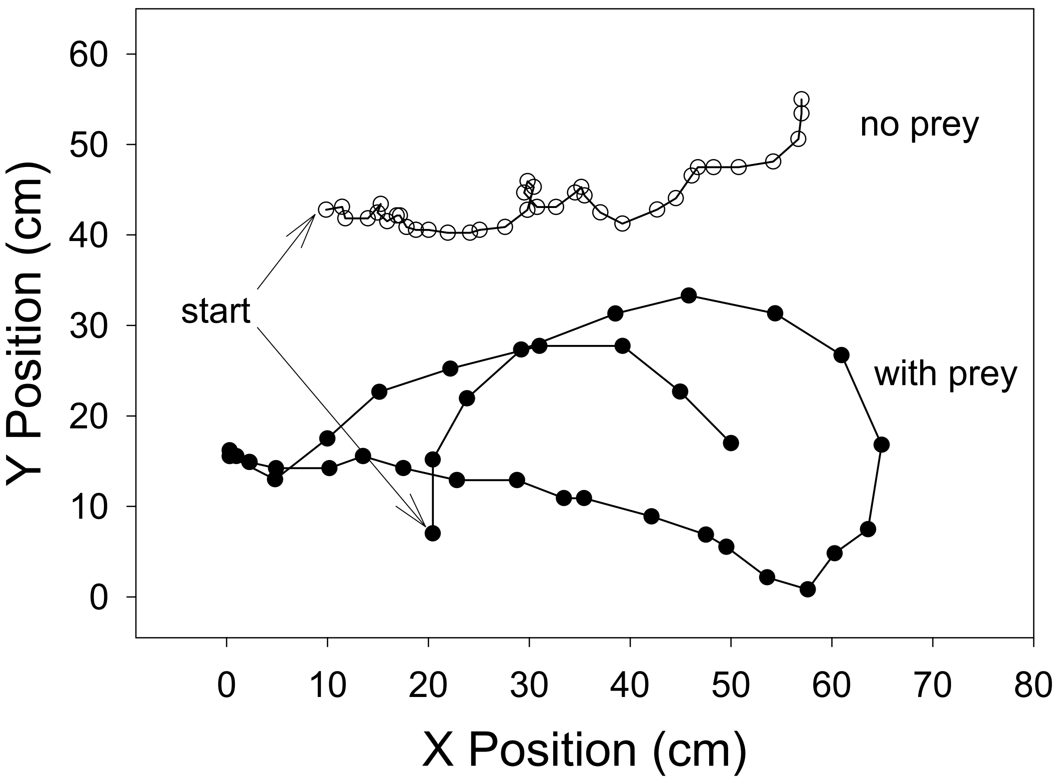

Figure 3.3 *Chrysaora quinquecirrha*. Plan view of swimming path of medusa C15, in the absence (open circles) and presence (filled circles) of prey. Position refers to location within filming tank. Symbols represent location of medusa every 5 s, and each trace is 180 s in duration.

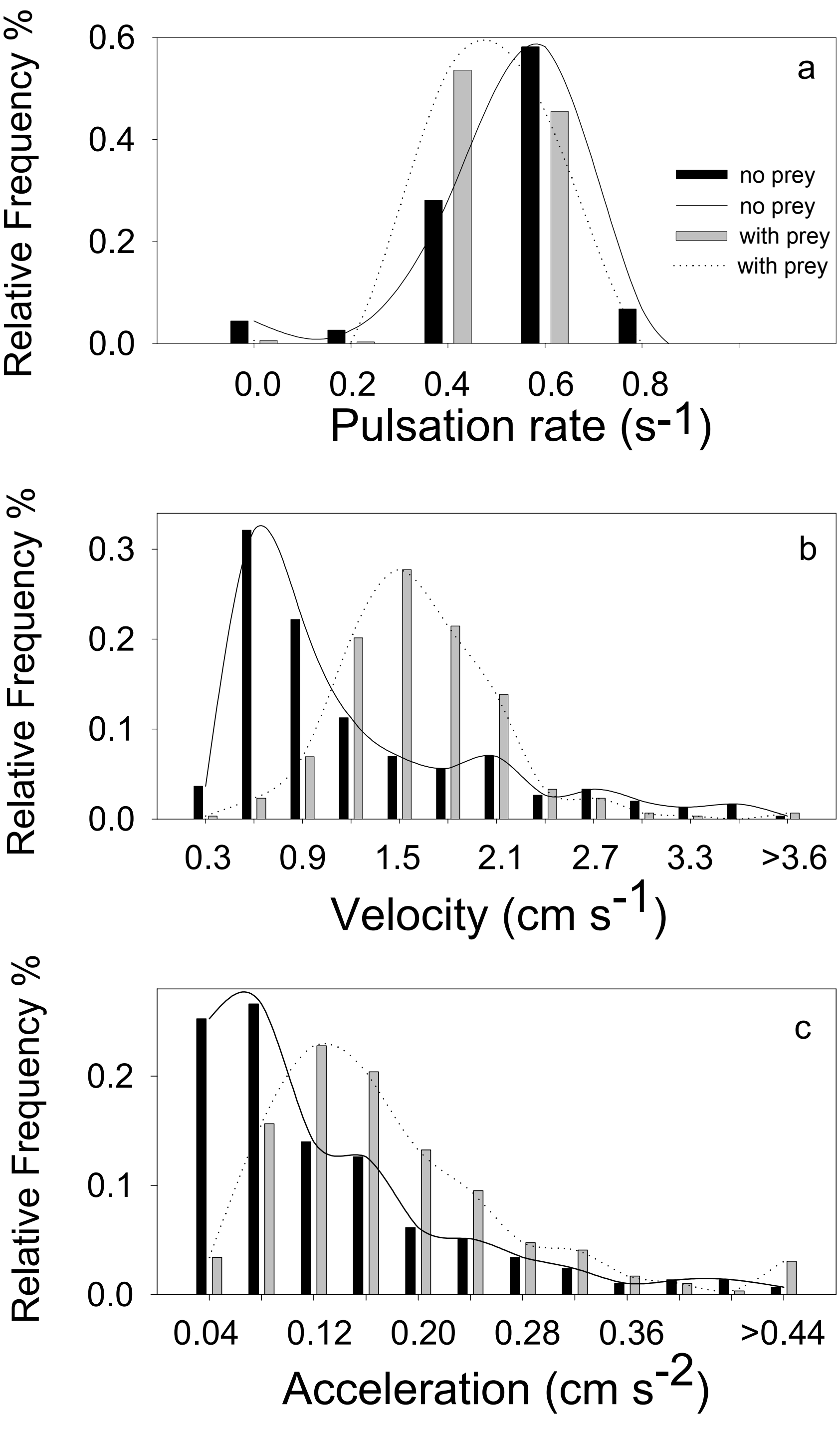

Figure 3.4 *Chrysaora quinquecirrha*. Frequency histograms for observations of (a) pulsation rate, (b) velocity, and (c) acceleration in the absence (n = 9) and presence (n = 9) of prey. Cubic spline interpolations of histograms have been overlaid to aid in comparisons.

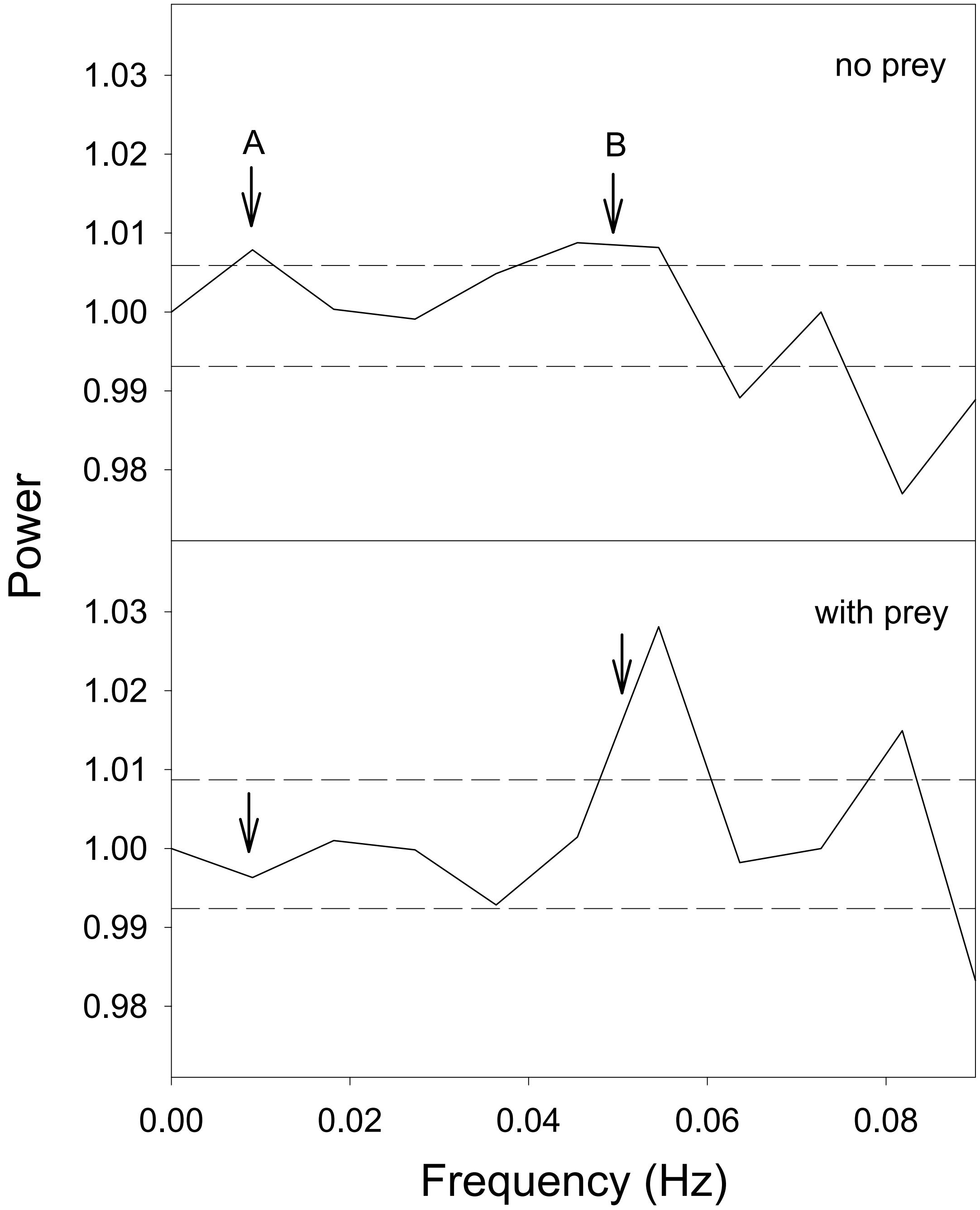

Figure 3.5 *Chrysaora quinquecirrha*. Average power spectra of pulsation rate in the absence (n = 9) and presence (n = 9) of prey. Low frequency cycle (A, 0.01 Hz) is absent in the presence of prey. Dashed lines represent 95% confidence intervals.

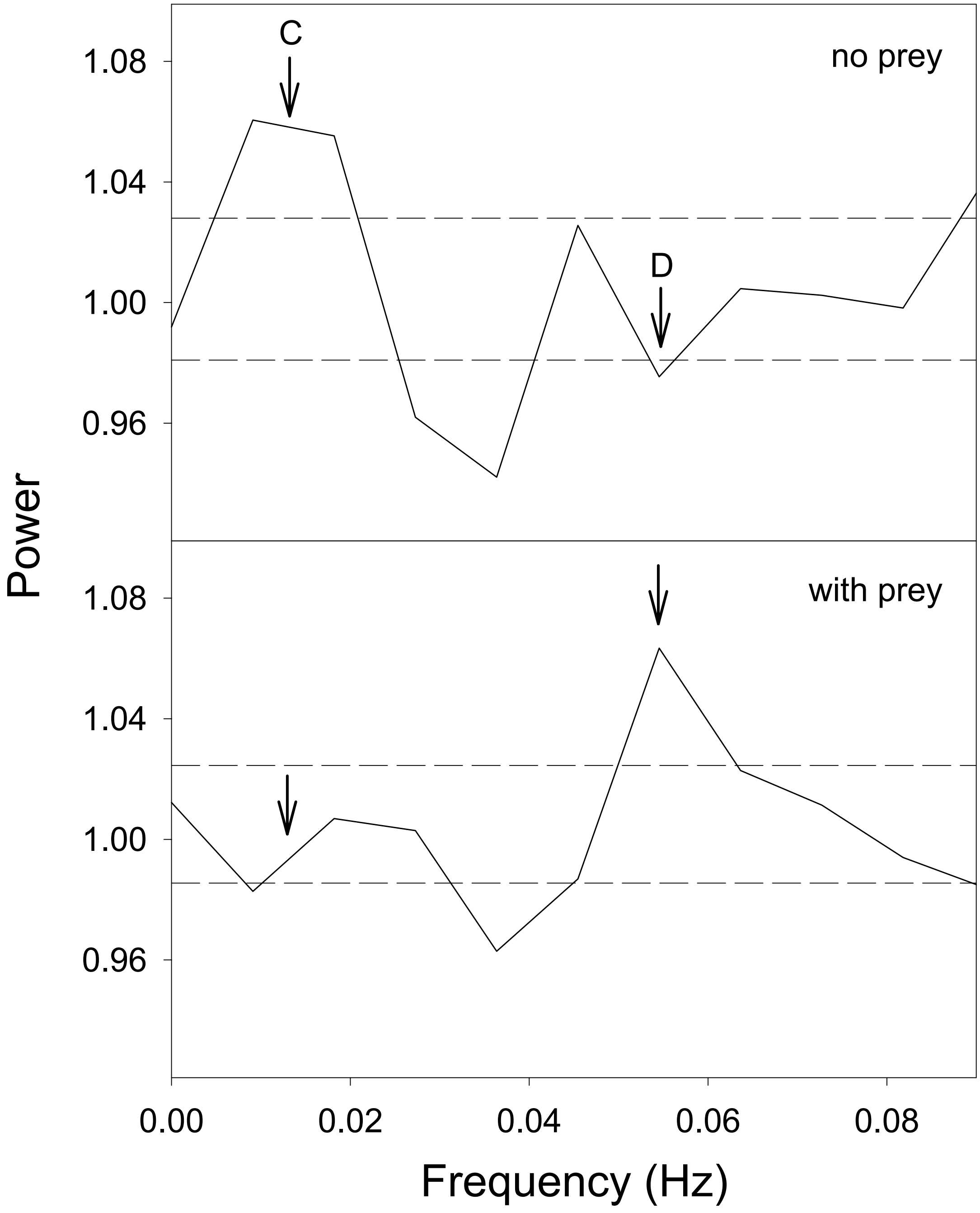

Figure 3.6 *Chrysaora quinquecirrha*. Average power spectra of velocity for groups in the absence (n = 9) and presence (n = 9) of prey. Low frequency components (C, 0.01-0.02 Hz) disappear in the presence of prey. Dashed lines represent 95% confidence intervals.

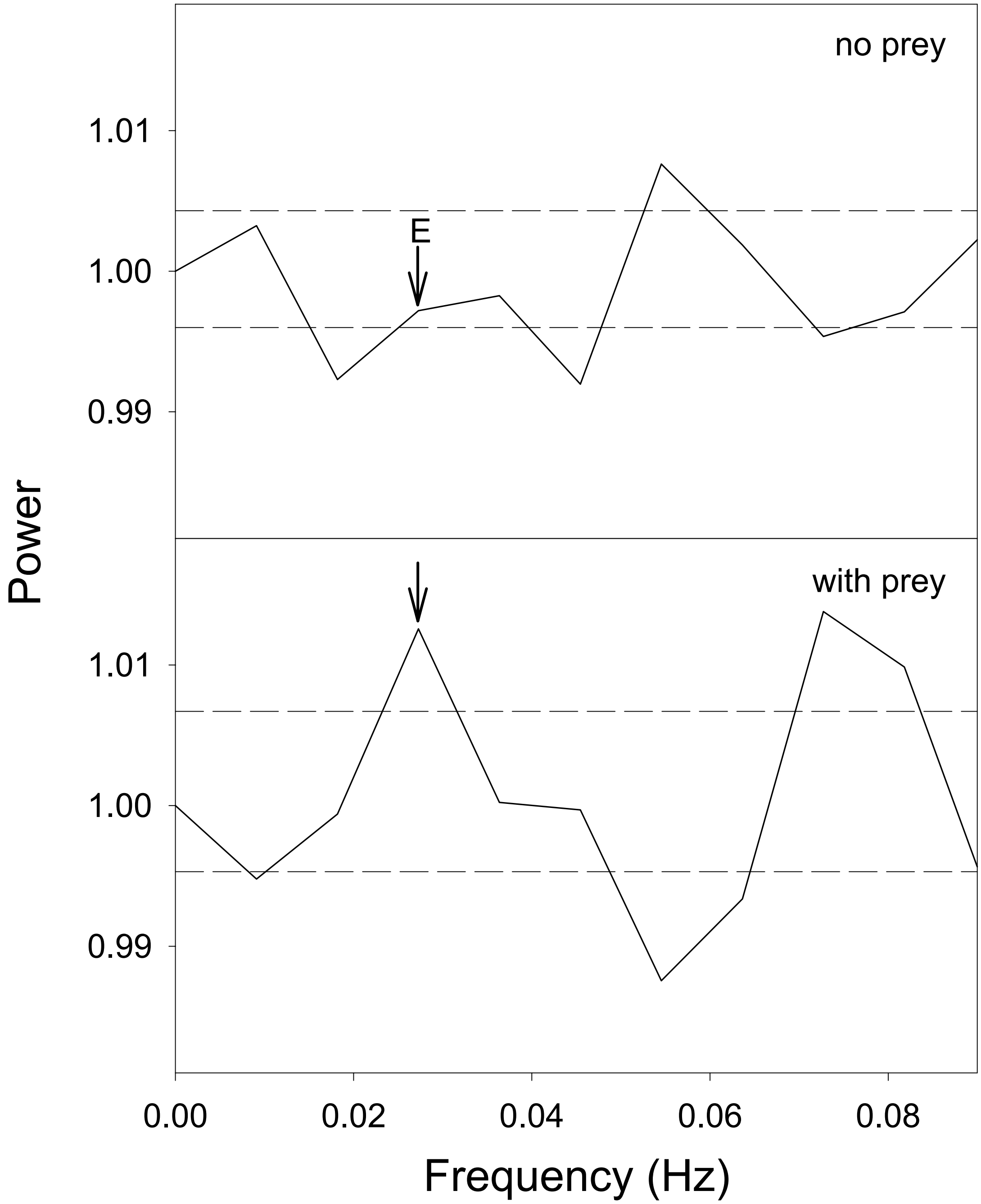

Figure 3.7 *Chrysaora quinquecirrha*. Average power spectra of acceleration for groups in the absence (n = 9) and presence (n = 9) of prey. Low frequency cycle (E, 0.03 Hz) appears in the presence of prey. Dashed lines represent 95% confidence intervals.

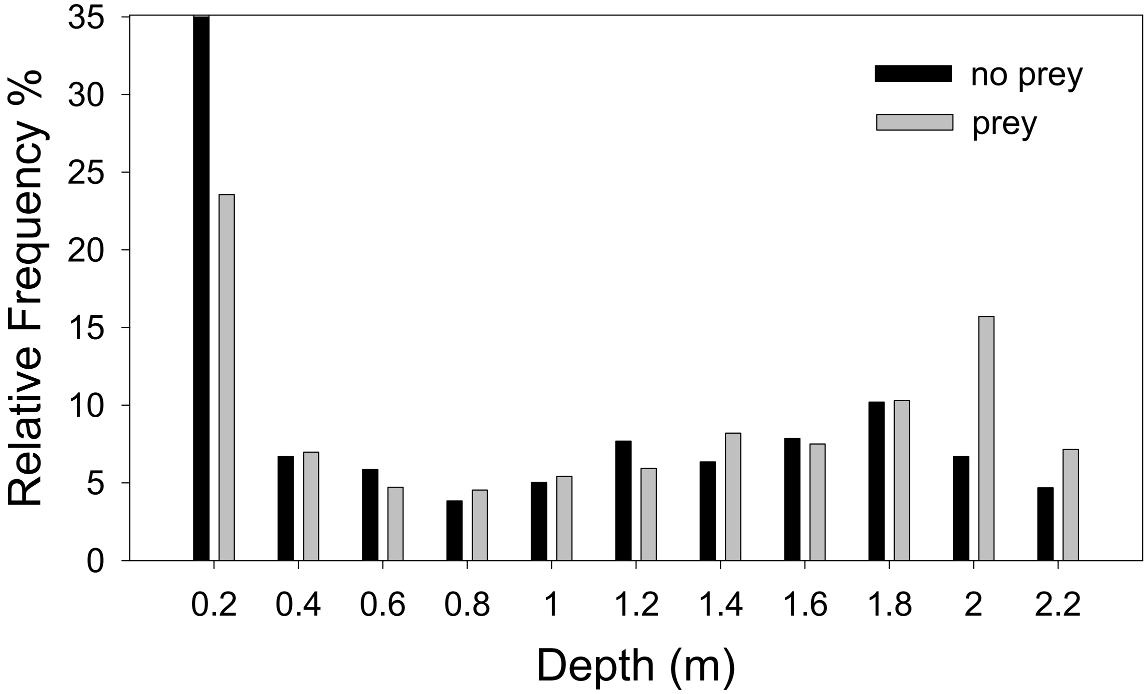

Figure 3.8 *Chrysaora quinquecirrha*. Frequency histograms for observations of medusa depth in absence (n = 11) and presence (n = 8) of prey.

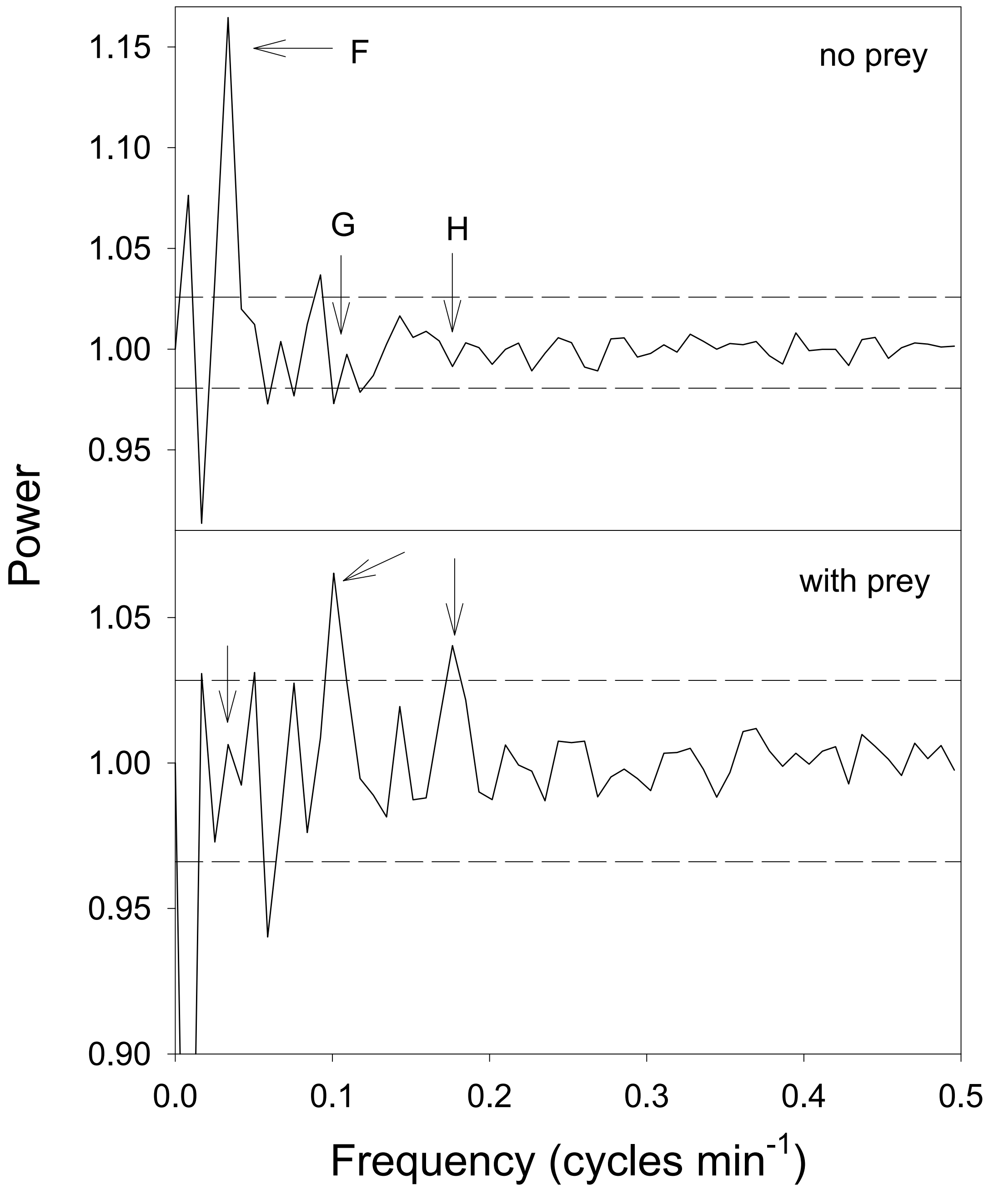

Figure 3.9 *Chrysaora quinquecirrha*. Average power spectra of depth in the absence (n = 9) and presence (n = 9) of prey. Presence of prey causes low frequency cycle (F, 0.03 cycles min $^{-1}$) to disappear and two higher frequency components (G and H, 0.10 and 0.18 cycles min $^{-1}$) to appear. Dashed lines represent 95% confidence intervals.

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CHAPTER 4

An individual-based numerical model of medusa swimming behavior

ABSTRACT

Scyphomedusae are ubiquitous in marine and estuarine systems, where they frequently play an important role in trophodynamics. Feeding rates of scyphomedusae are highly variable both spatially and temporally and depend, in part, on behavior. Many scyphomedusae are cruising predators and rely on swimming to produce feeding currents, yet no model exists of their swimming. I developed an individual-based correlated random walk (CRW) model of medusa swimming behavior in three dimensions, which was validated using a dataset of the swimming of 19 medusae observed in either the presence or absence of prey. Medusae searching for prey alternated periods of slow and fast swimming with variable timing. When prey were located, medusae swam at a constant moderate rate and began area-restricted searching, with more looping trajectories. The model reproduced these patterns by simulating switching in the behavior that controls the strength of swimming bell pulsations using a probabilistic function. However, there was marked anisotropy in the looping trajectories of feeding medusae that could only be reproduced when changes in movement by medusae were oriented to local stimuli (e.g. simulating contact with prey). Model results also demonstrate a bias by medusae to swim toward the surface and avoid contact with the bottom. There were significant periodicities in medusa swimming patterns, which appear to be the result of deterministic behavior. The implications of these behaviors for foraging efficiency and spatial distribution are discussed.

INTRODUCTION

Movement is an integral part of most processes necessary for an organism's survival. Although some motions are due to external forcing (e.g. currents), many are an active behavioral response by individuals to capture food, locate mates, avoid predators, or select favorable habitats (reviewed in Manning and Dawkins 1998). Pelagic organisms, in particular, are in nearly continuous motion because of their own swimming and the movement of the dynamic fluid medium surrounding them. These individual movement patterns scale up and have an important role in determining species distribution, abundance, and population and community dynamics (Levin 1978; Okubo 1980; Kareiva 1982; Turchin 1991, 1998).

Scyphomedusae swim most of the time (Costello et al. 1998) and modify their swimming behavior in response to prey, touch, changes in illumination, and chemical gradients (Mackie et al. 1981; Strand and Hamner 1988; Arai 1991; Schuyler and Sullivan 1997; Matanoski et al. 2001). Medusae swim to locate and capture prey, move into aggregations that may increase reproductive success, and avoid predators (Strand and Hamner 1988; Malej 1989; Costello and Colin 1994, 1995; Hamner et al. 1994). These movements alter spatial distributions, enhance predation rates, increase abundance and, ultimately, change the ecological effect medusae have on their communities (Hamner and Hauri 1981; Hamner et al. 1982; Purcell et al. 1992, 2000; Keister et al. 2000).

Considerable attention has been devoted to formulating quantitative models that describe and predict animal movement because of its importance in many life processes (reviewed in Turchin 1998). Numerous models of swimming, feeding and reproductive behavior have been developed for pelagic species, including planktonic organisms like copepods (Bundy et al. 1993; Leising and Franks 2000; Tittensor et al. 2003) and juvenile fish (Coughlin et al. 1992; Rose and Cowan 1993; DeAngelis and Petersen 2001). By contrast, no model exists of medusa movement. Of particular interest is medusa movement related to feeding since most swim to capture prey, which contributes directly to growth and survival (Costello and Colin 1994, 1995; Ford et al. 1997). Consequently, there is a need for a quantitative model of medusa movement, especially as it relates to locating and capturing prey. A model capable of characterizing the dynamic spatial-temporal processes involved in medusa movement behavior would facilitate predictions of their ecological effects (e.g. Cowan and Houde 1992; Brown et al. 2002) and would be generally useful because of the important role swimming plays in their survival.

One class of model that has been used extensively to describe animal motion is the correlated random walk (CRW). CRW models simulate animal motion as a succession of discrete movements over time. The length and direction of each movement differs slightly from the one preceding it, and the magnitude and sign of these changes is determined by random draws from a probability distribution. The width of the distribution determines how correlated an animal’s path is over time. CRW models are biologically relevant because they explicitly recognize the tendency of animals to move straight ahead (Bovet and Benhamou 1988). At the same time, they implicitly simulate movement controlled by Markovian behavior, that is, where movement decisions in one time step depend on past movement. In addition, the movement of many animals is significantly influenced by non-random responses (e.g. behavior) to local conditions.

CRW models reproduce these changes by altering the degree of correlation in the animal's movement, which simulates directed motion (Kareiva and Shigesada 1983; Grunbaum 1998; Turchin 1998).

Individual movement decisions (e.g. foraging behaviors, search tactics) influence population predation rates, spatial distributions, and reproductive success (Crist and Machmahon 1991; Banks and Yasenak 2003; Seymour et al. 2003). Recent works propose explicitly recognizing the contribution individual responses have on group attributes using individual-based models (IBMs) (Huston et al 1988; DeAngelis and Gross 1992; DeAngelis and Petersen 2001). The movement of individual animals in response to local environmental heterogeneities (e.g. prey patches) can have a profound effect on the distribution, abundance and, thus, the ecological effect of a species (Turchin 1998). For example, IBMs have already demonstrated the role that feeding success by individual larvae has on the growth and survival of fish populations (Rice et al. 1993; Letcher and Rice 1996). In addition, IBMs of animal behavior explicitly recognize two fundamental biological principles: (1) that behavior varies among individuals and (2) that behavior is influenced by the local environment.

In this paper, I describe the development and validation of an individual-based CRW model of the swimming behavior of the scyphomedusa *Chrysaora quinquecirrha* in three dimensions. The development of this model revealed that many aspects of *C. quinquecirrha* movement can be reproduced using a simple CRW model, i.e., they are essentially random motions. However, reproducing the full suite of statistical properties of the motion (e.g. mean and variance of velocity and acceleration, turning rates) presented significant challenges that required major modifications to the model and the coordinate system. Moreover, the development process revealed deterministic properties in the swimming patterns of the medusae that appear to be linked to their foraging behavior. These include the frequency of switching between fast and slow swimming that is part of a search pattern, a tendency to swim toward the surface, and a distinct anisotropy in 3-dimensional movement.

This study also demonstrated a unique approach to the development of IBMs, in which the behavioral attributes of a modeled individual are statistically compared to identical measures of an individual drawn from an empirical dataset (Matanoski et al. 2004). The test results determine both the accuracy of the model in simulating the observed behavior and, in an iterative process, inform the changes necessary for each succeeding step in the development.

MATERIALS AND METHODS

The goal of this modeling effort was to simulate the swimming behavior of 19 specimens of the scyphomedusa *Chrysaora quinquecirrha* that were observed in either the presence or absence of a natural prey assemblage (Matanoski et al. 2001). Medusae were videotaped singly in a cylindrical tank, 2.3 m in depth and 2.4 m in diameter. The model simulates medusa swimming behavior using an individual-based correlated random walk (CRW) of velocity vectors. Medusa paths are the summation of position vectors independently determined at consecutive time steps and set in a three-dimensional rectangular coordinate framework. Time-dependent changes in the x-position vector are represented by the equation

$$\frac{\partial \mathbf{x}}{\partial t} = \mathbf{u} \tag{1}$$

where $\mathbf{u}$ is the swimming velocity vector in the x direction resulting from the propulsive force generated by medusa swimming bell contractions. The x-velocity vector is described by the equations

$$\mathbf{u}(t) = \mathbf{u}_{t-1}\left(1 - \left(\frac{dt}{T_L}\right)\right) + \mathbf{p}(t) \tag{2}$$

$$\mathbf{p}(t) = \mathbf{p}_{t-1}\left(1 - \left(\frac{dt}{B_L}\right)\right) + \partial \mu_x \tag{3}$$

where dt is the time step of integration, T_L the physical decorrelation time scale, B_L the behavioral decorrelation time scale, $\mathbf{p}(t)$ the velocity vector at time t resulting from swimming bell pulsations, and $\partial\mu_x$ random changes in the x direction component of propulsive force from swimming bell pulsations. Position vectors $\mathbf{y}$ and $\mathbf{z}$ and velocity vectors $\mathbf{v}$ and $\mathbf{w}$ are determined in an identical fashion.

According to this model, medusa momentum is correlated over time due to physical constraints on velocity by the surrounding fluid medium as determined by T_L, and by behavioral constraints on changes in motion, that is, the degree to which the medusa maintains a similar speed and direction over time, as determined by B_L. The behavioral correlation timescale, B_L, simulates a Markovian behavioral process in which the behavior at one time step depends on the behavior of preceding time steps. Model runs 1-8 (Table 4.1) were parameterized with a behavioral decorrelation time scale, B_L, equal to the integration time step, *dt*. Thus, the first term on the right side of the equality in (3), above, becomes zero, and the velocity vector due to swimming bell pulsations ($\mathbf{p}$), a function of completely random changes in strength and direction ($\partial\mu_x$). In effect, this assumes that there is no correlation between time steps due to behavior. To simulate the periodic changes in swimming characteristics observed in empirical medusae, model runs 9-11 were re-parameterized with appropriate physical and behavioral correlation terms. In calculations of velocity vectors ($\mathbf{u}, \mathbf{v}, \mathbf{w}$), the terms $\frac{dt}{T_L}$ and $\frac{dt}{B_L}$ determine the magnitude of the change in momentum between time steps and can range from 0 (completely correlated linear motion) to 1 (random motion).

The effect of random changes in the magnitude and direction of swimming bell pulsations on the x-velocity vector is specified by $\partial\mu_x$, the incremental velocity vector. The vector $\partial\mu_x$ is independently drawn from a normal (Gaussian) distribution with mean ψ_x and variance $\sigma_b \frac{dt}{T_L}$, where σ_b is, in this application, a behaviorally determined constant and dt and T_L are as defined above. Here, σ_b can be considered to represent the strength and variability of propulsive swimming bell pulsations, which are determined by the behavior of the medusa. In addition, pulsations require conformational changes in the swimming bell and thus $\frac{dt}{T_L}$ can be interpreted as representing the physical constraints on these conformational changes due to the fluid medium. Incremental changes in velocity vectors in the y and z directions were calculated in an identical fashion.

To simulate the anisotropic vertical movement of medusae, a directional bias was introduced into model runs 2 and 7-11 by centering the distribution from which $\partial\mu_z$ is drawn on a non-zero value ($\psi_z \neq 0$) when calculating the z-position vector. This can be considered to represent a propensity of the medusa to turn up or down. Note that there was no directional bias in all other model runs (1, 3-6).

Boundaries are parameterized identically to the cylindrical tank used in the empirical studies. The position of the medusa at the start of each simulation is set to the center of a horizontal circular plane (2.2 m diam) that is equidistant (1.15 m) from the surface and bottom. At each time step, the position of the medusa is evaluated and, if the modeled medusa's velocity vector at time step t would take it outside the boundaries of the tank, the medusa is returned to the position at time $t - 1$.

To simulate changes in behavioral state observed in empirical medusae in the absence of prey, I formulated the model to alternate between two levels of swimming bell pulsation strength by changing the variance of the distribution, σ_b, from which incremental velocity vectors, $\partial\mu$, are drawn. Furthermore, I modeled these changes as a stochastic process using a time-dependent conditional distribution. Initially, the medusa is randomly assigned one of two variances, σ_{b1} or σ_{b2}. At each time step, the behavioral state changes if a random draw from a uniform distribution exceeds a threshold value that declines as a time-dependent linear function.

The modeled switch was governed by the conditional

$$\text{if } g > 1 - \left(\frac{h}{n} * N\right) \qquad \text{then alternate variance of } \sigma_b \tag{5}$$

where g and h are independent random draws from a uniform distribution ranging from 0 to 1, n is a user-specified constant that describes the average interval between switches, and N is the number of time steps since the previous switch. A new value of g is randomly drawn after each switch, representing the stochastic nature of the timing of switches for an individual medusa. By contrast, h remains constant throughout the duration of the simulation, is unique to each medusa, and represents the propensity of a given medusa to switch between behavioral states (e.g. a high value of h would make frequent switching more likely). The constant n determines the average duration of remaining in a behavioral state for a group of medusae, although the average interval differs among medusae and depends on the particular value of h that is randomly drawn for that individual. In addition, the timing between switches by an individual medusa is variable and depends on the value of g drawn after each switch.

In model runs 1-2 and 5-11, the incremental changes in velocity vectors are determined relative to the fixed three-dimensional rectangular coordinate system that formed the framework of the modeled tank and, therefore, are immediately translatable into time-dependent changes of medusa position within the tank. To simulate the looping behavior exhibited by medusae in the presence of prey, in model runs 3 and 4, velocity vectors in each direction (designated $\mathbf{a}, \mathbf{b}, \mathbf{c}$) are determined using a “natural coordinate system”, that is, relative to the current position of the medusa, but in all other respects, in an identical fashion using (2) and (3) above. Incremental changes in velocity vectors in each direction ($\partial\mu_a, \partial\mu_b, \partial\mu_c$) are random draws from a normal distribution as above, except the distribution from which $\partial\mu_a$ is drawn is centered on a positive non-zero value ($\psi_a \neq 0$), such that, $\partial\mu_a >> \partial\mu_b = \partial\mu_c$, which represents the propensity of medusae to move primarily straight ahead.

The three-dimensional velocity vector relative to the current position is calculated as

$$\mathbf{r} = \sqrt{\mathbf{a}^2 + \mathbf{b}^2 + \mathbf{c}^2} \qquad (6).$$

The angle between $\mathbf{r}$ and the plane formed by axes a and b is calculated as,

$$\phi = \arctan\left(\frac{\sqrt{\mathbf{a}^2 + \mathbf{b}^2}}{\mathbf{c}}\right) \qquad (7)$$

and between $\mathbf{r}$ and the plane formed by axes a and c as

$$\theta = \arctan\left(\frac{\mathbf{b}}{\mathbf{a}}\right). \qquad (8)$$

The vertical and horizontal heading of the medusa relative to the fixed coordinate system of the tank is the sum of the incremental changes in ϕ and θ

$$\Phi = \sum \phi \text{ and } \Theta = \sum \theta \qquad (9), (10)$$

The components of $\mathbf{r}$ in each direction relative to the fixed coordinate system are calculated using

$$\mathbf{u} = \mathbf{r}\sin\Phi\,\cos\Theta\;,\; \mathbf{v} = \mathbf{r}\sin\Phi\,\sin\Theta\;, \text{ and } \mathbf{w} = \mathbf{r}\cos\Phi\;. \qquad (11), (12), (13)$$

To simulate the anisotropic looping behavior observed in empirical medusae in the presence of prey, changes in the vertical velocity vector, $\mathbf{w}$, between time steps are reduced by a damping factor, κ, between 0 and 1, such that,

$$\mathbf{w} = \kappa\mathbf{w}\,. \qquad (14)$$

During model development, I used a statistical approach developed by Matanoski et al. (2004) to compare behavior between individuals. In this study, I compared swimming trajectories of individual medusae by applying a suite of statistical techniques (random series analysis, analysis of variance (ANOVA), and Kolmogorov-Smirnov goodness-of-fit tests of frequency histograms) to the time-dependent change in velocity and acceleration. In addition, the time-dependent variability of swimming behavior of individual medusae (intra-individual variability) was quantified as the variance of observations of velocity and acceleration. In an iterative process, I compared the swimming characteristics of a modeled medusa to identical measures of an empirically observed medusa. Differences between model output and empirical data were used to inform the change in model parameters prior to the next simulation.

When there was no significant difference between modeled and empirical observations, then the model was considered to be simulating the behavior of the empirical medusa, and the parameter set was used to simulate the behavior of several medusae. This group was then compared to an equal number of empirical medusae. I used 2-sample t-tests to compare means of observations and means of variances (the intra-individual variability). In addition, I quantified the variability in swimming behavior among medusae (inter-individual variability) as the variance of the mean velocity and acceleration of all individuals in a group (e.g. empirical medusae in the presence of prey) and the variance ratio test to determine significant differences between groups (Zar 1984).

I analyzed time series of velocity and acceleration using a finite Fourier transformation available in the spectra procedure of SAS (v. 8.02, SAS Institute, Inc., Cary, NC) and created power spectra for each medusa. The mean power at each frequency for all medusae was calculated. To determine if the power at any frequency in the average spectrum was different from the mean power of the spectrum, I used the repeated measures option of the linear mixed models procedure of SAS.

I defined the vertical successive turning angle, ω_{vj}, as the angle between the medusa's three-dimensional position vector and the plane formed by the x and y axes at time step j relative to the vector at time step $j-1$ for each time step. The horizontal turning angle, ω_{hj}, was calculated similarly as the angle between the position vector and the plane formed by the x- and z-axes. To compare the sinuosity of trajectories, the mean successive turning angles of groups of medusae were calculated and compared using the Watson-Williams test (Batschelet 1981, Zar 1984).

To characterize looping patterns in medusa trajectories, I defined the vertical turning rate for a medusa swimming sequence of n time steps as

$$T = \frac{\sum_{j=1}^{j=n} \omega_{vj}}{t} \qquad (16)$$

where ω_{vj} is the vertical successive turning angle at time step j and t is the duration of the swimming sequence. The horizontal turning rate was calculated in an identical fashion. Summing turning angles in the calculation of turning rates creates a linear measure, which I compared between medusa groups using a two-sample t-test for means (Zar 1984).

Sampling of the swimming characteristics of the modeled medusae was identical to that in Matanoski et al. (2001). The position of the medusa was determined at an interval sufficient to render each independent for the various statistical tests: 5-s intervals for random series and spectral analyses, Watson-Williams tests, and t-tests of turning rates; 15-s intervals for Kolmogorov-Smirnov goodness-of-fit tests, ANOVA, and variance ratio tests; 60-s intervals for frequency histograms of depth in the modeled tank. To avoid boundary effects only swimming sequences in which the medusa's velocity vector did not carry it outside the boundary for at least 3 min were used in analyses, which is similar to the constraint applied to the empirical data.

Comparisons between both individual modeled and empirical medusae and groups of meduase was based on a suite of statistical techniques. The approprate significance level for each test was determined using the Dunn-Šidák method so that the experimentwise significance level was 0.05 (Sokal and Rohlf 1995).

RESULTS

In the empirical study, medusa swimming patterns depended on the availability of prey (Fig. 4.1) (Matanoski et al. 2001). Medusae observed in the absence of prey swam slower and turned less than those in the presence of prey. In addition, swimming patterns of medusae without prey were more variable than medusae with prey. Specifically, 3 of 11 medusae without prey swam in a constant high velocity pattern with frequent turning that resembled the pattern observed in medusae in the presence of prey, 2 in a constant low velocity linear pattern, and the remaining medusae exhibited periods of swimming in both patterns switching between the two at characteristic frequencies. Matanoski et al. (2001) speculated that this switching was part of a general foraging strategy that allows medusae to periodically sample the prey environment while conserving energy in regions where prey patches are widely spaced.

Foraging behavior

I found that a correlated random walk model parameterized with a single value of σ_b, representing a constant strength of swimming bell pulsations (Table 4.1, model run 1), reproduced means and variabilities of velocity and acceleration of medusa trajectories in the presence of prey (Table 4.2). In addition, the cumulative frequency distribution of observations of velocity and acceleration of the modeled medusae were statistically identical to the empirical observations (Fig. 4.2; $p>0.05$, Kolmogorov-Smirnov goodness-of-fit test).

By contrast, the same model solution could not simultaneously reproduce the mean values and interindividual and intraindividual variability of velocity and acceleration of empirical medusae observed in the absence of prey (Table 4.3). In addition, there were obvious (although non-significant) differences in the cumulative distribution of observations of velocity and acceleration between the empirical and modeled medusae (Fig. 4.2). Specifically, the variability in velocity and acceleration among empirical medusae increased dramatically when swimming in the absence of prey when compared with those in the presence of prey, a difference the model could not simulate.

There were indications that swimming patterns in the absence of prey resulted from medusae exhibiting two behavioral states (Matanoski et al. 2001). Additionally, the distributions of velocity and acceleration observations (Fig. 4.2) are characteristic of populations in which individuals engage in more than one movement behavior (Turchin 1998; Skalski and Gillam 2000; Okubo and Levin 2002). Therefore, the model was formulated to alternate between two levels of σ_b, simulating behaviorally induced changes in pulsation strength. A model solution (run 5) parameterized to switch between weak pulsations and pulsations of a strength similar to those that accurately simulated the prey pattern ($\sigma_b = 0.8$) still lacked the variability observed empirically (data not shown). However, parameterizing the model to switch between weak pulsations and much stronger ones than required to reproduce the prey pattern (model run 6), reproduced the mean and variability of velocity and acceleration observed in the empirical medusae in the absence of prey (Table 4.3). Moreover, I was able to simulate the interindividual variability observed empirically by switching between these two behaviors with an equal probability, that is, g, which controls the interval between switches, was determined identically after each switch. This model solution resulted in an identical number of individuals swimming fast, slow, and in a pattern that combines periods of fast and slow swimming (3, 2, and 6 medusae, respectively) as the empirically observed medusae. Those medusae that mixed both patterns during a swimming sequence accounted for the high intraindividual variability of the group, similar to the situation observed in the empirical medusae (Fig. 4.3).

Vertical distribution

Empirical medusae observed in the absence of prey swam near the surface (depth < 20 cm) more than three times as often as any other depth (Fig. 4.4). In the presence of prey, medusae were found near the surface more frequently than any other depth, but there was a marked increase in the number of medusae observed from 1.8-2.0 m (i.e. 30-50 cm away from the bottom) when compared to medusae observed in the absence of prey. Modeled medusae were also observed more often at the surface and bottom than at any other depth although with equal frequency and within 20 cm of both boundaries.

When a bias by medusae to swim toward the surface was simulated in the model (runs 2, 7-11), the depth profiles of modeled medusae in both the absence and presence of prey appeared remarkably similar to empirical observations, including the shift of medusae in the presence of prey toward the bottom. However, at the bottom, modeled medusae were observed most frequently within 30 cm of the boundary whereas the empirical medusae were twice as likely to be found in a layer 30-50 cm from the bottom as in a layer within 30 cm of the bottom.

Looping and turning

The pattern of turning in empirical medusae depended on the availability of food. In the presence of prey, medusae had a significantly higher turning rate (i.e. more looping) in the horizontal compared with the vertical plane (Fig. 4.5; t-test, $p<0.05$). By contrast, medusae observed in the absence of prey turned at the same rate in both planes, that is, less in the horizontal and more in the vertical than medusae in the presence of prey. The mean turning angle (i.e. sinuosity) of trajectories was the same in both the horizontal and vertical directions and between both groups (Watson-Williams test, $p>0.05$). Indeed, there were no differences in mean turning angles in comparisons among any of the model solutions and the empirical groups.

There was no difference between turning rates (Fig. 4.5; t-test, $p>0.05$) of trajectories of empirical medusae in the absence of prey and the modeled medusae simulated with two behavior states and oriented to a fixed coordinate system (model run 6). However, the model formulated to simulate medusa swimming in the presence of prey and oriented to a fixed coordinate system (model run 2) produced less looping in the horizontal plane than empirical medusae (t-test, $p<0.05$). When medusa swimming was oriented to their current position (model run 3), looping increased markedly (Fig. 4.6). However, the model simulated isotropic movement (i.e. identical parameterization for velocity vectors in each of the three directions) and did not reproduce the difference in horizontal and vertical looping that was observed in empirical medusae. Reducing changes in vertical velocity using the damping factor, κ (model run 4) reproduced the anisotropic movement observed in empirical medusae (t-test, $p>0.05$), increased the vertical linearity of trajectories, and had the effect of simulating vertically spiraling patterns similar to those of empirical medusae in the presence of prey.

Cyclical behavior

There were significant periodicities in the time series of velocity and acceleration of empirical medusae in the presence of prey (Table 4.2)(Matanoski et al. 2001). Medusae exhibited a significant high frequency cycle at 52 mHz that was associated with low amplitude (0.4-0.6 cm s^{-1}) changes in velocity. At the same time, medusae exhibited a very high frequency cycle in acceleration at 80-90 mHz resulting from these same changes in velocity (i.e. ~ twice the frequency of the velocity cycle). In addition, there is a low frequency cycle in acceleration at 36 mHz that is associated with large amplitude (0.5-2.0 cm s^{-1}) changes in velocity due to turning. In the absence of prey, periodicities in medusa swimming patterns are markedly different. There are significant changes in the velocity time series at 9 and 17 mHz (Table 4.3). The 17 mHz cycle is a result of periodic increases in velocity associated with changes from slow to fast swimming by those medusae that mix both patterns in their searching.

All model solutions simulate incremental changes in velocity vectors by randomly drawing values from a normal distribution, that is, as a stochastic process. Therefore, none reproduced the significant periodicities observed in empirical medusae. The prominent low frequency peak in the power spectra of velocity and acceleration observations of modeled medusae resulted from truncating these smoothed (correlated) time series. Model solutions that simulate the switching behavior observed in empirical medusae in the absence of prey (e.g. run 6) vary speeds markedly as a result of simulated changes in swimming bell pulsation strength. However, the switching is controlled by a probabilistic function and did not produce the significant periodicities that were observed in empirical medusae.

Furthermore, I did not recover significant periodicities in the time series of a model (run 8) that simulated a deterministic cycle of changes (frequency = 50 mHz) in swimming patterns of medusae, that is, similar to the pattern changes observed in empirical medusae in the absence of prey (Fig. 4.7). The model was parameterized so that the interval between switches (g) and among medusae (h) was identical. However, when deterministic swimming pattern changes were accompanied by changes in behavior as simulated by a momentary reduction in the behavioral correlation of swimming trajectories, B_L (model run 9), significant cycles in velocity and acceleration were observed.

I observed periodicities in a group of empirical medusae (i.e. in the absence of prey) that varied in both their propensity to switch behavior states (e.g. some remained in one behavior for long periods, others changed often) and, of those that switched, varied in the interval between switches. To explore the effect of this variability on the periodicities observed, I simulated populations that varied in either the timing between switches (g) or the propensity to switch (h). I did not observe any significant periodicities at the expected average frequency of 50 mHz in a population (run 10) in which each individual maintained identical intervals between switches ($g_1 = g_2$, etc.) but where the propensity to switch varied, that is, where some medusae switched frequently while others remained in the same pattern throughout (Fig. 4.7). I also found no significant periodicities in a group of medusae (run 11) in which all medusae had the same likelihood of switching patterns, but the timing between switches varied.

DISCUSSION

I found that some elements of the swimming trajectories of *Chrysaora quinquecirrha* medusae were simulated with a simple correlated random walk (CRW) model of velocity vectors. CRW models have proven successful for modeling movement in heterogeneous environments, simulating the tendency of organisms to move straight ahead, but also the effect of small-scale directed motion by individuals in response to local conditions (Turchin 1998). The fact that a CRW model simulates medusa movement may indicate selective pressure to evolve swimming behaviors that suit the generally heterogeneous conditions of their biotic and abiotic environments (Purcell et al. 1994; Keister et al. 2000). At the same time, I noted departures of medusa movement from the CRW model that reflected the influence of more complex behaviors, for example, in elements of foraging, anisotropic patterns of looping and vertical movement, and periodicities in swimming behavior.

Foraging behavior

An efficient foraging pattern for widespread and patchy resources is to move in a highly correlated straight-line manner, which increases the area searched between patches (Dixon 1959; Smith 1974; Kareiva and Shigesada 1983; Root and Kareiva 1984; Zollner and Lima 1999). When a patch is encountered, speed is reduced and turning increased (i.e. correlation reduced) increasing the likelihood of remaining in a patch. An effective search strategy may be especially important to medusae since they forage in a three-dimensional environment for planktonic prey, which are often moving and whose abundance varies in both time and space (Steele 1978; Davis et al. 1991). Modeling results are consistent with a medusa foraging behavior similar to that described above for heterogeneously distributed prey, with two important exceptions: (1) medusae periodically increase speed between patches; and (2) medusae speed up, not slow down, when prey are encountered.

Following their empirical studies, Matanoski et al. (2001) speculated that medusae searching for prey switch between two swimming patterns as part of a foraging behavior that conserves energy moving between prey patches while periodically achieving the necessary velocity to generate prey-capturing vortices at the swimming bell margin. The addition to the model of a probabilistic function that simulates periodic increases in the variability and strength of swimming bell pulsations produced similar trajectories to those of the empirical medusae with respect to means and variability of velocity and acceleration. The model confirms that medusa searching behavior comprises two states, a slower linear pattern and a faster more curvilinear one.

Interestingly, to reproduce the “fast” pattern of medusae in the absence of prey required greater simulated pulsation strength than was necessary to reproduce the pattern of medusae in the presence of prey. In other words, medusae are not merely switching between a slow pattern and the feeding pattern. Despite a lower mean velocity, medusae in the absence of prey swim very fast (> 2.7 cm/s) more frequently than medusae in the presence of prey (Matanoski et al. 2001). Clearly, medusae are briefly switching to a very high velocity pattern in the absence of prey. This “ bursting” of speed may be related to the biomechanics of medusa prey capture because the velocity and areal extent of prey capturing vortices are linearly related to medusa swimming speed (Ford et al. 1997). Bursts of very high velocity would briefly increase the size of the medusa encounter zone and the volume of water passing through the tentacles (Madin 1988). Chemical stimuli associated with prey elicited similar pattern changes in marine crustaceans (Hindley 1975; Smith and Baldwin 1982). Buskey (1984) noted that faster swimming would increase the flow across the antennae and enhance the ability of copepods to detect the chemical signature of prey in the water. Whatever the reason for this high velocity "bursting" by medusae, it would appear to be an integral, albeit subtle, component of medusa foraging because swimming trajectories from models lacking it (e.g. run 5) were significantly different from those observed empirically.

I found that an equal probability of switching between the two behavior states produced the same proportion of medusae swimming in each of the three patterns (i.e. fast, slow, or a mixture of fast and slow) as was observed in the empirical medusae suggesting that the same neurophysiological mechanism controls switching into each behavior. Reflexive behaviors commonly exhibit exhaustion with repeated stimulation and on a time scale similar to that used to parameterize the model switching function (seconds to minutes) (Slater 1999; Purves et al. 2001). If the observed behaviors, fast and slow swimming, were reflexive reactions to the same stimulus (in this case a negative one, an absence of prey), then I might expect a similar duration for each of the behaviors and an equal probability of switching between them.

Most organisms reduce speed after encountering prey both to increase the probability of remaining in a patch and because the physical manipulations required in capturing and ingesting prey require them to slow down (Smith 1974; Kareiva and

Shigesada 1983; Buskey and Stoecker 1988; Zollner and Lima 1999). By contrast, *Chrysaora quinquecirrha* medusae swim faster in the presence of prey (Matanoski et al. 2001), which may be a consequence of the linear dependence between medusa velocity and that of prey-entraining vortices along the swimming bell margin (Ford et al. 1997). In addition, medusa prey capture occurs on numerous independently acting tentacles and oral arms (Costello and Colin 1995; Arai 1997), which eliminates the need to slow down while prey are consumed. The model reproduces the swimming pattern of medusae in the presence of prey by simulating stronger swimming bell pulsations, which resulted in faster swimming but would also tend to increase the velocity and extent of prey-entraining vortices along the bell margin. This supports the idea that faster swimming by medusae in the presence of prey is linked to stronger swimming bell pulsations required to generate feeding currents.

Vertical distribution

Medusae simulated swimming both in the absence and presence of prey were observed most frequently within 20 cm of the surface and bottom of the tank despite the absence of net vertical movement (i.e. distribution of incremental changes in velocity were centered on zero). A similar vertical distribution has been observed in *Pelagia noctiluca* medusae near shore (Zavodnik 1987). Model results indicate that the accumulation of medusae at the air-sea interface and near the bottom in shallow systems is largely the result of simple boundary effects, that is, the interaction of randomly swimming medusae with a barrier. These results also suggest that shallow systems may be more generally limiting to medusae than previously thought and create heterogeneous vertical distributions, which may be especially important because many medusa species inhabit coastal or estuarine systems.

Modeled medusae in both the absence and presence of prey were observed swimming near the top and bottom boundaries with similar frequency, but the behavior of empirical medusae depended on whether they were near the surface or the bottom of the tank and on the availability of food. Empirical medusae observed in the absence of prey aggregate near the surface but not near the bottom. Introducing a bias by modeled medusa to swim toward the surface created a similar vertical distribution. The bias was surprisingly small, 0.2 mm s^{-1} or about 2% of the mean 3-D velocity of the group. Hamner et al. (1982) observed repeated vertical shifts of as much as 16 m by *Mastigias* sp. medusae in a single night. Model results suggest that these types of vertical migrations may be accomplished by exceedingly small changes in net vertical movement either by active swimming or, alternatively (with very low energy expenditures), by changing buoyancy (Bidigare 1980, Wright and Purcell 1997).

Similarly, small directed movements toward an orienting stimulus (e.g. a current) or a center of attraction (e.g. a prey patch) could be a mechanism for migrating or aggregating behavior in the horizontal plane as well. Light, prey, touch, and currents are orienting cues for directed movement by medusae (Shanks and Graham 1987; Strand and Hamner 1988; Hamner et al. 1994; Schuyler and Sullivan 1997; Purcell et al. 2000; Matanoski et al. 2001) and could cause local migrations or aggregations. Similar responses to physical barriers and discontinuities (e.g. fronts) could create large-scale heterogeneous distributions (Arai 1973, 1976; Graham et al. 2001).

Model results demonstrate that empirical medusae avoid contact with the bottom. Empirical medusae in the presence of prey were observed twice as often in a layer 30-50 cm from the bottom as in the layer adjacent to it suggesting they are avoiding direct contact with the bottom and similar behavior has been observed in the scyphomedusa *Pelagia noctiluca* near shore (Zavodnik 1987). Medusae may detect the boundary with their tentacles, which have a wider displacement than their swimming bell and swim upward to avoid potentially entangling structures on the bottom. Modeled medusae do not show a similar response, swimming directly adjacent to the bottom.

Turning and Looping

Turning and looping were prominent features of empirical medusa trajectories and depended on the availability of prey. The initial formulation of the model (run 1) was not able to reproduce these features because medusae were modeled such that random changes in velocity vectors of the CRW were independently determined in each direction and relative to a fixed coordinate system. Model formulations in which random changes in velocity were relative to the current medusa trajectory (runs 3 and 4) resulted in marked increases in turning rate.

The fact that random changes relative to a fixed coordinate system could not generate loops is not surprising. Consider that looping requires that the medusa's heading sweep through all the points on a circle. In a CRW of velocity vectors, this would require a highly ordered and improbable sequence of random increments of alternating sign (e.g. positive x and positive y velocity increments followed by positive x and negative y increments, etc.). By contrast, if changes are relative to the current position (i.e. a natural coordinate system), a turn can be accomplished by a short sequence of values of the same sign in one of the directions (Smith 1974; Turchin 1998). When subsequently translated to the fixed coordinate system, these changes are mathematically partitioned into the positive and negative values of x, y, and z, direction that create a loop.

The natural coordinate system is also biologically relevant because it simulates the biomechanical process of medusa turning. To turn, a medusa deforms one side of the swimming bell prior to the other to create a pivot point (Gladfelter 1972). Repeating this action through several cycles of pulsations creates a loop. The numerical equivalent of this sequence is several positive incremental changes to the velocity vector in one direction.

I show, for the first time, anisotropy in medusa swimming patterns that depend on food. While searching for prey, medusae exhibited little difference in looping and sinuosity between the horizontal and vertical planes, however, when feeding, medusae looped more in the horizontal than the vertical despite having similarly sinuous paths. Not unexpectedly, model run 3 that was formulated for isotropic movement (i.e. the parameter set for calculating velocity vectors in all 3 directions was identical) could not simulate the anisotropic patterns of looping of empirical medusae. However, by reducing the magnitude of changes in vertical velocity (run 4), I created trajectories that were more linear, and therefore less looping, in the vertical plane.

Interestingly, the effect of linear vertical movements combined with horizontal looping produced vertically spiraling trajectories. In effect, anisotropic changes in looping when prey were encountered created volume-restricted searching. A vertical spiral can be an efficient search pattern for encountering horizontally distributed prey (Gerritsen and Strickler 1977; Turchin 1998). The change in swimming pattern would also alter the shape and orientation of the tentacle net and increase the volume of water contacted by medusa tentacles (Madin 1988). Thus, it was shown that anisotropic changes in the linearity of swimming paths could create changes that enhance capture efficiency. Similar spiral trajectories have been observed in *Phacellophora camtschatica* (Strand and Hamner 1988) and may be a general response of medusae consistent with typical spatial patterns of their prey (Steele 1978; Haury et al. 1978).

The choice of coordinate system used to model medusa swimming patterns may also reflect the stimuli governing movement behavior. A natural coordinate system simulates organisms responding to cues in their local environment and a fixed coordinate system to stimuli perceived across long distances (Marsh and Jones 1988). The requisite coordinate system to simulate the two swimming patterns suggests that medusae respond to different stimuli depending on whether they are searching or feeding. In the presence of prey, motion may be governed by local movement processes (e.g. turn left, turn right), which are influenced by stimuli perceived over short distances, for example, mechanical disturbances. In the absence of prey, medusae may orient to long-range stimuli (e.g. gravity) and move accordingly (e.g. swim up). Austin et al.

(2004) found that a CRW model based on local considerations did not accurately predict the movement of far ranging grey seals, but could simulate ones engaging in area-restricted movement.

Cyclical behavior

There were significant periodicities in the velocity and acceleration observations of empirical medusae, but no formulation of the model simulated similar cyclical changes in swimming. I did not expect any statistically significant cycles in groups of medusae modeled by a CRW because changes in velocity and acceleration are the result of a stochastic function. However, the model also failed to generate significant periodicities in trajectories when deterministic changes in velocity parameters were added to the simulation (run 8). This outcome occurred because the correlation term, which is integral to producing the smooth trajectories observed in empirical medusae, reduced the stepped changes that were part of the deterministic function, with unpredictable effects on the timing of those changes.

I was able to recover the cycle resulting from a deterministic change in swimming behavior in the time series of velocity and acceleration if the correlation of movement was abruptly reduced when swimming patterns changed. Clearly, instantaneous changes in the physical correlation due to the fluid medium do not occur, however correlation in movement due to behavior might reasonably be expected to vary with changes in behavioral response, which can happen very suddenly. Similar shifts in the degree of correlation of animal movement occur, for example, when organisms change from wide-ranging searching behavior to area-restricted feeding (Kareiva and Shigesada 1983). Therefore, model results indicate that swimming by empirical medusae are a result of behavior induced changes in swimming patterns.

It is informative to note the uniformity of behavioral changes in medusa swimming necessary to create significant cycles in the time series of their velocity and acceleration. I could not recover a simulated deterministic cycle of changes in medusa behavior in the time series of their velocity and acceleration when each medusa maintained a fixed interval between changes in behavior but the duration of the interval was unique to each medusa in the group. Nor was a significant cycle recovered if a group of medusae had the same average interval between changes in behavior, but the duration of the interval varied during a swimming sequence. Only if all medusae were identical in the timing of changes could the deterministic cycle be recovered. Therefore, it appears that the periodicities observed in the swimming patterns of empirical medusae were caused by deterministic changes in speed and turning as part of searching and feeding behaviors. Furthermore, the timing of these changes was similar in a sufficient number of medusae that comprise the population to produce a significant cycle in the average power spectrum of the group. Behavior patterns (i.e. well-defined sequences of actions) can be highly invariant, changing little among individuals or in the timing of each component of the sequence in the same individual (Slater 1999). Such deterministic components have been observed in the strongly correlated movements of swimming sperm, for example (Alt 1990). The similarity in timing of changes in swimming patterns among and within medusae may reflect strong selective pressure that creates common traits in their foraging behavior.

The framework model I describe is a generalized model of medsua swimming. Swimming patterns vary among medusa species differing with regard to speed, turning, proportion of horizontal versus vertical movement and allocation of time spent moving or at rest (Mills 1983; Strand and Hamner 1988; Kreps et al. 1997; Costello et al. 1998; Matanoski et al. 2001; Matanoski et al. 2004). These differences are a result of interspecific variability of swimming bell size and shape, tentacle size and deployment and its constraint on movement in a fluid medium as well as behavioral responses to heterogeneities in the abiotic and biotic environment. The model can reproduce interspecific variability in swimming patterns by varying model parameters simulating physical and behavioral controls on swimming bell pulsations as well as the correlatedness of medusa motion over time.

The model is also a unique application of the CRW to animal movement because it correlates velocity vectors rather than move length and turning angles as is common (Turchin 1998). In this aspect, the model resembles a particle trajectory model (e.g. Dutkiewicz et al. 1993). I have shown that such a model can simulate the movement of a planktonic organism. In addition, because of its unique formulation of animal movement, it can readily be incorporated into predictive models of plankter distributions set in a large-scale current framework (Hinckley et al. 1996; Hood et al. 1999; Johnson et al. 2001; Scheibe and Richmond 2002), and used to investigate coupling of physical and behavioral processes.

Medusae are neurologically simple organisms and may be incapable of the more complex behavioral patterns found in higher animals. However, I have observed swimming patterns in foraging medusae that resemble some of these higher order behaviors (e.g. area-restricted searching) and that may contribute to foraging efficiency because they are complementary to the spatial distributions commonly observed in various medusa prey. For example, I demonstrated a search pattern consistent with patchy prey, and a feeding pattern consistent with horizontally distributed prey, both features of mesozooplankton spatial dynamics. Additionally, these behaviors can be simulated with random processes and probabilistic functions, which may reflect the simple arrangement of the medusa nervous system.

TABLES

Table 4.1 Parameter sets for all model runs. Refer to text for details on parameter selection.

Model run	Coordinate system	Behavioral switch			$\frac{dt}{T_L}$	$\frac{dt}{B_L}$	$\sigma_{b x,y,z}$	$\sigma_{b a,b,c}$	$\psi_{x,y}$	ψ_z	κ	ψ_a	$\psi_{b,c}$	Differences between model and empirical observations
		g	h	n										
1	fixed	none			0.025	1	0.8	-	0	0	1.0	-	-	no prey: variability of vel, acc with prey: vertical distribution
2	fixed	none			0.025	1	0.8	-	0	0.02	1.0	-	-	horizontal turning rate
3	natural	none			0.050	1	-	0.04	-	-	1.0	1.5	0	vertical turning rate
4	natural	none			0.050	1	-	0.04	-	-	0.3	1.5	0	periodicities of vel, acc
5	fixed	g*	h*	10	0.025	1	0.06 / 0.8	-	0	0	1.0	-	-	mean and variability of vel, acc
6	fixed	g*	h*	10	0.025	1	0.06 / 1.6	-	0	0	1.0	-	-	vertical distribution
7	fixed	g*	h*	10	0.025	1	0.06/ 1.6	-	0	0.02	1.0	-	-	periodicities of vel, acc
8	fixed	g**	h**	10	0.025	1	0.06 / 1.6	-	0	0.02	1.0	-	-	periodicities of vel, acc
9	fixed	g**	h**	10	0.125	0.083	0.06 / 1.6	-	0	0.02	1.0	-	-	frequency of periodicities
10	fixed	g**	h*	10	0.125	0.083	0.06 / 1.6	-	0	0.02	1.0	-	-	periodicities of vel, acc
11	fixed	g*	h**	10	0.125	0.083	0.06 / 1.6	-	0	0.02	1.0	-	-	periodicities of vel, acc

vel: velocity   acc: acceleration

coordinate system   fixed: relative to the framework of tank   natural: relative to medusa position

behavioral switch:
g* interval between switches is recalculated after each switch ($g_1 \neq g_2$)
g** interval between switches is constant throughout swimming sequence ($g_1 = g_2$)
h* threshold for switch is unique to each medusa ($h_1 \neq h_2$)
h** threshold for switch is identical for all medusae ($h_1 = h_2$)

n determines average interval between switches $\frac{dt}{T_L}$ physical correlation parameter $\frac{dt}{B_L}$ behavioral correlation parameter

$\sigma_{b x,y,z}$ $\sigma_{b a,b,c}$ variance of incremental velocity vectors for fixed, natural coordinate systems, respectively

$\psi_{x,y}$ mean of incremental x, y velocity vectors ψ_z mean of incremental z velocity vector

$\psi_{b,c}$ mean of incremental b,c velocity vectors ψ_a mean of incremental a velocity vector

κ damping factor for vertical velocity vector

Table 4.2 Means, individual and population variability, and results of spectral analysis of velocity and acceleration for empirical and modeled medusae (n = 8 for each) in the presence of prey. Refer to Table 4.1 for details of parameter set for each model run.

		Source of data		
	Statistical measures	Empirical	Model run 1	Model run 4
Velocity	Mean ± SE (cm s^{-1})	1.35 ± 0.063	1.30 ± 0.105	1.43 ± 0.045
	Variance of means (cm^{-2} s^{-2}) (interindividual variability)	0.031	0.087	0.016
	Mean ± SE of variances (cm^{-2} s^{-2}) (intraindividual variability)	0.149 ± 0.044	0.191 ± 0.022	0.164 ± 0.039
	Significant cycles (mHz)	52	9	9
Acceleration	Mean ± SE (cm s^{-1})	0.140 ± 0.016	0.140 ± 0.008	0.145 ± 0.007
	Variance of means (cm^{-2} s^{-2}) (interindividual variability)	1.97×10^{-3}	4.87×10^{-4}	3.83×10^{-4}
	Mean ± SE of variances (cm^{-2} s^{-2}) (intraindividual variability)	$6.73 \times 10^{-3} \pm 2.40 \times 10^{-3}$	$3.82 \times 10^{-3} \pm 8.00 \times 10^{-3}$	$4.87 \times 10^{-3} \pm 1.22 \times 10^{-3}$
	Significant cycles (mHz)	36, 82, 91	none	none

Table 4.3 Means, individual and population variability, and results of spectral analysis of velocity and acceleration for empirical and modeled medusae (n = 11 for each) in the absence of prey. Refer to Table 4.1 for details of parameter set for each model run. Statistically significant differences between empirical observations and output of each model are denoted by asterisks (t-test of means and variance ratio test; * $p<0.05$, ** $p<0.01$, *** $p<0.001$).

	Statistical measures	Source of data		
		Empirical	Model run 1[†]	Model run 6
Velocity	Mean ± SE (cm s^{-1})	1.06 ± 0.161	1.05 ± 0.059	1.04 ± 0.132
	Variance of means (cm^{-2} s^{-2}) (interindividual variability)	0.285	0.038 **	0.193
	Mean ± SE of variances (cm^{-2} s^{-2}) (intraindividual variability)	0.248 ± 0.058	0.211 ± 0.024	0.368 ± 0.094
	Significant cycles (mHz)	9,17	9	9
Acceleration	Mean ± SE (cm s^{-1})	0.113 ± 0.015	0.095 ± 0.002	0.094 ± 0.014
	Variance of means (cm^{-2} s^{-2}) (interindividual variability)	2.33×10^{-3}	5.80×10^{-5} ***	2.11×10^{-3}
	Mean ± SE of variances (cm^{-2} s^{-2}) (intraindividual variability)	$4.25 \times 10^{-3} \pm 1.00 \times 10^{-3}$	$1.63 \times 10^{-3} \pm 1.00 \times 10^{-4}$ *	$4.35 \times 10^{-3} \pm 6.00 \times 10^{-3}$
	Significant cycles (mHz)	55	9	9

[†] Parameter set identical to model run 1 in Table 4.1 except $\sigma_{bx,y,z} = 0.65$ to simulate lower mean velocity and acceleration of empirical medusae in the absence of prey.

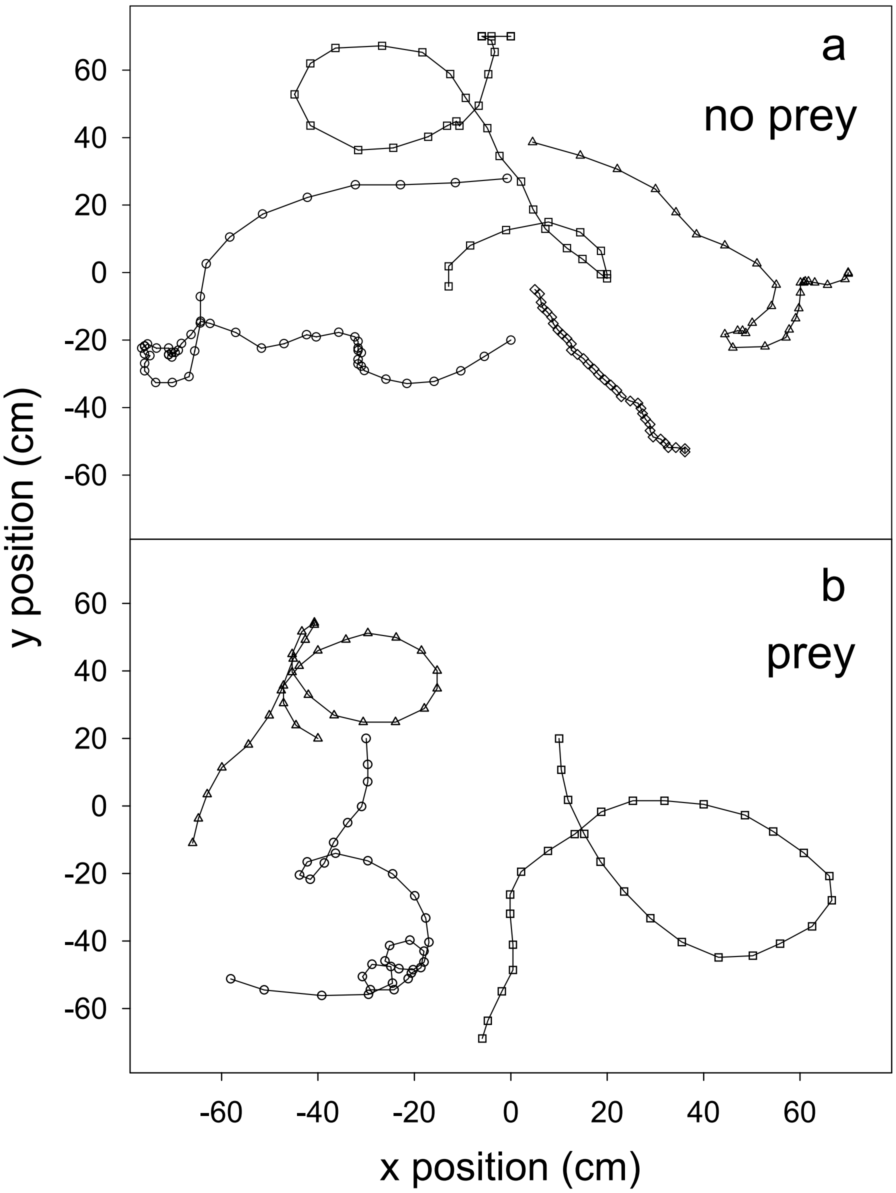

Figure 4.1 Representative trajectories for swimming of empirical medusae in absence (a) and presence (b) of prey. Symbols denote position of medusa at 5-s intervals. Initial positions were assigned to avoid overlapping paths.

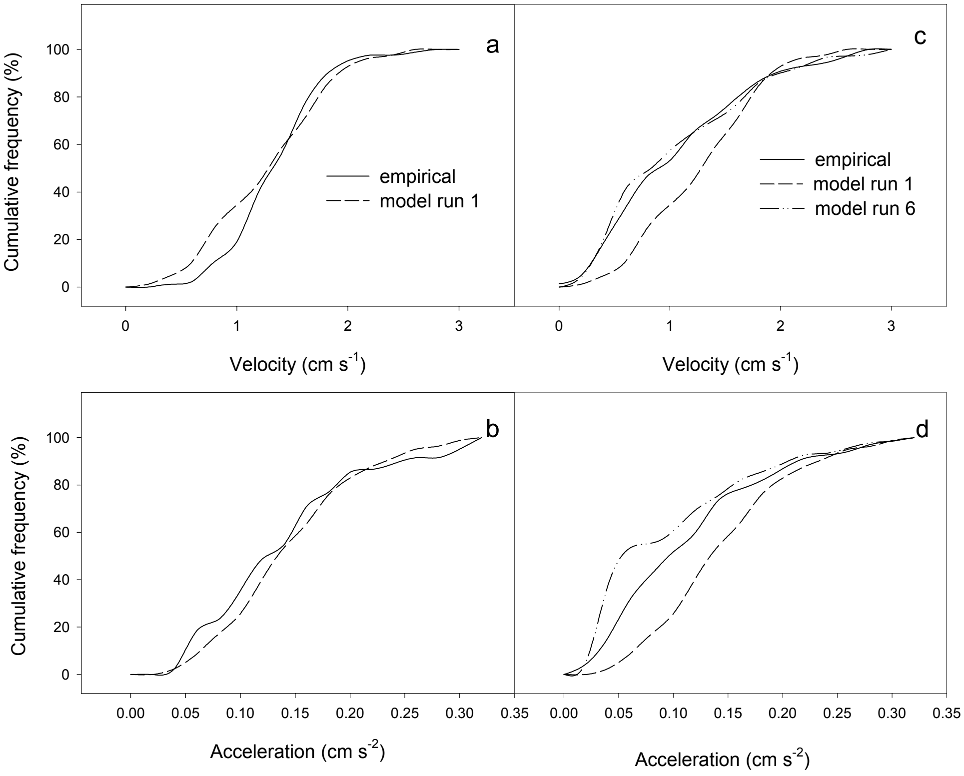

Figure 4.2 Cumulative frequency distributions of velocity and acceleration observations of empirical and modeled medusae in presence (a, b; n = 8 each) and absence (c, d; n = 11 each) of prey simulated swimming in one behavior state (model run 1) or alternating between 2 behavior states (i.e. strength of swimming bell pulsations) (model run 6).

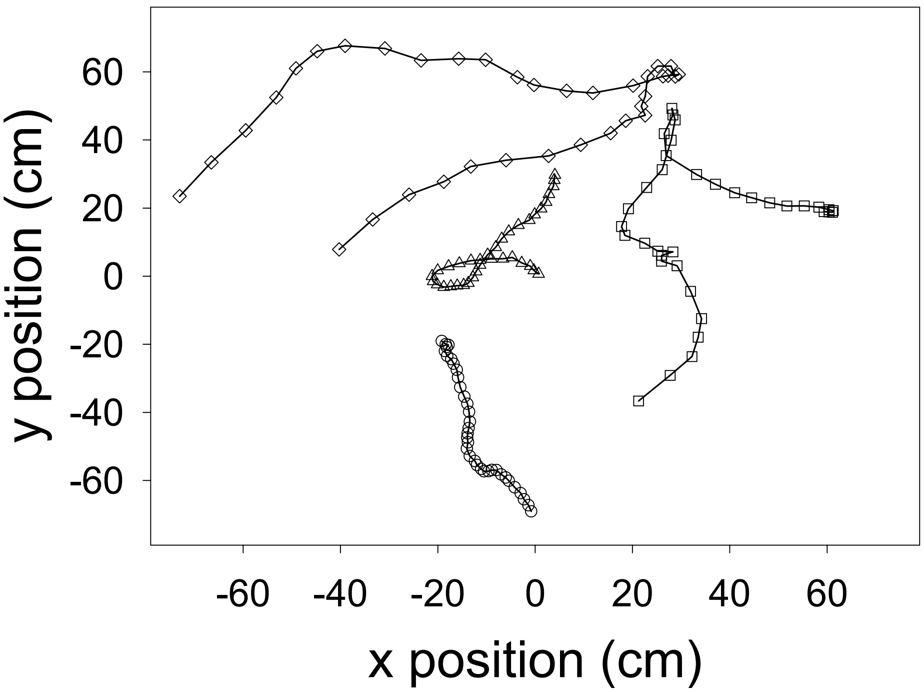

Figure 4.3 Representative trajectories for simulated swimming of 4 medusae in absence of prey and alternating between 2 behavioral states (i.e. strength of swimming bell pulsations) (model run 6). Symbols denote position of medusa at 5-s intervals. Initial positions were assigned to avoid overlapping paths.

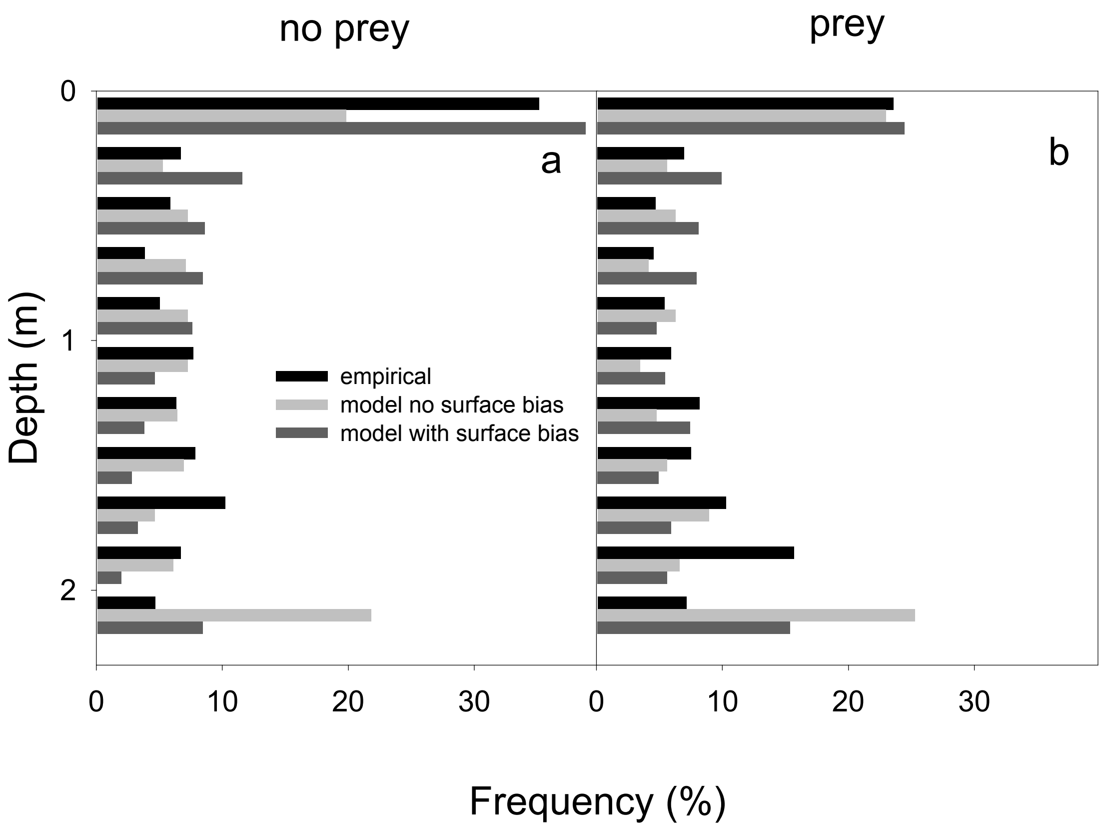

Figure 4.4 Depth profiles of empirical medusae observed singly in cylindrical tank 2.3 m in depth and 2.4 m in diameter in absence (a, n=11) and presence (b, n=8) of prey and modeled medusae simulated under identical conditions of prey without (runs 6 and 1) and with (runs 2 and 7) a bias to swim toward surface. The depth of each medusa was observed every min for 2 h.

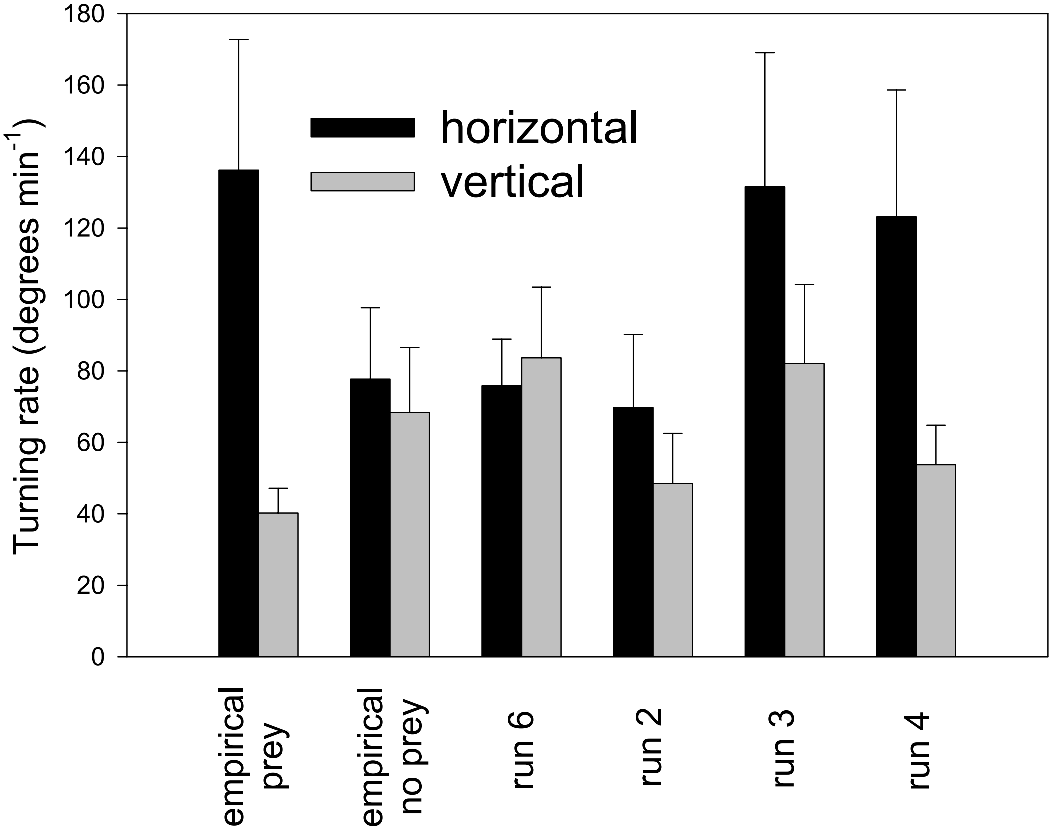

Figure 4.5 Mean turning rates (± SE) for empirical and modeled medusae in presence (n=8 each) and absence (n=11 each) of prey. Refer to Table 4.1 for details of parameter set for each model run.

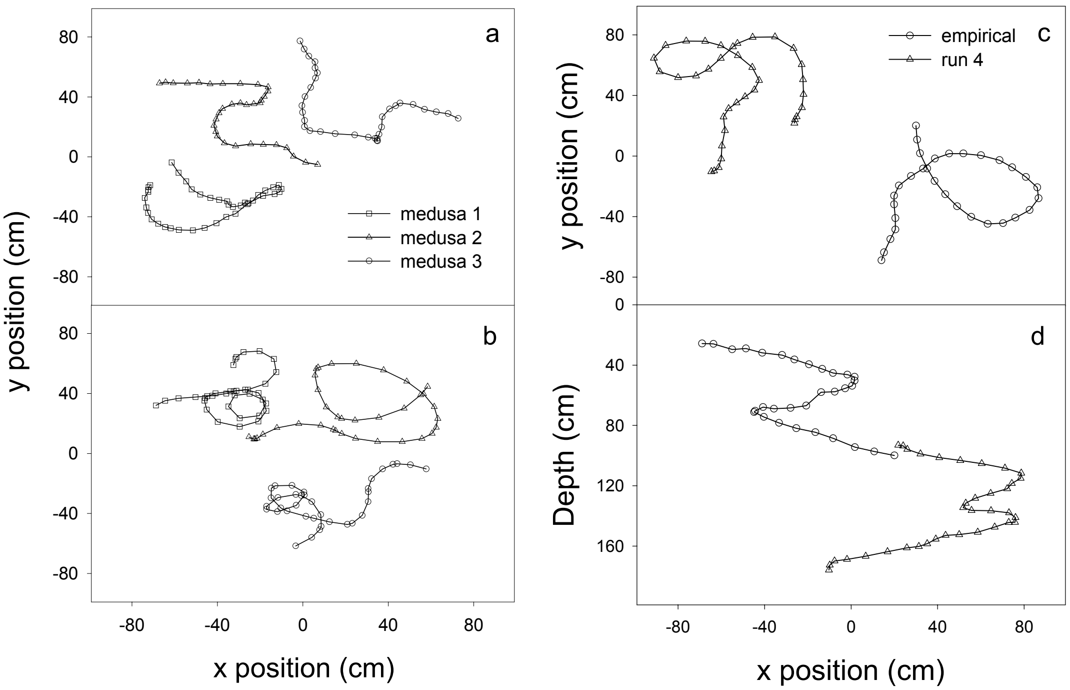

Figure 4.6 Representative trajectories for simulated swimming of 3 modeled medusae in presence of prey with random changes in velocity relative to framework tank (a; model run 2) or relative to position of medusa (b; model run 3). Representative trajectories of empirical medusae in absence and presence of prey and modeled medusa (model run 4) simulated using natural coordinate system with damped changes in vertical movement from plan view (c) and side view (d).

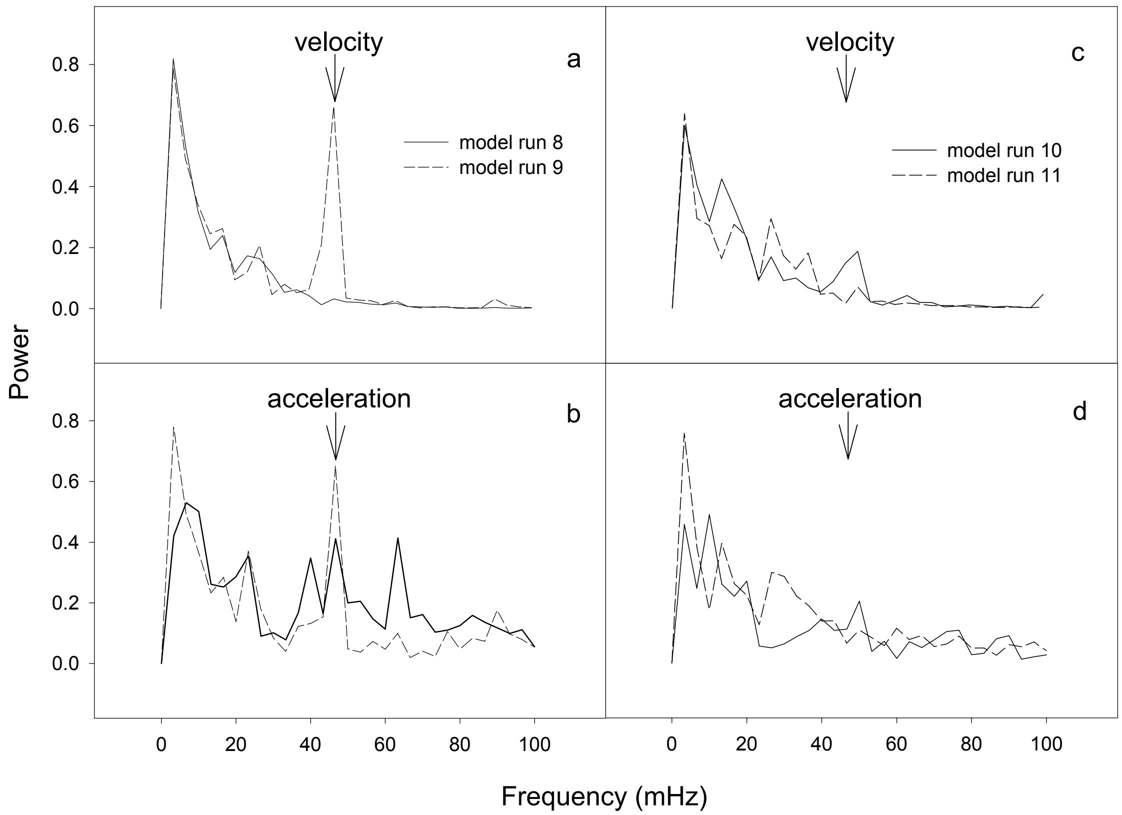

Figure 4.7 Average power spectra of velocity and acceleration time series for four groups of modeled medusae (n = 11 each) with simulated cycle (arrow, average frequency = 50 mHz) of changes in patterns during 5 min swimming sequence. Refer to Table 4.1 and text for details of parameter set for each model run.

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CHAPTER 5

Conclusions

SUMMARY OF RESULTS

In this dissertation, I reported the development of an approach to differentiate behavior between individuals. The approach relies on the fact that behavior often comprises repeated sequences of actions (Slater 1999) and that individuals may differ in the timing (i.e. variability) of these sequences. Time-dependent changes in patterns of swimming behavior of four individual scyphomedusae, *Aurelia aurita*, were analyzed using a suite of statistical techniques, random series analysis, analysis of variance, goodness-of-fit tests of frequency histograms, and spectral analysis. I found that each medusa swam in a unique pattern, which differed, among other things, in their mean velocity and the frequency of turning. Furthermore, this approach was used in mesocosm studies of foraging behavior and the development of a model of medusa swimming behavior (Chapters 3 and 4, respectively) and demonstrated that the variability of behavior (i.e. changes in velocity, acceleration, etc.) among individuals and in a single individual over time were fundamental components of swimming and foraging behaviors.

I also reported the results of studies of foraging behavior in the scyphomedusa *Chrysaora quinquecirrha*. Using the statistical approach of Chapter 2, I found swimming behavior varied more when medusae were searching for food largely because they exhibited two behavioral states, one of slow, linear swimming and the other faster and more curvilinear. Intraindividual variability was a result of medusae alternating between the two states while variability among individuals was a result of the frequency at which they alternated; some medusae remained in one state for periods of several minutes or more while others changed more frequently. By contrast, feeding medusae swam at a constant moderate velocity and with increased turning. In these respects medusa swimming resembled area-restricted patterns observed in other species (Dixon 1959; Fraenkel and Gunn 1961; Smith 1974; Kareiva and Shigesada 1983; Turchin 1991). Furthermore, turning by feeding medusae was markedly anisotropic with increased looping in the horizontal plane and reduced looping in the vertical plane as compared with medusae searching for prey, a characteristic of animal feeding behavior that has not been previously reported. The effect created vertically spiraling trajectories. Overall, the foraging behavior (searching and feeding patterns) is well suited to prey that are distributed in horizontally compressed patches (Gerritsen and Strickler 1977; Turchin 1998). However, medusa foraging also differed from typical foraging patterns (Dixon 1959; Smith 1974; Kareiva and Shigesada 1983) in being faster (not slower) in the presence of prey, which I attribute to the direct relationship between medusa swimming velocity and that of feeding currents. Medusae also periodically increased speed in the absence of prey patches, which may be necessitated by their inability to detect prey except by capture and the need to generate prey-entraining feeding currents while searching.

I developed an individual-based model of medusa swimming behavior, which is unique in simulating motion as a correlated random walk (CRW) of velocity vectors rather than move length and turning angle. Model results support the idea that medusa foraging is adapted for a patchily distributed prey. A simple CRW model simulated some aspects of medusa foraging behavior including means and variability of velocity and acceleration of feeding patterns and mean turning angles (i.e. sinuosity) of both search and feeding patterns. The alternation between velocities that is part of medusa search patterns is an integral part of medusa foraging because a model of medusae swimming behavior that did not simulate these changes could not reproduce empirically observed trajectories. The model was formulated with a probabilistic function simulating stepped changes in swimming bell pulsation strength, which reproduced this switching behavior including increased variability in swimming patterns. Anisotropy in looping behavior in feeding medusae was simulated by reducing changes in vertical velocity, which also created vertically spiraling trajectories. Model results showed that foraging medusae tend to swim toward the surface and that this behavior, when combined with a boundary condition effect, resulted in aggregations of medusae at the surface and bottom. This effect appears to dissipate in deeper systems. Model results also highlight an avoidance behavior by empirically observed medusae of the bottom but not the surface. In addition, periodicities in velocity outside prey patches and looping behavior within patches in empirical medusae were a result of deterministic cycles of behavior at a frequency that was common to several medusae in the population. Formulation of this model also validated a new approach to development of individual-based models. At each step of model development, the output of a modeled individual was compared to a single empirically observed individual (using statistical methods described in Chapter 2) to assess the accuracy of the model in simulating the observed behavior and to inform changes in the model prior to the next step in development.

IMPLICATIONS

Several results from this dissertation demonstrate the important effect that individual behavior has on population-level processes. In chapter 3, I showed that variability of behavior among individuals (interindividual variability) and by a single individual over time (intraindividual variability) depended on environmental conditions, specifically the availability of prey. Modeling studies showed that both types of variability resulted from individual medusae alternating between two behavioral states and that this switching was an integral part of the searching behavior of medusae. Models that lacked this variability did not simulate the observed behaviors. In addition, individual variability was responsible for the differences between search and feeding behaviors because a single correlated random walk model reproduced most aspects of both patterns if it allowed for variability of individual behavior in response to changing environmental conditions. These results show how a population-level process (e.g. predation effect) can be affected by how individuals respond to local conditions (e.g. presence of prey) and, in particular, by the variability of responses among members of the population and in the same individual over time. These results suggest that greater attention be focused in empirical studies on quantitatively assessing the various responses of individuals and incorporating these data into population and ecosystem models.

Quantifying the behavioral response of individuals to environmental conditions is especially important in marine systems because they are dynamic. Mobile individuals confront conditions that change as they move (Steele 1976; Abbott 1993), and even sedentary marine animals will experience rapid changes in abiotic and biotic environments as currents bring a mosaic of nutrients, oxygen, other animals, etc. past their location. Many of these physical and biological features (e.g. turbulence, plankton patches) vary over scales relevant to the individual (e.g. cm to m) (Davis et al. 1991). For example, using the approach developed in chapter 2, I showed that individual medusae change from searching behavior when prey were absent to feeding behavior when prey were present, a change that would occur when they move into a prey patch.

Studying individual behavior is also necessary to understand behavioral mechanisms because behavior begins with the individual. Studies in mesocosms showed that each of several *Chrysaora quinquecirrha* medusae change from searching behavior to feeding behavior when they encounter prey. This type of behavioral plasticity is implicit in numerous mechanisms that have been proposed wherein marine animals orient to environmental gradients of pressure, salinity or temperature to maintain a relative position in the water column. For example, Hough and Naylor (1992) observed that populations of the estuarine copepod *Eurytemora affinis* located up-estuary move to the surface on ebbing tides while those located down-estuary do so on a flooding tide. The result is to concentrate *E. affinis* near the midpoint of the estuary. They speculated that these spatially dependent behaviors were in response to salinity gradients. A similar mechanism has been proposed for crab larvae in response to the vertical pressure gradient (Sulkin and Van Heukelem 1982; Sulkin 1984). These types of behavioral mechanisms require the animal to reverse its behavior (i.e. behavioral plasticity) or risk overshooting the desired position. I compared the response of individual medusae to the availability of prey and found their behavior changed from searching to feeding when prey were present. Quantifying an organism’s response to environmental factors postulated to control their movement would determine whether such mechanisms are responsible for in situ distributions.

Predation effects of scyphomedusae are highly variable both spatially and temporally (reviewed in Arai 1997), yet little is known about how behavioral processes affect feeding. Among other factors, rates depend on the co-occurrence of medusae and their prey, the size of the tentacle capture area and the range of their perceptive field (Madin 1988; Purcell 1997), all factors potentially influenced by behavior. I have shown that medusa foraging behavior creates swimming patterns that can be expected to increase feeding rates by decreasing the time spent between prey patches and increasing the likelihood of remaining in a patch once located. Furthermore, anisotropic looping patterns that are part of medusa feeding behavior create vertically spiraling trajectories, which may increase the capture rate by expanding tentacle deployment. In addition, I have shown that medusa search patterns include periods of very fast swimming, which may enhance their perceptive range. Similar behaviors are likely in other scyphomedusae because of shared morphological traits and feeding mechanisms (Arai 1997).

I showed that medusae went from searching to feeding when prey concentrations increased, as might be experienced when encountering a patch; but of equal importance is the point at which medusae abandon feeding and return to searching for prey, that is, the degree to which they exhibit patch fidelity. The degree of patch fidelity an animal exhibits is related to energetic returns from feeding in an area compared with the expenditures of moving to a new patch (Schoener 1971). It is a fundamental behavior that governs animal distributions (Root 1984) and about which little is known in medusae. In the mesocosm experiments of chapter 3, prey conditions changed in a stepped fashion (i.e. prey were absent or present). We might ask, at what concentration of prey does a medusa change behavior? Goldfish, *Carassius auratus*, begin area-restricted searching after capturing a first prey item, but if no others are caught (e.g. if prey are sparsely distributed), they gradually increase the range of their searching (Mikeheev et al. 1992). That is, the likelihood of remaining in an area decreases as the average energetic return from the patch declines. This graded response permits area-restricted feeding in a prey patch but also efficient searching if prey are not all confined to a single patch (Grunbaum 1998b). Using the approach of Chapter 2, one could examine the behavioral changes in individual medusae with increasing concentrations of prey to determine at what concentration medusae change from feeding to searching, that is, when do they abandon a patch and return to a linear, large displacement, search pattern. One can easily imagine a direct relationship between the level of nervous stimulation of nematocyst discharge caused by contact with prey (Watson et al. 2000) and nervous control of swimming bell muscles responsible for turning that would create a graded response in turning behavior due to prey.

I observed changes in swimming patterns in response to prey assemblages comprising mesozooplankton. Further investigation is needed to explore the response of medusae to larger prey. Chrysaora and other medusae slow down and turn toward points of contact with larger prey, presumably to involve more tentacles in their capture (Bailey and Batty 1983; Strand and Hamner 1988; Kreps et al. 1997). Whether medusae maintain a different pattern and if so for what duration after encountering large prey is unknown. In addition, the effect of any change in pattern may alter the spatial distribution. The model of medusa swimming behavior is sufficiently flexible that differences in medusa swimming patterns due to variability in type and size of prey could be simulated by altering correlation parameter and frequency and magnitude of changes in bell pulsation strength.

I found that medusae swam faster, without interruption, and in more circular trajectories in the presence of prey, a pattern consistent with cruising predation in a patch of prey (Kareiva and Shigesada 1983; Greene 1985). An interesting question would be whether medusae could change their foraging mode (e.g. from cruising to ambush predation) dependent on conditions. For example, can *Chrysaora quinquecirrha* adopt an ambush foraging pattern? This might also explain their efficiency as generalist feeders (Purcell 1992). Cruising predation is favored for relatively slow, patchily distributed prey (e.g. copepods), while ambush predation is advantageous when prey are fast moving and wide-ranging (e.g. fish) (Huey and Pianka 1981; Greene 1985). Members of stream-dwelling fish populations can assume different foraging tactics to reduce intraspecific competition for food or to exploit changes in the prey composition (Fausch et al. 1997; McGlaughlin et al. 1999). Generalist feeders would be uniquely suited to engage in such responses because they can feed on prey with varying speeds and distributions. Strand and Hamner (1988) observed *Phacellophora camtschatica* altering the orientation of search patterns from vertical to horizontal to match the various distributions of their prey, however, they remained cruising predators in both patterns. Although for some animals there may be morphological constraints to switching feeding modes (Huey and Pianka 1981), web building spiders, for example, can’t become cruising raptors, the entangling tentacles of medusae are well suited to both cruising entangling and ambush entangling modes. I observed behavioral switching between fast and slow swimming by medusae searching for prey and similar changes in swimming patterns could result in appropriate deployment of medusa tentacles (e.g. for cruising or entangling) for the prey available.

Although I have demonstrated how swimming patterns changed when medusae switch from searching to feeding, detailed information on how searching patterns change with hunger would further enhance predictions of medusa distribution, especially if dynamically coupled to data on the spatial distribution of their prey. Foraging patterns of some animals depend on level of hunger or satiation (Huey and Pianka 1981; Kareiva and Odell 1987; Wallin 1991; Mikheev et al. 1992; Grunbaum 1998b). Ladybird beetles reduce their turning rate as hunger increases creating more linear paths, greater displacement, and increasing the probability of encountering a patch of prey (Kareiva and Odell 1987). Similarly, Wallin (1991) found that the insectivorous beetle *Calosoma affine* exhibits more directed movements when it is hungry than when it is satiated, which reduces the time spent moving between prey patches. Medusae used in the mesocosm studies were freshly collected. Therefore, their feeding history was unknown, and further research is needed to determine if medusa foraging behavior also depends on the level of hunger.

Very little is known about prey detection by scyphomedusae. I found conflicting evidence regarding prey detection by *Chrysaora quinquecirrha* medusae. While searching, medusae periodically increased speed, and I suggested that this is a necessity of periodically generating prey-entraining vortices. This implies that medusae ultimately detect prey only when they impinge on tentacles. By contrast, model results suggested that medusae orient their search patterns to long-range stimuli. It may be that search patterns are oriented to long-range stimuli, for example gravity or light, stimuli for which

C. quinquecirrha are known to have receptors (Arai 1997), but that detection itself occurs only by contact with prey. It is unclear whether medusae can detect, and, therefore, orient their movement to, prey over long distances. A single example exists of a scyphomedusa responding to chemical stimuli (Arai 1991) and a similar reaction has been observed in another cnidarian, the hydromedusa *Mitrocoma cellularia* (Tamburri et al. 2000). However, no sensory structures have been identified to explain these responses. Although receptors sensitive to chemicals associated with prey have been shown to induce nematocyst firing, their range of detection has never been assessed, but appears limited (Watson and Hessinger 1994). The means by which medusae detect prey is vital to making predictions of their ecological effect. For example, it has been proposed that reductions in available light associated with increased phytoplankton growth in eutrophied systems favor non-visual predators such as medusae at the expense of visual predators such as fish (Eiane et al. 1999).

Dramatic examples of aggregating behavior have been well documented in several species of scyphozoa (Hamner and Hauri 1981; Larson 1992; Hamner et al. 1994; Purcell et al. 2000). I found that medusae exhibit preytaxis, engaging in area-restricted searching once prey are located. The effect of this behavior would be to concentrate medusae in prey patches (Fraenkel and Gunn 1961; Kareiva and Odell 1987; Leising and Franks 2000). Grunbaum (1998a) showed that individual animals could increase their foraging efficiency by forming groups. The effective size of an individual’s perceptive field is expanded if it responds to the actions of others, for example, in the schooling behavior of some fish. Tentacle discharge is sensitive to the presence of conspecifics (Hannson and Kultima 1995), but it is not known whether other nervous system responses are also affected. This behavior would be especially advantageous to medusae because their perceptive field is limited (see above). Medusae could increase their probability of finding prey while searching by aggregating and increasing the volume of water within which prey are detected. Therefore, I expect in situ medusa aggregations to be a common occurrence, that is, medusae will be found together more than apart, because of behaviors related to feeding on and searching for prey and regardless of physical processes (e.g. convergences) that concentrate them. Significantly, many of the instances of scyphomedusa aggregations that have been identified found animals actively feeding (Malej 1989; Fossa 1992; Purcell et al. 2000).

In general, little is known about how medusae perceive the presence of nearby animals. They respond to tactile stimulation and can differentiate contact with conspecifics (Shanks and Graham 1987; Hannson and Kultima 1995; Arai 1997; Kreps et al. 1997). Whether this perceptive ability also controls swimming patterns is unknown. Such abilities might further explain the frequency which medusae are found in aggregations, especially those in which medusae are spawning.

The model of medusa swimming behavior reported in chapter 4 was formulated to resemble a particle trajectory model akin to the type used to model large-scale flow fields (e.g. Dutkiewicz et al. 1993). This will allow the incorporation of the effect of medusa swimming and behavior into a predictive model of their large-scale distribution. I have already demonstrated that vertical distributions of medusae depended on their interaction with boundaries as well as their swimming patterns. Similarly, coupling behavioral and physical models will create a spatially explicit dynamical simulation of behavior. For example, movement, as in a large-scale current, exposes medusae to variable environmental conditions that will elicit changes in their behavior. If these behavioral responses affect swimming (e.g. as the presence of prey did to *Chrysaora quinquecirrha* medusae), they would amplify or reduce the effect of currents on medusa movement. Spatially explicit models that couple physiological processes (e.g. respiration) with environmental conditions (e.g. dissolved oxygen) enhance predictions of survival rates of populations of juvenile fish (Scheibe and Richmond 2002). Similarly, spatial consideration of individual behavior in relation to physical conditions should enhance model predictions of how small-scale behavioral responses affect medusa growth, survival and large-scale distribution. For example, the hydromedusa *Sarsia tubulosa* swims less near haloclines, which causes them to aggregate near these boundaries (Arai 1973). The reaction of medusae to large-scale flows would be important when it brings them into proximity with gradients of physical and biological conditions (e.g. fronts, patches), which cause changes in behavior.

I found that the movement of *Chrysaora quinquecirrha* medusae in shallow systems is vertically limited in what appears to be a boundary condition effect. Presumably, shallow areas would not allow medusae to engage in their full range of searching and feeding patterns. Paradoxically, in Chesapeake Bay, this is where medusa densities are highest (Purcell 1992) and raises the question of why medusae aggregate in shallow tributaries where their range of motion is restricted. Although shallow areas are where the benthic polypoid stage occurs (Cargo and Schultz 1966), net estuarine circulation should flush medusae from these areas (Schubel and Pritchard 1987). In addition, medusae in these areas exhibit a full range of sizes from ephyrae to medusae >

10 cm diameter, and, therefore, do not represent merely a cohort of newly strobilated medusae (Cargo and Schultz 1967; Purcell 1992).

Preytaxis cannot be ruled out as a cause of the observed distribution. Preytaxis has been observed in *C. quinquecirrha* medusae (Matanoski et al. 2001) and creates overlapping distributions of predator and prey (Fraenkel and Gunn 1961; Kareiva and Odell 1987; Leising and Franks 2000). Although planktonic, medusa aggregations observed in tributaries might be a result of preytaxis toward high prey concentrations, especially if it occurs in conjunction with a general mechanism that promotes estuarine retention. Clearly more research is needed to explain the distribution of *C. quinquecirrha* medusae in systems like Chesapeake Bay, but it seems likely that behavior influences their distribution in tributaries.

We should also expect a similar boundary effect at pycnoclines, which would act as barriers to movement for neutrally buoyant medusae. Medusae are osmoconformers and, in the short term, before osmotically regulated changes in buoyancy can occur, medusae may accumulate at density discontinuities (Bidigare and Biggs 1980; Wright and Purcell 1997). Thus, aggregations of medusae may be observed in systems with stable pycnoclines, regardless of depth.

The model also provides a tool for investigating behavioral mechanisms controlling aggregations. In situ medusa aggregations are associated with increased predation and reproduction (Malej 1989; Hamner et al. 1994). Quantifying the spatial and temporal extent of aggregations would improve predictions of the ecological effect of medusae (Graham et al. 2001). I showed that medusa aggregations at the surface were a result of swimming that was directed upwards. Other behaviors have been suggested as mechanisms that create and shape aggregations observed in situ including swimming oriented to currents and the sun (Larson 1992; Hamner et al. 1994; Purcell et al. 2000). Comparisons of observed distributions and a model simulating the proposed behavior could confirm the controlling mechanism. For example, Larson (1992) observed aggregations of the scyphomedusa *Linuche unguiculata* in the convergences formed by Langmuir circulations and speculated that swimming in circles maintained the patch. Model simulations could determine the relative effect directed swimming would have on medusa position in the face of convergent flows and whether it is sufficient to explain the aggregations observed.

I observed substantial changes in the vertical distribution of medusa populations that were caused by a very small bias of individuals to swim toward the surface. This suggests an efficient mechanism for control of medusa migrating behavior. Migrations could be accomplished if medusae move toward a common orienting stimulus, for example, a current, light source, or along a chemical gradient (Mackie et al. 1981; Shanks and Graham 1987; Arai 1991; Purcell et al. 2000). Currents would tend to disrupt the orderly movements necessary for migrating. However, I simulated large spatial shifts in medusa populations with a very small orienting bias and in a relatively short time (e.g. minutes to hours). Thus, even in the face of strong currents, migrations may be accomplished if the propensity to orient swimming is large or a small bias is maintained for longer periods.

Similarly, the fact that a very small bias to swim upward caused large shifts in the medusa population to the surface supports the proposal that estuarine plankters maintain their relative position in the estuary by migrating vertically and using horizontal shear to counteract the net estuarine flow (Hill 1991). These animals may be using salinity changes to orient and time these changes in behavior (Hough and Naylor 1992). The model could also be used to investigate these proposed mechanisms. More detailed observations of the reaction of medusae in variable salinity conditions could be parameterized in the model, and, coupled with a large-scale framework of tidal currents (see above), used to test whether such a behavioral mechanism could affect net horizontal movement of estuarine plankton.

I observed *Chrysaora quinquecirrha* avoiding contact with the bottom but not the surface. Presumably, the bottom presents the medusa with potentially hazardous structures that the surface would not. *Pelagia noctiluca* form wedge-shaped groups moving up from the bottom and down from the surface (Zavodnik 1987), and Hamner et al. (1982) observed similar avoidance behavior of mangrove roots fringing a marine lake. These responses of medusae to boundaries suggest that behaviors aimed at avoiding other hazards (e.g. predators) may have evolved in scyphozoa.

Boundary avoidance behavior also raises questions about how medusae differentiate among boundaries. Certainly, medusae can distinguish their orientation in space (i.e. up versus down) through stimulation of gravity-sensitive statocysts (Arai 1997) and may differentiate between the surface and the bottom in this way. This behavior also implies that medusae can detect boundaries at a sufficient distance to maintain a safe separation. For medusae in the tank, the distance is small enough that they could use contact between the boundary and their widely dispersed tentacles to direct the swimming bell to a safe distance. In situ, the distances observed between medusae and boundaries are much larger. Grunbaum (1998a) showed that forming groups effectively increases the perceptive range of an individual fish by massing numerous overlapping perceptive fields. It is interesting to note that the two examples of this behavior by medusae in situ occurred in aggregations.

Scyphomedusae are ubiquitous in marine and estuarine systems worldwide and are increasingly recognized as having varied and important roles in the trophic and community structure of these systems. Their significance to human endeavors will increase in the future because they are often found in coastal areas (Arai 1997) where anthropogenic influences are growing rapidly. In addition, it appears that many medusa populations are increasing their range and abundance (Mills 2001). Behavior can have a significant influence on medusa survival, growth, abundance and distribution, and further research is required if we are to make more accurate assessments and predictions of the importance of medusae in marine ecosystems.

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