

Gelatinous Zooplankton Trophodynamics: Ecological & Biogeochemical Influences on Pelagic Food Webs

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A handwritten signature in black ink, consisting of a stylized 'L' shape with a loop at the top and a horizontal stroke at the bottom.

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SUMMARY

Gelatinous zooplankton play important, but relatively poorly understood, roles in pelagic trophodynamics. Within this context, the tendency for gelatinous zooplankton to aggregate at discontinuities heightens their influences. Discontinuities generate spatial and temporal heterogeneity in chemical, physical and biological factors, which affect resource use. In particular, the ability of organisms to locate and exploit patches of food concentrated at discontinuities exerts considerable influence on trophodynamics. Such situations involve mechanisms that operate at multiple scales ranging from larger scale, passive forcing associated primarily with physical heterogeneity to fine-scale behavioral responses to localized heterogeneity, including patchy food. In fact, (1) passive responses to hydrodynamics, (2) increased reproduction that generate blooms, or (3) behaviors that limit dispersal create aggregations of gelatinous zooplankton that can intensify predation, microbial degradation, and remineralization. Gelatinous zooplankton often constitute a predatory biomass large enough to exert strong top-down influences on productivity and survival of zooplankton and ichthyoplankton, yet they also can exert bottom-up influences on energy transfer to fish and higher predators by altering fluxes of particulate organic matter. However, such influences remain poorly quantified due to a lack of reliable data. In an attempt to fill several gaps in our understanding of gelatinous zooplankton and their trophodynamics, this thesis employed a variety of novel methods, including meso-scale field sampling examining *in situ* distributions and trophic linkages relative to a thermal discontinuity, fine-scale laboratory experiments investigating behavior of individual gelatinous zooplankton and their potential prey at physical or biological discontinuities, and a laboratory investigation of the potential consequences associated with the decomposition of gelatinous zooplankton.

Although gelatinous zooplankton represent a conspicuous component of planktonic assemblages throughout the pelagic zone, there is an inherent difficulty in capturing, preserving and quantifying them due to their fragile and transparent bodies. However, recent efforts to elucidate key interactions of the world's oceans have been enhanced by advances in acoustic and optical technology and sampling techniques. Nonetheless, a number of ecological questions related to the tendency for gelatinous zooplankton to aggregate remain unanswered. Key questions are: (1) Are gelatinous zooplankton differentially distributed around discontinuities?, (2) If differential distributions exist, are they related to trophic interactions with differentially distributed prey?, (3) If differential distributions related to trophodynamics exist, how do individual behaviors generate or sustain such distributions?, and (4) If aggregations of gelatinous zooplankton exist, can they generate biogeochemical pulses when the organisms die and sink? These questions are addressed using original investigations in four manuscripts that document a meso-scale field study of *in situ* distributions and trophic linkages of gelatinous zooplankton and their potential prey, two laboratory experiments that elucidate fine-scale behavior of gelatinous zooplankton and one of their potential prey at discontinuities, and another laboratory experiment documenting potential influences of dying gelatinous zooplankton on biogeochemical cycles.

In **MANUSCRIPT 1**: “Distribution and trophic links of gelatinous zooplankton on Dogger Bank, North Sea,” small gelatinous zooplankton (generally < 50 mm) and their potential prey were sampled in June 2007 along a transect across Dogger Bank, North Sea, where thermal stratification regularly occurs from May to September. Eleven species of small medusae and ctenophores were collected, with six of the most abundant taxa occurring in greater numbers below the thermocline and in the shallower, southeastern portion of the bank throughout days and nights. Of these species, eight have benthic forms and bloom-forming potential. In contrast, potential prey for the gelatinous zooplankters were distributed more

evenly across the bank and throughout the water column. Isotopic analyses revealed that gelatinous zooplankton fed on multiple size classes of mesozooplankton, but also potentially on each other. This study provided evidence that small medusae and ctenophores should be integrated into ecological studies to support sustainable management of the highly productive areas like the Dogger Bank because of their potential influence on local trophodynamics.

The differential distribution of gelatinous zooplankton relative to a thermal discontinuity on Dogger Bank in raises questions about how the behavior of individual, small gelatinous zooplankton generate aggregations and how individuals affect trophodynamics. Such individual behaviors will not be captured by net tows or even by technologically-advanced, *in situ*, optical instruments, such as a towed Video Plankton Recorder. Investigating individual behavior requires fine-scale observations, which, nevertheless, may have substantial ecological relevance. For example, fine-scale discontinuities with narrow vertical extents and high concentrations of organisms (e.g., thin layers) create patches of food, and aggregations of gelatinous zooplankton can exploit such resources in pelagic systems. Some studies have shown significant effects of thin layers on the distribution of hard-bodied, adult zooplankton, which may be suitable prey for some gelatinous zooplankton, but there is a notable gap in the literature concerning responses of other life-history stages. Thus, **MANUSCRIPT 2**: “Comparative behavior of three developmental stages of *Acartia tonsa* Dana, 1849 (Copepoda: Calanoida) relative to physical gradients and biological thin layers,” used laboratory experiments to test the hypothesis that *Acartia tonsa* nauplii, copepodites and adults respond similarly to fine-scale, physical gradients with and without thin layers of algae. Results indicated that both physical gradients and biological thin layers affected the behavior of *A. tonsa*. Notably, all developmental stages aggregated at the upper and lower boundaries of physical gradients or biological discontinuities. When algae were present, all developmental stages also exhibited evidence of area-restricted search behavior

by increasing their speeds and number of turns, especially near a thin layer. Such behavior was most evident for the more active copepodites and adults. Frequency distributions of distances traveled did not provide evidence of Lévy flight behavior, an indicator of searches for new patches of food. Overall, this study provided evidence that all developmental stages detected and responded to discontinuities with behaviors that likely enhanced successful feeding, especially near biological thin layers.

Based on results in **MANUSCRIPT 2** adults of *A. tonsa* were chosen as prey for subsequent laboratory experiments to explore predation dynamics of gelatinous zooplankton. In **MANUSCRIPT 3**: “Behavior of *Nemopsis bachei* L. Agassiz, 1849 medusae in the presence of physical gradients and biological thin layers,” laboratory experiments were used to test the hypothesis that a common and abundant hydromedusa predator, *Nemopsis bachei*, would respond similarly to salinity gradients with and without a biological thin layer comprising algae and copepods. Approximately 75% of the hydromedusae remained in both types of discontinuities. These distributions were not created solely by passive responses related to osmoconformation or an inability to swim through salinity gradients because approximately 25% of hydromedusae swam through or away from salinity gradients or biological thin layers. Biological thin layers stimulated feeding. Feeding success was related directly to encounter rates and it was independent of swimming, as expected for an ambush predator. Feeding increased at higher prey concentrations, and capture, handling time, and ingestion were not saturated even at 150–200 copepods l^{-1} . The proportion of *N. bachei* that ceased feeding and began swimming increased when encounters with prey decreased to approximately 2 encounters hydromedusa $^{-1}$ 10 min $^{-1}$. Thus, hydromedusae may seek new patches of prey once encounter rates and subsequent feeding success fall below a threshold. Exposing *N. bachei* to salinity gradients with and without biological thin layers indicated that

these hydromedusae will remain in discontinuities and exert predation pressure that should be considered when assessing trophic webs and estimating carbon flux.

Beyond the effects on trophodynamics in the water column, aggregations and blooms of gelatinous zooplankton may yield substantial ecological effects when the animals are damaged or die because bacteria readily decompose their tissues releasing carbon and nutrients into the surrounding water. In an effort to elucidate such bottom-up effects, **MANUSCRIPT 4**: “Pulse perturbations from bacterial decomposition of *Chrysaora quinquecirrha* (Scyphozoa: Pelagiidae)” details a laboratory experiment that examined decomposition of whole *Chrysaora quinquecirrha* and pieces created to simulate damage. Tissue of *C. quinquecirrha* decomposed in 5–8 d, with wet biomass having a half-life of 3 d at 22°C. Decomposition raised concentrations of total organic carbon, total nitrogen and total phosphorus by 1–2 orders of magnitude above controls. A large increase in mean total nitrogen lagged increases in mean total phosphorus and mean total organic carbon by 24 h. Cocci were the sole microbial morphotype observed in control incubations, where their numbers did not increase significantly. In incubations with *C. quinquecirrha* tissue, bacilli increased exponentially from 6 h onward to become the dominant morphotype, although cocci remained and reproduced at a rate that was 0.7× slower. These results, and those from previous studies, suggested that certain bacteria decompose medusae and other forms benefit from the release of carbon and nutrients. In addition, contrasts between this experiment and previous studies indicated that proteins and other nitrogenous compounds are less labile in damaged medusae than in dead or homogenized individuals. Overall, dense patches of medusae are likely to act as a trophic shunt that diverts carbon and nutrients into microbial trophic webs.

Within the scope of this thesis, a variety of novel methods were employed to investigate fragile, transparent and enigmatic gelatinous zooplankton at ecologically

important time and space scales, including episodic events, diel variation and fine-scale vertical resolution. In essence, the collective results highlighted top-down trophic linkages between gelatinous zooplankton and hard-bodied zooplankton and among gelatinous zooplankton; effects of discontinuities on the behavior and trophodynamics of gelatinous zooplankton and their prey; and bottom-up contributions to biogeochemical fluxes through episodic release of carbon, nitrogen and phosphorus from damaged and dying gelatinous zooplankton. The original work in this thesis emphasizes the value of using complimentary, novel methods to help resolve the roles gelatinous zooplankton play in top-down and bottom-up regulation of processes in marine ecosystems. The conclusions also provide insights into the ecology of gelatinous zooplankton that can act as a basis for evaluating future changes in key interactions due to local or global anthropogenic pressures.

OUTLINE OF PUBLICATIONS

The following overview outlines the four manuscripts included in this thesis, as well as contributions from various co-authors. A section from a fifth manuscript (Koppelman & Frost 2008) is included as an appendix for the purpose of summarizing general background information on gelatinous zooplankton and select gaps in knowledge. The primary objectives of this thesis were funded by the Eur-Oceans Network of Excellence fellowship WP4-SYSMS-1101, with the exception of manuscript 4 that was funded by the University of Florida, USA but still considered a contribution to the fellowship award.

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MANUSCRIPT 1

Distribution and trophic links of gelatinous zooplankton on Dogger Bank, North Sea

Jessica R. Frost*, Anneke Denda, Clive J. Fox, Charles A. Jacoby, Rolf Koppelman, Morten Holtegaard Nielsen, Marsh J. Youngbluth

Jessica R. Frost organized the sampling protocol, collected and analyzed all data, and drafted the manuscript. Students and staff from Universität Hamburg assisted with collection and sorting of specimens while onboard the FS Alkor. Anneke Denda identified and enumerated mesozooplankton under the direction of and with funding from Jessica R. Frost. Charles A. Jacoby performed statistical analyses of the data, with assistance from Jessica R. Frost. All co-authors provided editorial comments. The work was funded by Eur-Oceans fellowship WP4-SYSMS-1101. The manuscript was published in *Marine Biology* (2012), a peer-reviewed journal.

MANUSCRIPT 2

Comparative behavior of three developmental stages of *Acartia tonsa* Dana, 1849 (Copepoda: Calanoida) relative to physical gradients and biological thin layers

Jessica R. Frost*, Fabien Lombard, Charles A. Jacoby

Jessica R. Frost designed and conducted the experiments, analyzed the data, and drafted the manuscript. Fabien Lombard provided the particle tracking script used for video analysis and assisted in editorial comments. Charles A. Jacoby assisted in analyzing the data, statistical analysis and editorial comments. The work was funded by Eur-Oceans fellowship WP4-SYSMS-1101. The manuscript was submitted for publication in a peer-reviewed journal.

MANUSCRIPT 3

Behavior of *Nemopsis bachei* L. Agassiz, 1849 medusae in the presence of physical gradients and biological thin layers

Jessica R. Frost*, Charles A. Jacoby, Marsh J. Youngbluth

Jessica R. Frost designed and conducted the experiments, analyzed the data, and drafted the manuscript in collaboration with Charles A. Jacoby, who also assisted in the statistical analysis. Marsh J. Youngbluth provided helpful editorial comments which improved the manuscript. The work was funded by Eur-Oceans fellowship WP4-SYSMS-1101. The manuscript was published in *Hydrobiologia* (2010), a peer-reviewed journal.

MANUSCRIPT 4

Pulse perturbations from bacterial decomposition of *Chrysaora quinquecirrha* (Scyphozoa: Pelagiidae)

Jessica R. Frost*, Charles A. Jacoby, Thomas K. Frazer, Andrew R. Zimmerman

Jessica R. Frost designed the experiment, collected and analyzed the data, and drafted the manuscript in collaboration with Charles A. Jacoby, who also assisted in the statistical analysis. Thomas K. Frazer and the University of Florida provided the funding for this work. Andrew R. Zimmerman provided analyses of organic carbon. All co-authors provided editorial comments. The manuscript was published in *Hydrobiologia* (2012), a peer-reviewed journal.

APPENDIX:

MANUSCRIPT 5 (EXCERPT)

The ecological role of zooplankton in the twilight and dark zones of the ocean

Rolf Koppelman* and **Jessica Frost**

Rolf Koppelman wrote sections 1-3 and 5. Jessica Frost wrote section 4 and edited the manuscript in its entirety. The section written by Jessica Frost is included in this thesis, along with the references in their entirety. The manuscript was published as a chapter in the book *Biological Oceanography Research Trends* published by Nova Science Publishers, Inc., New York (2008). Jessica Frost was supported by Eur-Oceans fellowship WP4-SYSMS-1101.

CHAPTER 1**GENERAL INTRODUCTION — GELATINOUS ZOOPLANKTON***Biology and Ecology*

The term gelatinous zooplankton encompasses, but is not limited to, members of two distantly related phyla: Cnidaria and Ctenophora. Zooplanktonic Cnidaria include cubomedusae, hydromedusae, and scyphomedusae, which typically possess tentacles, cnidae (explosive, intracellular structures used in predation and defense), and muscular bells that contract and produce a propulsive force. The phylum Ctenophora, or ctenophores, may possess tentacles, use adhesive cells called colloblasts to capture prey, and move by beating rows of fused cilia, or ctenes. Gelatinous zooplankton are ubiquitous in marine environments, with relatively few occurring in freshwater. They occupy the entire extent of water columns, with representatives found in shallow, nearshore, coastal waters and the bathypelagic zone of the open ocean (Wrobel & Mills 1998; Koppelman & Frost 2008).

As per their name, gelatinous zooplankton possess soft bodies that are often transparent, radially symmetrical and comprised of $\geq 95\%$ water. Unlike fish and crustaceans, which retain their shape outside of water, gelatinous zooplankton lack rigid skeletons, so they often collapse if not supported by an aqueous environment. The organic matter that comprises 1–3% of their bodies is approximately 72% protein, 22% lipid and 7% carbohydrate (Larson 1986; Schneider 1988; Arai et al. 1989; Clarke et al. 1992; Lucas 1994, 2009; Pitt et al. 2009). Gelatinous zooplankton vary from 5 mm in diameter (i.e., *Carukia barnesi*) to greater than 2 m (i.e., *Nemopilema nomurai*). In general, these animals do not swim rapidly, and many can remain buoyant because the mixture of salts in their tissue is less dense than the surrounding seawater. Some gelatinous zooplankton enhance their buoyancy by excluding certain ions (i.e., sulfate) or accumulating other ions (i.e., ammonium; Wrobel & Mills 1998; Graham et al. 2001).

The life cycle of most cnidarians is complex, with generations alternating between two morphological forms: polyp and medusa. Polyps arise from a larval stage, where a planula swims out of the oral arms of a medusa and attaches to a hard substrate, including the sea floor. Polyps are sessile and perform asexual budding to create additional polyps. Once environmental conditions are favorable, polyps undergo strobilation, during which they segment to produce tiny, juvenile medusae called ephyrae. Ephyrae are released individually into the water column, where they mature into adults. Once mature, medusae reproduce sexually, with males releasing sperm that is taken into the oral cavities of females to fertilize eggs. Eggs develop into embryos that eventually are released as planulae, which complete the life cycle by attaching to a substrate and forming polyps (Arai 1997).

Unlike cnidarians, ctenophores have a simple life cycle. Almost all ctenophores are hermaphroditic, whereby they release both their sperm and eggs into the water column to be fertilized. However, there are a few exceptions, with some species having the ability to self-fertilize (Ruppert et al. 2004). Some ctenophores have the ability to produce both eggs and sperm at the same time (simultaneous hermaphrodites), while others have the ability to produce eggs and sperm that mature at different times (sequential hermaphrodites). Generally, fertilization takes place externally and young ctenophores are planktonic, gradually morphing into their adult shape as they grow. However, species from the genera *Beroe* are an exception because their young look like miniatures of their adult form, with large mouths and no tentacles. Certain juvenile ctenophores are capable of reproducing before reaching their adult size and shape. Consequently, the combination of hermaphroditism and early reproduction enables small populations to grow at an explosive rate (Mianzan et al. 2009).

Dietary needs of cnidarians and ctenophores can be met from a variety of sources, such as animal prey, dissolved organic matter and compounds derived from symbiotic algae

(Sebens 1987; Arai 1997). In general, cnidarians and ctenophores are considered carnivorous, feeding on plankton, crustaceans, fish eggs, larval fish, and other gelatinous zooplankton. They typically employ one of two foraging modes, either cruising or ambush. Cruising predators sweep relatively large volumes of water to capture prey as they swim, whereas ambush predators sit and wait for encounters with drifting or swimming prey (Gerritsen & Strickler 1977; Costello 1992; Costello et al. 2008). In either mode, feeding success is likely to increase if prey are concentrated at discontinuities.

Aggregation at Discontinuities

Generally, zooplankton are unevenly distributed within the water column in both the vertical and horizontal extents. In many cases, zooplankton are concentrated where differences in the biological, chemical or physical properties of the water column create distinct, rapidly changing gradients or discontinuities, which typically are far more pronounced in the vertical extent. These discontinuities serve as important cues for physiological, behavioral or ecological processes that give rise to aggregations of zooplankton. Aggregations can result from active and passive responses to differences in currents, light, pressure, turbulence, salinity, temperature, and density (often a combination of differences in temperature and salinity), as well as from trophic interactions and reproduction. The assemblage composition, magnitude and extent of an aggregation can vary among geographic locations, species and life history stages, as behavioral responses to and interactions with discontinuities and other organisms can be species-specific and age-related (Omori & Hamner 1982; Arai 1992; Graham et al. 2001; Greer et al. 2013; Luo et al. 2014).

Aggregations of gelatinous zooplankton have been recorded throughout the world for decades, with local densities being high enough to interfere with fisheries operation by clogging nets and straining wire wraps (Omori & Hamner 1982; Arai 1992; Purcell 2005). Previous reports demonstrate that gelatinous zooplankton, including ctenophores, medusae

and siphonophores, tend to aggregate at density, salinity, and temperature discontinuities that develop in coastal transition zones, estuaries and fjords (Owen 1989; Graham et al. 2001).

Discontinuities affect the spatial and temporal heterogeneity of resources, which in turn affects movement and resource use by animals (Levin et al. 2000). In particular, behaviors that allow organisms to locate and exploit patches of food exert considerable influence on trophodynamics. For plankton, external forcing (e.g., currents, shear and turbulence) combines with behavioral responses to determine the structure and function of assemblages, access to food, and the flow of carbon across a range of spatial and temporal scales (e.g., Bochdanský & Bollens 2004). At a micro-scale, biological thin layers represent persistent, spatially coherent patches of plankton (Donaghay et al. 1992; Cowles et al. 1998). Thin layers that are decimeters to meters thick; extend several kilometers horizontally; and persist for minutes, hours or days have been identified with the aid of technologically advanced instruments (e.g., acoustic Doppler current profilers; Flagg & Smith 1985; Cowles et al. 1990; Cowles & Desiderio 1993; Holliday et al. 1998). The formation of thin layers requires the creation of a stable discontinuity, typically associated with a pycnocline at the boundary of two water masses, and threefold increases in densities of phytoplankton or zooplankton that arise passively, primarily due to neutral buoyancy, or actively, as a outcome of behavior (Osborn 1998; Dekshenieks et al. 2001; Alldredge et al. 2002; McManus et al. 2003; Gallagher et al. 2004; Rawlinson et al. 2004). In thin layers, competition and predation can be intensified, rates of nutrient uptake can be enhanced, chemical wastes and toxins can accumulate, and rates of microbial degradation and remineralization can be higher (Mason et al. 1993; Sieburth & Donaghay 1993; Johnson et al. 1995; Donaghay & Osborn 1997; Cowles et al. 1998). The chemical, physical and biological characteristics of thin layers have been documented (Donaghay et al. 1992; Hanson & Donaghay 1998; Holliday et al. 1998; Widder et al. 1999; McManus et al. 2005). In all their forms, dense concentrations of

organisms within discontinuities, like thin layers, have the potential to influence the ecology of systems by altering behavior, feeding, growth, and reproduction (e.g., McManus et al. 2003). As yet, relatively few studies have examined the behavioral responses that allow individual organisms to remain within and exploit thin layers, in spite of the recognition that such coupling can alter the abundance and species composition of planktonic assemblages (Denman & Powell 1984; Mackas et al. 1985; Yamazaki et al. 2002; Clay et al. 2004; Ignoffo et al. 2005; Woodson et al. 2005, 2007a, b). In addition, to my knowledge, there is no study that has examined the influence of thin layers on the behavior of individual gelatinous zooplankton.

Individual gelatinous zooplankton swim to feed, breed and disperse (Strand & Hamner 1988; Malej 1989; Costello & Colin 1994, 1995; Hamner et al. 1994), and in so doing, they may encounter discontinuities. If discontinuities act as a physical or physiological barrier or if detectable boundary conditions stimulate coherent behavioral responses in multiple individuals, gelatinous zooplankton will aggregate. For instance, responses to osmotic stress at sharp haloclines may cause animals to either slow their swimming to allow osmoconformation or turn away to remain in a specific range of physiological tolerance (Graham et al. 2001). As stated previously, the resulting aggregations can affect ecological dynamics by altering local abundances and rates of feeding, growth and reproduction (Hamner & Hauri 1981; Hamner et al. 1982; Purcell 1992; Purcell et al. 2000; Keister et al. 2000; Matanoski et al. 2004).

In summary, the formation and persistence of discontinuities and aggregations of gelatinous zooplankton are influenced by varied factors, remain largely unquantified, and are predicted to increase as oceans become more stratified (Cox et al. 2000; Gregg et al. 2003). In many cases, these features will alter biogeochemical cycles, define food webs, affect fisheries production, and even affect carbon flux by replacing classic vectors of particulate

organic matter (e.g., phytodetritus) with particulate organic matter derived from the increasingly abundant gelatinous zooplankton (Dekshenieks et al. 2001; Stacey et al. 2007; Birch et al. 2008; Jackson 2008; Richardson et al. 2009). In terms of trophodynamics, the enhanced biological productivity found at discontinuities generates exploitable patches of abundant food resources that may cause behavioral responses by gelatinous zooplankton.

Role in Pelagic Food Webs

Current global policies call for an ecosystem approach to managing marine natural resources. Attempts to manage an ecosystem can generate unexpected consequences in the absence of a solid understanding of trophic dynamics. In large part, such consequences arise from the complexity of food webs, i.e., the multiple and shifting interactions that transfer energy among organisms. For example, as some organisms grow, their diets change and, consequentially, they may change trophic levels. In addition, competition for food can cause consumers to shift their diets (Barnes 1980).

Trophic interactions among cnidarians and ctenophores include competition for prey and intraguild predation, and cnidarians and ctenophores also prey on and compete with larval fish (Purcell & Arai 2001; Robison 2004). Members of the phyla Cnidaria and Ctenophora are almost entirely carnivores, with the exception of some species that exhibit omnivory or receive nutrition from various symbionts (Sommer & Stibor 2002; Arai 2005; Colin et al. 2005; Pitt et al. 2009). Predation and competition generated by gelatinous zooplankton can yield severe consequences for fishery resources. A classic example is the collapse of commercial fishing in the Black Sea attributed to the invasion of the ctenophore *Mnemiopsis leidyi* (Vinogradov et al. 1989). *Mnemiopsis leidyi* also was a factor in the collapse of the beluga caviar industry and reductions in abundance of sturgeon and anchovy kilka in the Caspian Sea (Stone 2005; Daskalov & Mamedov 2007; Richardson et al. 2009). Gelatinous zooplankton also have been implicated in declines or collapses of fisheries in the

Bering Sea (Brodeur et al. 2002, 2008), Gulf of Mexico (Graham 2001; Graham et al. 2003), Irish Seas (Doyle et al. 2008), East Asian Marginal Seas (Uye 2008), and Benguela upwelling system (Lynam et al. 2006; Utne-Palm et al. 2010).

Competition and predation are not the only means by which gelatinous zooplankton exert deleterious effects on pelagic food webs. For example, major fish kills were documented when the medusae *Pelagia noctiluca* and the siphonophore *Apolemia uvaria* got entangled with caged, farm-raised salmon (Båmstedt et al. 1998; Doyle et al. 2008). Other studies have implicated gelatinous zooplankton as intermediate vectors of fish parasites (Martorelli 2001; Hay 2006). Nevertheless, competition and predation represent key ecological pressures exerted by gelatinous zooplankton.

Contributors to the Pelagic Organic Matter Cycle

Aggregations of gelatinous zooplankton have the potential to generate a significant flux of organic matter to the sea floor because many of them are mucus-net feeders, and their prolific egesta (feeding nets and external houses) and digesta (feces) constitute important components of particulate organic matter (Morris et al. 1988; Robison et al. 2005; Koppelman & Frost 2008). As fecal aggregates and mucous sheets sink, they provide a relatively labile food source for microbes. In fact, previous studies have shown that salp fecal aggregates make a major contribution to oceanic biogeochemical fluxes (Wiebe et al. 1979; Iseki 1981; Pfannkuche & Lochte 1993; Madin et al. 2006). Concerns about changes to the global carbon cycle have focused considerable attention on the role of gelatinous zooplankton and their aggregations in the transfer of carbon and nutrients (Riemann et al. 2006; Titelman et al. 2006; Condon & Steinberg 2008; Yamamoto et al. 2008; Murty et al. 2009; Alamaru et al. 2009; West et al. 2009; Sexton et al. 2010; Condon et al. 2011).

Mass occurrences of medusae generally last for weeks to months (Mills 2001; Sexton et al. 2010), and during this time, they assimilate and release carbon and nutrients creating a

relatively protracted, press perturbation (*sensu* Glasby & Underwood 1996). For example, medusae can consume significant numbers of zooplankton and larval fish and assimilate up to 88% of the carbon in their prey (Mills 1995; Arai 1997; Purcell 1997; Purcell & Arai 2001; Pitt et al. 2009). In turn, medusae excrete and secrete carbon, nitrogen and phosphorus, primarily as mucus, ammonium and phosphate (Pitt et al. 2009; Condon et al. 2011). Rapidly accumulating evidence suggests that these releases support phytoplanktonic and bacterial production, although the magnitude of their influence depends heavily on the availability of carbon and nutrients from other sources and rates of flushing (Pitt et al. 2005; Malej et al. 2007; Condon et al. 2010, 2011). Yet, what happens to carbon and nutrients when the medusae in an aggregation are damaged or die?

Damaged, moribund or dead medusae should begin to decompose as they sink or drift, in part because the continuous release of organic matter while they were alive ensures they are surrounded by a thriving bacterial assemblage (Doores & Cook 1976; Heeger et al. 1992; Hansson & Norrman 1995; Riemann et al. 2006). In some cases, decomposition is not completed in the water column, and carcasses of medusae carry hundreds of grams of carbon to the sea floor (Miyake et al. 2002, 2005; Billett et al. 2006; Koppelman & Frost 2008; Yamamoto et al. 2008; Murty et al. 2009). Observations of other carrion falls suggest that benthic scavengers will feed on dead and moribund medusae (Lebrato & Jones 2009). In addition, one set of field observations in deep water and one set of mesocosm experiments in shallow water indicate that medusae will decompose (Billett et al. 2006; West et al. 2009). Over a period of days, bacterial decomposition and respiration created pulse perturbations (*sensu* Glasby & Underwood 1996) consisting of increased nutrients and reduced oxygen concentrations as evidenced by the production of hydrogen sulfide (Billett et al. 2006; West et al. 2009). Depending on the system's response, these two perturbations could yield discrete or protracted responses (*sensu* Glasby & Underwood 1996). For example, nutrients could

stimulate a discrete increase in primary productivity if there is sufficient light, and hypoxia/anoxia could create a protracted decrease in the abundance of infauna that persists through multiple cycles of recruitment. Thus, an understanding of impacts from carrion falls of medusae requires an understanding of their decomposition.

Gaps in Knowledge

Despite increases in frequency of occurrence and widely acknowledged as key predators in marine environments, gelatinous zooplankton have earned a reputation as the least understood group of planktonic animals because they are more difficult to capture, preserve and quantify (Omori & Hamner 1982; ICES 2003; Raskoff et al. 2003; Haddock 2004). Nevertheless, gelatinous zooplankton have been documented to form a predatory biomass large enough to exert significant top-down influences on the productivity and survival of other zooplankton and ichthyoplankton (Purcell & Arai 2001; Brodeur et al. 2002; Lynam et al. 2005; Attrill et al. 2007; Koppelman & Frost 2008). Such accumulations of gelatinous zooplankton also can exert bottom-up influences by altering fluxes of carbon and nutrients that support primary productivity (Feigenbaum & Kelly 1984; Pitt et al. 2009; West et al. 2009; Condon et al. 2010; Koppelman & Frost 2008).

Given the influences exerted by gelatinous zooplankton and the import of understanding the global carbon cycle, several challenges confront ecologists. These challenges include understanding the formation of aggregations at discontinuities where the uptake of carbon and nutrients may be significantly higher (e.g., Purcell et al. 2001; Billet et al. 2006; Condon et al. 2010, 2011). Following uptake, questions arise regarding the transfer of resources, including transfer from surface waters down through the mesopelagic and into the bathypelagic zone. Transfer seldom appears to be through direct consumption of gelatinous zooplankton, but indirect transfers through release of mucus and feces, as well as bacterially mediated decomposition of damaged, moribund or dead gelatinous zooplankton

appear to be important (Robison et al. 2005; Madin et al. 2006; Titelman et al. 2006; Condon et al. 2011).

Objectives

Gelatinous zooplankton that represented key organisms in this thesis included ctenophores, hydromedusae, and scyphomedusae. The framework of this thesis comprises three objectives:

- (1) Quantify the distribution of gelatinous zooplankton relative to discontinuities and assess behavioral factors contributing to this distribution.
- (2) Identify predatory role of gelatinous zooplankton in relation to the abundance and taxonomic composition of their potential prey at discontinuities.
- (3) Document the form and magnitude of pulse impacts arising from decomposition of gelatinous zooplankton.

In particular, this thesis attempts to answer four key questions: (1) Are gelatinous zooplankton differentially distributed around discontinuities?, (2) If differential distributions exist, are they related to trophic interactions with differentially distributed prey?, (3) If differential distributions related to trophodynamics exist, how do individual behaviors generate or sustain such distributions?, and (4) If aggregations of gelatinous zooplankton exist, can they generate biogeochemical pulses when the organisms die and sink? These questions were addressed using original investigations in **MANUSCRIPTS 1–4**. Objective 1 was met by the combination of conducting a meso-scale field study using modified nets and vertical hydrographic profiling, along with two laboratory experiments that documented fine-scale behavior of gelatinous zooplankton and their prey. This work resulted in the publication of **MANUSCRIPTS 1** and **3**, with **MANUSCRIPT 2** submitted for publication in the *Journal of Experimental Marine Biology and Ecology*. Objective 2 was met by using stable isotope analysis, typically employed in terrestrial research, and a modern mixing model, IsoSource, to determine trophic links between gelatinous zooplankton and their potential

prey, which formed part of **MANUSCRIPT 1**. Lastly, Objective 3 was met by conducting a laboratory experiment involving new techniques to document potential influences on biogeochemical cycles from decomposing gelatinous zooplankton. Few similar studies exist, and the work resulted in the publication of **MANUSCRIPT 4**.

Overall, this thesis aims to improve our understanding of the basic ecology of gelatinous zooplankton, including their predatory and biogeochemical influence on marine ecosystems. In particular, my original research elucidates the import of aggregations near discontinuities, with emphasis on behaviors that promote formation of aggregations, trophic links for gelatinous zooplankton, and biogeochemical pulses of organic matter generated by dissolution of aggregations. The results also may support modelling to predict the top-down and bottom-up controls that regulate marine ecosystems. Additionally, an improved understanding of the formation, persistence and dissolution of aggregations in and around discontinuities, including biological thin layers, will help policy makers manage food webs, sustain fisheries productivity, and respond prudently to climate change.

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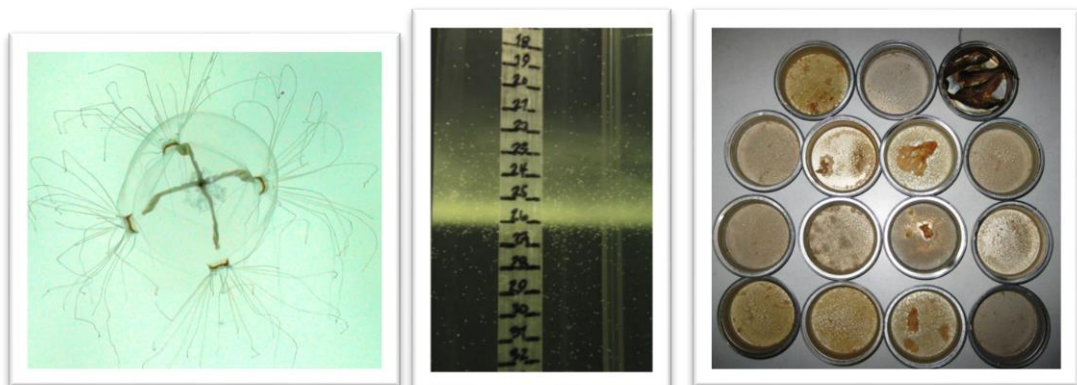
CHAPTER 2

INFLUENCE OF DISCONTINUITIES ON THE DISTRIBUTION, BEHAVIOR, AND
TROPHIC INTERACTIONS BETWEEN GELATINOUS ZOOPLANKTON
AND THEIR PREY

MANUSCRIPT 1: *Distribution and trophic links of gelatinous zooplankton on Dogger Bank, North Sea*

MANUSCRIPT 2: *Comparative behavior of three developmental stages of *Acartia tonsa* Dana, 1849 (Copepoda: Calanoida) relative to physical gradients and biological thin layers*

MANUSCRIPT 3: *Behavior of *Nemopsis bachei* L. Agassiz, 1849 medusae in the presence of physical gradients and biological thin layers*



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ORIGINAL PAPER

Distribution and trophic links of gelatinous zooplankton on Dogger Bank, North Sea

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Abstract The ecology of small, gelatinous zooplankton is not integrated into management of Dogger Bank (54° 00' N, 3° 25' E to 55° 35' N, 2° 20' E). In pursuit of this goal, gelatinous zooplankton and their potential prey were sampled along a transect across the bank on June 10–16, 2007. Eleven species of small medusae and ctenophores were collected, with six abundant taxa occurring in greater numbers below the thermocline and in the shallower, southeastern portion of the bank. There were no statistically significant diel changes in distribution. In contrast, potential prey were

distributed more evenly across the bank and throughout the water column. Isotopic analyses revealed that gelatinous zooplankton fed on both smaller (100–300 µm) and larger (>300 µm) mesozooplankton, but also potentially on each other. These ecological insights suggest that small medusae and ctenophores should be integrated into sustainable management of Dogger Bank.

Introduction

Current global and European policies call for an ecosystem approach to managing marine natural resources. Attempts to manage an ecosystem can generate unexpected consequences in the absence of a solid understanding of trophic dynamics. The North Sea demonstrates the value of such an understanding because over-exploitation combined with an environmental regime shift in the 1980s significantly restructured trophic webs resulting in negative consequences for humans, especially reduced availability of gadoid fish (Reid and Edwards 2001).

Application of ecosystem management to the North Sea must consider the trophic dynamics of Dogger Bank. The bank, which is located in the central North Sea (54–56° N, 1–5° E), is a shoal of sandy and muddy sediments rising from 60 to <20 m across its center (Kröncke and Knust 1995; Gubbay et al. 2002). It lies at the intersection of two water masses; Atlantic water from the north meets residual currents exiting the English Channel via the Straits of Dover in the south. Tidal mixing dominates in waters to the south of the bank throughout the year, but thermal stratification in late spring and early summer characterizes water above the bank and to the north (Kröncke and Knust 1995). In the region of thermal stratification, a subsurface chlorophyll maximum develops at approximately 30 m depth

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(Holligan et al. 1984; Weston et al. 2005). By August, the thermocline typically has deepened, and the water above the shallowest part of the bank can become thermally homogenous (Weston et al. 2005). Nutrients supplied by tidal mixing fronts and relatively clear water over the bank fuel enhanced productivity (Reiss et al. 2007) that supports higher trophic levels.

In fact, Dogger Bank acts as a nursery ground for many commercial fish species, including cod, plaice, sole, and sand eels (Fox et al. 2008; Joint Nature Conservation Committee 2008; Munk et al. 2009). In recognition of its importance as a habitat for a suite of species, most of Dogger Bank is likely to receive protection in the next few years under the European Natura 2000 program (Joint Nature Conservation Committee 2008; Jak et al. 2009). Recently, there were proposals to designate Dogger Bank as a Special Area of Conservation with primary reason being its rank as a major, shallow sandbank that supports an ecologically important sand eel community that provides food for cetaceans, piscivores, and sea birds (Centre for Environment, Fisheries and Aquaculture Science 2007; Joint Nature Conservation Committee 2008).

Past investigations of the bank's ecology have focused on its physics, phytoplankton, hard-bodied zooplankton, fish, benthic assemblages, and use by seabirds and marine mammals (Reid et al. 1990; Fransz and Gonzalez 2001; Reid and Edwards 2001; Krause et al. 2003; Joint Nature Conservation Committee 2008; Jak et al. 2009). Studies of gelatinous zooplankton have focused on larger scyphomedusae or other regions of the North Sea (Nicholas and Frid 1989; Hay et al. 1990; Lynam et al. 2004, 2005a, b, 2010; Atrill et al. 2007; Barz and Hirche 2007). Beyond the seminal work of Russell (1953), relatively little information is available regarding the abundance, distribution and ecology of small gelatinous zooplankton on Dogger Bank. Given the documented importance of small gelatinous zooplankton as consumers of other zooplankton, fish eggs, and larvae (Purcell and Nemazie 1992; Mills 1995; Purcell and Arai 2001; Daskalov 2002), this gap may hamper ecosystem management. For example, small gelatinous zooplankton could compete with sand eels for food.

The role of small gelatinous zooplankton in pelagic trophic webs at Dogger Bank is likely to be amplified during early summer because their numbers increase throughout the region (Greve and Reiners 1988). In addition, thermal stratification from May to September regularly creates discontinuities (Kröncke and Knust 1995), and gelatinous zooplankton often aggregate and feed at such features (Hansen 1951; Arai 1976; Southward and Barrett 1983; Pagès and Gili 1992), with access to abundant prey potentially triggering behaviors that generate and maintain aggregations (Frost et al. 2010). Thus, oceanographic conditions and the biology of small gelatinous zooplankton make early summer

a suitable time to examine the distribution and abundance of these predators in this productive region of the North Sea.

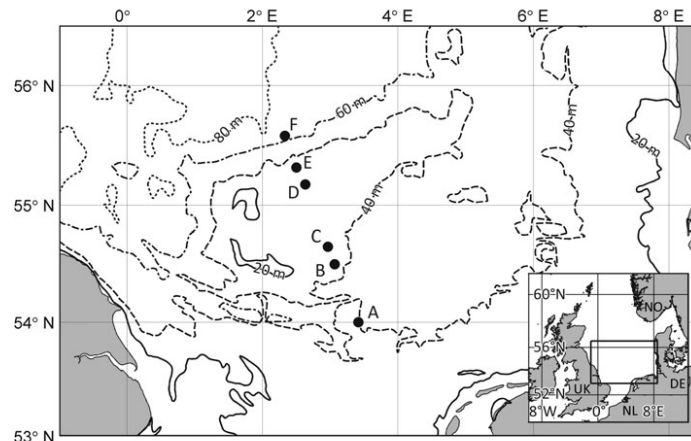
In an effort to enhance the existing knowledge of the ecology of Dogger Bank, this study documented the gelatinous zooplankton assemblage (especially smaller forms), their potential prey, and the resulting trophic interactions above, within and below thermal discontinuities at six locations across the bank during June 2007. Sampling tested the hypotheses that assemblages of gelatinous zooplankton and their potential prey would (1) differ between the northern and southern edges of the bank due to the influence of different water masses, (2) be differentially associated with discontinuities, and (3) exhibit diel variation in their distribution. In addition, a mixing model identified trophic links for common and abundant gelatinous zooplankton.

Materials and methods

Field sampling

Sampling was conducted from the FS Alkor between 10 and 16 June 2007 at six stations along a transect from 54°00'N, 3°25'E to 55°35'N, 2°20'E, with the stations divided evenly between the northern and southern edges of Dogger Bank (Fig. 1). Each station was occupied twice, with daytime and nighttime sampling conducted at stations A, B, D, E, and F and two daytime sampling events at station C (Table 1). At the beginning of each sampling event, conductivity, temperature, and depth were profiled with a Hydro-Bios CTD (Meerestechnik Elektronik, Kiel, Germany) mounted on a rosette of Niskin bottles. The depth and vertical extent of thermoclines extracted from the resulting vertical profiles determined depth strata for sampling of gelatinous zooplankton.

Gelatinous zooplankton were collected in vertical hauls of a closing WP2 net (57-cm diameter mouth; 300- μ m mesh; Hydro-Bios, Kiel, Germany) through three discrete depth strata: from approximately 3 m off the bottom to the lower boundary of the thermocline, within the thermocline, and from the upper boundary of the thermocline to the surface. Physical damage to gelatinous zooplankton was mitigated by hauling the net slowly (~ 2.0 m min⁻¹) and by replacing the filtering cod end with a 50-l plastic bag (Youngbluth and Båmstedt 2001). In combination, calm conditions, vertical hauls at a relatively slow speed, and the ability to open and close the net minimized sampling across two depth strata. During each of the 12 sampling events, five sequential hauls were performed in each of the three depth strata yielding 180 hauls. Immediately after each haul, the net was thoroughly rinsed with seawater, and the pelagic fauna in the cod-end bag were emptied gently into a

Fig. 1 Map showing stations occupied along a transect across Dogger Bank, North Sea from 10 to 16 June 2007**Table 1** Station details from the transect across Dogger Bank, North Sea sampled from 10 to 16 June 2007

Station	Coordinates	Portion of transect	Depth (m)	Date sampled (dd-mm-yy)	Time of day	Depth of thermocline (m)	Temperature differential (°C)
A	54° 00' N; 03° 25' E	SE	43	10-06-07	Day	15–18	3.10
				15-06-07	Night	14–22	1.96
B	54° 30' N; 03° 04' E	SE	37	16-06-07	Day	22–27	2.77
				11-06-07	Night	7–9	4.16
C	54° 39' N; 02° 58' E	SE	34	11-06-07	Day	8–16	3.25
				16-06-07	Day	22–28	2.01
D	55° 10' N; 02° 37' E	NW	32	12-06-07	Day	6–12	3.47
				14-06-07	Night	6–12	2.39
E	55° 19' N; 02° 30' E	NW	36	14-06-07	Day	10–24	3.69
				12-06-07	Night	8–15	4.42
F	55° 35' N; 02° 20' E	NW	70	13-06-07	Day	10–30	5.60
				14-06-07	Night	10–35	5.50

300-l rectangular, plastic bucket. To compensate for zero catches, the contents of the five independent hauls were pooled to create 36 samples, i.e., three replicate samples for each combination of station, depth stratum, and time of day.

After collection, all gelatinous zooplankton were removed by hand using 3-ml Sarstedt disposable Pasteur pipettes with integral bulbs (7 mm Ø) for smaller specimens and plastic 500-ml Kautex bottles (5.5 cm Ø) for larger specimens. The larger or more abundant gelatinous zooplankton were identified to the lowest possible taxonomic level, enumerated, and placed in separate Kautex bottles for storage at -80°C prior to analysis of elemental composition and isotopic ratios. The smaller and less abundant gelatinous zooplankton, which would not yield the 5–6 mg of dried biomass required for elemental and

isotopic analyses, were preserved for identification and enumeration in the laboratory. The preservative, a 4% solution of formaldehyde and seawater buffered with sodium-tetraborate, was effective except for two specimens of the ctenophore *Bolinopsis* sp. (Appendix 1).

Hauls that yielded sufficient gelatinous zooplankton for elemental and isotopic analyses were sampled for potential mesozooplanktonic prey. The WP2 net retained mesozooplankton $>300\ \mu\text{m}$, and the non-filtering cod ends retained some mesozooplankton smaller than $300\ \mu\text{m}$, which offered an opportunity to identify trophic links to two size classes. Therefore, water from the cod ends was sieved through nested meshes (300 and $100\ \mu\text{m}$) to generate a 100 – $300\ \mu\text{m}$ size fraction and a $>300\ \mu\text{m}$ size fraction. These samples were frozen for elemental and isotopic analyses.

Quantitative estimates of the abundance and distribution of potential mesozooplanktonic prey were derived from samples taken with an opening and closing MultiNet® (Hydro-Bios, Kiel, Germany) immediately following sampling with the WP2 net. The five nets had 0.25-m² mouths and 300-µm mesh. The water column was partitioned into contiguous 10-m depth strata, and beginning at depth, one net was hauled vertically through each stratum at approximately 3 m min⁻¹. Once onboard, the nets were rinsed with seawater, and the resulting samples were preserved in the buffered solution of formaldehyde and seawater for subsequent identification and enumeration. For statistical analyses, samples from the 10-m depth strata at the six stations were allocated to the three positions identified in vertical profiles, i.e., above, within and below the thermocline, based on where the majority of sampling occurred.

Laboratory processing and statistical analyses

In the laboratory, preserved gelatinous zooplankton were identified to genus or species and counted using a Heerbrugg Wild M3 microscope. Sample volumes were calculated using the radius of the WP2 net and the vertical distances sampled during hauls. Counts were scaled to densities 100 m⁻³.

Summed densities for all gelatinous zooplankton were tested for normality with Kolomogorov–Smirnov tests, tested for homoscedasticity with Cochran's tests, and log₁₀-transformed to meet these assumptions. The resulting data were used in an analysis of variance (ANOVA). In the ANOVA, location on the transect across Dogger Bank (southeast or northwest) and vertical position relative to a detectable thermocline (above, within, or below any temperature discontinuity) represented orthogonal, fixed factors. Time of day (day or night) was treated as a random factor nested in the interaction between location and position because samples were collected on different dates (Table 1). If the term containing time, the nested factor, was non-significant at $P \geq 0.25$, that term was pooled with the residual to create an analysis with more power to detect differences between locations and among positions.

Densities of individual gelatinous taxa were used in permutation analyses of variance (PERMANOVA; Anderson et al. 2008). These multivariate analyses tested for differences in the taxonomic composition of the gelatinous assemblage among levels of location (fixed factor; southeast or northwest portions of the transect across Dogger Bank), position relative to a detectable thermocline (fixed factor; above, within, or below any temperature discontinuity), and time of day (random factor nested in the interaction between location and position; day or night). In an effort to distinguish between variations in density and variations in commonness (i.e., the number of samples containing

each taxon), similar PERMANOVAs were applied to raw data and data transformed to presence/absence. If the term containing time, the nested factor, was non-significant at $P \geq 0.25$, that term was pooled with the residual to create an analysis with more power to detect differences between locations and among positions. For significant factors, a permutational analysis of multivariate dispersion (PERMDISP; Anderson et al. 2008) was used to determine whether significant differences among the levels of the factor were due solely to increased variability in the numbers of taxa or their densities. The multivariate analyses were based on Bray–Curtis resemblance measures, with a dummy variable added to account for paired zeros.

In the laboratory, mesozooplankton from the MultiNet® samples, representing potential prey for gelatinous zooplankton, were sorted into major taxonomic groups and counted, with all exuviae excluded. Abundant Copepoda were identified to genus or species. Counts were scaled to yield densities, numbers of individuals 10 m⁻³, by calculating sample volumes using the surface area of the net aperture and vertical distances sampled during hauls.

Predation pressure from gelatinous zooplankton tends to be correlated strongly with encounter rates, and prey density represents a key determinant of those rates (Purcell 1997; Costello et al. 2008). Therefore, potentially important prey for gelatinous zooplankton were selected as those taxa that represented at least 5% of the total numbers of zooplankton captured in at least one MultiNet® sample. Summed and scaled counts for the appropriate taxa were tested for normality and homoscedasticity as described previously and log₁₀-transformed to meet these assumptions. The resulting density data were used in an ANOVA that treated location on the Dogger Bank transect (southeast or northwest) and position relative to a detectable thermocline (above, within, or below) as orthogonal, fixed factors.

The densities of individual prey taxa and a presence/absence transformation of those data were used in PERMANOVAs that treated location on the Dogger Bank transect and position relative to the thermocline as fixed factors, with PERMDISP tests used to determine whether significant differences were due solely to differences in variability among replicate samples within the factors of interest. The primary taxa contributing to any significant differences not related to increased variability were identified by an analysis of similarities and differences (SIMPER; Anderson et al. 2008).

Elemental compositions, isotopic analyses, and trophic links

Prior to elemental and isotopic analyses, all samples were thawed, weighed, and dried to a constant weight at 82–89°C. Wet and dry weights were measured to the nearest

0.001 g using an analytical balance. Once dried samples reached a constant weight, they were ground to fine powder using a ceramic mortar and pestle. Powdered samples were stored in screw-cap glass vials that were sent to the Museum für Naturkunde, Humboldt Universität zu Berlin, where a Thermo Finnigan Delta V Isotope Ratio Mass Spectrometer (IRMS) was used to determine proportions of carbon (C) and nitrogen (N), along with stable isotope ratios, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. The instrument was calibrated against international standards obtained from the International Atomic Energy Agency (IAEA).

Trophic relationships were assessed by analyzing stable isotope ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures) for gelatinous zooplankton and their potential prey using IsoSource, a mixing model that generates distributions of feasible solutions for diets in datasets with more potential sources than isotopic signatures (Phillips and Gregg 2003). Dietary contributions were iterated in 1% steps, and the mass balance tolerance for feasible mixtures, i.e., the acceptable deviation from the true $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures, was adjusted from 0.1 to 0.5‰ in an attempt to generate feasible and constrained solutions (i.e., unimodal distributions of percentage contributions to diets not located near zero).

Two common adjustments to isotopic signatures were considered prior to IsoSource analyses. If the range of $\delta^{15}\text{N}$ signatures was greater than 6‰, which equates to average enrichment across 2 trophic levels (Minagawa and Wada 1984; Hobson and Welch 1992), these values were adjusted to a common baseline. In addition, separate analyses were conducted for both unadjusted $\delta^{13}\text{C}$ signatures and signatures that were adjusted according to overall carbon to nitrogen ratios to account for a potential bias toward depleted signatures due to the presence of lipids (Smyntek et al. 2007). Both types of signatures were analyzed because adjustments were not derived specifically for gelatinous zooplankton, which tend to contain fewer lipids than other zooplankton (Carli et al. 1991; Malej et al. 1993; Lucas 1994).

Results

Oceanographic conditions

All six stations had detectable thermoclines whenever they were sampled (Table 1). Stations A–E had maximum depths ranging from 32 to 43 m, and station F was deeper (70 m). Salinity, as measured in practical salinity units, remained nearly constant at 35 throughout the water column at all stations. Water temperatures varied from 14.99°C at the surface to 8.11°C at depth. Thermoclines were 2–25 m thick, with temperature differentials from 1.96 to 5.60°C. Broader thermoclines with slightly larger

temperature differentials were found at the northwestern end of the transect, especially during the day (Fig. 2). Vertical density fields reflected the relatively large variations in temperature due to consistent salinity, as illustrated by profiles from station F at the northwestern end of the transect and station B in the southeast (Fig. 3).

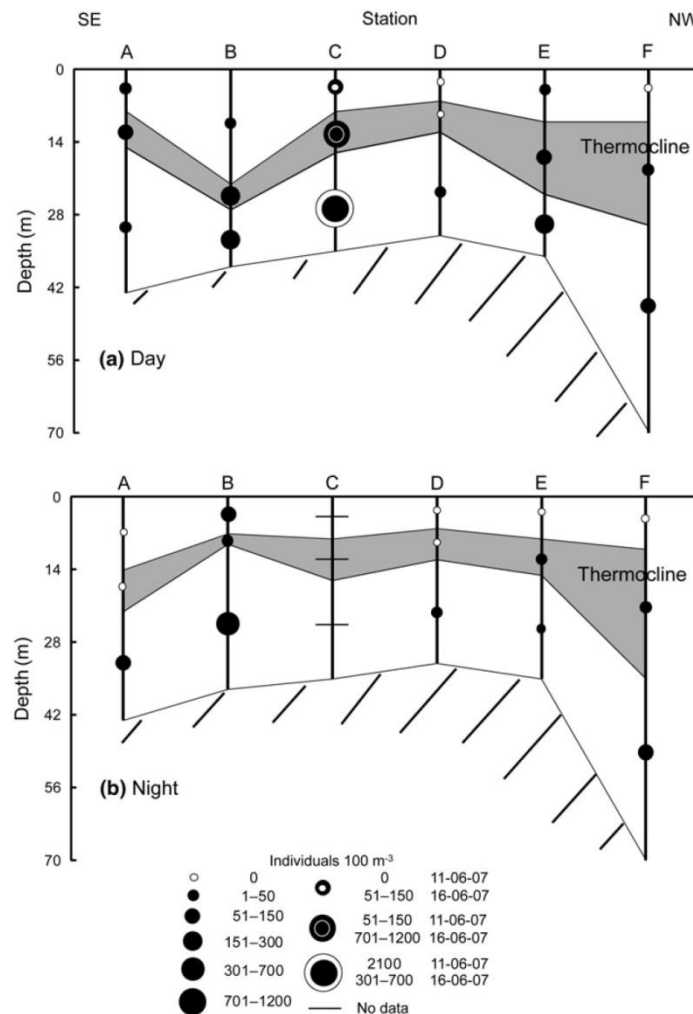
Biological conditions

Seven species of hydromedusae, one species of scyphomedusa, and three species of ctenophores were collected at stations along the transect across Dogger Bank (Appendix 1). In samples containing gelatinous zooplankton, densities ranged from 4 to 2,100 individuals 100 m^{-3} , with an overall mean and standard error of 234 ± 89 individuals 100 m^{-3} ($N = 26$). The range, mean and standard error were reduced to 4–1,136 and 159 ± 50 individuals 100 m^{-3} ($N = 25$), respectively, when one anomalously large daytime catch of 245 *Pleurobrachia pileus* from below the thermocline at station C was excluded.

Counts for 11 gelatinous taxa, *Aglantha digitale*, *Beroë* sp., *Bolinopsis* sp., cf. *Bougainvillia* sp., *Cyanea capillata*, *Eutonina indicans*, *Leuckartiara* sp., *Phialella quadrata*, *Phialidium* sp., *Pleurobrachia pileus*, and *Tima bairdi*, were summed and scaled to yield densities of gelatinous zooplankton. After \log_{10} -transformation, the data were homoscedastic and normal ($P > 0.01$). In the full model, there was no significant variation for the factor involving time of day ($P \geq 0.25$); therefore, this term was pooled to yield a more powerful test of variation between locations and among positions relative to the thermocline (Table 2). In the pooled analysis, there was significant variation both between locations and among positions (Table 2). Back-transformed means and 95% confidence limits indicated that more gelatinous zooplankton were captured at stations in the southeast and below the thermocline (Fig. 4).

The PERMANOVAs based on raw densities and presence/absence data yielded similar results (Table 3). There was no significant variation for the factor involving time of day ($P \geq 0.25$); therefore, this term was pooled to yield a more powerful test of variation between locations and among positions relative to the thermocline. In the pooled analysis, there was significant variation both between locations and among positions, and these significant differences were not due to differences in variability among replicate samples for those factors (Table 3). For the six gelatinous taxa with densities >1 individual 100 m^{-3} , the highest abundances of five taxa were recorded at stations in the southeast, with *Eutonina indicans* being the exception (Fig. 5a). Out of these six taxa, four had higher abundances below the thermocline, whereas *Leuckartiara* sp. and *Pleurobrachia pileus* were collected in reasonable numbers throughout the water column, even if the leverage exerted

Fig. 2 Diagram illustrating the thermocline and sum of total numbers of gelatinous zooplankton across 5 net hauls per depth stratum during **a** daytime and **b** nighttime sampling along a transect across Dogger Bank, North Sea from 10 to 16 June 2007



by the large catch of *P. pileus* was moderated by replacing it with the mean of all other catches from below the thermocline in the southeast portion of the transect (new mean \pm SE = 62.6 ± 42.0 individuals 100 m^{-3} ; Fig. 5b).

Potential mesozooplanktonic prey were identified and enumerated in samples from stations where gelatinous zooplankton were numerous; therefore, samples from station D were not included. Seventeen prey taxa, i.e., appendicularians, fish larvae, fish eggs, bivalves, gastropods, amphipods, cladocerans, crustacean larvae, harpacticoids, *Oithona* spp., other cyclopoids, *Acartia clausii*, *Temora longicornis*, *Centropages* spp., *Pseudocalanus elongatus*, *Metridia* spp.,

and other calanoids, met the criterion set of representing at least 5% of the total numbers in one or more MultiNet® samples. The summed and scaled counts for these taxa were normal and homoscedastic after \log_{10} -transformation. The resulting densities of potential prey did not differ significantly between locations or among positions relative to the thermocline (Table 4).

The PERMANOVA based on raw data indicated no significant variation between prey assemblages found at different locations on the Dogger Bank transect or at different positions relative to the thermocline, whereas the PERMANOVAs based on presence-absence data indicated

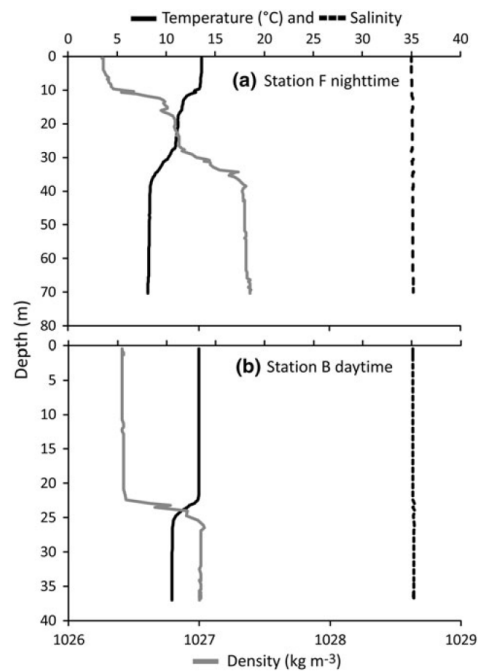


Fig. 3 Profiles of the water column along a transect across Dogger Bank, North Sea taken during a nighttime at station F and b daytime at station B

significant variation in occurrences of prey species between locations (Table 5). The significant difference was not due to differing variability among replicate samples for the location factor. Results from SIMPER indicated that the significant difference was due primarily to 11 of the 17 taxa. More hauls at stations in the northwest portion of the transect across Dogger Bank contained *Metridia* spp. and gastropods, whereas bivalves, cladocerans, *Acartia clausii*, fish larvae, fish eggs, *Centropages* spp., amphipods, crustacean larvae, and *Temora longicornis* were collected in a greater number of hauls in the southeast. In combination, the results of the two analyses indicate that the density of potential prey did not differ significantly between locations or among positions, but the identities of commonly occurring taxa did vary consistently among locations.

Elemental compositions, isotopic signatures, and trophic links

In total, 82 hydromedusae from three species, 313 ctenophores from two species, six samples of mesozooplankton in the 100–300 μm size class, and six samples of mesozoo-

Table 2 Results of analysis of variance for \log_{10} (total gelatinous zooplankton $100\text{ m}^{-3} + 1$)

Model (source)	df	MS	F	P
Full model				
Location	1	4.610	7.34	0.035
Position	2	4.836	7.70	0.022
Location \times position	2	0.064	0.10	0.905
Time (location \times position)	6	0.628	0.91	0.504
Residual	24	0.689		
Pooled model				
Location	1	6.201	9.16	0.005
Position	2	5.041	7.44	0.002
Location \times position	2	0.037	0.05	0.947
Residual	30	0.677		

plankton in the $>300\text{ }\mu\text{m}$ size class were analyzed for elemental content and stable isotope ratios (Tables 6 and 7). As expected, gelatinous zooplankton contained large amounts of water ($>96\%$), which dictated the need for pooling relatively large numbers of individuals to generate sufficient dried biomass. In fact, prior to IsoSource analyses, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures were averaged across samples from different locations and positions for *Eutima indica*, *Tima bairdi*, *Pleurobrachia pileus*, and *Beroe* sp., because only samples of *P. pileus* and *Beroe* sp. yielded sufficient dried biomass from more than one location or position (Figs. 5, 6). Based on their size, *Tima bairdi* and *Beroe* sp. were considered as prey only for each other.

The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of potential prey were averaged within size classes for IsoSource analyses. The only statistically significant variation identified for the prey assemblage was a difference in relative commonness among taxa in the southeast and northwest portions of the transect (Tables 4 and 5). One-way ANOVAs based on homoscedastic and normal $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ signatures indicated that the significant variation in commonness did not translate into a significant difference in isotopic signatures between locations ($\delta^{13}\text{C}$ signatures, $F_{1,9} = 0.007$, $P = 0.949$; $\delta^{15}\text{N}$ signatures, $F_{1,9} = 4.48$, $P = 0.063$).

The $\delta^{15}\text{N}$ signatures were not adjusted because the range was 4.9% , which spanned less than the average enrichment across two trophic levels, but $\delta^{13}\text{C}$ signatures of mesozooplankton were adjusted for lipid content. Analyses that included adjusted $\delta^{13}\text{C}$ signatures for gelatinous zooplankton did not yield feasible solutions because the signatures of putative predators became more extreme than the signatures of all available prey. In contrast, analyses including adjusted $\delta^{13}\text{C}$ signatures for the two size classes of mesozooplankton did yield feasible solutions (Table 7).

Analyses based on $\delta^{15}\text{N}$ signatures paired with either unadjusted or adjusted $\delta^{13}\text{C}$ signatures indicated that

Table 3 Results of PERMANOVAs and PERMDISP tests based on raw densities of gelatinous zooplankton 100 m⁻³ and data transformed to presence/absence

Model (source)	PERMANOVA					PERMDISP		
	df	MS	F	P	Unique permutations	df	F-perm	P
Full model raw densities								
Location	1	8,203.9	2.68	0.065	992			
Position	2	8,578.4	2.80	0.034	999			
Location × position	2	3,466.5	1.13	0.331	998			
Time (location × position)	6	3,066.0	0.96	0.528	998			
Residual	24	3,193.1						
Pooled model raw densities								
Location	1	10,906.0	3.44	0.010	999	1, 34	0.68	0.453
Position	2	8,373.0	2.64	0.004	999	2, 33	3.28	0.092
Location × position	2	4,029.9	1.27	0.214	998			
Pooled residual	30	3,167.6						
Full model presence/absence								
Location	1	3,655.4	3.84	0.064	993			
Position	2	6,010.7	6.32	0.015	999			
Location × position	2	971.8	1.02	0.441	999			
Time (location × position)	6	952.2	1.18	0.324	998			
Residual	24	806.7						
Pooled model presence/absence								
Location	1	4,684.6	5.60	0.004	999	1, 34	0.16	0.713
Position	2	5,560.4	6.65	0.001	998	2, 33	2.91	0.057
Location × position	2	1,346.2	1.61	0.179	998			
Pooled residual	30	835.8						

Eutima indicans had been feeding on the smaller mesozooplankton fraction (100–300 µm; Figs. 7, 8). The analysis based on unadjusted $\delta^{13}\text{C}$ signatures also pointed to a trophic link to *Pleurobrachia pileus* (Fig. 7), and the analysis based on adjusted signatures indicated a link to *Leuckartiara* sp. (Fig. 8).

In analyses with *Leuckartiara* sp. as the consumer, combining $\delta^{15}\text{N}$ signatures with either adjusted or unadjusted $\delta^{13}\text{C}$ signatures for mesozooplankton highlighted somewhat different trophic links (Figs. 7, 8). The analysis based on unadjusted signatures indicated that *Leuckartiara* sp. fed on both size classes of mesozooplankton and had a link to *P. pileus* (Fig. 7). On the other hand, the analysis based on adjusted signatures only yielded links to *E. indicans* and *P. pileus* (Fig. 8).

Analyses with *P. pileus* as the consumer and either type of $\delta^{13}\text{C}$ signatures indicated that this ctenophore fed on mesozooplankton larger than 300 µm (Figs. 7, 8). The analysis based on adjusted $\delta^{13}\text{C}$ signatures indicated a trophic link to *Leuckartiara* sp. (Fig. 8).

For *Tima bairdi*, analyses highlighted two trophic links. Analyses based on either unadjusted or adjusted $\delta^{13}\text{C}$ signatures paired with $\delta^{15}\text{N}$ signatures indicated trophic links

to *Beroe* sp. (Figs. 7, 8), with the analysis based on adjusted values also indicating that *T. bairdi* fed on 100–300 µm mesozooplankton (Fig. 8).

Two sets of analyses yielded constrained solutions for *Beroe* sp. as a consumer. Analyses based on combining $\delta^{15}\text{N}$ signatures with both unadjusted and adjusted $\delta^{13}\text{C}$ signatures provided strong evidence of a link to *T. bairdi* (Figs. 7, 8), and an analysis based on unadjusted $\delta^{13}\text{C}$ signatures also indicated a link to mesozooplankton larger than 300 µm (Fig. 7).

Overall, IsoSource analyses indicated trophic links from gelatinous zooplankton to mesozooplankton and among gelatinous zooplankton (Figs. 7, 8). In general, the $\delta^{15}\text{N}$ signatures provided little insight into which gelatinous taxon was the predator in potential examples of intraguild predation (Fig. 6).

Discussion

In June 2007, 11 species of gelatinous zooplankton were collected on Dogger Bank, with over 50% of these taxa and 70% of the individuals collected from the shallower,

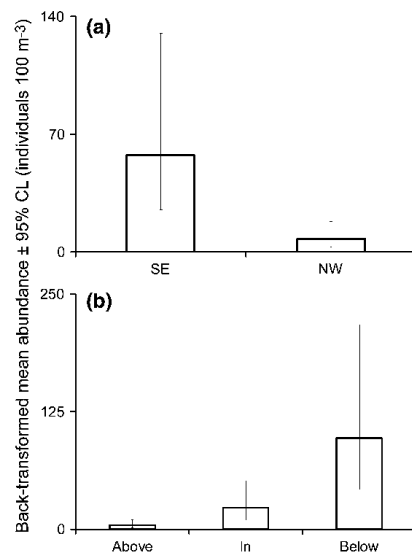


Fig. 4 Back-transformed mean abundances \pm 95% confidence limits (CL) for total gelatinous zooplankton caught at **a** stations in the southeast and northwest portions of Dogger Bank and **b** above, within and below the thermocline

southeastern portion of the transect and below the thermocline. In contrast, the densities of 17 taxa of potential prey did not differ significantly across Dogger Bank or throughout the water column, although the most common species on the northern edge of the bank differed from the most common species on the southern edge. There were no significant diel changes in the distributions of either gelatinous zooplankton or their potential prey, with the result for mesozooplanktonic prey matching previously reported results for copepods in the stratified waters above Dogger Bank (Koski et al. 2011). Stable isotope signatures from five taxa of gelatinous zooplankton (*Eutonina indicans*, *Leuckartiara* sp., *Tima bairdi*, *Pleurobrachia pileus*, and *Beroe* sp.) indicated predation on two size classes of mesozooplankton and the potential for intraguild predation. Thus, results from this study provide information on the distribution and trophic links of small gelatinous zooplankton on Dogger Bank that augments other studies of larger gelatinous zooplankton in the greater North Sea.

Significant variation in densities and diversity of gelatinous zooplankton and the assemblage composition of mesozooplanktonic prey may have reflected the influence of the different water masses on the southeast and northwest portions of the transect. Cooler, Atlantic water arrives on the bank from the north, and warm, nutrient-rich water from the English Channel bathes the southern edge of the

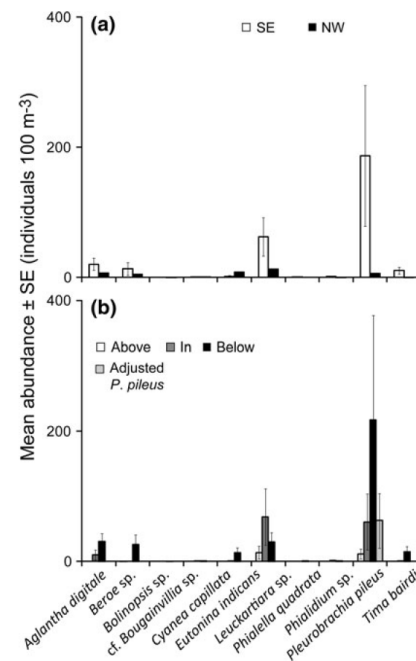


Fig. 5 Mean abundances \pm standard errors (SE) for gelatinous zooplankton captured at **a** stations in the southeast and northwest portions of Dogger Bank and **b** above, within and below the thermocline, with an adjusted mean shown for *Pleurobrachia pileus* from below the thermocline

Table 4 Results of an analysis of variance using \log_{10} (potential prey $10 \text{ m}^{-3} + 1$)

Source	df	MS	F	P
Location	1	0.027	0.08	0.779
Position	2	0.514	1.59	0.257
Location \times position	2	0.147	0.45	0.648
Residual	9	0.324		

bank (Kröncke and Knust 1995; Joint Nature Conservation Committee 2008). In particular, *Pleurobrachia pileus* has been shown to generate a wave of higher abundance that propagates seaward from the coastal waters of the United Kingdom and Germany in early summer (Williams and Collins 1985; Greve and Reiners 1988). In fact, Båmstedt (1998) attributed the presence of large numbers of *P. pileus* off the northwest coast of Norway to an intrusion of North Sea water.

The vertical distribution of gelatinous zooplankton relative to a persistent thermocline indicated a differential association with density discontinuities, which is consistent

Table 5 Results of PERMANOVAs and PERMDISP tests based on raw densities of potential prey 10 m^{-3} and data transformed to presence/absence

Data (source)	PERMANOVA					PERMDISP		
	df	MS	F	P	Unique permutations	df	F-perm	P
Raw densities								
Location	1	4,739.7	2.12	0.084	998			
Position	2	3,085.4	1.38	0.208	998			
Location \times position	2	2,728.0	1.22	0.273	999			
Residual	9	2,240.7						
Presence/absence data								
Location	1	2,094.8	6.70	0.002	999	1, 13	0.82	0.502
Position	2	277.3	0.89	0.538	998			
Location \times position	2	227.7	0.73	0.652	999			
Residual	9	312.8						

Table 6 Details regarding samples, weights, and elemental compositions of gelatinous zooplankton collected over Dogger Bank, North Sea from 10 to 16 June 2007

Station	Time of day	Depth range (m)	Position relative to thermocline	Species	Individuals sample ⁻¹	Weight (g)		Proportion (%)			Content (mg)	
						Wet	Dry	H ₂ O	C	N	C	N
B	Night	30–9	Be	<i>Beroe</i> sp.	47	28.37	0.81	97	1.6	0.4	13.1	2.9
B	Night	30–9	Be	<i>Tima bairdi</i>	19	39.43	1.31	97	2.2	0.5	6.0	6.5
B	Night	7–0	Ab	<i>Leuckartiara</i> sp.	11	6.08	0.23	96	2.2	0.5	5.0	1.1
B	Night	30–0	Be, In, Ab	<i>Pleurobrachia pileus</i>	14	5.65	0.21	96	2.1	0.4	4.4	0.9
C	Day	30–20	Be	<i>P. pileus</i>	245	53.15	1.41	97	2.1	0.5	14.6	3.3
F	Day	68–30	Be	<i>Beroe</i> sp.	4	41.18	1.24	97	5.9	1.0	74.0	12.9
F	Day	68–30	Be	<i>Eutonina indicans</i>	24	27.30	0.68	97	1.2	0.3	7.9	1.8
F	Night	68–35	Be	<i>E. indicans</i>	27	34.10	1.08	97	0.6	0.1	6.1	1.6

Ab, In and Be = above, within and below the thermocline

with findings from other studies. For example, Jacobsen and Norrbin (2009) used a video plankton recorder (VPR) to sample along a transect in a semi-enclosed bay in northern Norway that had depths similar to this study (max. 55 m; avg. 30 m), a similar assemblage of gelatinous zooplankton, including small hydromedusae and the ctenophore *Pleurobrachia pileus*, and an even distribution of mesozooplanktonic prey. In contrast to this study, 79% of gelatinous zooplankton captured in the bay came from within the density discontinuity, whereas the majority of gelatinous zooplankton on Dogger Bank was found below the thermocline. The less saline water above the thermocline and the 5°C water below the thermocline may have influenced the distribution of gelatinous zooplankton in the Norwegian bay, whereas the salinity was essentially constant and temperatures remained around 10°C throughout the water column over Dogger Bank. In fact, vertical distributions of small gelatinous zooplankton and their tendency to migrate may vary. During 1991–1995, *P. pileus* in the Black Sea was found to remain primarily below the thermo-

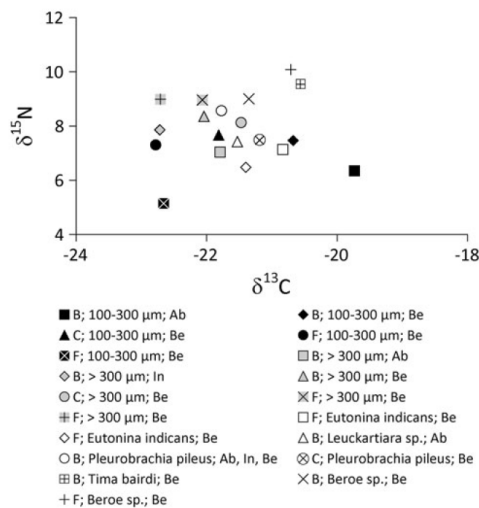
cline, with a small proportion of the population migrating through it at night (Mutlu and Bingel 1999), but this ctenophore was more evenly distributed and showed no evidence of vertical migration during 1996–1999 (Kideys and Romanova 2001). Off the Norwegian coast, *P. pileus* was found primarily above the thermocline (Båmstedt 1998), whereas off the west coast of South Africa, *P. pileus* was found throughout the water column, with larger individuals nearer the surface and no evidence of vertical migration (Gibbons et al. 2003). Further work is needed to determine how salinity, temperature, the presence of prey, and other factors that vary at discontinuities influence the behavior of individual gelatinous zooplankton to generate patterns in vertical distribution at the population level (Frost et al. 2010). In particular, sampling specifically designed to elucidate the distribution of mesozooplankton above, within, and below thermoclines on Dogger Bank would be valuable.

In addition to environmental influences and the presence of prey, disjunct distributions may arise from interactions among gelatinous zooplankton. A lack of overlap in the

Table 7 Details regarding samples, weights, and elemental compositions of WP2 mesozooplankton in two size classes collected over Dogger Bank, North Sea from 10 to 16 June 2007

Location (station)	Time of day	Depth range (m)	Position relative to thermocline	Size class	Weight (g)		Proportion (%)		Content (mg)	
					Wet	Dry	C	N	C	N
B	Night	30–9	Be	Small	96.05	0.24	8.6	1.1	20.5	3.2
B	Night	30–9	Be	Large	71.10	0.61	13.9	2.4	86.2	16.4
B	Night	9–7	In	Small	23.83	0.02	–	–	–	–
B	Night	9–7	In	Large	58.32	0.08	35.2	4.1	28.8	3.3
B	Night	7–0	Ab	Small	83.02	0.09	15.4	1.9	14.0	1.8
B	Night	7–0	Ab	Large	25.89	0.16	33.6	6.8	54.9	10.8
C	Day	30–20	Be	Small	28.52	0.09	9.8	1.2	8.3	1.2
C	Day	30–20	Be	Large	50.54	0.34	25.9	4.2	87.8	13.0
F	Day	68–30	Be	Small	28.96	0.05	24.6	2.8	12.7	1.4
F	Day	68–30	Be	Large	79.76	0.63	38.0	6.9	239.8	45.5
F	Night	68–35	Be	Small	25.21	0.06	15.4	2.5	8.4	1.1
F	Night	68–35	Be	Large	25.44	0.41	39.9	6.7	164.0	27.8

Small = 100–300 μm zooplankton; large = zooplankton >300 μm ; Ab, In and Be = above, within and below the thermocline; – = insufficient sample material

**Fig. 6** Isotopic signatures for gelatinous zooplankton and mesozooplankton. B, C and F = stations along the transect across Dogger Bank; Ab, In and Be = hauls above, within or below the thermocline

vertical and horizontal distributions of *Pleurobrachia pileus* and *Beroe* sp. have been attributed to predator–prey interactions in the southeastern North Sea (Greve 1971; Greve and Reiners 1988) and off the west coast of Norway (Båmstedt 1998). In this study, the distributions of these ctenophores were not completely disjunct, with both taxa being more numerous in the southeast, *Beroe* sp. captured

primarily below the thermocline, and *P. pileus* found in only slightly lower numbers at those depths. Similar overlap in vertical distribution was reported for these ctenophores off the west coast of South Africa where *Beroe* sp. remained above the thermocline and the bulk of the *P. pileus* population, especially smaller individuals, was found below the thermocline (Gibbons et al. 2003). *Pleurobrachia pileus* may be less numerous where *Beroe* sp. is found simply because of predation, but avoidance also may play a role because *P. pileus* has been shown to detect and avoid potential predators (Esser et al. 2004). Again, there is a need for an improved understanding of the link between individual responses to various cues and the distribution of populations.

In this study, trophic interactions were investigated through analysis of stable isotope signatures. Although $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for consumers vary through time and in space due to variation in the signatures of their primary foods, a comparison to previously reported values will help identify any methodological problems. The unadjusted $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures recorded for mixed mesozooplankton in this study (-22 to -21 and 7 to 8‰) were in the mid-range of values reported from the Baltic Sea (-27 to -18 and 2 to 11‰ ; Rolff 2000) and depleted relative to those reported from the eastern North Sea in June and July (-21 to -19 and 11 to 12‰ ; Hamer et al. 2011). *Pleurobrachia pileus* in this study had a slightly depleted $\delta^{13}\text{C}$ signature (-21‰) and a depleted $\delta^{15}\text{N}$ signature (8‰) relative to specimens from the eastern North Sea (-20 to -19 and 13 to 14‰ ; Hamer et al. 2011). The difference in $\delta^{13}\text{C}$ signatures is expected given the signatures of mesozooplanktonic prey in the two systems, and the larger difference in

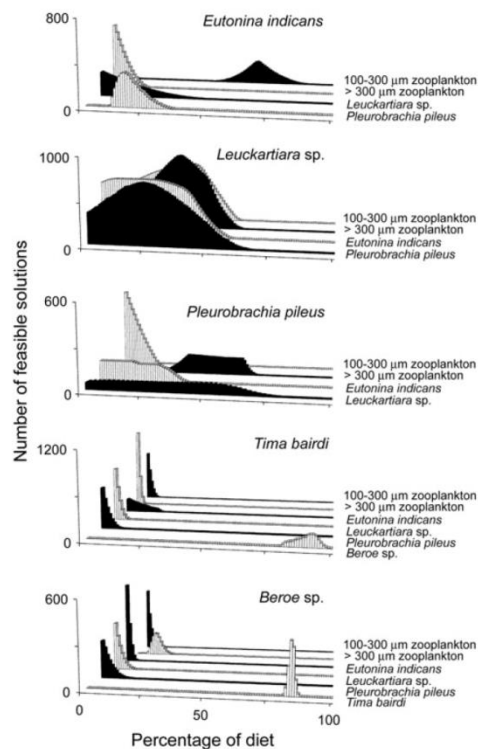


Fig. 7 Results of IsoSource analyses based on raw $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ signatures. Relevant gelatinous predator and prey shown for each graph

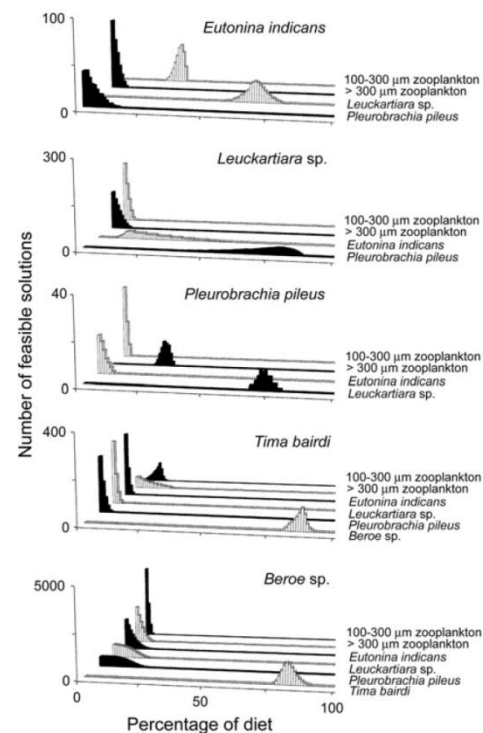


Fig. 8 Results of IsoSource analyses based on raw isotopic signatures for gelatinous zooplankton and $\delta^{13}\text{C}$ signatures adjusted for lipid content of mesozooplankton. Relevant gelatinous predator and prey shown for each graph

$\delta^{15}\text{N}$ signatures can be attributed to extensive predation on fish eggs ($\delta^{15}\text{N} = 16\text{‰}$) by *P. pileus* in the Eastern North Sea (Hamer et al. 2011). Overall, evidence suggested that the isotopic signatures reported in this study were reliable.

In general, variations in $\delta^{15}\text{N}$ signatures are used to differentiate trophic levels, but the limited range of signatures recorded here precludes this approach. Without this guidance, trophic links indicated by similar $\delta^{13}\text{C}$ signatures need to be interpreted on the basis of other information about trophic interactions.

In fact, the results of IsoSource analyses differed according to which $\delta^{13}\text{C}$ signatures were combined with $\delta^{15}\text{N}$ signatures, which would be expected given the similarity of $\delta^{15}\text{N}$ signatures for gelatinous zooplankton and their potential mesozooplanktonic prey. Based on unadjusted $\delta^{13}\text{C}$ signatures, the constrained solutions generated in IsoSource analyses indicated trophic links to small mesozooplankton for *Eutonina indicans* and *Leuckartiara* sp.; links to large mesozooplankton for *Leuckartiara* sp., *Pleurobrachia*

pileus, and *Beroe* sp.; and a link between *Beroe* sp. and *Tima bairdi* that suggested intraguild predation. Results of analyses based on adjusted $\delta^{13}\text{C}$ signatures suggested intraguild predation between *E. indicans* and *Leuckartiara* sp., *Leuckartiara* sp. and *P. pileus*, and *T. bairdi* and *Beroe* sp. In addition, these results linked *E. indicans* and *T. bairdi* to small mesozooplankton and *P. pileus* to large mesozooplankton.

The dietary contribution from large mesozooplankton identified for *Beroe* sp. probably reflects an isotopic signature obtained through predation on *P. pileus* because species of *Beroe* are thought to consume only gelatinous zooplankton, and they are known to consume *P. pileus* (Greve 1971; Greve and Reinert 1988; Purcell 1991; Båmstedt 1998). In addition, the isotopic signatures in this study and a study in the eastern North Sea (Hamer et al. 2011), along with gut contents from other studies, indicate that *P. pileus* feeds heavily on larger copepods including genera captured in this study, e.g., *Pseudocalanus* sp., *Acartia* sp.,

Metridia sp., *Temora longicornis*, *Centropages* sp., and *Oithona* sp. (Båmstedt 1998; Mutlu and Bingel 1999).

The link between *Tima bairdi* and *Beroe* sp. probably reflects predation by the medusa on the ctenophore. Species in the genus *Beroe* have been documented to feed primarily on other ctenophores (Purcell 1991), and *T. bairdi* belongs to a family of medusae possessing nematocysts that are effective at capturing soft-bodied prey such as *Beroe* sp. (Purcell and Mills 1988).

According to their isotopic signatures, *Tima bairdi* and *Eutonina indicans* fed on small mesozooplankton, and *Leuckartiara* sp. fed on both size classes of mesozooplankton. *Eutonina indicans* and *T. bairdi* are in the same family, so both species likely possess nematocysts that are known to capture small crustaceans effectively, as shown by copepod nauplii and barnacle larvae found in the gut contents of *E. indicans* (Purcell and Mills 1988). Species in the same family as *Leuckartiara* sp. possess two types of nematocysts, those that can penetrate crustaceans and those that primarily penetrate soft-bodied prey (Purcell and Mills 1988), so a diet including mesozooplankton that are larger than 300 μm is possible.

Beyond the links between *Beroe* sp. and *Tima bairdi*, the results of five IsoSource analyses suggested intraguild predation among *Eutonina indicans*, *Leuckartiara* sp., and *Pleurobrachia pileus*. *Leuckartiara* sp. and *E. indicans* probably preyed on *P. pileus* because medusae in these genera are known to eat gelatinous zooplankton, including ctenophores, the medusae tend to be larger, and they should possess the appropriate nematocysts (Purcell and Mills 1988; Purcell 1991). The outcome of trophic interactions between *Leuckartiara* sp. and *E. indicans* may vary because they are similar in size, have similar nematocysts, and feed on gelatinous zooplankton according to data for *E. indicans* and two species of *Leuckartiara* (Purcell and Mills 1988; Purcell 1991).

Further work is needed to fully elucidate the diets of small gelatinous zooplankton over Dogger Bank. If such work combined analysis of stable isotopes with empirical evaluation of the need to adjust signatures for lipid content, identification of gut contents, tracing of lipid biomarkers, and laboratory feeding experiments, it could overcome the weaknesses associated with each method (Pitt et al. 2009).

This study yields initial insights into the abundance, distribution and trophic links of small, gelatinous zooplankton on Dogger Bank. A few studies have documented the abundance and distribution of gelatinous zooplankton in the greater North Sea, but those studies primarily reported on a limited range of large scyphomedusae (Hay et al. 1990; Lynam et al. 2004, 2005a, b, 2010; Attrill et al. 2007; Barz and Hirche 2007; Gibbons and Richardson 2009). Although large gelatinous zooplankton are more visible, small species can exert equal or greater predation pressure. For

instance, the scyphomedusae *Aurelia aurita* (max $\varnothing \sim 50$ cm), *Cyanea capillata* (max $\varnothing \sim 2$ m), and *Chrysaora quinquecirrha* (max $\varnothing \sim 30$ cm) dominate the macrozooplankton of Chesapeake Bay in summer, but in spring, the much smaller, hydromedusa *Nemopsis bachei* (max $\varnothing \sim 1$ cm) reaches abundances of 74 individuals m^{-3} and consumes an average of 471 copepodites $\text{m}^{-3} \text{day}^{-1}$ (Purcell and Nemazie 1992). In another example, during the 1970s and 1980s, jellyfish biomass in the Black Sea increased to over 1 kg m^{-2} due to the large scyphozoans *Rhizostoma pulmo* (max $\varnothing \sim 60$ cm) and *A. aurita*, respectively (Daskalov 2002); however, the collapse of fisheries in this system has been attributed to the ctenophore *Mnemiopsis leidyi* (max size ~ 10 cm), which achieved standing stocks of $\sim 2 \text{ kg m}^{-2}$. *Mnemiopsis leidyi* is also a factor in the commercial collapse of the beluga caviar industry and reductions in abundance of sturgeon and anchovy kilka in the Caspian Sea (Stone 2005; Daskalov and Mamedov 2007; Richardson et al. 2009). In addition, at densities of $\leq 160 \text{ m}^{-3}$ or about $10\times$ the mean density recorded in this study, *Pleurobrachia pileus* was estimated to sweep zooplankton from 27% of the water column (Gibbons et al. 2003). At Dogger Bank in June 2007, abundances of small gelatinous zooplankton ($1\text{--}1,231$ individuals 100 m^{-3}) were not at the levels implicated in major ecological changes, but evidence of a diverse assemblage and aggregation at thermoclines highlights a need to better understand the population and trophic dynamics of these taxa.

Although the North Sea represents one of the most investigated Large Marine Ecosystems in the world, the ecology of small gelatinous zooplankton has not been integrated into four decades of health assessments (Quality Status Reports 1987, 1993, 2000a, b, 2010) or the “Synthesis and New Conception for North Sea Research” (SYCON Synthesis and New Conception for North Sea Research, <http://www1.uni-hamburg.de/SYCON>). Further data on gelatinous zooplankton of all size classes may contribute significantly to sustainable management of natural resources on Dogger Bank and in the North Sea because gelatinous taxa have been implicated in declines or collapses of fisheries in the Bering Sea (Brodeur et al. 2002, 2008), Gulf of Mexico (Graham 2001; Graham et al. 2003), Irish Seas (Doyle et al. 2008), Japan (Uye 2008), Benguela upwelling system (Lynam et al. 2006; Utne-Palm et al. 2010), and Black Sea (Daskalov 2002; Daskalov et al. 2007).

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Appendix 1. Gelatinous zooplankton captured at Dogger Bank, North Sea from 10 to 16 June2007. Ab, In and Be = above, within and below the thermocline; *Bolinopsis* sp. not preserved

Location	Species	Day	Night	Position	Number sample ⁻¹	Individuals 100 m ⁻³
A	<i>Cyanea capillata</i>	+		Be	1	5
	<i>Leuckartiara</i> sp.	+		In	1	11
	<i>Pleurobrachia pileus</i>	+		In, Ab	5, 4	56, 39
	<i>Aglantha digitale</i>		+	Be	16	78
	<i>Leuckartiara</i> sp.		+	Be	2	10
	<i>Phialella quadrata</i>		+	Be	1	5
	<i>Phialidium</i> sp.		+	Be	1	5
	<i>Pleurobrachia pileus</i>		+	Be	10	49
B	<i>Aglantha digitale</i>	+		Be	13	127
	<i>Eutonina indicans</i>	+		Be	3	29
	<i>Leuckartiara</i> sp.	+		Be, In, Ab	2, 8, 2	20, 125, 7
	<i>Phialidium</i> sp.	+		In	1	16
	<i>Pleurobrachia pileus</i>	+		Be, In, Ab	6, 4, 2	59, 39, 7
	<i>Tima bairdi</i>	+		Be, In	5, 1	49, 10
	<i>Aglantha digitale</i>		+	Be	11	41
	<i>Beroe</i> sp.		+	Be	47	175
	<i>Bolinopsis</i> sp.		+	Be, Ab	1, 1	4, 11
	<i>Leuckartiara</i> sp.		+	Be, In, Ab	3, 1, 11	11, 39, 123
	<i>Tima bairdi</i>		+	Be	19	71
		+				
C	<i>Aglantha digitale</i>	+		Be	3	24
	<i>Beroe</i> sp.	+		Be	7	55
	<i>Cyanea capillata</i>	+		Be	1	8
	<i>Leuckartiara</i> sp.	+		Be	11	86
	<i>Phialella quadrata</i>	+		Be	1	8
	<i>Pleurobrachia pileus</i>	+		Be	245	1920
		+				
C	<i>Aglantha digitale</i>	+		In	7	91
	<i>Beroe</i> sp.	+		Ab	1	4
	<i>Leuckartiara</i> sp.	+		Be, In, Ab	8, 40, 3	157, 523, 11
	<i>Pleurobrachia pileus</i>	+		Be, In, Ab	24, 40, 25	470, 523, 89
	<i>Tima bairdi</i>	+		Be	3	59
	<i>Beroe</i> sp.	+		Be	2	9
	<i>cf. Bougainvillia</i> sp.	+		Be	1	5
D	<i>Pleurobrachia pileus</i>	+		Be	1	5
	<i>Beroe</i> sp.		+	Be	2	12
	<i>Aglantha digitale</i>	+		Be	9	71
	<i>Beroe</i> sp.	+		Be	5	39
	<i>Eutonina indicans</i>	+		Be	2	16
	<i>Leuckartiara</i> sp.	+		Be, In, Ab	9, 20, 3	71, 112, 24
	<i>Pleurobrachia pileus</i>	+		Be	13	102
E	<i>Beroe</i> sp.		+	Be	1	5
	<i>Cyanea capillata</i>		+	In	1	11
	<i>Leuckartiara</i> sp.		+	Be, In	1, 1	5, 11
	<i>Aglantha digitale</i>	+		Be	4	8
	<i>Beroe</i> sp.	+		Be	6	12
	<i>Eutonina indicans</i>	+		Be, In	24, 1	50, 4
	<i>Leuckartiara</i> sp.	+		Be	2	4
	<i>Phialidium</i> sp.	+		Be	1	2
	<i>Pleurobrachia pileus</i>	+		Be	2	4
	<i>Tima bairdi</i>	+		Be	2	4
	<i>Aglantha digitale</i>		+	Be, In	8, 9	19, 28
	<i>Beroe</i> sp.		+	Be	2	5
F	<i>Eutonina indicans</i>		+	Be, In	30, 2	71, 6
	<i>Phialidium</i> sp.		+	Be	1	2

Comparative behavior of three developmental stages of *Acartia tonsa* Dana, 1849 (Copepoda: Calanoida) relative to physical gradients and biological thin layers

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Abstract

Heterogeneous physicochemical conditions within water columns drive large-scale patterns in plankton, including formation of biological thin layers (organisms concentrated in horizontally extensive and vertically constrained discontinuities). Individual behavioral responses to thin layers determine key ecological interactions, such as feeding; however, responses to patchy resources and ontogenetic changes in those responses remain largely unknown. Laboratory experiments tested the hypothesis that *Acartia tonsa* nauplii, copepodites and adults respond similarly to fine-scale, physical gradients with or without thin layers of green algae. Results indicated that both physical gradients and biological thin layers affected the behavior of *A. tonsa*. Notably, all developmental stages aggregated at the upper and lower boundaries of physical gradients or biological discontinuities. When algae were present, all developmental stages also exhibited evidence of area-restricted search behavior by increasing their swimming speeds and number of turns, especially near a thin layer. Such behavior was most evident for the more active adults and copepodites. Frequency distributions of distances traveled did not provide evidence of Lévy flight behavior, an indicator of searches for new patches of food. Overall, this study provided evidence that all developmental stages detected and responded to discontinuities with behaviors that likely enhanced successful feeding, especially near biological thin layers.

Introduction

Large-scale, physical forcing in the oceanic environment has long been accredited with structuring planktonic assemblages (Landry, 1977; Legendre and Demers, 1984; Daly and Smith, 1993). However, increasing evidence indicates that behavioral interactions with biological, chemical and physical forcing conditions generate ecologically important patterns in planktonic assemblages (Franks, 1995; Yamazaki *et al.*, 2002; Lougee *et al.*, 2002;

Bochdansky and Bollens, 2004; Gallagher *et al.*, 2004; Woodson *et al.*, 2005). In particular, studies have shown that physicochemical factors (e.g. currents, shear, turbulence, and pycnoclines) operating at a range of spatial scales combine with behavioral responses to determine the structure of assemblages and associated functional relationships, such as access to food and the flow of carbon (e.g. Bochdansky and Bollens, 2004; Woodson *et al.*, 2005).

While it is well-documented that zooplankton tend to aggregate in patches at density, salinity and temperature discontinuities that develop in coastal transition zones, estuaries and fjords (Owen, 1989; Graham *et al.*, 2001; Lougee *et al.*, 2002; Genin *et al.*, 2005), the ability of zooplankters to influence their own displacement over a wide range of spatial and temporal scales has recently drawn increased attention (Genin *et al.*, 2005; Woodson and McManus, 2007; Frost *et al.*, 2010). Behavior may vary in response to structure in the water column (vertical or horizontal), availability of food or presence of predators. For example, zooplankton have demonstrated ecologically important behavioral responses when encountering a halocline, including remaining in the vicinity; maintaining a position above, in or below the cline; or simply migrating through it (Hansen, 1951; Williams, 1985; Morgan *et al.*, 1997; Lougee *et al.*, 2002; Frost *et al.*, 2010). The importance of individual behavior also is manifested through strategies employed to optimize feeding while avoiding predation (Sih, 1980; Landry and Fagerness, 1988; Ohman, 1988; Lima and Dill, 1990; Tiselius and Jonsson, 1990; Kiørboe *et al.*, 1996; Titelman, 2001). In fact, trophodynamics are altered substantially by spatial and temporal heterogeneity in food resources and accompanying changes in movement and resource use by animals (Levin, 1992; Levin *et al.*, 2000; Bochdansky and Bollens, 2004; Benoit-Bird *et al.*, 2009).

For copepods, flexibility in behaviors, such as feeding and mating, represents a key adaptation that deserves further study. For example, it has been shown that swimming behavior can vary markedly with species, developmental stage, gender, reproductive state and

the presence of predators (Titelman and Kiørboe, 2003; Dur *et al.*, 2010 and references therein; Kiørboe, 2011). In terms of trophodynamics, pelagic copepods have been shown to respond to patches of food (Tiselius, 1992; Saiz *et al.*, 1993, Bochdansky and Bollens, 2004; Woodson *et al.*, 2007a; Benoit-Bird *et al.*, 2009) and switch between scanning currents and ambush attack jumps; behaviors that are present in few other zooplankters (Kiørboe, 2011). Changes in the appendages used in swimming and capturing food will lead to differences in both behaviors among different developmental stages (Rosenberg, 1980; Tiselius and Jonsson, 1990; Leising and Franks, 2002). Thus, exposing different developmental stages of copepods to resource-rich discontinuities, e.g. phytoplankton in thin layers, will improve our understanding of ecologically significant variation in individual behavior.

The importance of individual behavior in copepods may be amplified near thin layers, which represent persistent, spatially coherent patches of plankton at discontinuities (Donaghay *et al.*, 1992; Cowles *et al.*, 1998). Thin layers that are decimeters to meters thick, extend several kilometers horizontally, and persist for minutes, hours or days have been identified with the aid of technologically-advanced instruments (e.g. acoustic Doppler current profilers; Flagg and Smith, 1985; Cowles *et al.*, 1990, 1993; Holliday *et al.*, 1998). The formation of thin layers requires the creation of a stable discontinuity, typically associated with a pycnocline at the boundary of two water masses, and up to threefold increases in densities of phytoplankton and zooplankton that arise passively, primarily due to neutral buoyancy, or actively, as an outcome of behavior (Osborn, 1998; Dekshenieks *et al.*, 2001; Alldredge *et al.*, 2002; McManus *et al.*, 2003; Gallagher *et al.*, 2004; Rawlinson *et al.*, 2004). In thin layers, competition and predation can be intensified, rates of nutrient uptake can be enhanced, chemical wastes and toxins can accumulate, and microbial degradation and remineralization can be higher (Mason *et al.*, 1993; Sieburth and Donaghay, 1993; Johnson *et al.*, 1995; Donaghay and Osborn, 1997; Cowles *et al.*, 1998). Aspects of the chemistry,

physics, and biology of thin layers have been documented (Donaghay *et al.*, 1992; Hanson and Donaghay, 1998; Holliday *et al.*, 1998; Widder *et al.*, 1999; McManus *et al.*, 2005). As yet, relatively few studies have examined the behavioral responses that individual organisms employ to remain within and exploit thin layers, in spite of the recognition that such coupling can alter the abundance and species composition of plankton assemblages (Denman and Powell, 1984; Mackas *et al.*, 1985; Yamazaki *et al.*, 2002; Clay *et al.*, 2004; Ignoffo *et al.*, 2005; Menden-Deuer and Grünbaum, 2006; Woodson *et al.*, 2005, 2007a, b). In addition, to our knowledge, no study has examined the behavioral responses of different developmental stages of a single pelagic copepod to thin layers containing phytoplankton.

The abundance, widespread occurrence, and ability to switch between scanning currents and attack jumps make the pelagic calanoid copepod, *Acartia tonsa*, a useful model for studies to elucidate functional relationships between foraging copepods and phytoplankton thin layers. To examine these relationships, laboratory experiments tested the hypothesis that *A. tonsa* nauplii, copepodites, and adults respond similarly to fine-scale physical gradients with or without biological thin layers of green algae, *Nannochloropsis* sp.

Materials and methods

Sources and maintenance of water and algae for thin layers

All water used in this study originated from the North Sea and was held with constant aeration in storage tanks at the University of Hamburg Institute for Hydrobiology and Fisheries Science (UHH-IHF). Filtered North Sea water was prepared using a two-step process: (1) water was filtered sequentially through three, in-line, wound cotton-fiber filters with nominal pore sizes of 100, 10, and 1 μm , and (2) the filtrate was filtered sequentially through Whatman™ glass fiber (GF/C) and Millipore membrane filters with nominal pore sizes of 1.0 and 0.1 μm , respectively. Experimental salinities of 8.0, 12.0, and 18.0 ± 0.1 were made by adding fresh water to filtered North Sea water with a salinity of 35.0. Salinities

were measured with a WTW TetraCon® 325 conductivity meter. The water for experiments was stored in 113-L, plastic buckets that were aerated inside a climate-controlled room under a 12:12 light:dark cycle at 14 °C. The salinities used in this study were chosen to create narrow and distinct discontinuities and to bracket the typical salinities of brackish waters where the estuarine copepod, *Acartia tonsa*, is commonly found.

Thin layers typically involve several trophic levels (e.g. Cowles *et al.*, 1998); therefore, small (2-µm spherical diameter), non-motile, unicellular green algae, *Nannochloropsis* sp., were added to half of the experimental discontinuities to provide food for *Acartia tonsa*. In preliminary trials, visual observations indicated that all three developmental stages of *A. tonsa* fed readily on *Nannochloropsis* sp., which remained in the thin layer, whereas the grow-out feed, cryptophyte *Rhodomonas* sp., sank out of the thin layer. *Nannochloropsis* sp. used in the experiments were drawn from cultures maintained at UHH-IHF. The inoculum was obtained in 2007 from Dansk Skaldyrcenter, a shellfish hatchery located near Limfjord, Denmark. The culture medium comprised filtered and autoclaved North Sea water of salinity 12.0, nutrient and vitamin solutions (Walne, 1970), and 50 mg L⁻¹ biotin (Støttrup and Jensen, 1990). The algal culture was continuously aerated and stored in the same climate-controlled room as the water.

Collection and maintenance of *Acartia tonsa*

Acartia tonsa were hatched from resting eggs that were stored at 4 °C after being collected from continuous stock cultures maintained by UHH-IHF. Approximately 2 million eggs were placed in gently aerated, filtered North Sea water lowered from a salinity of 35.0 to 18.0. After 24 h, viable eggs hatched and resulted in a batch culture containing 220 nauplii 100 mL⁻¹. According to UHH-IHF standard practice, nauplii were fed daily with 200 ml of *Rhodomonas* sp. (> 50,000 cells mL⁻¹). Using a 35-µm sieve on day 3, a subsample from the batch culture of *A. tonsa* was transferred to filtered, aerated water of salinity 12.0. Using a

90- μm sieve on day 5, a subsample of the copepods from the 12.0 salinity water was transferred to filtered, aerated water of salinity 8.0. Developmental stages of *A. tonsa* were confirmed by subsampling, magnifying with a dissecting microscope, and validating a set of morphologic criteria: 2 terminal setae, 2 ventral and 2 terminal spines characterized naupliar stage 5; 4 pairs of swimming legs and 2 urosome segments distinguished copepodite stage 3; and 5 pairs of swimming legs and at least 3 urosome segments differentiated adult stage 6. According to these criteria, nauplii reached stage 5 on approximately day 4, copepodites reached stage 3 on approximately day 12, and adults entered stage 6 on approximately day 28, which is consistent with Titelman (2001). All copepods were held in the same climate-controlled room as the water and algae. *A. tonsa* were fed daily until 2–4 d prior to experimentation.

Experimental system

Each experiment occurred in a 1-cm thick, columnar, glass tank (15 x 15 x 50 cm; Fig. 1), on which a scale with 1-cm markings was fixed to an outside edge. In each experiment, a consistent light regime was supplied by an 11-W lamp transmitting light through a diffuser comprising a pane of glass fitted with a sheet of vellum paper. This diffuser functioned like milk glass commonly used in photography. A black, fabric backdrop enhanced contrast in video images captured with a SONY Handycam® DCR-HC96 miniDV camcorder operating at 30 frames sec^{-1} , with a 3.3 MP optical sensor resolution. The camcorder was mounted on a LINOS™ vertical motion, rail profiler in a position that yielded a 13 x 13 x 7.5 cm or approximately 1.3 L field of view. Recording focused on four layers relative to the discontinuity (above the discontinuity or top, at the upper boundary of the discontinuity or upper, at the lower boundary of the discontinuity or lower, and below the discontinuity or bottom). The camcorder was positioned to record each layer for 10–15 min several times during each 5-h experiment. Video records and direct observations were conducted for 5 h so

that records included both delayed responses to salinity gradients and food, such as osmoconformation and satiation, and more immediate responses, such as swimming and feeding (Tiselius, 1992).

All experiments involved a stratified water column with a salinity gradient representing the physical discontinuity. Gradients were created by carefully and slowly pouring water of salinity 18.0 along the walls of the tank while it was held at an angle, to avoid generating air bubbles, and then layering water of salinity 8.0 into the upper portion of the tank. The less saline water was dispensed from a carboy fitted with a tap and tubing that ended in a t-valve. At the end of this process, the top and bottom portions of the water column each were approximately 22-cm high, and these portions were separated by a 5-cm thick salinity gradient. Each salinity gradient was profiled using a WTW TetraCon® 325 conductivity meter at the end of the observations to confirm its persistence.

The experiments were designed to compare and contrast responses from three developmental stages of *Acartia tonsa* to sharply-defined physical discontinuities and to biological thin layers, comprising similar micro-scale discontinuities with high concentrations of food (Dekshenieks *et al.*, 2001; Cowles, 2004). Therefore, half of the 12 experiments, termed treatments, included biological thin layers containing green algae, *Nannochloropsis* sp. To create these treatments, aliquots of *Nannochloropsis* sp. were prepared so as to contain, on average, 3.05×10^6 cells mL⁻¹ (particle diameters 2.38–5.00 µm) as measured with a Beckman Multisizer™ 3 Coulter Counter® within 20 min of the beginning of each experiment. Thin layers containing algae were formed by slowly introducing the algae into the salinity gradient with a 60-mL, plastic syringe barrel connected to tubing that ended in a t-valve. Flow was controlled with a tubing clamp. The resulting biological thin layers were 6–7 cm thick, with volumes of 1.0–1.2 L. For all experiments, the boundaries of salinity

gradients or biological thin layers were located near the middle of the tank (i.e. 22–28 cm from the top).

For each control (no algae) and treatment, a 100-mL sample from the batch culture containing the appropriate developmental stage of *Acartia tonsa* was concentrated on a sieve (35-, 90- or 224- μ m mesh for nauplii, copepodites and adults), transferred to a Bogorov chamber, and enumerated using magnification from a dissecting scope. After preparation of the stratified water column with or without a biological thin layer of algae, aliquots from the batch culture containing approximately 300 copepods were uniformly distributed throughout the three salinity zones in the water column using a plastic syringe barrel and tubing attached to a 5-mm OD glass rod. The flow was controlled in the same way as during addition of algae. Thus, a total of approximately 900 copepods were added in each experiment.

Video analysis

Video recordings from the miniDV camcorder were captured in audio video interleaved (AVI) format using Microsoft® Windows Movie Maker. Using the VirtualDub 1.9.11 freeware (www.virtualdub.org, verified February 2011), the AVIs were segmented into 15-s files, or 450 frames, that documented copepods in each of the four layers relative to the discontinuity (top, upper, lower, and bottom).

Metrics extracted from the video records included the relative abundance of *Acartia tonsa* in each of the four layers and six reliably discernible behaviors. Relative abundance of copepods was determined from a 2D screen shot of the initial frame using the Image-based Tool for Counting Nuclei (ITCN) plugin within the ImageJ freeware (<http://rsb.info.nih.gov/ij/>, verified October 2012). Parameters for detecting the nuclei to be counted varied among the developmental stages of *A. tonsa* given the size difference between naupliar stage 5, copepodite stage 3 and adult stage 6. Behavioral metrics were derived from tracks of up to 25 *A. tonsa* per developmental stage, experiment, layer, and time interval

using the segmented files and custom-built particle tracking scripts in Mathworks MATLAB® 7.0.4. The trajectories followed by individual copepods were examined to generate behavioral metrics.

Analysis of videos generated seven metrics characterizing the behavior of *Acartia tonsa*. To generate comparable measures of abundance, counts of individuals in video frames were standardized to 300,000 pixels ($\sim 25 \text{ cm}^2$). Counts of individuals remaining stationary or moving were standardized to the total number of individuals tracked to yield proportions of individuals remaining stationary or moving. Stationary was defined as no travel in any direction, whereas moving was defined as the displacement of more than one body length in a given direction over the 15 s. For moving individuals, distances traveled between frames (0.333 s) were scaled to speeds in cm s^{-1} , and the median and quartiles were calculated for each developmental stage. Counts of individuals moving upward, downward or horizontally were standardized to the total number of individuals tracked to yield proportions of individuals moving in a given direction. Counts of individuals following ballistic (linear) or convoluted (non-linear) trajectories were standardized to the total number of individuals tracked to yield proportions of individuals following each type of trajectory. Convoluted trajectories involved turns, which were defined as the combination of moving more than one body length in a new direction. Turning rates were calculated by dividing the number of turns by the duration of the observation, which was generated by dividing the number of frames by 30 s, and the resulting data were scaled to number of turns 10 s^{-1} . In an effort to detect the presence of Lévy flight behavior, the exponent that parameterizes a power-tail law, μ (Edwards, 2008), was calculated from the distances traveled by all individuals that had been aggregated according to combinations of developmental stage, treatment or control, layer, and time. Lévy flights are random walks with a relatively large number of long distance

flights as indicated by $1 < \mu < 3$. Such search patterns have been implicated as effective when the distribution of food resources is unknown (Edwards, 2008; Sims *et al.*, 2008).

Data analysis

Five metrics were analyzed with analyses of variance (ANOVAs). In all cases, the residuals were tested for normality using Anderson–Darling tests and for homoscedasticity using Cochran’s tests. If necessary, data were transformed, and if the residuals remained non-normal or heteroscedastic, ANOVAs were interpreted conservatively. The ANOVAs for abundance, proportions of individuals remaining stationary, proportions of individuals following ballistic trajectories, and number of turns 10 s^{-1} were analyzed with ANOVAs that treated (1) developmental stage as a fixed factor with three levels (naupliar stage 5, copepodite stage 3 and adult stage 6), (2) treatment as a fixed factor with two levels (discontinuity termed control and discontinuity with algae termed thin layer), (3) layer as being nested in treatment with four levels (top, upper, lower, and bottom), and (4) time since the start of the experiments as being nested in the combination of treatment and layer with three levels (early = 30–65 min, mid = 150–190 min and late = 210–270 min). Proportions of individuals moving in a given direction were analyzed with an ANOVA that had an additional fixed factor, direction of movement, with three levels (up, down and horizontal).

Results

Vertical distribution relative to discontinuity

Profiles of salinity indicated that physical gradients were located between 22 and 28 cm from the top of the tank (Fig. 2). Within the gradients, which spanned approximately 6 cm, salinities increased from 10.0 to 17.0. In experiments with biological thin layers, visual observations confirmed that *Nannochloropsis* sp. remained concentrated at the physical gradients throughout the 5-h period. Although *Acartia tonsa* were evenly distributed

throughout the water column at the start of all experiments, individuals became significantly more abundant at the upper and lower boundaries of the discontinuities with and without algae from early in and throughout the 5-h experiments (Fig. 3). In fact, the vertical distribution of *A. tonsa* differed significantly among developmental stages and layers over time in both controls and treatments with algae (Table I). Such distributions suggest that neither negative nor positive phototaxis was a dominant influence on the behavior of *A. tonsa*.

Behavior of *Acartia tonsa*

From the 12 experiments, a total of 144, 15-s video segments was generated over a total of 90 h, resulting in the tracking of 3476 individuals. The number of stationary individuals varied significantly among combinations of developmental stage and layer relative to the physical and biological discontinuities (Table II). In fact, there were significantly more nauplii moving at the upper and lower boundaries in experiments with biological thin layers than in those with only a physical discontinuity (Fig. 4). In general, a greater proportion of copepodites and adults moved, with movement at the upper and lower boundaries of the discontinuities being more common for stage 3 copepodites (Table II; Fig. 4).

For moving individuals, overall median speeds increased with development, with nauplii being the slowest at 0.74 cm s^{-1} and adults being the fastest at 3.69 cm s^{-1} . Copepodites were intermediate at 2.50 cm s^{-1} . In experiments without a biological thin layer, speeds of *Acartia tonsa* varied among developmental stages and layers relative to the discontinuities (Table III). For instance, nauplii and adults moved more slowly when they were at the physical gradient than when they were in the top and bottom portions of the water column. In contrast, copepodites moved faster at the physical gradient. In experiments with a biological thin layer, all developmental stages moved faster at the upper and lower boundaries of the thin layer than in the top and bottom portions of the water column (Table

III). These median speeds near thin layers increased with developmental stage from 1.77 to 3.57 to 3.62 cm s⁻¹ for nauplii, copepodites and adults, respectively.

Moving nauplii, copepodites and adults generated trajectories that were characterized by intermittent swimming, sinking, and jumping (Fig. 5). These trajectories were examined to determine direction of movement (i.e. upward, downward or horizontal) and shape of movement (i.e. ballistic or convoluted).

The proportion of individuals moving in a particular direction was compared using a multi-factor ANOVA, which was interpreted conservatively because the arcsine-transformed data were not normally distributed or homoscedastic (Table IV). A significant interaction among direction, developmental stage and layer, along with examination of mean proportions indicated that, although movement tended to be downward in all cases, nauplii generally exhibited more upward movement than copepodites or adults (Fig. 6).

The proportion of individuals exhibiting ballistic movements varied significantly among combinations of developmental stage, experiments with and without biological thin layers, position in the water column, and time (Table V). In general, the mean proportion of individuals demonstrating ballistic movements decreased with increasing development (Fig. 7). In addition, the proportion of individuals exhibiting ballistic movements tended to be lower above and below the discontinuity, especially if it contained algae (Fig. 7). Thus, trajectories followed by older *A. tonsa* contained more turns near discontinuities containing algae, i.e. thin layers.

Convoluted trajectories were examined to determine the number of turns taken. Although the transformed data were not normally distributed, the mean numbers of turns were significantly different among combinations of developmental stage, experiment, layer, and time (Table VI; Fig. 8). In general, older *A. tonsa* consistently made more turns and turns were more common at the upper and lower boundaries of the physical and biological

discontinuities (Fig. 8). The presence or absence of algae had little effect on the number of turns made (Fig. 8).

Random Walk

All developmental stages exhibited little evidence of Lévy flight behavior, with μ -values ranging from 1.13 to 1.30 across all experiments (Table VII). In particular, μ -values were relatively consistent in experiments with and without algae in the discontinuities, i.e. thin layers.

Discussion

In this study, we investigated the effects of physical gradients and biological discontinuities on the behavior of three morphologically different developmental stages of the calanoid copepod, *Acartia tonsa* (i.e. nauplii, copepodites and adults). Seven metrics characterizing fine-scale behaviors of individual were examined using video recordings, an image-based tool for counting and a particle tracking script. In part, motivation for comparing behavior among developmental stages stemmed from marked differences reported for the same species during general observations of swimming and encounters with food (Titelman and Kiørboe, 2003; Dur *et al.*, 2010).

Results from this study indicated that both physical gradients and biological thin layers affected the behavior of *Acartia tonsa* across all developmental stages. Notably, all developmental stages aggregated at the upper and lower boundaries of the physical gradients or biological discontinuities. Evidently, all *A. tonsa* were capable of detecting and remaining near discontinuities.

When algae were present, all developmental stages altered their behavior. Although median speeds increased as copepods matured (adults moved more than five times faster than nauplii), all developmental stages moved faster near biological thin layers. In the upper and

lower portions of the biological thin layers, more trajectories included turns. Thus, *Acartia tonsa*, especially older developmental stages, exhibited some characteristics of area-restricted search behavior (Tinbergen *et al.*, 1967; Leising and Franks, 2002).

Although trajectories with turns (convoluted paths) were more common near biological thin layers, the number of turns 10 s^{-1} did not differ significantly, regardless of the presence or absence of algae in the discontinuity. Furthermore, no developmental stage showed strong evidence of Lévy flight behavior. The lack of a significant difference in number of turns and the absence of Lévy flight behavior may be due to the relatively short periods of observation. The behavior of *A. tonsa* around discontinuities may have changed if searching for food beyond 270 min did not yield success or if encounters with food particles fell below some threshold (Frost *et al.*, 2010). Overall, the results indicated that *Acartia tonsa* detected discontinuities with and without algae, and they adjusted their behavior to remain near the discontinuity.

Behaviors exhibited by *Acartia tonsa* in this study showed similarities to those recorded for the same species in studies of predator-prey relationships, escape responses and factors affecting encounter rates with predators. First, trajectories of nauplii involved more lateral movements than adults, as described by Buskey (1994), and second, trajectories generally matched the three patterns described by Titelman and Kiørboe (2003): (1) a straight line, (2) a sawtooth pattern with an occasional loop, or (3) a helical, corkscrew pattern. Trajectories of copepodites and adults included more sawtooth and corkscrew patterns, with the sawtooth pattern being comparable to the “hop and sink” behavior observed for other copepod species (Bainbridge, 1952). Third, speeds from undisturbed *A. tonsa* in this study (i.e. $0.34\text{--}4.71\text{ cm s}^{-1}$) spanned the range found in studies that focused on eliciting a response to a disturbance. For instance, speeds of stimulated *A. tonsa* nauplii recorded by Buskey

(1994), Titelman (2001) and Titelman and Kiørboe (2003) ranged from 0.01 to 1.04 cm s⁻¹, while speeds of adults ranged from 0.20 to 2.00 cm s⁻¹ (Buskey, 1994).

While other studies have tested the effect of physical gradients or biological thin layers on copepods, to our knowledge, this is the first study to examine fine-scale, individual behaviors across three developmental stages from one species using a single methodology. Notably, this study provided evidence that all developmental stages detected and responded to discontinuities with behaviors that likely enhanced successful feeding (e.g. Tinbergen *et al.*, 1967; Cowles *et al.*, 1998; Leising and Franks, 2002). Further work on the persistence of such behavior would yield additional insights into the importance of individual behavior in determining ecological patterns.

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Table and Figure legends

Table I. Results of an analysis of variance examining variation in vertical distribution of *Acartia tonsa*. DS = developmental stage (naupliar, copepodite or adult); Treat = discontinuity without algae (control) or with algae (thin layer); Lay = section of the water column relative to the discontinuity (top = above, upper = near upper boundary, lower = near lower boundary and bottom = below); Ti = time since the beginning of the experiment (early = 30–65 min, mid = 150–190 min and late = 210–270 min)

Table II. Results of an analysis of variance examining variation in numbers of *Acartia tonsa* remaining stationary. DS = developmental stage (naupliar, copepodite or adult); Treat = discontinuity without algae (control) or with algae (thin layer); Lay = section of the water column relative to the discontinuity (top = above, upper = near upper boundary, lower = near lower boundary and bottom = below); Ti = time since the beginning of the experiment (early = 30–65 min, mid = 150–190 min and late = 210–270 min)

Table III. Median speeds for *Acartia tonsa*.

Table IV. Results of an analysis of variance examining variation in numbers of *Acartia tonsa* moving in a particular direction. Dir = direction of movement (up, down or horizontal); DS = developmental stage (naupliar, copepodite or adult); Treat = discontinuity without algae (control) or with algae (thin layer); Lay = section of the water column relative to the discontinuity (top = above, upper = near upper boundary, lower = near lower boundary and bottom = below); Ti = time since the beginning of the experiment (early = 30–65 min, mid = 150–190 min and late = 210–270 min)

Table V. Results of an analysis of variance examining variation in numbers of *Acartia tonsa* exhibiting ballistic (linear) trajectories. DS = developmental stage (naupliar, copepodite or adult); Treat = discontinuity without algae (control) or with algae (thin layer); Lay = section

of the water column relative to the discontinuity (top = above, upper = near upper boundary, lower = near lower boundary and bottom = below); Ti = time since the beginning of the experiment (early = 30–65 min, mid = 150–190 min and late = 210–270 min)

Table VI. Results of an analysis of variance examining variation in number of turns 10 s^{-1} performed by *Acartia tonsa*. DS = developmental stage (naupliar, copepodite or adult); Treat = discontinuity without algae (control) or with algae (thin layer); Lay = section of the water column relative to the discontinuity (top = above, upper = near upper boundary, lower = near lower boundary and bottom = below); Ti = time since the beginning of the experiment (early = 30–65 min, mid = 150–190 min and late = 210–270 min)

Table VII. Mean exponents that parameterized power tail laws (μ) for *Acartia tonsa* observed in the experiments. DS = developmental stage (naupliar = N5, copepodites = C3 or adult = C6); Treat = discontinuity without algae (control = C) or with algae (thin layer = TL); Lay = section of the water column relative to the discontinuity (top = above = T, upper = near upper boundary = U, lower = near lower boundary = L, and bottom = below = B); Ti = time since the beginning of the experiment (early = 30–65 min, mid = 150–190 min and late = 210–270 min)

Fig. 1 Experimental system for testing the behavior of the copepod, *Acartia tonsa*. A physical gradient with a biological thin layer of algae is shown. Salinities of the water column were 8.0 above, 10.0–16.0 within and 18.0 below the gradient. Algae was absent in control experiments involving a salinity gradient without a biological thin layer. Figure is not drawn to scale.

Fig. 2 Examples of salinity and temperature profiles for experiments with *Acartia tonsa* at (A) naupliar stage 5, (B) copepodite stage 3 and (C) adult stage 6 of development.

Fig. 3 Variation in mean abundances \pm standard errors (SE) for *Acartia tonsa* during experiments. (A–C) = control experiments for nauplii at early, mid and late; (G–I) = control experiments for copepodites at early, mid and late; (M–O) = control experiments for adults at early, mid and late; (D–F) = thin layer experiments for nauplii at early, mid and late; (J–L) = thin layer experiments for copepodites at early, mid and late; (P–R) = thin layer experiments for adults at early, mid and late. Control = discontinuity without algae; Thin layer = discontinuity with algae; Top = above discontinuity; Upper = at the upper boundary of the discontinuity; Lower = at the lower boundary of the discontinuity; Bottom = below the discontinuity; Early = 30–65 min since the beginning of the experiment; Mid = 150–190 min since the beginning of the experiment; Late = 210–270 min since the beginning of the experiment

Fig. 4 Variation in mean proportions of *Acartia tonsa* remaining stationary (white bars) or moving (gray bars) \pm standard errors (SE) during experiments. (A, C, E) = control experiments for nauplii, copepodites and adults, respectively; (B, D, F) = thin layer experiments with nauplii, copepodites and adults, respectively. Control = discontinuity without algae; Thin layer = discontinuity with algae; Top = above discontinuity; Upper = at the upper boundary of the discontinuity; Lower = at the lower boundary of the discontinuity; Bottom = below the discontinuity

Fig. 5 Examples of trajectories exhibited by adult *Acartia tonsa*, with trajectories 7 and 4 being ballistic and trajectories 2, 3 and 12 being convoluted.

Fig. 6 Variation in mean proportions of *Acartia tonsa* moving up (white bars), down (light gray bars) or horizontal (dark gray bars) \pm standard errors (SE) during experiments. (A, C, E) = control experiments for nauplii, copepodites and adults, respectively; (B, D, F) = thin layer experiments with nauplii, copepodites and adults, respectively. Control = discontinuity

without algae; Thin layer = discontinuity with algae; Top = above discontinuity; Upper = at the upper boundary of the discontinuity; Lower = at the lower boundary of the discontinuity; Bottom = below the discontinuity

Fig. 7 Variation in mean proportions of *Acartia tonsa* exhibiting ballistic (linear) trajectories \pm standard errors (SE) during experiments. (A–C) = control experiments for nauplii at early, mid and late; (G–I) = control experiments for copepodites at early, mid and late; (M–O) = control experiments for adults at early, mid and late; (D–F) = thin layer experiments for nauplii at early, mid and late; (J–L) = thin layer experiments for copepodites at early, mid and late; (P–R) = thin layer experiments for adults at early, mid and late. Control = discontinuity without algae; Thin layer = discontinuity with algae; Top = above discontinuity; Upper = at the upper boundary of the discontinuity; Lower = at the lower boundary of the discontinuity; Bottom = below the discontinuity; Early = 30–65 min since the beginning of the experiment; Mid = 150–190 min since the beginning of the experiment; Late = 210–270 min since the beginning of the experiment

Fig. 8 Variation in mean number of turns $10\text{ s}^{-1} \pm$ standard errors (SE) for *Acartia tonsa* during experiments. (A–C) = control experiments for nauplii at early, mid and late; (G–I) = control experiments for copepodites at early, mid and late; (M–O) = control experiments for adults at early, mid and late; (D–F) = thin layer experiments for nauplii at early, mid and late; (J–L) = thin layer experiments for copepodites at early, mid and late; (P–R) = thin layer experiments for adults at early, mid and late. Control = discontinuity without algae; Thin layer = discontinuity with algae; Top = above discontinuity; Upper = at the upper boundary of the discontinuity; Lower = at the lower boundary of the discontinuity; Bottom = below the discontinuity; Early = 30–65 min since the beginning of the experiment; Mid = 150–190 min since the beginning of the experiment; Late = 210–270 min since the beginning of the experiment

Table I. Results of an analysis of variance examining variation in vertical distribution of *Acartia tonsa*.

Anderson– Darling	Cochran's	Source	df	SS	MS	F	p
p > 0.05	p > 0.05	DS	2	14.411	7.206	14.54	0.001
		Treat	1	0.254	0.254	0.11	0.748
		Lay(Treat)	6	13.437	2.239	7.66	0.001
		Ti(Treat × Lay)	16	4.679	0.292	4.53	0.000
		DS × Treat	2	0.438	0.219	0.44	0.653
		DS × Lay(Treat)	12	5.948	0.496	4.78	< 0.001
		DS × Ti(Treat × Lay)	32	3.320	0.104	1.61	0.049
		Error	72	4.645	0.065		

Table II. Results of an analysis of variance examining variation in numbers of *Acartia tonsa* remaining stationary.

Anderson–Darling	Cochran's	Source	df	SS	MS	F	p
p > 0.05	p > 0.05	DS	2	6.666	3.333	12.13	0.001
		Treat	1	0.797	0.797	2.19	0.189
		Lay(Treat)	6	2.183	0.364	6.96	0.001
		Ti(Treat × Lay)	16	0.837	0.052	1.26	0.249
		DS × Treat	2	0.333	0.167	0.61	0.561
		DS × Lay(Treat)	12	3.296	0.275	4.23	0.001
		DS × Ti(Treat × Lay)	32	2.078	0.065	1.56	0.061
		Error	72	2.998	0.042		

Table III. Median speeds for *Acartia tonsa*.

Treatment	Developmental stage	Median	
		Discontinuity	Water column
Control	Naupliar stage 5	0.36	0.77
	Copepodite stage 3	3.33	1.31
	Adult stage 6	3.98	4.73
Thin layer	Naupliar stage 5	1.77	0.49
	Copepodite stage 3	3.57	1.47
	Adult stage 6	3.62	2.30

Table IV. Results of an analysis of variance examining variation in numbers of *Acartia tonsa* moving in a particular direction.

Anderson– Darling	Cochran's	Source	df	SS	MS	F	p
p < 0.01	p < 0.05	Dir	2	50.642	25.321	176.48	< 0.001
		DS	2	0.058	0.029	2.44	0.130
		Treat	1	0.003	0.003	0.20	0.671
		Lay(Treat)	6	0.080	0.013	1.46	0.255
		Ti(Treat × Lay)	16	0.146	0.009	0.18	1.000
		Dir × DS	4	1.655	0.414	3.24	0.029
		Dir × Treat	2	0.513	0.257	1.79	0.209
		Dir × Lay(Treat)	12	1.722	0.143	1.08	0.409
		Dir × Ti(Treat × Lay)	32	4.259	0.133	2.67	< 0.001
		DS × Treat	2	0.029	0.014	1.21	0.332
		DS × Lay(Treat)	12	0.143	0.012	1.34	0.245
		DS × Ti(Treat × Lay)	32	0.284	0.009	0.18	1.000
		Dir × DS × Treat	4	0.618	0.154	1.21	0.332
		Dir × DS × Lay(Treat)	24	3.062	0.128	1.85	0.027
		Dir × DS × Ti(Treat × Lay)	64	4.412	0.069	1.38	0.045
		Error	216	10.753	0.050		

Table V. Results of an analysis of variance examining variation in numbers of *Acartia tonsa* exhibiting ballistic (linear) trajectories.

Anderson–Darling	Cochran’s	Source	df	SS	MS	F	p
p < 0.001	p < 0.01	DS	2	0.212	0.106	2.19	0.155
		Treat	1	0.205	0.205	0.60	0.466
		Lay(Treat)	6	2.031	0.339	2.77	0.049
		Ti(Treat × Lay)	16	1.958	0.122	1.76	0.055
		DS × Treat	2	0.276	0.138	2.85	0.097
		DS × Lay(Treat)	12	0.580	0.048	0.36	0.968
		DS × Ti(Treat × Lay)	32	4.293	0.134	1.92	0.011
		Error	72	5.021	0.070		

Table VI. Results of an analysis of variance examining variation in number of turns 10 s^{-1} performed by *Acartia tonsa*.

Anderson– Darling	Cochran's	Source	df	SS	MS	F	p
p < 0.001	p > 0.01	DS	2	262.52	131.26	14.28	0.001
		Treat	1	12.13	12.13	1.32	0.294
		Lay(Treat)	6	301.49	50.25	27.22	< 0.001
		Ti(Treat × Lay)	16	29.53	1.85	1.86	0.020
		DS × Treat	2	48.15	24.08	2.62	0.114
		DS × Lay(Treat)	12	110.26	9.19	2.93	0.007
		DS × Ti(Treat × Lay)	32	100.21	3.13	3.15	< 0.001
		Error	3367	3347.08	0.99		

Table VII. Mean exponents that parameterized power tail laws (μ) for *Acartia tonsa* observed in the experiments.

DS	Treat	Lay	μ	DS	Treat	Lay	μ	DS	Treat	Lay	μ
N5	C	T	1.25	C3	C	T	1.14	C6	C	T	1.19
		U	1.28			U	1.14			U	1.22
		L	1.29			L	1.15			L	1.21
		B	1.27			B	1.15			B	1.20
	TL	T	1.25		TL	T	1.14		TL	T	1.22
		U	1.23			U	1.14			U	1.21
		L	1.23			L	1.15			L	1.22
		B	1.27			B	1.15			B	1.22

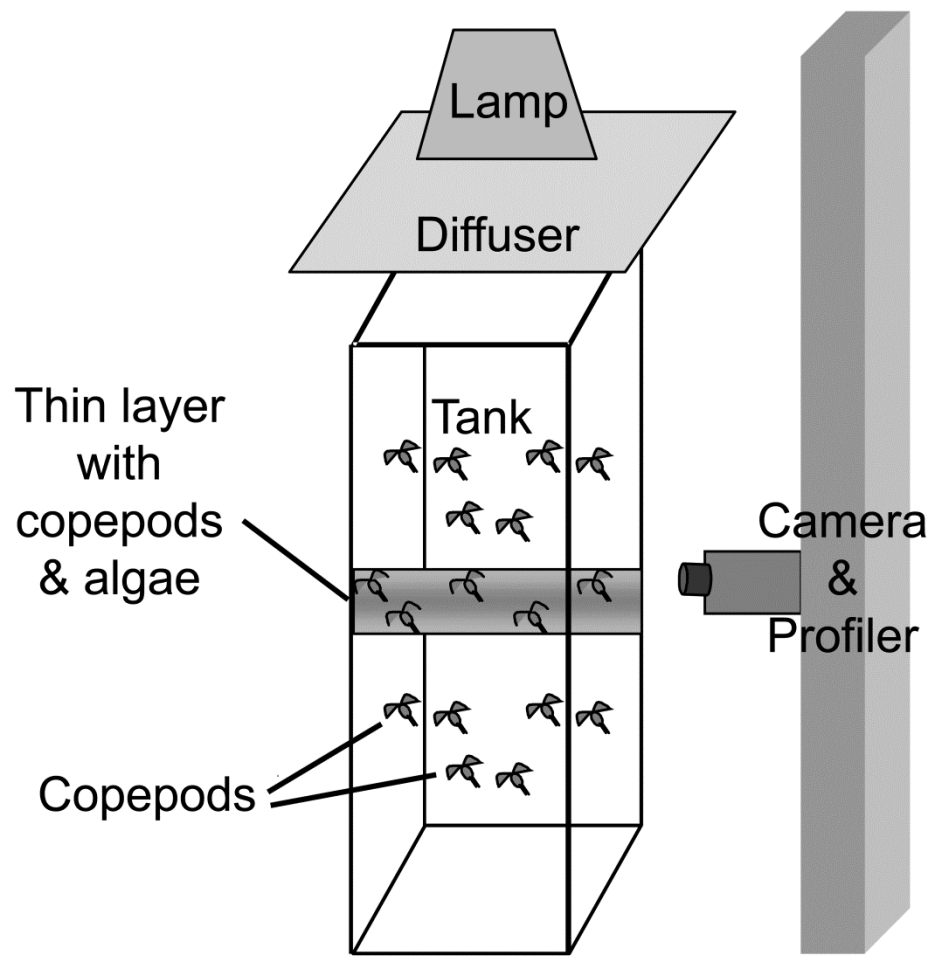


Fig. 1

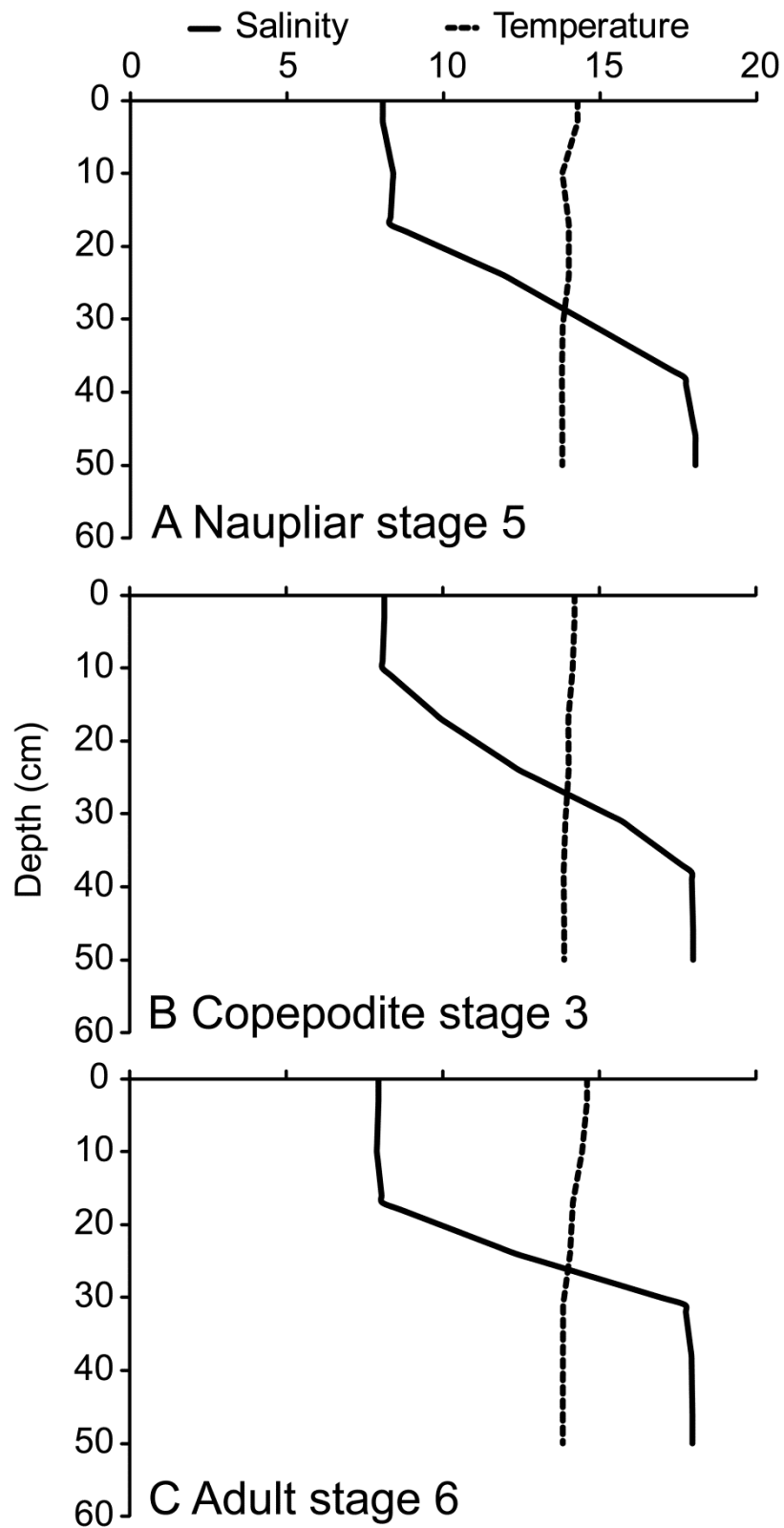


Fig. 2

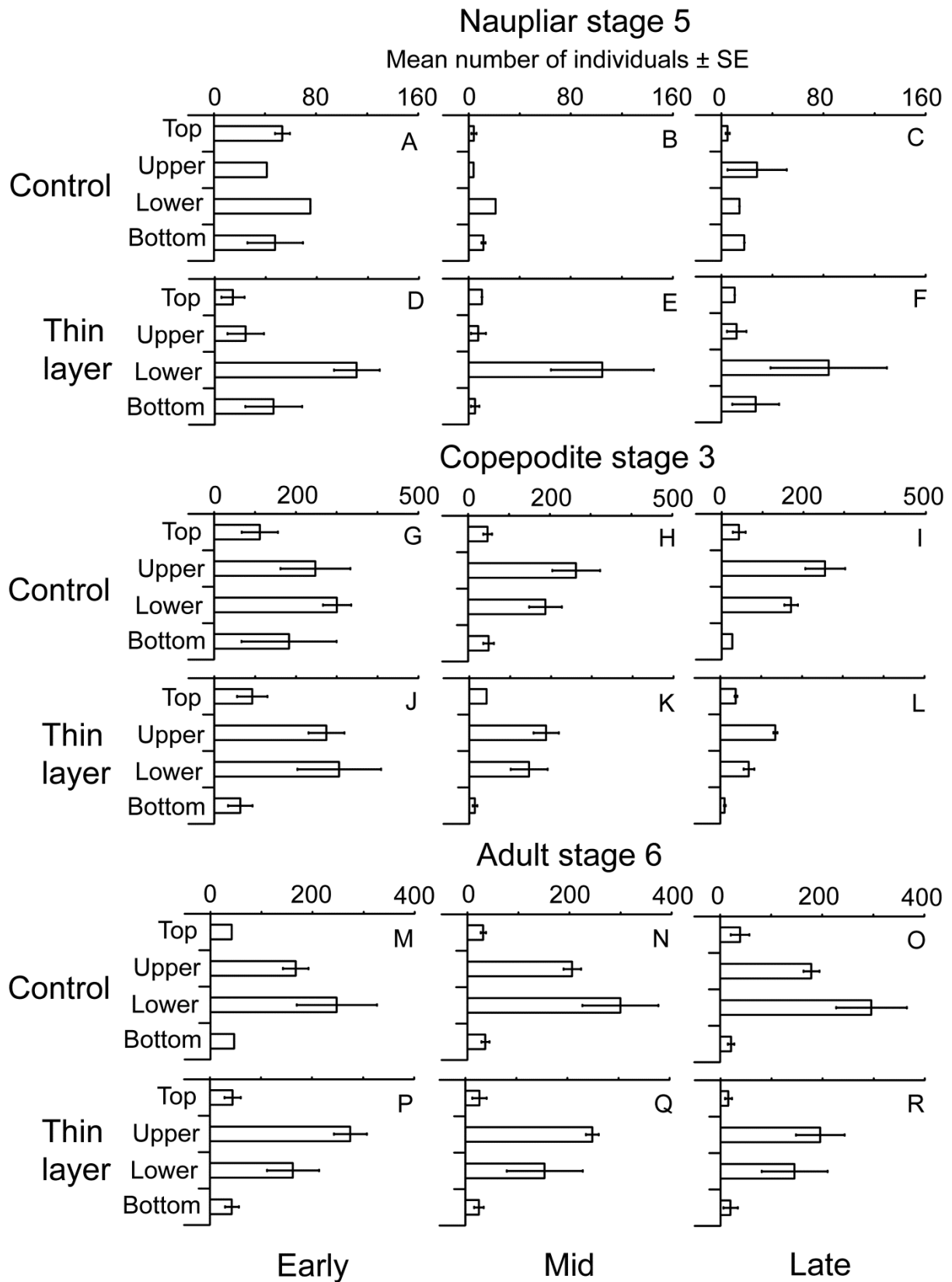


Fig. 3

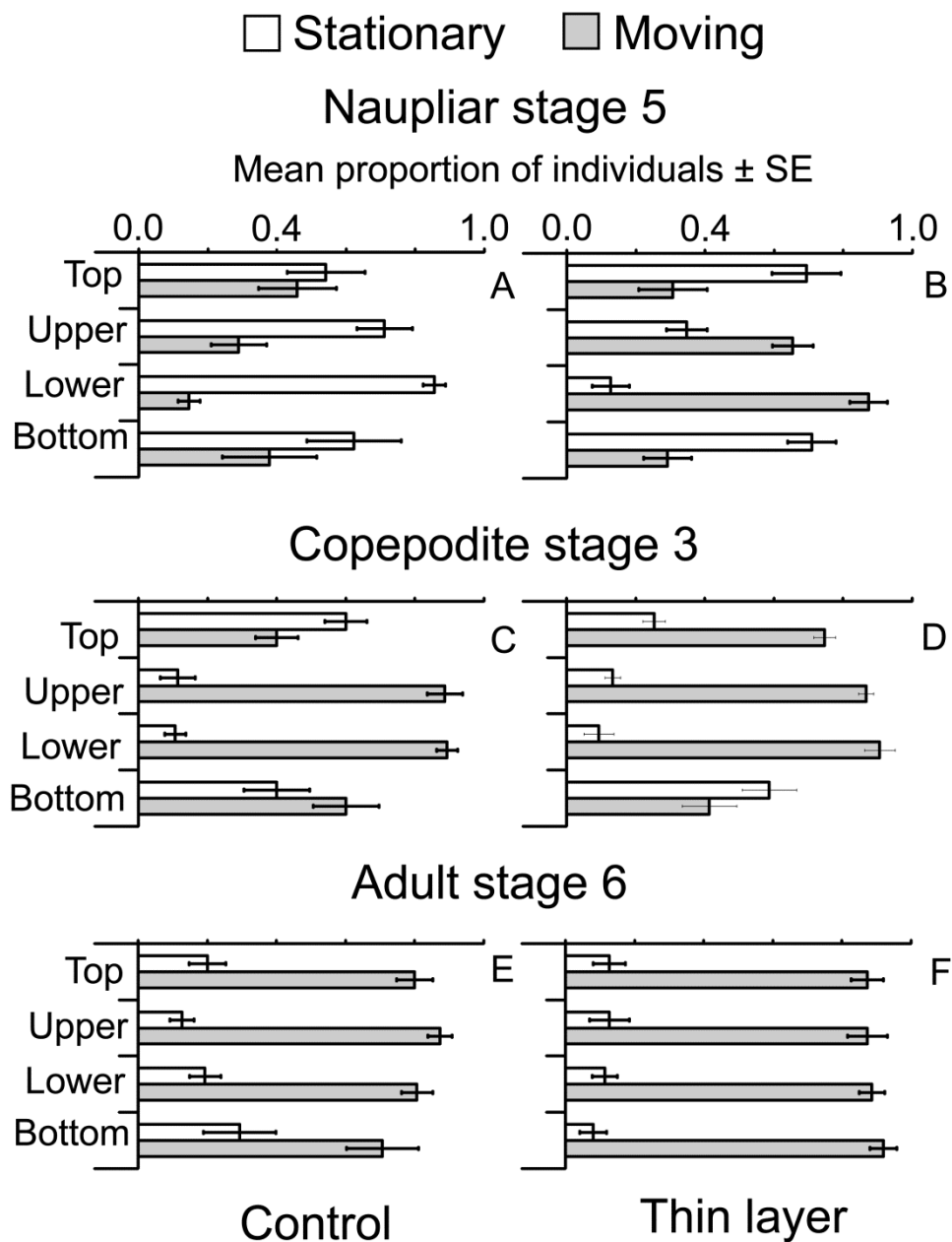


Fig. 4

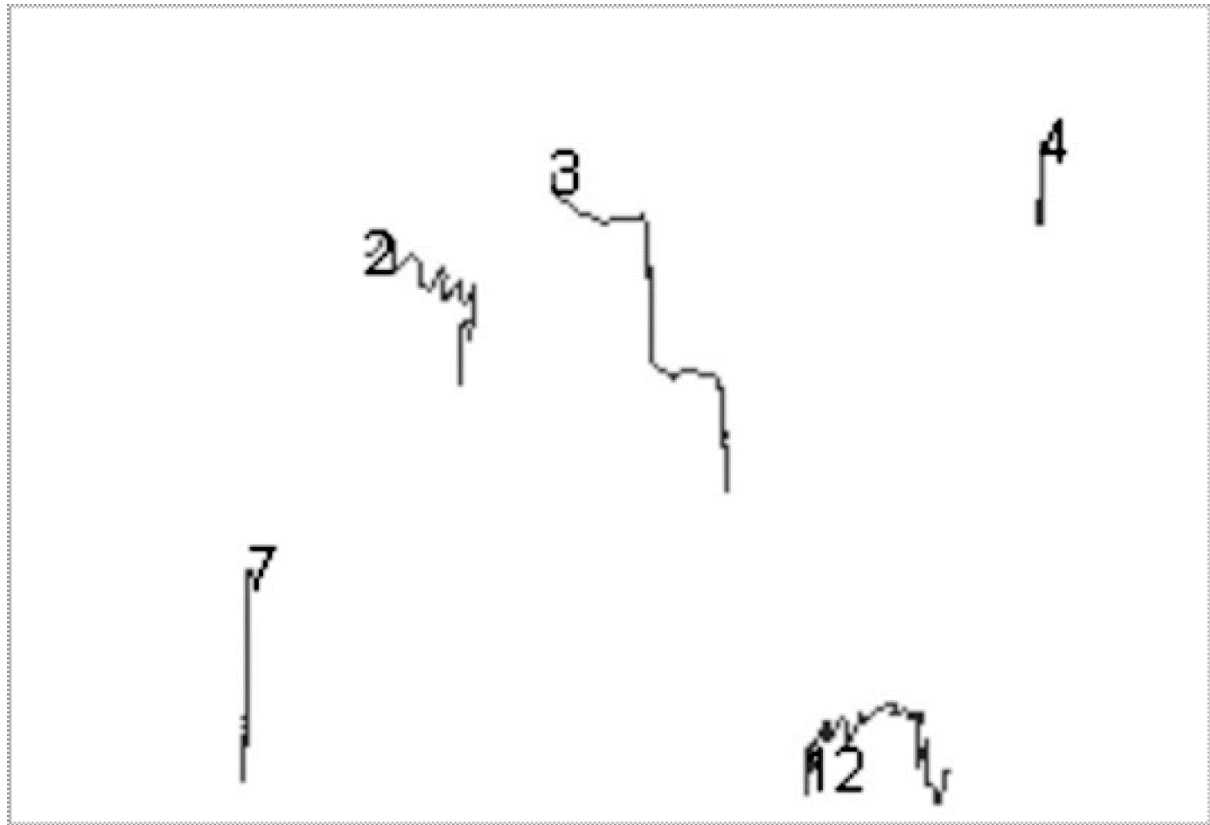


Fig. 5

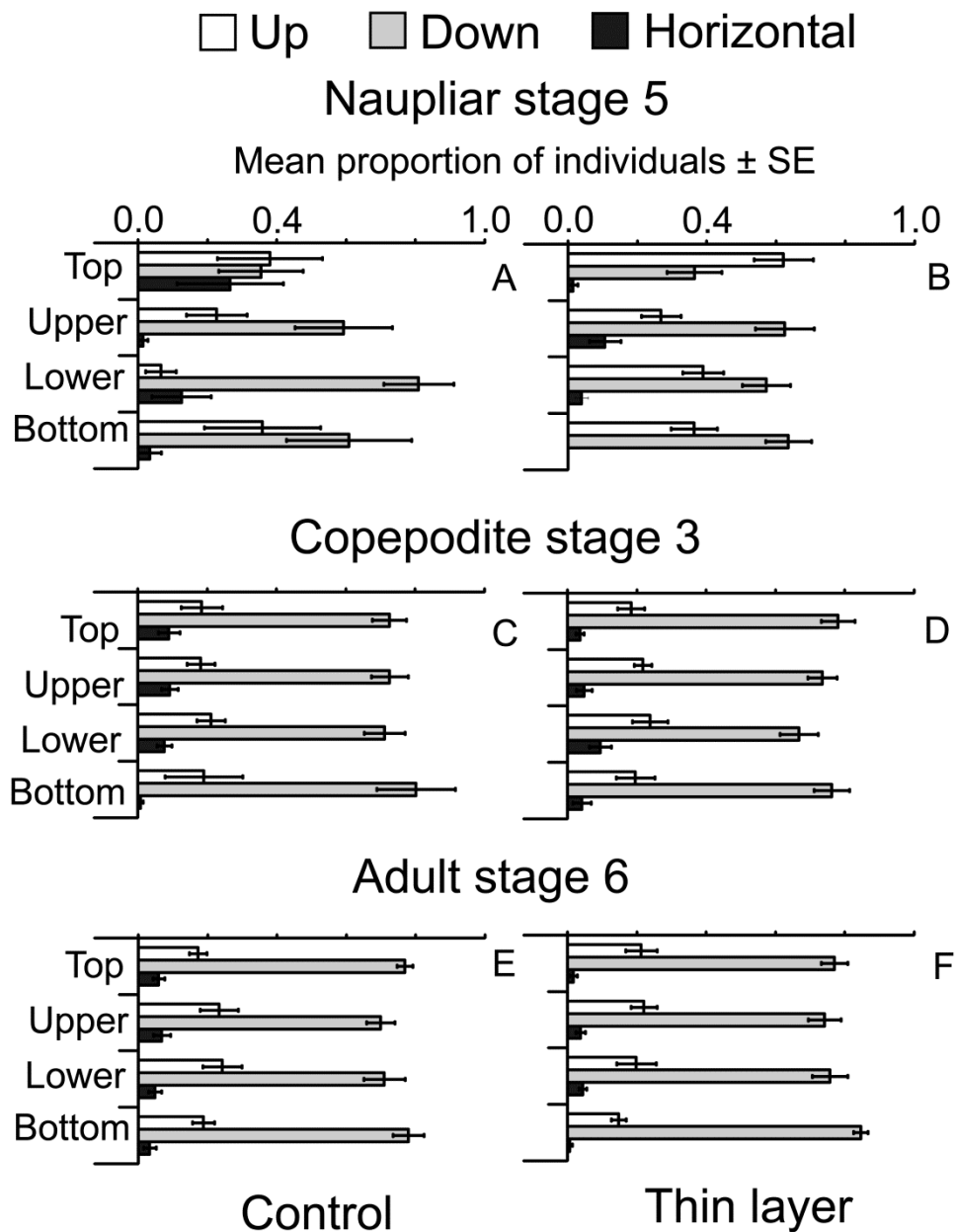


Fig. 6

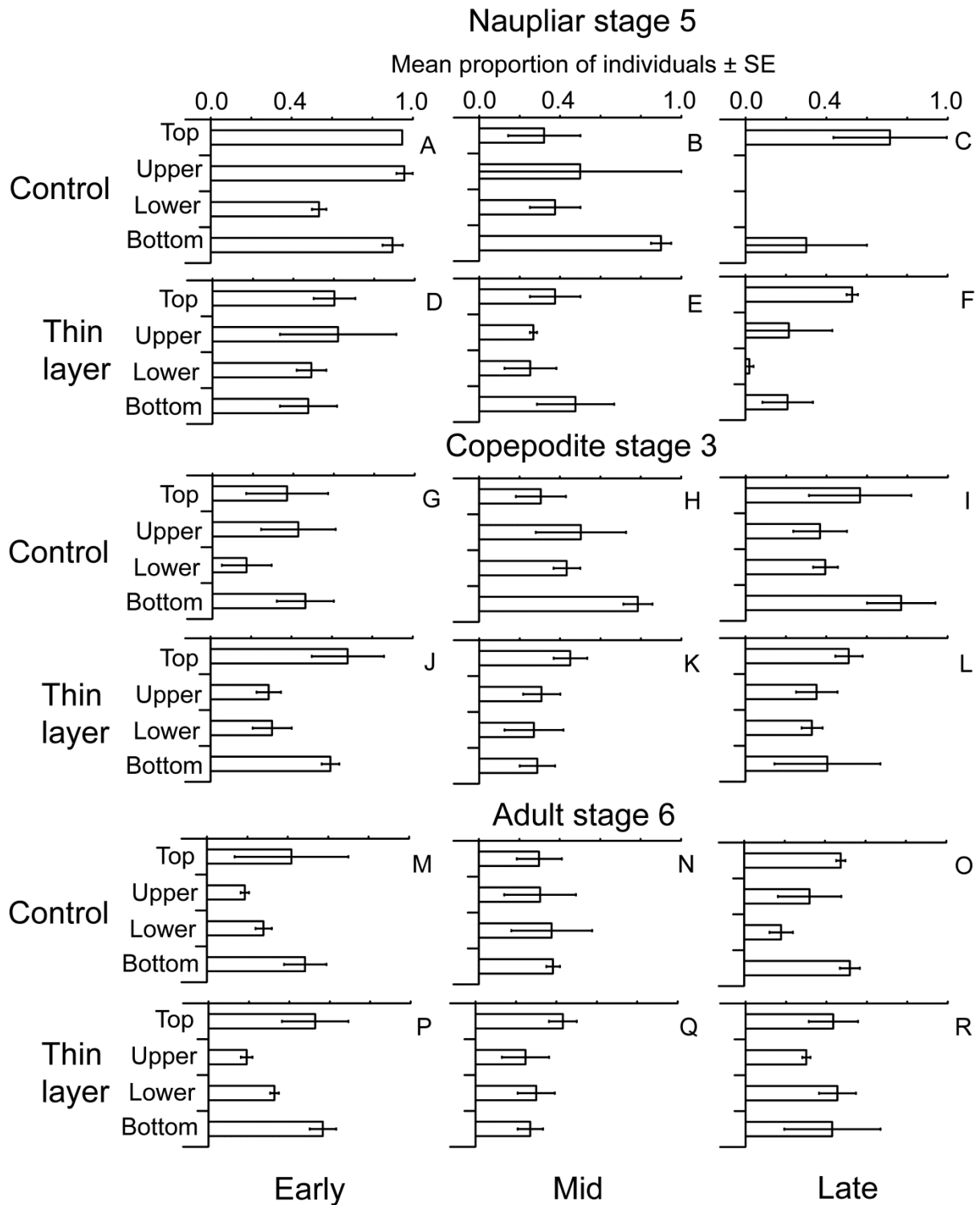


Fig. 7

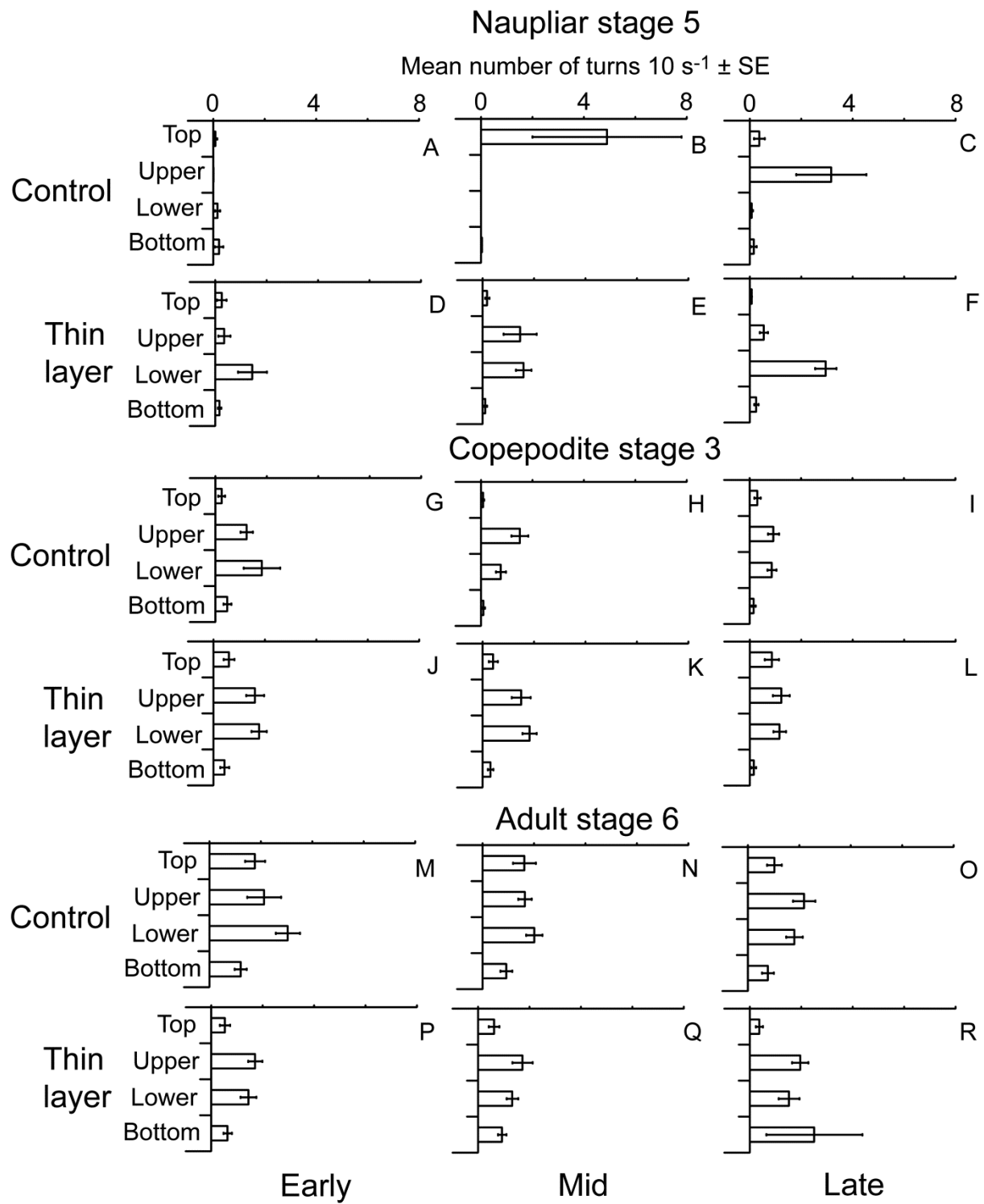


Fig. 8

Behavior of *Nemopsis bachei* L. Agassiz, 1849 medusae in the presence of physical gradients and biological thin layers

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Abstract In pelagic systems, thin layers (discontinuities with narrow vertical extents and high concentrations of organisms) create patches of food, and aggregations of gelatinous zooplankton can exploit such resources. The establishment, maintenance, and trophic effects of these functional relationships depend on behavioral responses to thin layers by individuals, which remain largely unexplored. In this study, we used laboratory experiments to test the hypothesis that a common and abundant

hydromedusa predator, *Nemopsis bachei* L. Agassiz, 1849, would respond similarly to salinity gradients with and without thin layers of algae and copepods. Approximately 75% of the hydromedusae remained in both types of discontinuities. These distributions were not created solely by passive responses related to osmoconformation or an inability to swim through salinity gradients because approximately 25% of hydromedusae swam through or away from salinity gradients or biological thin layers. Biological thin layers stimulated feeding. Feeding success was related directly to encounter rates and it was independent of swimming, as expected for an ambush predator. Feeding increased at higher prey densities, and capture, handling time, and ingestion were not saturated even at 150–200 copepods l⁻¹. The proportion of *N. bachei* that ceased feeding and began swimming increased when encounters with prey decreased to approximately 2 encounters hydromedusa⁻¹ 10 min⁻¹. Thus, hydromedusae may seek new patches of prey once encounter rates and subsequent feeding success fall below a threshold. Exposing *N. bachei* to salinity gradients with and without biological thin layers indicated that these hydromedusae will remain in discontinuities and exert predation pressure that should be considered when assessing trophic webs and estimating carbon flux.

Keywords Jellyfish · Hydromedusae · Zooplankton · Discontinuities · Feeding · Aggregation

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Introduction

Spatial and temporal heterogeneity affect movement and resource use by animals (Levin et al., 2000). In particular, behaviors that allow organisms to locate and exploit patches of food represent key influences on trophodynamics. For plankton, external forcing (e.g., currents, shear, and turbulence) combines with behavioral responses to determine the structure and function of assemblages, access to food, and the flow of carbon across a range of spatial and temporal scales (e.g., Bochdansky & Bollens, 2004).

At a micro-scale, thin layers represent persistent, spatially coherent patches of plankton (Donaghay et al., 1992; Cowles et al., 1998). Thin layers that are decimeters to meters thick, extend several kilometers horizontally, and persist for minutes, hours or days have been identified with the aid of technologically advanced instruments (e.g., acoustic Doppler current profilers; Flagg & Smith, 1985; Cowles et al., 1990; Cowles & Desiderio, 1993; Holliday et al., 1998). The formation of thin layers requires the creation of a stable discontinuity, typically associated with a pycnocline at the boundary of two water masses, and threefold increases in densities of phytoplankton and zooplankton that arise passively, primarily due to neutral buoyancy, or actively, as an outcome of behavior (Osborn, 1998; Dekshenieks et al., 2001; Alldredge et al., 2002; McManus et al., 2003; Gallagher et al., 2004; Rawlinson et al., 2004). In thin layers, competition and predation can be intensified, rates of nutrient uptake can be enhanced, chemical wastes and toxins can accumulate, and microbial degradation and remineralization can be higher (Mason et al., 1993; Sieburth & Donaghay, 1993; Johnson et al., 1995; Donaghay & Osborn, 1997; Cowles et al., 1998). The chemistry, physics, and biological compositions of thin layers have been documented (Donaghay et al., 1992; Hanson & Donaghay, 1998; Holliday et al., 1998; Widder et al., 1999; McManus et al., 2005). As yet, relatively few studies have examined the behavioral responses that allow individual organisms to remain within and exploit thin layers, in spite of the recognition that such coupling can alter the abundance and species composition of plankton assemblages (Denman & Powell, 1984; Mackas et al., 1985; Yamazaki et al., 2002; Clay et al., 2004; Ignoffo et al., 2005; Woodson et al. 2005, 2007a, b). In addition, we are

unaware of any study that has examined the influence of thin layers on the behavior of individual gelatinous zooplankton.

Gelatinous zooplankton, including ctenophores, medusae, and siphonophores, tend to aggregate at density, salinity, and temperature discontinuities that develop in coastal transition zones, estuaries, and fjords (Owen, 1989; Graham et al., 2001). Aggregations of gelatinous species can arise if discontinuities act as a physical or physiological barrier or if detectable boundary conditions stimulate appropriate behavioral responses. For example, field surveys showed that *Sarsia tubulosa* (M. Sars, 1835) aggregated at a discontinuity (Hansen, 1951), and in the laboratory, this species' ability to cross salinity and temperature discontinuities was limited by the magnitude and rate of its physiological adaptation (Arai, 1973, 1976). In contrast, *Aglantha digitale* (O. F. Müller, 1776) and *Proboscoidactyla ornata* (McCrady, 1857) ceased their typical vertical migrations in response to discontinuities (Hansen, 1951; Smedstad, 1972; Moreira, 1973; Southward & Barrett, 1983). Although laboratory and field studies have provided information about the behavioral responses of medusae to discontinuities, they have not focused at the fine scales typical of thin layers (Grindley, 1964; Hamner et al., 1975; Williams, 1985; Tiselius et al., 1994; Lougee et al., 2002).

Hydromedusae represent a widespread and diverse group of jellyfish (Boero et al., 2008). These medusae have been documented to be abundant predators in some systems (Huntley & Hobson, 1978; Matsakis & Conover, 1991; Costello, 1992; Purcell & Nemazie, 1992). One hydromedusa of particular interest is *Nemopsis bachei*, which seems to have extended its range. Populations of *N. bachei* have existed in Chesapeake Bay, the Atlantic coastal waters of North America, and the Gulf of Mexico (Purcell & Nemazie, 1992); and populations recently have become established in the North Sea, in the coastal waters of the Netherlands, and off the coast of Belgium (Dumoulin, 1997; ICES, 2006). Furthermore, *N. bachei* has been reported to be the numerically dominant gelatinous predator in North Inlet, South Carolina, USA during January 2006 (Marshallonis & Pinckney, 2008) and the most abundant and important gelatinous predator in Chesapeake Bay, USA during spring (Purcell & Nemazie, 1992). Results from investigations in Chesapeake Bay

showed that *N. bachei* generated greater predation pressure on copepods than has been reported for other predatory jellyfish (Fulton & Wear, 1985; Daan, 1986, 1989).

As an “ambush” predator, *Nemopsis bachei* does not swim as it feeds; rather it remains stationary and relies on prey colliding with its extended tentacles (Gerritsen & Strickler, 1977; Costello & Colin, 2002; Costello et al., 2008; Marshalonis & Pinckney, 2008). In contrast to “cruising” predatory jellyfish, like *Aurelia aurita* (Linnaeus, 1758), that increase swimming when prey are detected (Bailey & Batty, 1983; Costello, 1992), and copepods that employ area-restricted search behavior (Woodson et al., 2005, 2007a, b), *N. bachei* medusae may display a different set of behaviors in order to balance feeding with swimming that allows them to remain in or near a thin layer.

In combination, the abundance, range extension and foraging mode of *Nemopsis bachei* make this species a useful example for studies elucidating functional relationships between jellyfish and thin layers. To examine such relationships, laboratory experiments tested the hypothesis that *N. bachei* respond similarly to 5-cm salinity gradients with or without biological thin layers of adult copepods, *Acartia tonsa* Dana, 1849, and green algae, *Nannochloropsis* sp.

Materials and methods

Collection and maintenance of hydromedusae

Individual *Nemopsis bachei* were collected from the surface in approximately 1 m of water along the coastline of a bay located near Meldorf, Germany (54°05'32"N, 8°57'01"E) on 25 June; 2, 14, and 29 July; and 21 August 2008. During summer 2008, this hydromedusa was abundant at the site with collections being most successful in calm weather during 2-h period before high tides. Individual hydromedusae were collected by hand using wide-mouthed, glass jars. The hydromedusae were transferred from the jars into a 20-l bucket containing ambient seawater with a temperature of 21.8–24.8°C and salinity of 24.0–25.8, as measured on the practical salinity scale.

The bucket containing hydromedusae was nested in a container of ambient seawater for transport to a laboratory at the University of Hamburg Institute for

Hydrobiology and Fisheries Science (UHH-IHF). Transport was completed within 2.5 h, and water temperature in the bucket increased by no more than 1°C. The bucket with hydromedusae in seawater from the collection site was placed in a climate-controlled room at $18 \pm 0.5^\circ\text{C}$ and subjected to a 13:11 light:dark cycle until the hydromedusae were used in experiments. Initial attempts to modify the salinity of the ambient seawater by adding fresh water or filtered North Sea water of salinity 35.0 induced mortality. The water was aerated with minimal bubbling to ensure adequate oxygenation without causing physical damage to the hydromedusae.

Hydromedusae used for experiments were not fed. Initial experiments were conducted 24 h after each sampling. Subsequent experiments were conducted daily for a maximum holding time of 1 week. This maximum holding time was well below the 3–8 week periods of starvation tolerated by other hydromedusae (Arai, 1992), and the hydromedusae were deemed sufficiently healthy if they were swimming actively. Each hydromedusa was used only once; each experiment involved 10 individuals.

Sources and maintenance of water and organisms for thin layers

All water used in cultures and experiments was collected from the North Sea and held with constant aeration in storage tanks at UHH-IHF. Filtered North Sea water was prepared using a two-step process: (1) water was filtered sequentially through three, in-line, wound cotton-fiber filters with nominal pore sizes of 100, 10, and 1 μm and (2) the filtrate was filtered sequentially through Whatman glass fiber (GF/C) and membrane filters with nominal pore sizes of 1.0 and 0.1 μm , respectively. Experimental salinities of 18.0, 22.0, and 28.0 ± 0.1 were made by adding fresh water to filtered North Sea water with a salinity of 35.0. Salinities were measured with a WTW TetraCon[®] 325 conductivity meter. The water for experiments was stored in 113 l, plastic buckets inside the climate-controlled room. The salinities used in experiments were chosen to bracket the salinity recorded at the collection site and to create narrow and distinct discontinuities.

Acartia tonsa was chosen as a biological component of experimental thin layers because this calanoid copepod is cultivated at UHH-IHF and *Nemopsis*

bachei is known to feed on both copepodites and adults of *A. tonsa* in situ (Purcell & Nemazie, 1992). Resting eggs produced by copepods collected in the Kiel Bight (54°N, 10°E) during August 2003 were stored at 4°C until they were hatched in gently aerated, filtered North Sea water lowered to a salinity of 18.0. The newly hatched copepods were subjected to a 12:12 light:dark cycle and fed *Rhodomonas* sp. daily until they were adults and at least 14-day-old. At this stage, a sub-sample from the culture of *A. tonsa* then was transferred to a bucket containing filtered North Sea water of salinity 22.0, which was stored with continuous aeration in the same climate-controlled room as the hydromedusae.

Thin layers typically involve several trophic levels (e.g., Cowles et al., 1998); therefore, small (2- μ m spherical diameter), unicellular green algae, *Nannochloropsis* sp., were added to the thin layers as food for *Acartia tonsa*. In preliminary trials, visual observations indicated that *A. tonsa* aggregated near and fed readily on *Nannochloropsis* sp., which remained in the thin layers, whereas *Rhodomonas* sp. sank (Frost, unpublished data). *Nannochloropsis* sp. used in the experiments were drawn from cultures maintained at UHH-IHF. The inoculum was obtained in 2007 from Dansk Skaldyrcenter, a shellfish hatchery located near Limfjord, Denmark. The culture medium comprised filtered and autoclaved North Sea water of salinity 22.0, nutrient and vitamin solutions (Walne, 1970), and 50 mg l⁻¹ biotin (Støttrup & Jensen, 1990). The culture was continuously aerated and stored in the same climate-controlled room as the hydromedusae and copepods.

Experimental system

Each experiment occurred in a 1-cm thick, columnar, glass tank (15 × 15 × 50 cm; Fig. 1). A scale with 1-cm markings was affixed to the outside of the tank along one edge. In each experiment, a consistent light regime was supplied by an 11-W lamp transmitting light through a diffuser comprising a pane of glass fitted with a sheet of vellum paper. This diffuser functioned like milk glass commonly used in photography. A black, fabric backdrop enhanced contrast in video images captured with a SONY Handycam® HDR-SR12E high definition camcorder operating at 25 frames s⁻¹ and a resolution of 1,920 × 1,080 pixels. The camcorder was mounted on a LINOS™

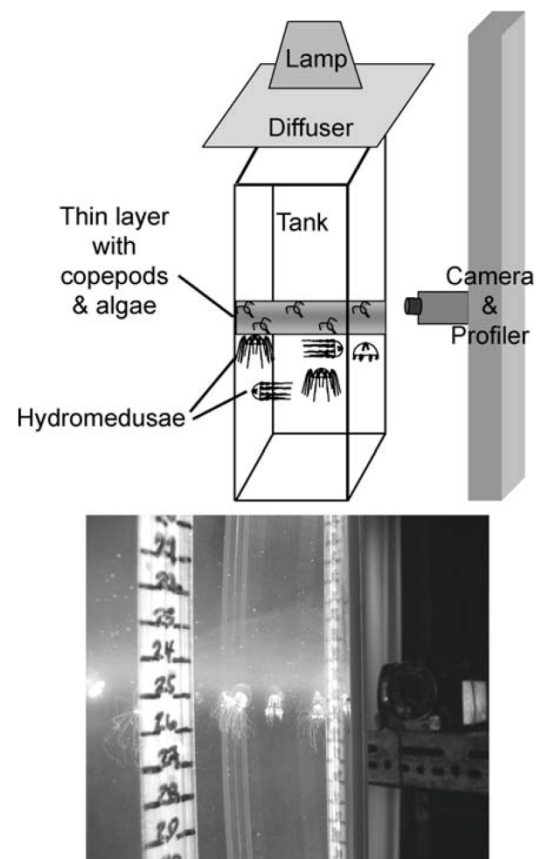


Fig. 1 Experimental system for testing the behavior of the hydromedusa, *Nemopsis bachei*. A salinity gradient with a biological thin layer of algae and copepods is shown. Salinities of the water were 18 above, 20–27 within, and 28 below the gradient. Algae and copepods were absent in experiments involving a salinity gradient without a biological thin layer. Inset is a photograph of an experiment using a biological thin layer. Figure is not drawn to scale

vertical motion, rail profiler in a position that yielded a 13 × 13 × 7.5 cm or 1.2–1.4 l field of view. The camcorder was panned manually every 10–15 min to scan the vertical extent of the tank. When not panning, the camcorder was focused on the biological thin layer or salinity gradient that had been established in the water column as described below. Video records and direct observations were conducted for 5 h so that delayed responses to salinity gradients and food, such as osmoconformation and satiation, could affect more immediate responses, such as swimming and feeding (Tiselius, 1992).

All experiments involved a stratified water column with a salinity gradient representing the physical discontinuity. Gradients were created by carefully and slowly pouring water of salinity 28.0 along the walls of the tank while it was held at an angle, to avoid generating air bubbles, and then layering water of salinity 18.0 into the upper portion of the tank. The less saline water was dispensed from a carboy fitted with a tap and tubing that ended in a t-valve. At the end of this process, the lower and upper portions of the water column each were approximately 22-cm high, and these layers were separated by a 5-cm thick salinity gradient. Each salinity gradient was profiled using a WTW TetraCon® 325 conductivity meter at the end of the observations to confirm its persistence.

Half of the 16 experiments with salinity gradients included biological thin layers containing green algae, *Nannochloropsis* sp., and adult copepods, *Acartia tonsa*. One 100-ml aliquot of *Nannochloropsis* sp. was prepared for each of these experiments. The aliquots contained an average of 3.04×10^6 cells ml⁻¹ (particle diameters 2.38–5.00 µm) as measured with a Beckman Multisizer™ 3 Coulter Counter® 20 min or less before the experiment. In addition, a 100-ml sample of *A. tonsa* was concentrated on a sieve (280-µm mesh), transferred to a Bogorov chamber, and enumerated using magnification from a dissecting microscope to determine the aliquot needed to obtain 400–500 individuals. Thin layers of algae and copepods were formed by slowly introducing the algae and then the copepods into the salinity gradient with a 60-ml, plastic syringe barrel connected to tubing that ended in a t-valve. Flow was controlled with a tubing clamp. On average, the resulting biological thin layers were 3–4 cm thick with volumes of 0.51–0.68 l.

After preparation of the stratified water column with or without a biological thin layer, 10 hydromedusae were introduced individually into the bottom portion of each water column using a polyvinylchloride (PVC) tube. For all 16 experiments, the lower boundaries of salinity gradients or biological thin layers were located near the center of the tank (i.e., 24–27 cm from the top). In order to minimize disruption to the stratified water columns and biological thin layers, the PVC tube was inserted and removed very slowly against one corner of the tank.

The two types of experiments compared and contrasted responses of hydromedusae to sharply defined physical discontinuities and to biological thin

layers comprising similar micro-scale discontinuities with high concentrations of organisms (Dekshenieks et al., 2001; Cowles, 2004).

Video analysis

Video streams were split and analyzed using the Sony Picture Utility software Picture Motion Browser Ver.3.0.00. Metrics recorded included the vertical distribution of hydromedusae and any reliably discernible activities, especially movement and feeding. In addition, the vertical distribution of copepods was recorded to track the availability of potential copepod prey.

Activities of hydromedusae were recorded from 1-min video segments beginning 10, 30, 50, 70, 90, 110, 180, and 300 min after each experiment began, and the vertical distributions of hydromedusae were determined from manual pans beginning 30 min after the start of each experiment and recurring every 10–15 min for 5 h. Tentacular bulbs at the intersections between the tentacles and umbrellar margins served as reference points for measuring vertical locations of hydromedusae.

The vertical distributions of copepod prey were quantified in video frames taken at 1, 3, and 5 h to show each of the three sections of the water column (6–14 cm or above, 19–27 cm or in, and 36–44 cm or below the biological thin layer). The positions of copepods were marked on a plastic transparency laid on top of each video frame, and the marks were counted and converted to numbers of copepods l⁻¹ using the volume of the field of view. In addition, the rates of changes in prey densities were not predictable within or between experiments. Therefore, the prey densities used in analyses of *Nemopsis bachei* behaviors were derived from counts of copepods in biological thin layers made from individual video frames captured in each of the eight time intervals allocated to observing the hydromedusae.

Data analyses

Analyses of variance (ANOVAs) were used to assess changes in the vertical distributions of copepods and hydromedusae, as well as differences in the activities exhibited by hydromedusae over time and versus

varying copepod densities. Prior to each ANOVA, normality was assessed with Ryan–Joiner tests, and homoscedasticity was assessed with Cochran’s tests. Data were transformed as necessary to satisfy these assumptions ($P > 0.05$). In cases where the assumptions were not met, the potential for increased Type I error was considered during interpretation of the ANOVAs. All statistical analyses were performed using MiniTab 15.1.00 Solutions (MiniTab Inc.) and functions within Microsoft Excel 2003 (Microsoft Inc.). In general, only significant F values and relevant means \pm standard errors (SEs) were reported.

In experiments with a biological thin layer, the vertical distributions of *Acartia tonsa* were compared among time intervals in order to track the availability of prey for the hydromedusae. Data comprised the proportions of copepods in the biological thin layer, and these data were arcsin transformed prior to analysis. The ANOVA treated time intervals as a random factor with three levels, 1, 3, and 5 h.

The vertical distributions of *Nemopsis bachei* were compared between experiments with and without a biological thin layer, among five time intervals (30–60, 61–90, 91–120, 121–180, and ≥ 181 min), and among copepod densities in the biological thin layers. Data comprised the proportions of hydromedusae aggregated at the biological thin layers, located within the depth range 19–27 cm. These data were calculated from the total number of hydromedusae observed during vertical pans, and they were arcsin transformed before analyses. In a two-way ANOVA, the presence and absence of a biological thin layer were treated as levels of a fixed factor, and time intervals were treated as levels of a random factor. In a one-way ANOVA, prey densities were treated as levels of a random factor.

Wherever appropriate, variations in the activities displayed by hydromedusae were compared between experiments with and without a biological thin layer, among time intervals, and among prey densities. In ANOVAs, the presence or absence of biological thin layers were treated as levels of a fixed factor and time intervals and prey densities were treated as levels of random factors, with the number and span of the levels chosen to yield balanced replication.

Results

Vertical distributions of copepods and hydromedusae

Profiles of salinity indicated that gradients were located between 19 and 27 cm from the top of the tank (Fig. 2). Within the gradients, which were approximately 5-cm deep, salinities increased from 20.0 to 27.0. In experiments with biological thin layers, visual observations confirmed that *Nannochloropsis* sp. remained concentrated at the salinity gradients throughout the 5-h period of observation, but *Acartia tonsa*, the prey provided for hydromedusae, dispersed during the same time periods (Fig. 2). A total of 72 observations indicated that on average 22.6 ± 1.8 , 73.8 ± 2.5 , and $3.6 \pm 1.0\%$ of the copepods were above, in, and below the layer of concentrated algae during the first hour, and these proportions shifted to 53.2 ± 4.4 , 33.8 ± 4.8 , and $13.0 \pm 3.7\%$ during the fifth hour. In fact, the proportion of copepods in the biological thin layer decreased significantly through time ($F_{2,21} = 24.60$, $P < 0.01$). The changes in copepod distributions occurred gradually over a relatively long time interval, which indicated that neither negative nor positive phototaxis was a dominant influence. These changes provided a basis for examining variation in the behavior of *Nemopsis bachei* from another viewpoint, i.e., relative to the changes in the density of prey remaining in the biological thin layers.

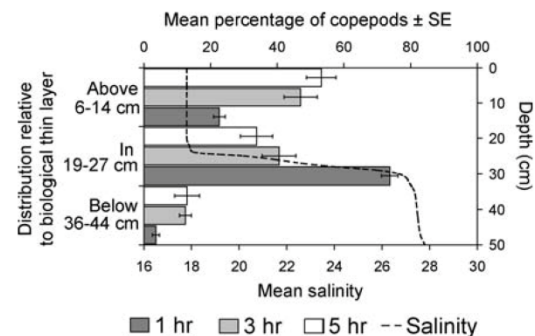


Fig. 2 Vertical distribution of available copepod prey (*Acartia tonsa*) relative to a salinity gradient with and without thin layers of algae during tests of the behavior of the hydromedusa, *Nemopsis bachei*. The percentages of copepods in different depth intervals and the salinities represent means from 16 experiments. SE standard error

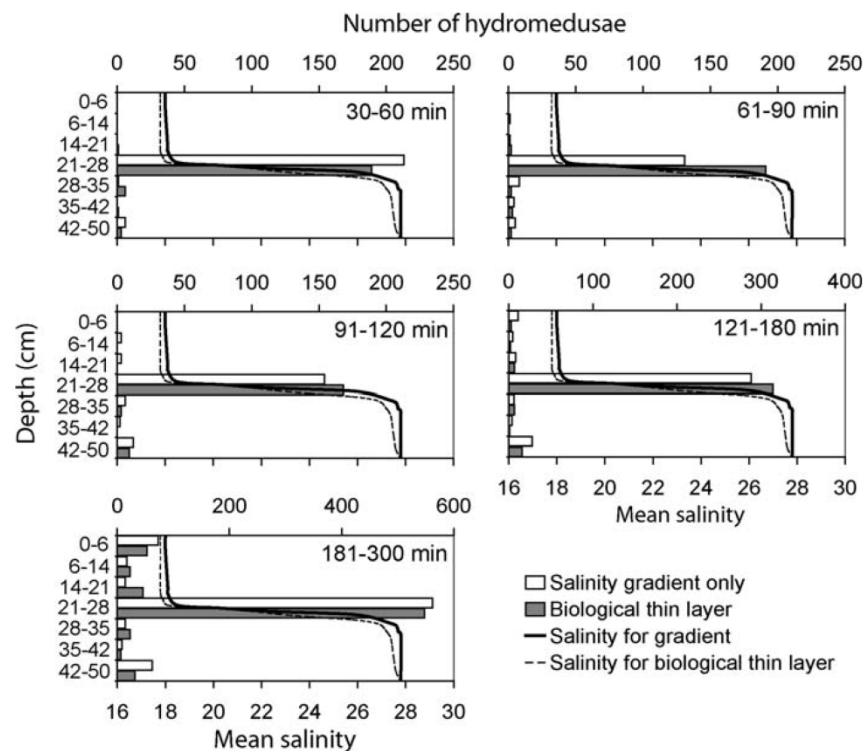
The vertical distributions of *Nemopsis bachei* medusae were determined from a total of 332 video scans equally divided between experiments with and without biological thin layers. The hydromedusae were strongly concentrated in the salinity gradients and in the thin layers (Fig. 3). Nevertheless, they were capable of traversing the entire water column, passing through the salinity gradient or biological thin layer into more or less saline seawater as indicated by the eventual presence of hydromedusae in all depth intervals. The vertical distribution of hydromedusae differed significantly among time intervals ($F_{4,69} = 6.03$, $P < 0.05$) but not between experiments with or without biological thin layers or among the combinations of these two factors. Thus, the overall trend was similar in experiments with and without biological thin layers, and the mean proportions of hydromedusae in the depth intervals could be averaged across all experiments. These mean proportions decreased from $95.5 \pm 1.9\%$ at the start of experiments to $75.6 \pm 4.4\%$ after 3 h. Approximately half of the dispersal occurred after 2 h of

observation, which suggested that dispersal of *N. bachei* was not caused primarily by a negative or positive phototaxis.

Activities of hydromedusae

During the 16 experiments, a total of 128, 1-min video segments were collected over a total of 80 h. *Nemopsis bachei* were classified as active (swimming or feeding) or non-active. Velocities (cm s^{-1}) were measured for swimming hydromedusae, with swimming defined as a minimum of five pulses yielding movement in any direction. Without these guidelines, swimming could be confused with pulses that regulated position in the water column. Furthermore, observations confirmed that swimming was not an integral part of prey capture, which was consistent with reports for other ambush predators (Costello, 1992). The numbers of hydromedusae feeding were counted in fields of view that included biological thin layers in those eight experiments. Steps in the feeding process were defined as contact and retention of a

Fig. 3 Vertical distributions of the hydromedusa, *Nemopsis bachei*, in experiments testing its behavior relative to a salinity gradient versus relative to a salinity gradient with a biological thin layer of algae and copepods. The numbers of hydromedusae represent the sums of all individuals in each depth interval across the appropriate experiments, and the salinities represent means across those same experiments



copepod on a tentacle, transfer of the copepod into the mouth, and return of the empty tentacle to an outstretched, sit-and-wait position. Every copepod captured was transferred successfully to the mouth of the hydromedusa; therefore, efficiencies of all steps in the feeding process were 100%. Additional information about feeding behavior was derived from encounter rates, defined as the elapsed time between successive captures by individual hydromedusae, and handling times, defined as the elapsed time from capture to transfer into the mouth.

The proportions of active hydromedusae (swimming or feeding) were examined with two ANOVAs. In one analysis, these proportions were compared among experiments with and without biological thin layers, among time intervals and among combinations of these two factors. The interaction term in this ANOVA was significant ($F_{7,112} = 5.99$, $P < 0.01$), indicating that the proportions of active hydromedusae differed among time intervals and that the pattern differed between experiments with and without biological thin layers. At 10–11 min, an average of $67.1 \pm 7.3\%$ and $42.1 \pm 7.1\%$ of hydromedusae were active in experiments with and without biological thin layers, respectively (Fig. 4a). At 300–301 min, an average of $92.6 \pm 3.9\%$ of hydromedusae were active in experiments with biological thin layers, but only $1.6 \pm 1.6\%$ of hydromedusae were active in experiments without biological thin layers (Fig. 4a). In experiments with biological thin layers, the proportions of hydromedusae recorded as active did not differ significantly among prey densities ($F_{6,57} = 2.21$, $P > 0.05$). On average, $92.4 \pm 2.6\%$ of hydromedusae were active at prey densities of 0–10 copepods l^{-1} and $62.5 \pm 13.8\%$ were active at prey densities of ≥ 151 copepods l^{-1} (Fig. 4b).

Swimming velocities were examined with two ANOVAs that paralleled those above. Swimming velocities differed significantly between experiments with and without biological thin layers ($F_{1,7} = 5.45$, $P < 0.05$), but not among time intervals or the interaction of these two factors. Although statistically different, the mean swimming velocities were very similar, i.e., 1.24 ± 0.28 and 0.95 ± 0.22 cm s^{-1} for hydromedusae in experiments with and without biological thin layers, respectively. In addition, swimming velocities did not differ significantly across the range of prey densities ($F_{6,38} = 0.94$, $P > 0.05$). Mean swimming velocities varied from

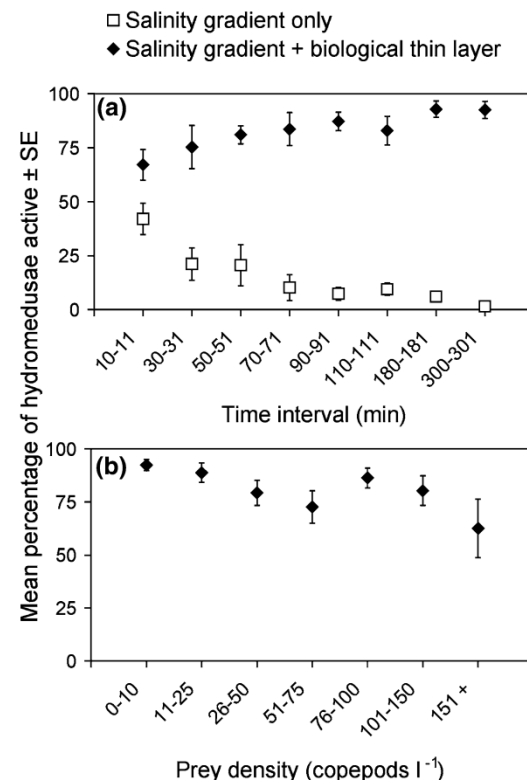


Fig. 4 Mean percentages of the hydromedusa, *Nemopsis bachei*, recorded as active (swimming or feeding) during experiments testing its behavior relative to a salinity gradient versus relative to a salinity gradient with a biological thin layer of algae and copepods. Means were calculated for (a) time intervals and (b) prey densities. Densities of copepod prey varied independently of elapsed time. SE standard error

0.72 ± 0.30 cm s^{-1} at prey densities of 26–50 copepods l^{-1} to 1.32 ± 0.30 cm s^{-1} at 51–75 copepods l^{-1} . The average bell height of *Nemopsis bachei* used in the experiments was 1 cm; therefore, the mean swimming velocities across all experiments ranged from 0.72 to 1.32 bell heights s^{-1} .

Numbers of hydromedusae feeding were compared with one-way ANOVAs. The numbers feeding differed significantly among time intervals ($F_{7,56} = 9.57$, $P < 0.01$) and across the range of prey densities ($F_{6,86} = 6.52$, $P < 0.01$). The mean number of hydromedusae feeding decreased from 3.9 ± 1.4 at 10–11 min to 0.4 ± 0.1 at 70–71 min (Fig. 5a). After that time, the mean number of hydromedusae feeding remained at or below 0.2 ± 0.1 for the duration of the experiments. In contrast, the mean number of

hydromedusae feeding increased significantly from 0.2 ± 0.1 to 3.0 ± 0.1 across prey densities ranging from 0–10 copepods l^{-1} to ≥ 151 copepods l^{-1} (Fig. 5b).

Mean encounter rates (encounters hydromedusa $^{-1}$ 10 min $^{-1}$) also were analyzed with one-way ANOVAs, which were interpreted cautiously because the transformed data were not normally distributed. The total number and distribution of encounters, which could not be controlled, meant that pooling was required to yield more balanced replication among time intervals and prey densities. The mean encounter rate at 10–11 min was 4.7 ± 1.1 encounters hydromedusa $^{-1}$ 10 min $^{-1}$, and the mean encounter rates at 30–31 min and beyond were $\leq 1.8 \pm 0.5$ encounters hydromedusa $^{-1}$ 10 min $^{-1}$, which represented a significant difference ($F_{4,19} = 3.96$, $P = 0.02$; Fig. 6a). In addition, encounter rates were significantly higher

when hydromedusae were exposed to ≥ 101 copepods l^{-1} ($F_{3,29} = 3.21$, $P = 0.04$). Encounter rates rose to 3.9 ± 0.6 encounters hydromedusa $^{-1}$ 10 min $^{-1}$ at ≥ 101 copepods l^{-1} from 1.5 ± 0.16 , 1.7 ± 0.26 , and 1.8 ± 0.7 encounters hydromedusa $^{-1}$ 10 min $^{-1}$ at 0–25, 26–75, and 76–100 copepods l^{-1} , respectively (Fig. 6b).

Mean handling times (s) were compared among time intervals and prey densities, with the non-significant results considered reliable even though transformed data were not normally distributed. Handling times did not differ significantly among time intervals or across the range of prey densities ($F_{4,41} = 0.37$, $P > 0.05$; $F_{5,40} = 1.64$, $P > 0.05$; respectively). Across all time intervals and prey

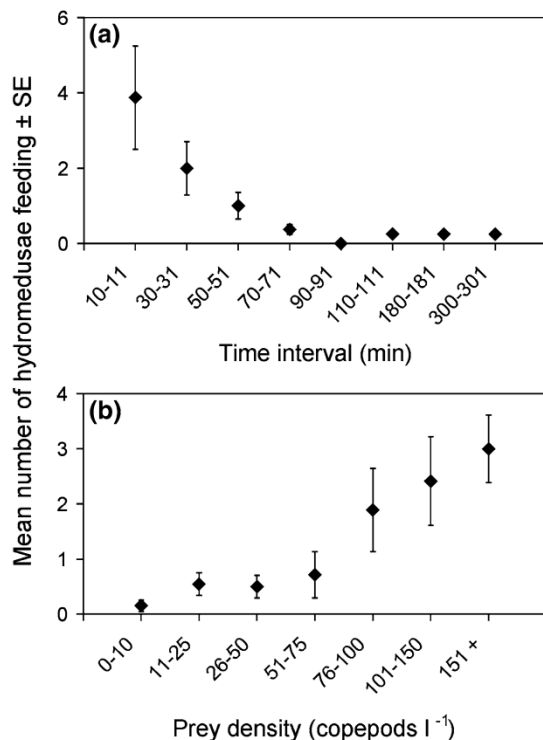


Fig. 5 Mean numbers of the hydromedusa, *Nemopsis bachei*, feeding during experiments testing its behavior relative to a salinity gradient versus relative to a salinity gradient with a biological thin layer of algae and copepods. Means were calculated for (a) time intervals and (b) prey densities. Densities of copepod prey varied independently of elapsed time. SE standard error

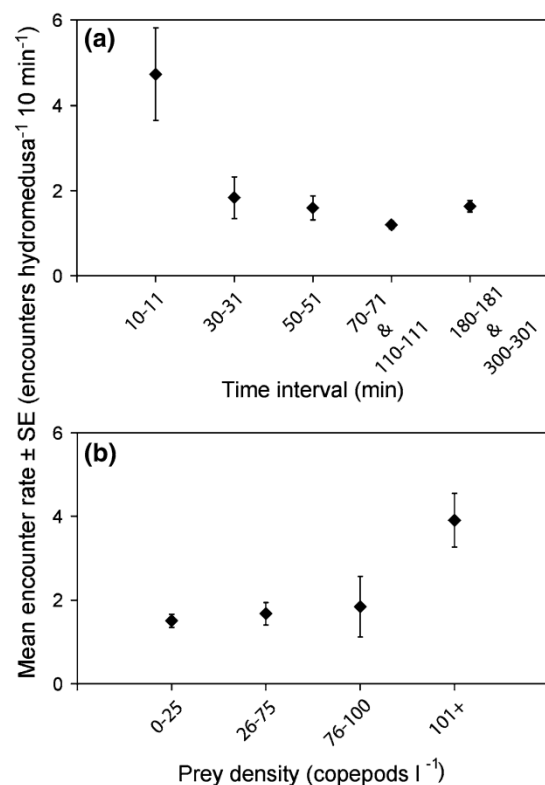


Fig. 6 Mean encounter rates between the hydromedusa, *Nemopsis bachei*, and its copepod prey, *Acartia tonsa*, during experiments testing the behavior of hydromedusae relative to a salinity gradient versus relative to a salinity gradient with a biological thin layer of algae and copepods. Means were calculated for (a) time intervals and (b) prey densities. Densities of copepod prey varied independently of elapsed time. SE standard error

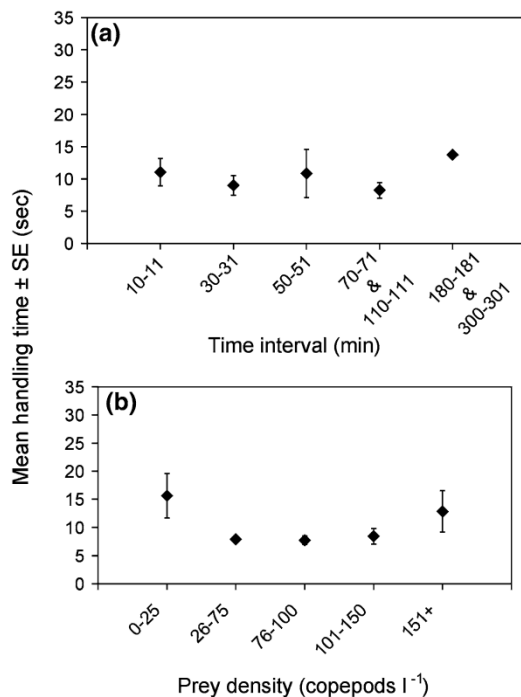


Fig. 7 Mean handling times for the hydromedusa, *Nemopsis bachei*, to transfer its prey, *Acartia tonsa*, into its mouth during experiments testing the behavior of hydromedusae relative to a salinity gradient versus relative to a salinity gradient with a biological thin layer of algae and copepods. Means were calculated for (a) time intervals and (b) prey densities. Densities of copepod prey varied independently of elapsed time. SE standard error

densities, mean handling times varied from 7.7 ± 0.8 to 15.6 ± 4.0 s (Fig. 7a, b).

Discussion

Dense concentrations of living material in thin layers have the potential to influence behaviors of organisms, feeding success, growth rates, reproductive rates, and predation pressure in coastal systems (McManus et al., 2003). The factors that drive the formation and maintenance of these layers are varied and largely unquantified, but nevertheless, the presence and persistence of thin layers are likely to alter biogeochemical cycles, define food webs, enhance fisheries productivity, and influence responses to climate change (Dekshenieks et al., 2001; Stacey et al., 2007; Birch et al., 2008).

Similarly, gelatinous zooplankton, a diverse and sometimes invasive faunal group, also are known to shape marine ecosystems (e.g., Boero et al., 2008). Unfortunately, the distribution and abundance of gelatinous zooplankton are generally underestimated, especially when these voracious consumers bloom or aggregate at discontinuities (Arai, 1992; Graham et al., 2001). In their review of the ecological value of gelatinous zooplankton, Boero et al. (2008) state that the life cycles and life histories of gelatinous zooplankton allow them to exploit temporarily abundant resources with irrefutable, but often overlooked, consequences for marine food webs that include direct effects from predation and indirect effects from disruption of trophic links. Thin layers represent patches of abundant resources that could be exploited by gelatinous zooplankton, such as jellyfish, but existing literature on thin layers is limited and largely focused on phytoplankton, microzooplankton, and ichthyoplankton, rather than predatory jellyfish.

This study addressed the nexus between these two issues by determining how a common and increasingly widespread hydromedusa predator, *Nemopsis bachei*, responded to salinity discontinuities with and without other plankton. Salinity gradients and biological thin layers were established successfully, and they persisted throughout all experiments. Careful handling, suitable experimental conditions, a 50-cm-tall experimental column, and multi-hour experiments provided ample space and time for hydromedusae to respond without a significant decrease in their health. In fact, there were no moribund hydromedusae, rather *N. bachei* medusae increased their activity, i.e., swimming or feeding, over time when biological thin layers were present. There also was no statistically significant change in swimming velocities over time, which further indicated that hydromedusae remained healthy. Finally, there also was evidence of feeding by hydromedusae throughout the duration of experiments with biological thin layers.

Distributions of hydromedusae

Over 75% of the hydromedusae aggregated at the salinity gradients with and without biological thin layers, with no statistically significant difference in their distribution between those conditions. These results indicate that the salinity gradient, not the

presence of copepod prey, was the primary influence on the vertical distribution of the hydromedusae.

The results also indicate that hydromedusae did not remain aggregated solely due to osmoregulatory limitations or their ability to swim. *Nemopsis bachei* medusae would have been expected to be able to conform to the salinity differential of 7 that they confronted during the 5-h experiments, because nine other species of hydromedusae conformed to salinity differentials of 3 within an hour (Mills, 1984). In fact, the salinity gradient did not prevent vertical excursions by the hydromedusae, which traversed the entire water column and gradually dispersed to yield minor concentrations at 0–6 cm (lower salinity) and 42–50 cm (higher salinity). In addition, the mean swimming velocities recorded during all experiments did not change significantly over 5 h; therefore, the hydromedusae remained capable of moving away from the salinity gradient.

The sustained aggregation of hydromedusae at salinity gradients was not solely passive or strongly influenced by the presence of organisms, including potential copepod prey. Regardless of the mechanism generating the aggregation, the results of experiments in the present study support previous reports that hydromedusae and other jellyfish will aggregate at discontinuities (Arai, 1992; Graham et al., 2001), which may enhance reproductive success, advection or retention, and feeding.

Changes in activity in response to biological thin layers

Although the vertical distributions of hydromedusae did not differ significantly between experiments with and without biological thin layers, results did indicate significant differences in behavior. The mean percentages of hydromedusae that were active, defined as feeding or swimming, differed significantly between experiments with and without biological thin layers. More hydromedusae were active at the beginning of experiments with biological thin layers (67% vs. 42%), and activity increased over time until 92% of hydromedusae were active after 5 h. In experiments without prey in biological thin layers, activity decreased to approximately 2% over 5 h. The decreased activity through time equates to decreased swimming in experiments without biological thin layers, because feeding could not occur. Nevertheless,

most hydromedusae remained in or near the salinity gradient, which involved limited pulsing of their bells to maintain their positions. In experiments with biological thin layers, the numbers of hydromedusae feeding decreased through time, which means that swimming must have increased in order for the levels of activity to increase. Thus, the biological thin layer did affect the behavior of hydromedusae beyond feeding, but the hydromedusae tended to aggregate in or near a physical gradient regardless of whether or not potential prey were present.

The relative effects of the physical and biological components of thin layers vary among planktonic fauna. For example, *Acartia hudsonica* Pinhey, 1926 aggregated consistently at salinity discontinuities, with exposure to thin layers of diatoms modifying this behavior, probably by inducing area-restricted searching and feeding (Bochdansky & Bollens, 2004). In contrast, other adult copepods displayed various responses to salinity gradients (three species crossed gradients, but four species did not; two species increased residence time in gradients, but seven species did not), with variations hypothesized to relate to species-specific sensory capabilities and adaptive responses to evolutionary pressures deriving from use of habitats with differing salinity regimes (Woodson et al., 2005, 2007a, b). All species remained longer in patches of food or exudates from food, with data suggesting area-restricted searching or slower swimming while feeding as the causes of aggregation, although not all statistical tests were significant. Thus, further research is required to elucidate how proximal cues and evolutionary pressures interact with the sensory capabilities, physiological limitations, and behavioral responses of organisms to yield aggregations at discontinuities like thin layers.

Feeding behavior and foraging strategy

As an ambush predator, *Nemopsis bachei* remains stationary when it feeds; therefore, the encounter rates and encounter radii that determine feeding rates depend heavily on the density or movement of prey (Gerritsen & Strickler, 1977; Costello, 1992; Costello et al., 2008). In experiments with biological thin layers, encounter rates for *N. bachei* reflected changes in the densities of copepod prey. These changes in encounter rates equate to changes in the mean

number of hydromedusae feeding because *N. bachei* displayed 100% capture, transfer, and ingestion efficiencies (as defined by Regula et al., 2009). Increased feeding with increased prey densities also has been reported for other hydromedusae (Fulton & Wear, 1985; Daan, 1986; Matsakis & Nival, 1989), ctenophores (Reeve et al., 1978), scyphomedusae (Båmstedt et al., 1994), and siphonophores (Purcell, 1982; Purcell & Kremer, 1983).

Results of the present study indicate that prey densities were not high enough to saturate the feeding process (Purcell & Nemazie, 1992; Regula et al., 2009). Ingestion rates, as estimated from encounter rates and 100% ingestion efficiency, increased at higher prey densities, with no evidence of a decrease that would indicate saturation. In addition, handling times did not vary significantly through time or across the full range of prey densities. In combination, these results indicate that hydromedusae were capable of consuming every copepod captured by the tentacles.

Given the observed efficiency of feeding and the lack of saturation, encounter rates can be extrapolated to estimate daily ingestion rates for *Nemopsis bachei*. The range of mean encounter rates, 1.5–4.7 encounters hydromedusa⁻¹ 10 min⁻¹, translates to ingestion rates of approximately 9–28 adult copepods h⁻¹, respectively. The high concentration of prey in thin layers may be why these ingestion rates were considerably higher than estimates of 2–15 *Acartia tonsa* copepodites d⁻¹ derived from laboratory experiments with *N. bachei* and 1–41 *A. tonsa* copepodites d⁻¹ derived from field sampling for *N. bachei* exposed to <25 prey l⁻¹ (Purcell & Nemazie, 1992). Ultimately, field surveys or experiments that account for variations in body size, prey densities, temperatures, salinities, and other potential influences will be needed to determine if ingestion rates vary consistently when gelatinous zooplankton encounter high concentrations of prey at narrow discontinuities.

Encounter rates also influenced the allocation of energy to feeding or swimming, which involves tradeoffs because swimming repositions hydromedusae while limiting feeding. Hydromedusae increased their swimming activity as encounter rates decreased to approximately 2 encounters hydromedusa⁻¹ 10 min⁻¹ and feeding success waned. In contrast, swimming did not vary significantly across the range of prey densities created in experiments, which spanned an order of magnitude. Thus, hydromedusae increased swimming

in response to decreased encounters with prey rather than variations in absolute densities of prey. This behavioral response may be the basis of a successful foraging strategy for a predator that remains stationary while ambushing prey, i.e., hydromedusae move from areas yielding low encounter rates and remain in areas yielding higher encounter rates, regardless of whether encounter rates are determined by the density or movement of prey.

Conclusions

This study examined the responses of an ecologically important hydromedusa, *Nemopsis bachei*, to salinity gradients and thin layers containing algae and copepods. The vertical distribution of hydromedusae was most strongly influenced by salinity gradients. The aggregation of hydromedusae at salinity gradients was not solely a passive response resulting from their inability to osmoconform or swim through the gradients. The presence of copepods stimulated feeding, which varied with encounter rates as expected for these ambush predators. Capture, transfer, and ingestion efficiencies were 100%, and feeding increased at higher prey densities without saturation. These results suggest that *N. bachei* can exert significant predation pressure on patches of prey found in thin layers. The frequency of swimming increased when encounters with prey decreased, which suggests that these hydromedusae may swim to new positions when encounter rates and feeding success decrease below some threshold. Such a strategy should increase their chances of finding and exploiting patches of prey, such as those found in thin layers, by balancing feeding with swimming to search for prey, which precludes feeding. In summary, hydromedusae can alter their distribution and feeding in response to salinity gradients and biological thin layers resulting in patches of enhanced predation that would affect the locations and magnitudes of carbon flux in the oceans.

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CHAPTER 3

INFLUENCE OF DECOMPOSING GELATINOUS ZOOPLANKTON AND ITS EFFECT
ON THE PELAGIC ORGANIC MATTER CYCLE

MANUSCRIPT 4: *Pulse perturbations from bacterial decomposition of Chrysaora quinquecirrha (Scyphozoa: Pelagiidae)*



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JELLYFISH BLOOMS

Pulse perturbations from bacterial decomposition of *Chrysaora quinquecirrha* (Scyphozoa: Pelagiidae)

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Abstract Bacteria decomposed damaged and moribund *Chrysaora quinquecirrha* Desor, 1848 releasing a pulse of carbon and nutrients. Tissue decomposed in 5–8 days, with 14 g of wet biomass exhibiting a half-life of 3 days at 22°C, which is 3× longer than previous reports. Decomposition raised mean concentrations of organic carbon and nutrients above controls by 1–2 orders of magnitude. An increase in nitrogen ($16,117 \mu\text{g l}^{-1}$) occurred 24 h after increases in phosphorus ($1,365 \mu\text{g l}^{-1}$) and organic carbon (25 mg l^{-1}). Cocci dominated control incubations, with no significant increase in numbers. In incubations of tissue, bacilli increased exponentially after 6 h to

become dominant, and cocci reproduced at a rate that was 30% slower. These results, and those from previous studies, suggested that natural assemblages may include bacteria that decompose medusae, as well as bacteria that benefit from the subsequent release of carbon and nutrients. This experiment also indicated that proteins and other nitrogenous compounds are less labile in damaged medusae than in dead or homogenized individuals. Overall, dense patches of decomposing medusae represent an important, but poorly documented, component of the trophic shunt that diverts carbon and nutrients incorporated by gelatinous zooplankton into microbial trophic webs.

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Blooms: Interactions with Humans and Fisheries

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Introduction

Medusae raise interesting questions for ecologists seeking to understand carbon and nutrient cycles in marine systems. Individual medusae do not sequester large quantities of carbon and macronutrients because their bodies typically comprise 97% water and 3% organic matter consisting of $72 \pm 14\%$ protein (mean \pm standard deviation), $22 \pm 12\%$ lipids, and $7 \pm 5\%$ carbohydrates (Larson, 1986; Schneider, 1988; Arai et al., 1989; Clarke et al., 1992; Lucas, 1994, 2009; Doyle et al., 2007; Pitt et al., 2009). Nevertheless, dense aggregations and blooms of medusae have been recorded (Graham et al., 2001; Mills, 2001; Richardson et al., 2009), and in such numbers, medusae irrefutably perturb the flow of energy and cycles of elements in an ecosystem.

Mass occurrences of medusae generally last for weeks to months (Mills, 2001; Sexton et al., 2010), and during this time, they assimilate and release carbon and nutrients creating a relatively protracted, press perturbation (sensu Glasby & Underwood, 1996). For example, medusae can consume significant numbers of zooplankton and larval fish and assimilate up to 88% of the carbon in their prey (Mills, 1995; Arai, 1997; Purcell, 1997; Purcell & Arai, 2001; Pitt et al., 2009). In turn, medusae excrete and secrete carbon, nitrogen, and phosphorus, primarily as mucus, ammonium, and phosphate (Pitt et al., 2009; Condon et al., 2011). Excretion rates vary among species, as well as with temperature and feeding history, but releases of $1,114 \mu\text{mol g DW}^{-1} \text{d}^{-1}$ of dissolved organic carbon, $187 \mu\text{mol g DW}^{-1} \text{d}^{-1}$ of ammonium, $137 \mu\text{mol g DW}^{-1} \text{d}^{-1}$ of dissolved organic nitrogen, $36 \mu\text{mol g DW}^{-1} \text{d}^{-1}$ of phosphate, and $12 \mu\text{mol g DW}^{-1} \text{d}^{-1}$ of dissolved organic phosphorus have been recorded (Morand et al., 1987; Malej, 1989, 1991; Schneider, 1989; Nemazie et al., 1993; Hansson & Norrman, 1995; Shimauchi & Uye, 2007; Pitt et al., 2009; Condon et al., 2010, 2011). Rapidly accumulating evidence suggests that when medusae reach sufficient densities, these releases create a press response (sensu Glasby & Underwood, 1996) by supporting phytoplanktonic and bacterial production, although the magnitude of their influence depends heavily on the availability of carbon and nutrients from other sources and rates of flushing (Pitt et al., 2005; Malej et al., 2007; Condon et al., 2010, 2011). Yet, what happens when the medusae in an aggregation or bloom are damaged or die?

Damaged, moribund, or dead medusae should begin to decompose as they sink or drift, in part because the continuous release of organic matter while they were alive insures they are surrounded by a thriving bacterial assemblage (Doores & Cook, 1976; Heeger et al., 1992; Hansson & Norrman, 1995; Riemann et al., 2006). In some cases, decomposition is not completed in the water column, and carcasses of medusae carry hundreds of grams of carbon to the seafloor (Miyake et al., 2002, 2005; Billett et al., 2006; Koppelman & Frost, 2008; Yamamoto et al., 2008; Murty et al., 2009). Observations of a carrion fall of *Pyrosoma atlanticum* Peron, 1804 (Lebrato & Jones, 2009) suggest that benthic scavengers will feed on accumulations of dead and moribund medusae. In addition, one set of field observations in deep water and one set of mesocosm experiments in shallow water indicate that medusae will decompose (Billett et al., 2006; West et al., 2009). Over a period of days, bacterial decomposition and respiration created pulse perturbations (sensu Glasby & Underwood, 1996) consisting of increased nutrients and reduced oxygen concentrations as evidenced by the production of hydrogen sulfide (Billett et al., 2006; West et al., 2009). Depending on the system's response, these two perturbations could yield discrete or protracted responses (sensu Glasby & Underwood, 1996). For example, nutrients could stimulate a discrete increase in primary productivity if there is sufficient light, and hypoxia/anoxia could create a protracted decrease in the abundance of infauna that persists through multiple cycles of recruitment. Thus, an understanding of impacts from carrion falls of medusae requires an understanding of their decomposition.

The three previous studies that examined decomposition of Scyphomedusae used suffocated, frozen or homogenized medusae, without controls for the effects of these treatments (Titelman et al., 2006; West et al., 2009; Tinta et al., 2010). Nevertheless, all three studies indicate that the carcasses of scyphomedusae contain few refractory, structural compounds, so they decay readily as bacteria digest their tissue, thereby releasing carbon, nitrogen, and phosphorus (Titelman et al., 2006; West et al., 2009; Tinta et al., 2010). Bacteria typically increased in abundance by one or more orders of magnitude over a period of days in incubations of suffocated or homogenized medusae (Titelman et al., 2006; Tinta et al., 2010). Measurements of half-lives for carcasses depended on ambient temperatures and ranged from 0.6 to 1.0 d, but these measurements potentially included unquantified loss

of tissue and consumption by scavengers (Titelman et al., 2006). In all cases, concentrations of carbon, nitrogen, and phosphorus in incubations of suffocated, frozen, or homogenized Scyphomedusae were significantly higher than those measured in controls (Titelman et al., 2006; West et al., 2009; Tinta et al., 2010).

This study tests hypotheses arising from the results of the three previous investigations. It employs a laboratory experiment to test the overall hypothesis that a pulse perturbation will be created by decomposing *Chrysaora quinquecirrha* Desor, 1848, a scyphomedusa with a circumglobal distribution and tendency to form aggregations and blooms (Graham, 2001; Graham et al., 2001; Mills, 2001; Purcell, 2005; Purcell & Decker, 2005; Hammer & Dawson, 2009; Sexton et al., 2010). In particular, the experiment addresses three related sub-hypotheses: (i) the half-life of tissue from damaged medusae will be longer than 24 h, (ii) the abundance and composition of bacterial assemblages will differ between incubations with and without tissue from damaged medusae, and (iii) concentrations of total organic carbon, total nitrogen, and total phosphorus will increase in incubations with tissue.

Materials and methods

Collection and handling

Individual Scyphomedusae, *Chrysaora quinquecirrha*, and ambient seawater were collected in 2–3 m of water near the mouth of the Steinhatchee River along Florida's west coast (N 29.6°; W 83.4°). Snorkelers allowed each medusa to swim into a stationary, hand-held, 3-l polypropylene beaker (Kartell) that previously had been washed with a 10% hydrochloric acid solution to minimize contamination from beyond the sampling site. Onboard a boat, bell diameters and any visible signs of damage were recorded before each individual was placed in a new, labeled, 12-l plastic bag containing ambient seawater (Table 1). Each bag with its single medusa, was placed in a covered, 190-l bin containing ambient seawater. To alleviate heat stress, the water in the bin was replaced every 2–3 h. A total of 13 medusae was collected. At the same time, ambient seawater for use in experimental and control incubations was collected in an acid-washed 75-l carboy.

Table 1 Results of analysis of variance for \log_{10} -transformed concentrations of various elements and ratios of total organic carbon to total nitrogen during decomposition of quarters of *Chrysaora quinquecirrha* medusae

Parameter	Anderson–Darling <i>P</i>	Cochran's <i>P</i>	Source	<i>df</i>	SS	MS	<i>F</i>	<i>P</i>
$\text{Log}_{10}(\text{TOC})$	<0.01	<0.01	Tr	1	7.538	7.538	126.82	<0.001
			Dur	8	1.698	0.212	3.57	0.002
			Tr * Dur	8	1.052	0.131	2.21	0.041
			Error	54	3.209	0.059		
$\text{Log}_{10}(\text{TN})$	>0.01	>0.05	Tr	1	37.375	37.375	1989.21	<0.001
			Dur	8	2.120	0.265	14.10	<0.001
			Tr * Dur	8	2.671	0.334	17.77	<0.001
			Error	54	1.015	0.019		
$\text{Log}_{10}(\text{TP})$	>0.05	>0.05	Tr	1	70.307	70.307	1451.52	<0.001
			Dur	8	2.574	0.322	6.64	<0.001
			Tr * Dur	8	1.968	0.246	5.08	<0.001
			Error	54	2.616	0.048		
$\text{Log}_{10}(\text{TOC:TN})$	<0.01	<0.01	Tr	1	11.344	11.344	317.60	<0.001
			Dur	8	0.663	0.083	2.32	0.032
			Tr * Dur	8	0.854	0.107	2.99	0.008
			Error	54	1.929	0.036		

TOC total organic carbon (mg l^{-1}); TN total nitrogen ($\mu\text{g l}^{-1}$); TP total phosphorus ($\mu\text{g l}^{-1}$); TOC:TN ratio of total organic carbon to total nitrogen; Tr treatment, either with or without medusae; Dur duration of incubation

Experimental design

In the laboratory, medusae and water were held for less than 10 h in a climate-controlled room at 22°C (similar to conditions at the collection site) under a 12:12 light:dark cycle. Before processing, individual *Chrysaora quinquecirrha* were examined to ensure they were pulsing, swimming, and free from trapped air bubbles or visible damage to their bells in an effort to establish an unbiased starting point for decomposition. Three of the 13 medusae were classified as unhealthy, and they were held as whole specimens during the experiment. The remaining 10 healthy medusae were treated to simulate damage.

Individual medusae were removed from their plastic bags with acid-washed forceps, placed on a tared foil pan, blotted gently with a paper towel to remove excess water, and weighed to the nearest 0.1 g using an analytical balance. The balance and tared foil pan were cleaned prior to each measurement. With gloved hands, a scalpel was used to section each healthy individual into four, nearly equal pieces that were weighed separately. The 40 quarters created from these 10 medusae varied in weight from 9.6 to 19.6 g because all medusae had oral arms that differed in length and bell diameters that differed by 1–3 cm. According to previously determined random numbers, four replicate quarters were allocated to each of 10 durations, i.e., 0, 2, 6, 10, 24, 48, 72, 96, 120, and 200 h. In addition, previously selected random numbers were used to allocate four replicate controls to each duration.

Individual quarters and each of the three whole *Chrysaora quinquecirrha* medusae were incubated in an acid-washed, 1-l Nalgene plastic bottle that was loosely capped and contained 200 ml of ambient seawater drawn from the well-mixed carboy and 800 ml of air-filled headspace. The controls consisted of 200 ml of ambient seawater in similar, acid-washed, 1-l Nalgene plastic bottles. The water in experimental replicates and controls was devoid of visible zooplankters. Bottles were incubated at 22°C under a 12:12 light:dark cycle.

Sampling and analysis

The progress of decomposition was tracked by recording the state of tissue samples and associated water at least once each day. At each of the selected durations,

any remaining tissue in each experimental replicate was removed and weighed as described above.

Water for counts of bacteria was removed from the appropriate control and experimental bottles, preserved with buffered formalin (final concentrations 2%), and stored at –4°C until analysis. Bacteria in 1-ml aliquots were stained with acridine orange and filtered onto 0.22-μm, black, polycarbonate, membrane filters (Osmonics). Subsequently, filters were mounted onto microscope slides and bacteria enumerated at 1,000× magnification using immersion oil and a Nikon Labophot epifluorescence microscope. Numbers of bacteria per milliliter were estimated from counts of morphotypes in haphazardly chosen sets of five grids, until at least 100 specimens of a single morphotype were counted. Raw counts were scaled to account for dilution, number of grids examined, and the area of each grid.

Samples for carbon and nutrient analyses were preserved with 2 N sulfuric acid to pH <1 and stored at –4°C. Concentrations of total organic carbon (TOC), total nitrogen (TN), and total phosphorus (TP) were measured in aliquots of the appropriate water samples; if the initial value was beyond the relevant detection range, a second aliquot was analyzed after being diluted with pre-filtered, distilled water. Samples for analysis of TOC concentrations (mg l^{–1}) were sparged with carbon dioxide free air for 2 min to remove inorganic carbon prior to high temperature catalytic oxidation using a Shimadzu TOC-5000 analyzer with infra-red carbon dioxide detection. Each sample was analyzed twice, and each analytical run comprised 3–5, 60 μl injections, with injections ceasing when the coefficients of variation among replicates were <5%. Potassium hydrogen phthalate was used as a standard. Samples yielding total nitrogen concentrations (μg l^{–1}) were oxidized with persulfate, and the resulting nitrate was measured with second derivative spectroscopy (Bachmann & Canfield, 1996). Concentrations of TP (μg l^{–1}) were determined using an acidified solution of ammonium molybdate and antimony following a persulfate digestion (Murphy & Riley, 1962; Menzel & Corwin, 1965).

Statistical analyses

An exponential decay model was fitted to mean changes in wet weights of tissue over time. A half-life was calculated using the resulting decay coefficient. The relationship between degradation rates and initial

wet weights of quarters was evaluated by correlating proportional losses of wet weight with initial wet weights.

Linear regressions were used to compare temporal changes in counts of each bacterial morphotype between control and experimental treatments. Residuals were tested for normality with Anderson–Darling tests and equality of variance with Cochran's tests. Data were \log_{10} -transformed to improve normality and homoscedasticity. For each bacterial morphotype, an exponential growth curve was fitted to back-transformed mean counts and a doubling time calculated.

Differences in concentrations of TOC, TN, and TP, as well as ratios of TOC to TN, were tested with ANOVAs. Data were \log_{10} -transformed to improve normality and homoscedasticity, which were evaluated as described above. In ANOVAs, treatment (either control or experimental) and duration of incubation were treated as fixed factors. Data are presented as mean \pm standard error.

Results

Evidence of decomposition began with a smell of rotting tissue that was noted in some incubations at 48 h, but one quarter was still pulsing at 72 h, which highlighted variation in responses to sectioning. The release of hydrogen sulfide was noted at 120 h in some incubations, which indicated the onset of anaerobic decomposition. Through time, wet weights decreased, with no tissue remaining in any sample at 200 h. An exponential decay curve fit to mean weight losses for 0–120 h yielded a half-life of 3 days or 72 h (wet weight = $13.3 \times e^{-0.229 \times \text{days}}$, $r^2 = 0.883$). Proportional rates of tissue loss were not correlated with initial wet weights ($r = 0.272$, $P = 0.089$). In addition, three whole animals weighing 39.6–47.0 g were 92–100% decomposed by 120–200 h.

Samples from four controls spanning 120 h of incubation contained coccoid bacteria ($2.7 \times 10^5 \pm 4.8 \times 10^4$ cells ml^{-1}). Numbers of cocci did not vary significantly throughout the incubation period according to a linear regression (Fig. 1A; $F_{1,2} = 1.67$, $P = 0.326$, $r^2 = 0.45$).

The bacterial assemblage in experimental replicates containing quarters of *Chrysaora quinquecirrha* medusae diverged from that in controls. In analyses of abundance, one anomalously low value from 6 h

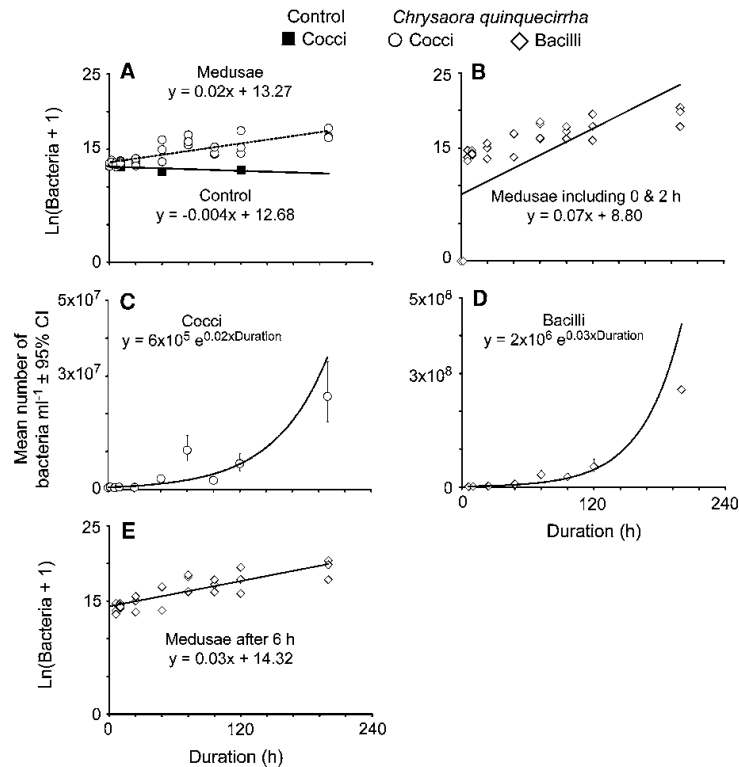
was excluded from the regressions to improve normality and homoscedasticity; the degrees of freedom were reduced accordingly. Cocci were the only bacteria observed through the second hour ($5.5 \times 10^5 \pm 5.0 \times 10^4$ cells ml^{-1}), and their numbers increased significantly throughout the incubation period (Fig. 1A; $F_{1,31} = 67.1$, $P < 0.001$, $r^2 = 0.68$). From the sixth hour, bacilli were visible, and their numbers also increased significantly (Fig. 1B; $F_{1,31} = 21.6$, $P < 0.001$, $r^2 = 0.41$). In fact, the slopes of regression lines for cocci (0.02) and for bacilli (0.03) were similar if the initial samples that did not contain bacilli were excluded (Fig. 1E; $F_{1,24} = 58.6$, $P < 0.001$, $r^2 = 0.70$). Near the end of the experiment, bacterial films formed in some replicates with quarters of *C. quinquecirrha*.

Furthermore, both forms of bacteria exhibited exponential growth through 200 h (Fig. 1C, D; r^2 for cocci = 0.83; r^2 for bacilli = 0.93), with bacilli predominating by an order of magnitude (raw counts at 200 h = $1.2 \times 10^8 \pm 8.8 \times 10^7$ bacilli ml^{-1} and $1.5 \times 10^7 \pm 1.2 \times 10^7$ cocci ml^{-1}). As expected given their predominance, bacilli had a shorter doubling time (24.8 h) than cocci (33.6 h).

As indicated by significant interactions in ANOVAs and comparisons of back-transformed means (Table 1; Fig. 2), the introduction and incubation of tissue from *Chrysaora quinquecirrha* medusae led to increased concentrations of TOC, TN, and TP in the seawater. Concentrations of all elements were elevated immediately, and increases in concentrations of TOC, TN, and TP followed different time courses to eventually become 1–2 orders of magnitude higher than the relatively stable concentrations measured in controls (Fig. 2). As tissue decomposed, TOC and TP concentrations exhibited a three-fold increase between 24 and 48 h, whereas, a similar increase in TN occurred 24 h later (Fig. 2).

The time courses followed by ratios of TOC to TN also differed significantly between control and experimental replicates (Table 1), with ratios in controls always being higher (Fig. 2; 16.9 ± 1.1 for control incubations and 3.1 ± 0.5 for experimental incubations). In experimental replicates, TN concentrations lagged TOC concentrations by 24 h, which led to a maximum ratio of 5.3 at 48 h (Fig. 2B–D). In control replicates, the maximum ratio of 31.1 at 72 h was due to a relatively low mean concentration of TN ($193 \mu\text{g l}^{-1}$ versus mean of all other values = $325 \mu\text{g l}^{-1}$) and a

Fig. 1 Linear regressions based on natural log transformed counts of bacteria versus duration of the experiment and exponential growth curves fitted to back-transformed mean counts of bacilli and cocci in incubations of quarters of *Chrysaora quinquecirrha* medusae. **A** regressions for counts of cocci in seawater controls and experimental incubations with medusae; **B** regression for counts of bacilli in experimental incubations; **C** exponential growth curve fit to counts of cocci in experimental incubations; **D** exponential growth curve fit to counts of bacilli in experimental incubations; **E** regression for counts of bacilli in experimental incubations after they become established at 6 h. *CI* confidence interval



slightly higher mean concentration of TOC (6 mg l^{-1} versus mean of all other values = 5 mg l^{-1}).

Mean TOC, TN, and TP concentrations in experimental replicates yielded an elemental ratio of 23:8:1 (TOC:TN:TP by weight) immediately after the introduction of *C. quinquecirrha* tissue. At 96–120 h, a ratio of 14:8:1 was calculated from the relatively stable mean concentrations of TOC, TN, and TP (Fig. 2). In comparison to the Redfield ratio of 40:7:1, nitrogen and phosphorus concentrations remained near the theoretical balance, whereas carbon was limiting throughout the incubations.

Discussion

Quarters of *Chrysaora quinquecirrha* medusae lost weight exponentially and at rates that were statistically similar for pieces of tissue weighing 9.6–19.6 g. As hypothesized, these rates of tissue loss were slower

than those reported for whole specimens of *Periphylla periphylla* Péron & Lesueur, 1810 (Titelman et al., 2006). In fact, the rate of tissue loss for quarters of *C. quinquecirrha* was 6.7–11.2× slower after using a Q_{10} of 2.3 to adjust the rates for *P. periphylla* from 10.1 or 12.5 to 22°C (Bidle et al., 2002; Titelman et al., 2006). Further evidence that tissue was lost over 8 days comes from observations that whole, unhealthy *C. quinquecirrha* decomposed in the same period of time as quarters of healthy individuals. In addition, previously frozen, whole *Catostylus mosaicus* Quoy & Gaimard, 1824 decomposed completely in approximately 9 days when resting on the bottom at 30°C (West et al., 2009). Although oxygen concentrations probably remained higher during the in situ incubations of *P. periphylla* in mesh bags, the most likely explanations for the more rapid change in wet weights would be the observed, but unquantified, loss of tissue during sample recovery and consumption by zooplankton that colonized the samples (Titelman et al., 2006).

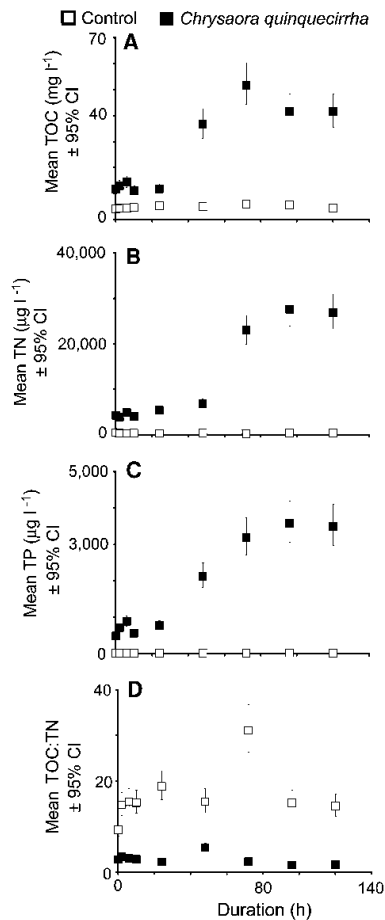


Fig. 2 Back-transformed mean concentrations of **A** total organic carbon (TOC in mg l^{-1}), **B** total nitrogen (TN in $\mu\text{g l}^{-1}$), and **C** total phosphorus (TP in $\mu\text{g l}^{-1}$), as well as **D** ratios of total organic carbon to total nitrogen in incubations containing quarters of *Chrysaora quinquecirrha* medusae and seawater controls. *CI* confidence interval

Tissue was not lost during *C. quinquecirrha* incubations, which did not contain visible zooplanktonic scavengers. Identifying the degree of consistency in decomposition rates and separating the consequences of scavenging and decomposition will be important for modeling of carbon and nutrient cycles.

Incubations with tissue from *Chrysaora quinquecirrha* exhibited changes in the abundance of bacteria as hypothesized. As the wet weight of tissue

declined, numbers of two bacterial morphotypes increased exponentially, a bacterial film formed in some experimental replicates, and hydrogen sulfide was produced. The presence of a bacterial film resembled observations of “slime” on a massive carrion fall of *Crambionella orsini* Vanhöffen, 1888 in the Arabian Sea (Billett et al., 2006). Evidence of decreased oxygen concentrations in the experiment with *C. quinquecirrha* matched observations of anoxic sediments associated with the *C. orsini* fall (Billett et al., 2006) and other experiments on decomposition (West et al., 2009; Tinta et al., 2010). Overall, the experiment with *C. quinquecirrha* appeared to simulate conditions associated with carrion falls of Scyphomedusae, which makes the data on the release of carbon and nutrients valuable for predicting the magnitude and duration of these pulse perturbations. In fact, the results will have direct application for the Gulf of Mexico and Chesapeake Bay where *C. quinquecirrha* and several congeners are known to form blooms (Graham, 2001; Graham et al., 2001; Mills, 2001; Purcell, 2005; Purcell & Decker, 2005; Hamner & Dawson, 2009; Sexton et al., 2010).

The hypothesis that incubations with tissue will contain a different bacterial assemblage also was supported. Initially, control and experimental samples contained cocci, with bacilli observed in experimental bottles from 6 h onward. Growth coefficients and doubling times indicated that bacilli grew 1.4-times faster than cocci, and bacilli abundances became an order of magnitude greater. Naturally occurring bacteria from two locations in the Adriatic Sea, with temperatures from 10 to 19°C, grew rapidly on homogenates of *Aurelia* sp., with bacterial abundances typically increasing 100-fold in 1–3 days and only one experiment exhibiting a 6-day lag to maximum densities (Tinta et al., 2010). Bacilli also predominated when homogenized *Periphylla periphylla* medusae were incubated with natural bacterial assemblages (Titelman et al., 2006) and on moribund *Chrysaora quinquecirrha* medusae in Chesapeake Bay (Doores & Cook, 1976). In addition, analyses of bacterial DNA indicated that assemblages differed between seawater controls and incubations with homogenized tissue (Titelman et al., 2006; Tinta et al., 2010). Incubations of medusa tissue with naturally occurring microbial assemblages and specific bacterial isolates showed that numbers of some bacteria decreased or remained static, with the strongest inhibitory effect on bacteria

attributed to the umbrella of *P. periphylla* (Titelman et al., 2006). Nevertheless, numerous bacteria decompose medusae because nine bacterial isolates increased in numbers over 10 h in other experiments (Titelman et al., 2006). In summary, available data indicate that certain bacteria may be primarily responsible for decomposition of medusae and grow more rapidly than other forms that may benefit from the ensuing release of carbon and nutrients. This interpretation receives further support from field observations of higher abundances of certain bacteria in depth zones where *P. periphylla* were abundant (Riemann et al., 2006) and a laboratory experiment demonstrating that *Brevibacterium* sp. JCM 6894, but not *Escherichia coli* ATCC 9637, decomposed tissue of an unspecified medusa (Mimura & Nagata, 2001). In our experiments with *C. quinquecirrha*, coccoid bacteria may have utilized carbon and nutrients released during decomposition driven by bacilli.

Incubations with tissue of damaged medusae yielded the hypothesized increases in carbon and macronutrients. In fact, the introduction of *Chrysaora quinquecirrha* tissue raised concentrations of TOC, TN, and TP by 3-, 9-, and 35-fold, respectively, within ~1 h, suggesting that damaged medusae leak carbon and nutrients. Concentrations of carbon and nutrients were elevated by approximately 1–2 orders of magnitude after 24–48 h in incubations containing tissue being decomposed by bacteria. A $16,117 \mu\text{g l}^{-1}$ increase in TN lagged a $1,365 \mu\text{g l}^{-1}$ increase in TP and a 25 mg l^{-1} increase in TOC by 24 h, which resulted in a maximum TOC:TN ratio at 72 h. Thus, it appeared that nitrogen-rich proteins were not degraded faster than polysaccharides and other carbon-rich compounds, as previously hypothesized (Titelman et al., 2006). Perhaps, the proteins in pieces of tissue were less labile than those in homogenized tissue (Titelman et al., 2006), and the observation that one quarter continued to pulse for 72 h suggests that resistance to decomposition varied among individual *C. quinquecirrha*. Ultimately, the overall TOC:TN ratio in the water from experimental replicates was 2.7 ± 0.4 , which was slightly lower than ratios of 3.4–4.1 previously reported for tissue of other medusae (Larson, 1986; Schneider, 1988; Clarke et al., 1992; Doyle et al., 2007). This discrepancy may have been due to mineralization of carbon during production of bacterial biomass, which would yield inorganic carbon that was not measured in our analyses. In fact,

carbon appeared to be the limiting element throughout the incubations, and changes in TOC:TN:TP ratios between 0 h and 96–120 h indicated that it became increasingly limiting. In combination with increases in bacteria, this relatively large decrease compared to changes in concentrations of nitrogen and phosphorus signified a conversion of “pelagic” TOC to “benthic” bacterial biomass.

In combination with previous reports, our data demonstrate that damaged medusae decompose readily, with carbon, nitrogen, and phosphorus released from relatively labile compounds. Certain bacteria appear to drive decomposition, and the resulting dissolved carbon and nutrients support the growth of other bacteria and phytoplankton as shown here and in other studies (Pitt et al., 2005; Riemann et al., 2006; Malej et al., 2007; Shimauchi & Uye, 2007; Pitt et al., 2009; Condon et al., 2010, 2011). Although they decompose rapidly, carcasses of medusae may reach the sea floor as carrion falls that should provide food for benthic scavengers, will create hot spots with elevated concentrations of key elements in the sediment and adjacent water column, and will contribute to low oxygen concentrations in bottom waters and sediments (Billett et al., 2006; Yamamoto et al., 2008; West et al., 2009; this study). In addition, the results of this and previous studies suggest that pulse perturbations generated by carrion falls of Scyphomedusae should be integrated into the conceptual model of a trophic shunt that diverts carbon, nitrogen, and phosphorus through living gelatinous zooplankton and into microbial trophic webs (Condon et al., 2011). Further work determining rates of decomposition in diverse and realistic situations will yield an improved understanding of differences among species; the influence of temperature, water movement, and other environmental conditions; and differences between dead and living yet damaged medusae.

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CHAPTER 4**DISCUSSION AND FUTURE RESEARCH**

In general, knowledge of the trophic ecology of gelatinous zooplankton grossly lags behind similar knowledge for their hard-bodied zooplanktonic and ichthyoplanktonic prey (Boero et al. 2008). Gelatinous zooplankton are challenging to sample and observe due to their fragility and transparency. However, the advent of improved technology (e.g., acoustics and optics) and sampling tools (e.g., modified nets, autonomous underwater vehicles and remotely operated vehicles) over the last 25 years has led to studies showing that gelatinous zooplankton create considerable predation pressure on hard-bodied zooplankton and ichthyoplankton, which may even cause the collapse of commercial fisheries (Purcell & Nemazie 1992; Mills 1995; Purcell & Arai 2001; Daskalov 2002). In an attempt to better understand the ecology and trophodynamics of gelatinous zooplankton, this thesis employed meso-scale field sampling to identify ecologically significant patterns in the abundance of gelatinous zooplankton and their prey at a discontinuity, experimentally examined the role of fine-scale behavior in creating patterns at discontinuities, and experimentally determined potential benefits and consequences associated with the decomposition of gelatinous zooplankton.

Gelatinous zooplankton represent a conspicuous component of planktonic assemblages throughout the pelagic zone, however, characterization of their distribution, diversity and activity (e.g., feeding rates and metabolic demands) remains inadequate, which may have a disproportionate impact on our current understanding of pelagic trophodynamics and carbon cycling in the global ocean. Strategies to improve our knowledge and understanding of the biogeochemical and ecological interactions in the pelagic zone must encompass novel methodologies to sample the biota at representative temporal and spatial scales, including episodic events, diel variation and fine-scale vertical resolution. Insights

gained from applying such methods will aid in predicting how key interactions may yield beneficial or harmful effects on marine ecosystems and how these interactions will change as the global climate shifts. Within the scope of this thesis, a variety of novel methods, including meso-scale field sampling and fine-scale laboratory experiments, were employed to generate the insights documented in **MANUSCRIPTS 1–4**. These insights contribute to an improved understanding of the trophodynamics and ecological influences of gelatinous zooplankton by determining how the formation, persistence and dissolution of their aggregations may influence interactions with potential prey and the surrounding environment, particularly at sites of discontinuity where such influences may be heightened.

Behavior and Distribution Relative to Discontinuities

Discontinuities represent sharp gradients in key abiotic and biotic factors that can affect how animals move and use resources, and these sites often support enhanced biological activity. To assess distributions of gelatinous zooplankton and their potential prey relative to discontinuities, this thesis used two approaches: one dealt with meso-scale, *in situ* conditions (**MANUSCRIPT 1**) and the other dealt with fine-scale, laboratory conditions (**MANUSCRIPTS 2 and 3**). Despite differences in the faunal assemblages and type of discontinuities, both approaches documented effects of discontinuities on distributions of gelatinous zooplankton and their potential prey.

In the first approach focusing on meso-scale, *in situ* conditions, a sampling net was modified to collect and maintain the integrity of small, fragile, gelatinous zooplankton. **MANUSCRIPT 1** reported that over 50% of 11 gelatinous taxa and 70% of individual gelatinous zooplankters were found below the seasonal thermocline in the shallower, southeastern portion of a transect across the Dogger Bank, North Sea. This differential association with a persistent thermal discontinuity was consistent with findings from other studies. For example, Jacobsen and Norrbin (2009) used a video plankton recorder to sample

along a transect in a semi-enclosed bay in northern Norway that had (1) depths similar to the sites on Dogger Bank (maximum 55 m; average 30 m), (2) a similar assemblage of gelatinous zooplankton (including small hydromedusae and the ctenophore, *Pleurobrachia pileus*), and (3) an even distribution of mesozooplanktonic prey. In contrast to my study, 79% of gelatinous zooplankton captured in the Norwegian bay came from within the density discontinuity, whereas the majority of gelatinous zooplankton on Dogger Bank was found below the thermal discontinuity. Less saline water above the thermocline and 5°C water below the thermocline may have influenced the distribution of gelatinous zooplankton in the Norwegian bay, whereas the salinity was essentially constant and temperatures remained close to 10°C throughout the water column over Dogger Bank. Several other studies also suggested that vertical distributions of this ctenophore can vary temporally and geographically. For example, during 1991–1995, *P. pileus* in the Black Sea was found to remain primarily below the thermocline (Mutlu & Bingel 1999), but this ctenophore was more evenly distributed during 1996–1999 (Kideys & Romanova 2001). Off the Norwegian coast, *P. pileus* was found primarily above the thermocline (Båmstedt 1998), whereas off the west coast of South Africa, *P. pileus* was found throughout the water column, with larger individuals nearer the surface (Gibbons et al. 2003).

In addition to environmental influences, disjunct distributions may arise from interactions among gelatinous zooplankton. A lack of overlap in the vertical and horizontal distributions of the ctenophores *Pleurobrachia pileus* and *Beroe* sp. were attributed to predator-prey interactions in the southeastern North Sea (Greve 1971; Greve & Reiners 1988) and off the west coast of Norway (Båmstedt 1998). In **MANUSCRIPT 1**, the distributions of these ctenophores were not completely disjunct on Dogger Bank, with both taxa being more numerous in the southeast, *Beroe* sp. captured primarily below the thermocline, and *P. pileus* found in only slightly lower numbers at those depths. Similar patterns in vertical distribution

were reported for these ctenophores off the west coast of South Africa where *Beroe* sp. remained above the thermocline and the bulk of the *P. pileus* population, especially smaller individuals, was found below the thermocline (Gibbons et al. 2003). *Pleurobrachia pileus* may be less numerous where *Beroe* sp. is found simply because of predation, but avoidance also may play a role because *P. pileus* has been shown to detect and avoid potential predators (Esser et al. 2004). Such *in situ* tracking of individual behavior has not been documented, despite the technological advances in optical sampling over the last 25 years. Thus, it is important to determine how salinity, temperature, presence of prey, and other factors that vary at discontinuities influence the behavior of individual gelatinous zooplankton and their potential prey in a way that generates vertical patterns in distributions.

In an attempt to address such issues, a novel video-imaging technique was used to assess the distribution and behavior of individual gelatinous zooplankton and their potential prey relative to discontinuities comprising physical gradients with and without biological thin layers. **MANUSCRIPT 2** documented how the hard-bodied zooplankton, *Acartia tonsa*, a potential prey item for a gelatinous predator, behaved in the presence of salinity gradients with and without biological thin layers of algae and whether their behavior differed across developmental stages. Results from **MANUSCRIPT 2** showed that both types of discontinuities affected the behavior of *A. tonsa*. Notably, all developmental stages of this calanoid copepod aggregated at the upper and lower boundaries of salinity gradients and biological discontinuities. In experiments with algae, all developmental stages also exhibited evidence of area-restricted search behavior by increasing their swimming speeds and number of turns, especially as they approached the thin layer where algae were concentrated. Such behavior was most evident for the more active copepodites and adults. Overall, these results indicated that *A. tonsa* detected discontinuities with and without thin layers of algae, and they adjusted their behavior to remain near those discontinuities.

Behaviors exhibited by *Acartia tonsa* in my study showed similarities to those recorded for the same species in studies of predator-prey relationships, escape responses and factors affecting encounter rates with predators. First, trajectories of nauplii involved more lateral movements than adults, as described by Buskey (1994), and second, trajectories generally matched the three patterns described by Titelman and Kiørboe (2003): (1) a straight line, (2) a sawtooth pattern with an occasional loop, or (3) a helical, corkscrew pattern. Trajectories of copepodites and adults included more sawtooth and corkscrew patterns, with the sawtooth pattern being comparable to the “hop and sink” behavior observed for other copepod species (Bainbridge 1952). Third, speeds from undisturbed *A. tonsa* in my study (i.e., 0.34–4.71 cm s⁻¹) spanned the range found in studies that focused on eliciting a response to a disturbance. For instance, speeds of stimulated *A. tonsa* nauplii recorded by Buskey (1994), Titelman (2001) and Titelman and Kiørboe (2003) ranged from 0.01 to 1.04 cm s⁻¹, while speeds of adults ranged from 0.20 to 2.00 cm s⁻¹ (Buskey 1994).

Although other studies have tested the effect of physical gradients or biological thin layers on copepods, to my knowledge, mine is the first study to examine fine-scale, individual behaviors across three developmental stages from one species using a single methodology. Notably, my study provided evidence that all developmental stages detected discontinuities and aggregated at them, with such behavior likely to enhance successful feeding (e.g., Tinbergen et al. 1967; Cowles et al. 1998; Leising & Franks 2002). Given literature that validated the ecological relevance of behaviors exhibited by individual *Acartia tonsa* in response to experimental physical and biological discontinuities, adult *A. tonsa* were deemed appropriate prey to use in subsequent experiments involving a gelatinous predator. The more pronounced movements and larger sizes of adults increased encounter rates with a tentaculate, gelatinous predator, and the sizes suited application of the novel video-imaging technique.

In **MANUSCRIPT 3**, a common and abundant hydromedusa predator was exposed to physical gradients with and without biological thin layers of algae and copepods to document the role of individual behavior in trophodynamics. Results reported in **MANUSCRIPT 3** revealed that the increasingly widespread *Nemopsis bachei* not only aggregated at the discontinuity but also exploited the thin layer of abundant copepod prey. Approximately 75% of *N. bachei* aggregated at the salinity gradients with and without biological thin layers, with no statistically significant difference in their distribution between those treatments. These results indicated that the salinity gradient, not the presence of copepod prey, was the primary influence on the vertical distribution of the hydromedusae. The results also indicated that *N. bachei* did not remain aggregated solely due to osmoregulatory limitations or their ability to swim. *Nemopsis bachei* would have been expected to be able to conform to the salinity differential of 7 that they confronted during the 5-h experiments, because nine other species of hydromedusae conformed to salinity differentials of 3 within an hour (Mills 1984). In fact, the salinity gradient did not prevent vertical excursions by the hydromedusae, which traversed the entire water column and 25% of individuals gradually dispersed into both the lower (0–6 cm) and higher (42–50 cm) salinity layers. Thus, the sustained aggregation of hydromedusae at salinity gradients was not solely passive or strongly influenced by the presence of organisms, including potential copepod prey. Regardless of the mechanisms generating the aggregation, the results from experiments in **MANUSCRIPT 3** conformed with previous reports that hydromedusae and other jellyfish will aggregate at discontinuities, which may enhance reproductive success, advection or retention, and feeding (Arai 1992; Graham et al. 2001).

Although the vertical distributions of *Nemopsis bachei* did not differ significantly between experiments with and without biological thin layers, results did indicate significant differences in behavior. Most hydromedusae remained in or near the salinity gradient, which

involved limited pulsing of their bells to maintain their positions. *Nemopsis bachei* remained healthy and increased their activity, i.e., swimming or feeding, over time when biological thin layers were present. There also was no statistically significant change in swimming velocities over time, which further indicated that hydromedusae remained healthy. Finally, there was evidence of feeding by hydromedusae throughout experiments with biological thin layers. The numbers of feeding hydromedusae decreased through time, which meant that swimming must have increased in order for the levels of activity to increase. Thus, the biological thin layer affected the feeding behavior of hydromedusae, but they tended to aggregate in or near a physical gradient regardless of whether potential prey were present.

In combination, results reported in **MANUSCRIPTS 2** and **3** provided substantial evidence that dense concentrations of living material in thin layers have the potential to influence behaviors of organisms. Although *Acartia tonsa* were distributed evenly throughout the water column at the start of all 12 experiments in **MANUSCRIPT 2**, individuals became significantly more abundant at the upper and lower boundaries of the discontinuities with and without algae over the course of the experimental periods. However, results from **MANUSCRIPT 3** showed that in the presence of a gelatinous predator, hard-bodied zooplankton, *A. tonsa*, moved away from the physical and biological discontinuities during similar experimental periods. In fact, the proportion of copepods remaining in the biological thin layer decreased significantly through time. By the end of the 16 experiments, the majority of *A. tonsa* were located above the discontinuity, with an increased proportion also located below the discontinuity. Thus, the copepods distanced themselves from the gelatinous predator, *Nemopsis bachei*, and the patch of phytoplankton. Importantly, the changes in copepod distributions reported in **MANUSCRIPTS 2** and **3** occurred gradually, which indicated that neither negative nor positive phototaxis was a dominant influence on the behavior of *A. tonsa*. Thus, predation pressure from a gelatinous predator was sufficient to

cause starved *A. tonsa* to avoid, rather than exploit, a patch of food. Given such changes in the behavior of *A. tonsa*, behavioral interactions between a gelatinous predator and their prey near thin layers may generate substantial effects on feeding success, growth rates, reproductive rates, and predation pressure, ultimately creating an ecologically significant top-down influence.

In summary, key information documented in **MANUSCRIPTS 1–3** was: (1) under *in situ* conditions, small gelatinous zooplankton on Dogger Bank primarily were located below a meso-scale thermal discontinuity, whereas their mesozooplanktonic prey were more evenly distributed in the water column; (2) in independent laboratory experiments, gelatinous zooplankton and their potential copepod prey aggregated and remained at fine-scale physical and biological discontinuities; and (3) in combined laboratory experiments, predation pressure from a gelatinous predator elicited behavioral responses from copepods that changed their distribution in the water column and caused them to move away from a patch of food. These results provided further evidence that interactions with discontinuities can be species-specific and individual behavior contributes to distributions and community structure around physical and biological discontinuities (Omori & Hamner 1982; Arai 1992; Graham et al. 2001).

Trophodynamics

Trophic linkages were investigated through the analysis of stable isotope signatures in **MANUSCRIPT 1**. Stable isotope signatures from five taxa of gelatinous zooplankton (*Eutonina indicans*, *Leuckartiara* sp., *Tima bairdi*, *Pleurobrachia pileus*, and *Beroe* sp.) indicated predation on two size classes of mesozooplankton and the potential for intraguild predation. In fact, the results differed according to which $\delta^{13}\text{C}$ signatures were combined with $\delta^{15}\text{N}$ signatures, which would be expected given the similarity of $\delta^{15}\text{N}$ signatures for gelatinous zooplankton and their potential mesozooplanktonic prey. Based on unadjusted

$\delta^{13}\text{C}$ signatures, the constrained solutions generated in IsoSource analyses indicated trophic links to small mesozooplankton for *Eutonina indicans* and *Leuckartiara* sp.; links to large mesozooplankton for *Leuckartiara* sp., *Pleurobrachia pileus* and *Beroe* sp.; and a link between *Beroe* sp. and *Tima bairdi* that suggested intraguild predation. Results of analyses based on $\delta^{13}\text{C}$ signatures adjusted for lipid content suggested intraguild predation between *E. indicans* and *Leuckartiara* sp., *Leuckartiara* sp. and *P. pileus*, and *T. bairdi* and *Beroe* sp. In addition, these results linked *E. indicans* and *T. bairdi* to small mesozooplankton and *P. pileus* to large mesozooplankton.

The dietary contribution from large mesozooplankton identified for *Beroe* sp. probably reflects an isotopic signature obtained through predation on *Pleurobrachia pileus* because species of *Beroe* are thought to consume only gelatinous zooplankton and they are known to consume *P. pileus* (Greve 1971; Greve & Reiners 1988; Purcell 1991; Båmstedt 1998). In addition, the isotopic signatures given in **MANUSCRIPT 1** and a study in the eastern North Sea (Hamer et al. 2011), along with gut contents from other studies, indicate that *P. pileus* feeds heavily on larger copepods including genera captured in the waters above Dogger Bank, North Sea, e.g., *Pseudocalanus* sp., *Acartia* sp., *Metridia* sp., *Temora longicornis*, *Centropages* sp. and *Oithona* sp. (Båmstedt 1998; Mutlu & Bingel 1999).

The link between *Tima bairdi* and *Beroe* sp. probably reflects predation by the medusa on the ctenophore. Species in the genus *Beroe* have been documented to feed primarily on other ctenophores (Purcell 1991), and *T. bairdi* belongs to a family of medusae possessing nematocysts that are effective at capturing soft-bodied prey such as *Beroe* sp. (Purcell & Mills 1988).

Beyond the links between *Beroe* sp. and *Tima bairdi*, the results of five IsoSource analyses suggested intraguild predation among *Eutonina indicans*, *Leuckartiara* sp. and *Pleurobrachia pileus*. *Leuckartiara* sp. and *E. indicans* probably preyed on *P. pileus* because

medusae in these genera are known to eat gelatinous zooplankton, including ctenophores, the medusae tend to be larger, and they should possess the appropriate nematocysts (Purcell & Mills 1988; Purcell 1991). The outcome of trophic interactions between *Leuckartiara* sp. and *E. indicans* may vary because they are similar in size, have similar nematocysts, and feed on gelatinous zooplankton according to data for *E. indicans* and two species of *Leuckartiara* (Purcell & Mills 1988; Purcell 1991).

In terms of trophodynamics, the results documented in **MANUSCRIPT 1** highlighted three key contributions. First, initial insights into the abundance, distribution and trophic links of small, gelatinous zooplankton illustrated the influence of discontinuities on trophic interactions. Second, although abundances at the time of sampling were not at the levels implicated in major ecological changes, comparisons with literature reports for similar small species confirmed that the gelatinous zooplankton assemblage could exert substantial predation pressure (Purcell & Nemazie 1992; Daskalov 2002; Gibbons et al. 2003; Stone 2005; Daskalov & Mamekov 2007; Richardson et al. 2009). Third, **MANUSCRIPT 1** provided a contribution at the regional level. As a contribution to an ecosystem approach to managing marine natural resources, results from **MANUSCRIPT 1** provided an initial evaluation of the ecology of small gelatinous zooplankton over Dogger Bank that had not been integrated into the last four decades of health assessments (Quality Status Reports 1987, 1993, 2000a, b, 2010) or the “Synthesis and New Conception for North Sea Research” (SYCON Synthesis and New Conception for North Sea Research, <http://www1.uni-hamburg.de/SYKON>).

To augment **MANUSCRIPT 1** by detailing fine-scale predatory behavior, **MANUSCRIPT 3** showed that, as an ambush predator, *Nemopsis bachei* remained stationary when it fed; therefore, the encounter rates and encounter radii that determined feeding rates depended heavily on the density or movement of prey (Gerritsen & Strickler 1977; Costello

1992; Costello et al. 2008). Encounter rates for *N. bachei* did reflect changes in the densities of copepod prey. These changes in encounter rates equated to changes in the mean number of hydromedusae feeding because *N. bachei* displayed 100% capture [no. captured/ no. encountered], transfer [no. transferred/ no. captured], and ingestion efficiencies [no. ingested/ no. encountered] (as defined by Regula et al. 2009). Increased feeding with increased prey concentrations also has been reported for other hydromedusae (Fulton & Wear 1985; Daan 1986; Matsakis & Nival 1989), ctenophores (Reeve et al. 1978), scyphomedusae (Clifford & Cargo 1978), and siphonophores (Purcell 1982; Purcell & Kremer 1983). Increased swimming when encounter rates fell below 2 encounters hydromedusa⁻¹ 10 min⁻¹ provided evidence that *N. bachei* can respond to depletion of a patch of prey with behavior that could relocate it to a new patch.

Results in **MANUSCRIPT 3** also indicated that prey concentrations were not high enough to saturate the feeding process (Purcell & Nemazie 1992; Regula et al. 2009). Ingestion rates, as estimated from encounter rates and 100% ingestion efficiency [no. ingested/ no. encountered], increased at higher prey concentrations, with no evidence of a decrease that would indicate saturation. Given this observed efficiency of feeding and lack of saturation, encounter rates were extrapolated to estimate daily ingestion rates for *Nemopsis bachei*, resulting in approximately 9–28 adult copepods h⁻¹. A concentration of prey in thin layers may explain why these ingestion rates were considerably higher than estimates of 2–15 *Acartia tonsa* copepodites d⁻¹ derived from laboratory experiments with *N. bachei* and 1–41 *A. tonsa* copepodites d⁻¹ derived from field sampling for *N. bachei* exposed to <25 prey l⁻¹ (Purcell & Nemazie 1992). Overall, these results suggest that *N. bachei* can exert significant predation pressure on patches of prey found in biological thin layers, with a consequent effect on the locations and magnitudes of carbon flux in the oceans.

Influence on Biogeochemical Cycling

Beyond the effects on trophodynamics in the water column, aggregations and blooms of gelatinous zooplankton may yield substantial ecological effects when the animals are damaged or die. Therefore, **MANUSCRIPT 4** expanded on the results in **MANUSCRIPTS 1–3**, which characterized formation, persistence and behavior within aggregations. Laboratory experiments in **MANUSCRIPT 4** simulated the dissolution of an aggregation with the aim of quantifying carbon and nutrients released during decomposition of damaged and whole scyphomedusae, *Chrysaora quinquecirrha*. As the wet weight of tissue decreased, numbers of two bacterial morphotypes increased exponentially, a bacterial film formed in some experimental replicates, and hydrogen sulfide was produced. The presence of a bacterial film resembled observations of “slime” on a massive carrion fall of *Crambionella orsini* in the Arabian Sea (Billett et al. 2006). Evidence of decreased oxygen concentrations in the experiment with *C. quinquecirrha* matched observations of anoxic sediments associated with the same event (Billett et al. 2006) and reports from other experimental evaluations of decomposition (West et al. 2009; Tinta et al. 2010). In these experiments with *C. quinquecirrha*, coccoid bacteria may have utilized carbon and nutrients released during decomposition mediated by bacilli bacteria. Overall, the experiments with *C. quinquecirrha* appeared to simulate conditions associated with carrion falls of scyphomedusae in warm, shallow water.

The simulated carrion falls significantly altered key biogeochemical parameters, suggesting that damaged or moribund gelatinous zooplankton can have a bottom-up influence. In particular, within approximately 1 h, the introduction of tissue from *Chrysaora quinquecirrha* raised concentrations of total organic carbon, total nitrogen and total phosphorus by 3, 9, and 35×, respectively, suggesting that damaged medusae leak carbon and nutrients. After 24–48 h, concentrations of carbon and nutrients were elevated by

approximately 1–2 orders of magnitude in incubations containing tissue that was being decomposed by bacteria. A $16,117 \mu\text{g l}^{-1}$ increase in total nitrogen lagged a $1,365 \mu\text{g l}^{-1}$ increase in total phosphorus and a 25 mg l^{-1} increase in total organic carbon by 24 h, which resulted in a maximum C:N ratio at 72 h. Thus, it appeared that nitrogen-rich proteins were not degraded faster than polysaccharides and other carbon-rich compounds, as previously hypothesized (Titelman et al. 2006). Perhaps, the proteins in pieces of tissue were less labile than those in homogenized tissue, which was used in Titelman et al. (2006). In fact, the observation that one section of tissue continued to pulse for 72 h suggests that resistance to decomposition varied among individual *C. quinquecirrha*. Ultimately, the overall mean C:N ratio \pm SE in the water from experimental replicates was 2.7 ± 0.4 , which was slightly lower than ratios of 3.4–4.1 previously reported for tissue of other medusae (Larson 1986; Schneider 1988; Clarke et al. 1992). This discrepancy may have been due to mineralization of carbon during production of bacterial biomass, which would yield inorganic carbon that was not measured in my analyses. In fact, carbon appeared to be the limiting element throughout the incubations, and changes in C:N:P ratios between 0 h and 96–120 h indicated that it became increasingly limiting. In combination with increases in bacteria, this relatively large decrease compared to changes in concentrations of nitrogen and phosphorus signified a conversion of “pelagic” total organic carbon to “benthic” bacterial biomass.

In combination, all available data demonstrate that damaged medusae decompose readily, with carbon, nitrogen and phosphorus released from relatively labile compounds. Certain bacteria appear to drive decomposition, and the resulting dissolved carbon and nutrients support the growth of other bacteria and phytoplankton (Pitt et al. 2005; Riemann et al. 2006; Malej et al. 2007; Shimauchi & Uye 2007; Pitt et al. 2009; Condon et al. 2010, 2011; this thesis). Although they decompose rapidly, carcasses of medusae may reach the sea floor as carrion falls that should provide food for benthic scavengers, will create hot spots

with elevated concentrations of key elements in the sediment and adjacent water column, and will contribute to low oxygen concentrations in bottom waters and sediments (Billett et al. 2006; Yamamoto et al. 2008; West et al. 2009; this thesis). In addition, the results in **MANUSCRIPT 4** and previous studies suggest that pulse perturbations generated by carrion falls of scyphomedusae should be integrated into the conceptual model of a trophic shunt that diverts carbon, nitrogen and phosphorus through living gelatinous zooplankton and into microbial trophic webs (Condon et al. 2011).

Future Research

Further research can improve answers to key ecological questions posed throughout **MANUSCRIPTS 1–4**. For instance, results from **MANUSCRIPT 1** are limited by the need to determine how salinity, temperature, the presence of prey, and other factors that vary at discontinuities influence the behavior of individual gelatinous zooplankton to generate patterns in vertical distribution at the population level. In particular, repeated spatial and temporal sampling specifically designed to elucidate the distribution of mesozooplankton, above, within and below thermoclines on Dogger Bank, North Sea would be valuable. Additionally, **MANUSCRIPT 1** draws attention to the need for further work to fully elucidate the diets of small gelatinous zooplankton. In fact, further data on gelatinous zooplankton of all size classes may contribute significantly to sustainable management of natural resources on Dogger Bank and in the North Sea because gelatinous taxa have been implicated in declines or collapses of fisheries in other systems (i.e., Bering Sea, Brodeur et al. 2002, 2008; Gulf of Mexico, Graham 2001, Graham et al. 2003; Irish Seas, Doyle et al. 2008; East Asian Marginal Seas, Uye 2008; Benguella upwelling system, Lynam et al. 2006, Utne-Palm et al. 2010; and Black Sea, Daskalov 2002, Daskalov et al. 2007). If such work combined analysis of stable isotopes with empirical evaluation of the need to adjust signatures for lipid content, identification of gut contents, tracing of lipid biomarkers, and

laboratory feeding experiments, it could overcome the weaknesses associated with each method (Pitt et al. 2009). In general, **MANUSCRIPT 1** is only a small part of a growing trend to employ stable isotope analysis to describe and better understand functional relationships within aquatic food webs. Boecklen et al. (2011) reviewed the use of stable isotopes in trophic ecology and found 119 representative studies (Fig. 1). Of those 119 studies, a scant few focused on Cnidaria, a taxon containing many gelatinous zooplankton. **MANUSCRIPT 1** helps to fill this gap, but there is an obvious need for more studies using stable isotope analysis; especially for plankton concentrated near discontinuities where trophic interactions are intensified, as documented in **MANUSCRIPTS 2** and **3**.

MANUSCRIPT 2 offered a unique characterization of fine-scale, individual behavior of one zooplanktonic species across three developmental stages, but further work on the persistence of such behavior is needed to yield additional insights into its importance in determining ecological patterns. Within the same context, work from **MANUSCRIPT 2** can be further improved by investigating linkages between individual responses to various cues and the distribution of populations. Results from my study suggested that individual behaviors can be species-specific; therefore, investigations of multiple species should be considered. These investigations should not only take place under controlled conditions, such as in laboratory experiments, but also under natural conditions. *In situ* investigations will pose more logistical challenges; consequently, there is a need to develop innovative technology that can allow for tracking of fine-scale, individual behavior, simultaneous quantification of multiple trophic levels, and synoptic sampling of related environmental parameters. Within the scope of this thesis, such an instrument would have improved *in situ* surveys examining how variations in body size, prey concentrations, temperatures, salinities and other potential influences affect ingestion rates when gelatinous zooplankton encounter high concentrations of prey at narrow discontinuities.

MANUSCRIPTS 1–3 attest to accumulating evidence that narrow discontinuities lead to aggregation, heightened biological activity, and increased production and remineralization. **MANUSCRIPT 4** complements **MANUSCRIPTS 1–3** by assessing biogeochemical effects generated through microbial degradation and remineralization of decomposing scyphomedusa that have a circumglobal distribution and a tendency to aggregate or bloom. When gelatinous zooplankton occur en masse at discontinuities, they have the potential to deposit more carbon to the seafloor in a pulse than phytoplankton-based export deposits as a continuous “rain.” However, few gelatinous zooplankton carrion-falls have been documented; therefore, future investigations should address the spatiotemporal scales at which these depositions occur and correlate those data with abiotic factors like climate and anthropogenic influences. In particular, work from **MANUSCRIPT 4** could be further improved by determining rates of decomposition in diverse and realistic situations to yield improved understanding of variation among species; the influence of temperature, water movement and other environmental conditions; and differences between dead and damaged medusae.

In conclusion, this thesis contributes to an improved understanding of the basic ecology of gelatinous zooplankton and their predatory role and biogeochemical influence on marine ecosystems. In particular, the results of original research highlight the import of aggregations near discontinuities. Formation of aggregations determines predation dynamics of gelatinous zooplankton, and dissolution of aggregations can generate substantial biogeochemical pulses of organic matter. Ultimately, the formation, persistence and dissolution of aggregations in and around discontinuities, including biological thin layers, will define food webs, affect fisheries production, alter biogeochemical cycles, and influence responses to climate change.

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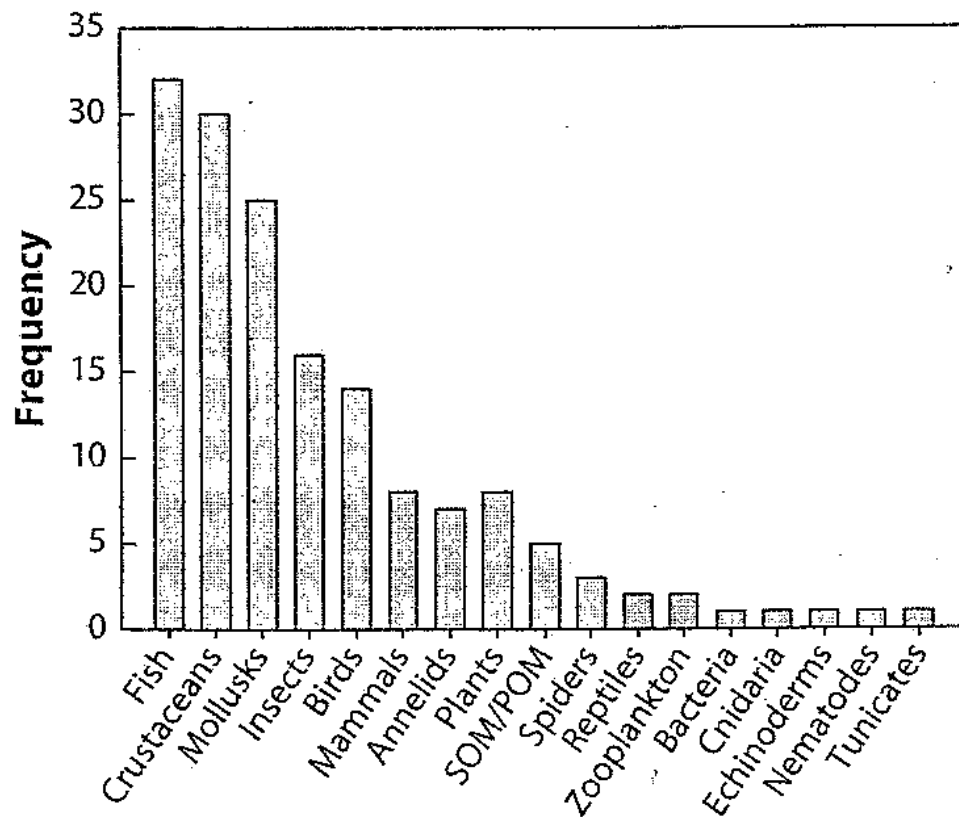


Fig. 1 Frequency histogram of metadata from studies using isotope mixing models for diet reconstruction. Models are characterized by taxonomic group. POM = particulate organic matter; SOM = soil organic matter. Taken from Boecklen et al. 2011.

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me patience, respect and how to enjoy the simplest of things in life. I am forever changed. To SKN, thank you for not allowing me to give up and always showing me your support and care through your gentle nudges.

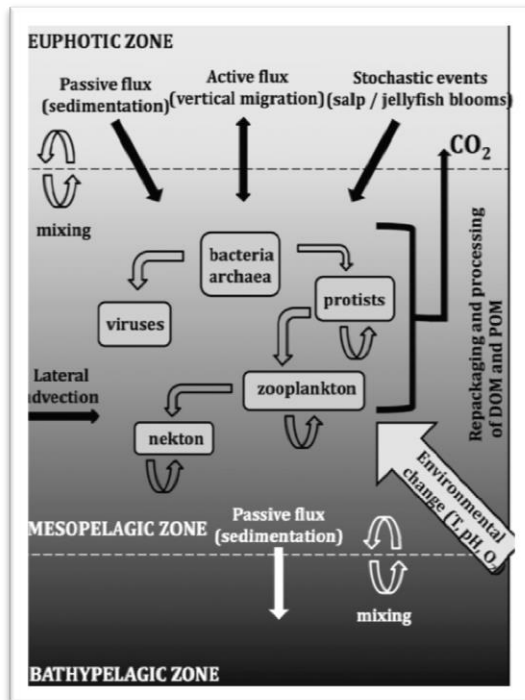
Finally, this thesis is dedicated to the BOZOs. BOZO #1, you have had an immeasurable impact on the person I am today. As a fellow researcher and friend, you have helped me see the many options in life, and you never wavered in support and care. Thank you for believing in me when certain others had their doubts and reminding me to reflect on what I have accomplished whenever I felt unworthy. I could not have managed this without you. BOZO #2, you are my inspiration. It is because of you that I have taken this direction in research, and I am forever appreciative of your enduring support, criticism and friendship. From the deepest recess of my heart, I thank you both for always being there for me.

With this thesis, I hope that I have contributed to the science and made everyone proud.

*Fame is a vapor, popularity an accident, and
riches take wings. Only one thing endures and
that is character.*

Horace Greeley

APPENDIX

MANUSCRIPT 5 (EXCERPT): *The Ecological Role of Zooplankton in the Twilight and Dark Zones of the Ocean*

Chapter 2

THE ECOLOGICAL ROLE OF ZOOPLANKTON IN THE TWILIGHT AND DARK ZONES OF THE OCEAN

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ABSTRACT

Cold temperatures, increased pressure, dim light and the absence of net primary production characterize the twilight zone between 200 and 1000 m of the open ocean. Below this depth is the dark zone consisting of stable abiotic conditions and perpetual darkness, with bioluminescence, the ability of organisms to produce their own light, being the only light source. These zones, also called the meso- and bathypelagic zones, are herein referred to as the deep-sea. The main food sources for organisms inhabiting these zones are vertically migrating animals, sinking carcasses and sinking particulate organic matter (POM) produced by autotrophic and heterotrophic organisms in the euphotic zone.

Approximately 90% of POM is remineralised as it sinks through the water column. Remineralization processes remain poorly characterized throughout the water column because they are difficult to observe and quantify. The character of the material transported to the deep-sea reflects the ecological structure of the upper ocean and influences the remineralization rate. Portions of sinking POM are transported from lower to higher trophic levels via the food chain. Longevity at these higher trophic levels probably exists in the deep-sea due to slow growth and maturity caused by low quantities of food reaching the deep.

A notable gap in understanding the linkage between trophic levels and remineralisation rates is the lack of information about gelatinous organisms. These organisms are widely distributed and occasionally occur in large numbers with biomass exceeding that of fish. This can greatly impact food web dynamics. A likely explanation

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for the paucity of knowledge of gelatinous organisms is the inherent difficulty of sampling them. Most gelatinous organisms are fragile and break into pieces when sampled with commonly used nets. Thus, information on their ecological role and physiological rates is very limited.

This paper will give an overview on deep-sea zooplankton ecology, its temporal distribution, and its role in organic matter cycling, while addressing gaps in knowledge. The following topics should be investigated in future research dealing with deep-sea zooplankton ecology: physiological rates and potentials of functional groups and key species, responses to different quantities and qualities of food (flux), responses to disturbances or changes in temperature, pH, O₂, pollutants etc. and, last but not least, effects of climate change on carbon transformation and storage in the twilight and dark zones.

1. INTRODUCTION

The pelagic environment is the part of the open ocean comprising the water column. It is the largest ecosystem on earth and can be divided into different zones (Figure 1). The euphotic, also known as epipelagic, zone from the surface down to approximately 200 m is illuminated with enough light for photosynthesis. Plants and animals are largely concentrated in this zone. Most of the food for animals living in deeper parts of the ocean is produced in this zone. The environment below the euphotic zone is referred to as the deep-sea in this paper. The twilight, also known as mesopelagic, zone between 200 and 1000 m of the open ocean is the area where only dim light penetrates the water and a net primary production is no longer possible. In the dark, also known as bathypelagic, zone, below 1000 m, light is virtually absent. It is completely dark being only lit by bioluminescence, the light produced by the animals themselves. A specialized zone is the dynamic environment between the deep water and the sea-floor called the benthic boundary layer. This zone is of considerable interest because of the presence of very strong gradients of energy, dissolved and solid chemical components, suspended and particulate organic matter, and the number of organisms living there.

Seasonal changes of plankton abundance in the euphotic zone are primarily due to changing abiotic parameters (temperature, light, nutrients) and are well known for different areas of the ocean (e.g. Parsons and Lalli 1988, Newton *et al.* 1994). While the chemical and physical properties in the twilight zone are still influenced by abiotic and biotic activities at the surface and large areas of oxygen minimum occurring in some ocean regions, these properties hardly vary in the dark zone. In this zone, seasonal differences have been rarely observed. Temperature is generally low (< 6-7 °C) and salinity (~35 PSU) and oxygen concentrations are stable throughout the year (Svedrup *et al.* 1942, Menzies 1965, Mantyla and Reid 1983, Tyler 1995). In some semi-enclosed parts of the ocean, like the Mediterranean and the Red Seas, however, higher temperatures and salinities are observed in the deep-sea (Weikert and Koppelman 1996). The distribution of animals inhabiting the benthic boundary layer is also influenced by tidal currents and benthic storms. Since no surface light penetrates the deep-sea, annual cycles cannot be triggered by changes in light intensity or length of daytime.

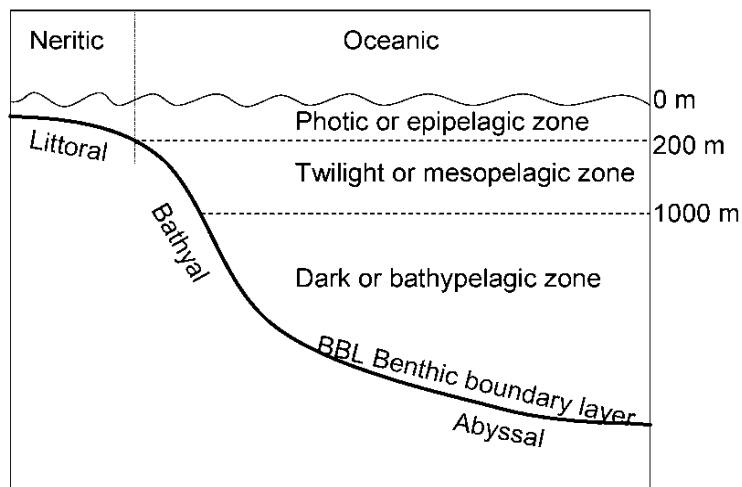


Figure 1. Habitat zones in the open ocean.

Despite these relatively stable conditions, living in the deep-sea is physiologically challenging due to limited resources. The deep-sea ecosystem depends mostly on organic material from the epipelagic zone. Food is transferred to greater depths by the vertical migration of plankton and micronekton (Vinogradov 1968, Vinogradov and Tseitlin 1983) in the form of gut contents or as a result of predation at depth (Angel 1989, Longhurst and Harrison 1989). Food is also transferred to a larger extent by the sinking of particulate organic material (Angel 1984, Fowler and Knauer 1986). Approximately 90% of the sinking POM is remineralized on its way through the water column, and the amount of available food decreases exponentially with increasing depth. This paper will give an overview on deep-sea zooplankton ecology, the temporal variability in distribution exemplified for three different oceanic regions, and its role in organic matter cycling, while addressing current gaps in knowledge.

4. GELATINOUS ORGANISMS - UNDERESTIMATED CONTRIBUTORS TO THE PELAGIC ORGANIC MATTER CYCLE?

We have learned through the previous chapters that temporal differences exist among deep-sea zooplankton and that these differences affect carbon utilization rates. This information, however, is primarily based on hard-bodied zooplankton. Literature related to soft-bodied gelatinous zooplankton, with special emphasis on abundance, distribution, carbon utilization rates and their ability to consume dissolved organic carbon, is even more scarce as compared to the available literature on hard-bodied zooplankton. A likely explanation for the paucity of information about gelatinous zooplankton is the inherent difficulty in sampling them due to their fragility and transparency. In this chapter, we present a general introduction to gelatinous organisms, including current knowledge and technological advances in sampling equipment. For the purpose of this paper, greater emphasis was placed on deep-sea gelatinous zooplankton and their potential role in the cycling of pelagic organic matter.

4.1. Introduction to Gelatinous Zooplankton

Gelatinous zooplankton consist of an assemblage of animals that are transparent, radially symmetrical invertebrates, owning soft bodies lacking hard skeletal components, and delicate with tissues composed of 95% or more of water, comparable to the consistency of gelatin. Unlike fish and hard-bodied zooplankton, which retain their form outside of water, gelatinous zooplankton require the support of their aqueous environment to avoid collapsing into an unidentifiable “blob”. Gelatinous zooplankton are fairly large animals, ranging from centimeters to meters in diameter. These animals do not swim rapidly but remain buoyant because the mixture of salts in their gelatinous tissue is lighter than the weight of the salt in the seawater within which they swim. However, they are not able to swim against currents and therefore belong to the plankton. Gelatinous zooplankton can enhance their ability to remain buoyant by excluding certain ions (primarily sulfate) or accumulating other ions, like ammonium, in their tissues (Wrobel and Mills 1998; <http://www.msc.ucla.edu/oceanglobe/investigations.htm>).

The term gelatinous zooplankton encompasses the two phyla Cnidaria and Ctenophora and members of Tunicata. The phylum Cnidaria includes Anthozoans, Cubomedusae, Hydromedusae and Scyphomedusae. The phylum Ctenophora is distantly related to cnidarians and consists of ctenophores. Tunicata are a subphylum within the phylum Chordata. The class Thaliacea consists of salps and doliolids. Salps may occur as single individuals or chains of individuals. A unique characteristic of doliolids is their ability to feed on planktonic particles using currents created by cilia rather than using their muscle bands to pulse the body like most members of gelatinous zooplankton. The class Larvacea/ Appendicularia consists of appendicularians, which are unique among the tunicates because they take the form of a “tadpole” with a tail containing a notochord.

Gelatinous zooplankton are ubiquitous in marine environments with few occurring in freshwater. Habitats range from coastal nearshore to the open ocean and down into the deep pelagic zone. Species found within such habitats typically have a wide tolerance for environmental variation (Wrobel and Mills 1998). Gelatinous zooplankton deserve their

reputation as the most enigmatic of plankton because they are difficult to capture, preserve and quantify, yet they often constitute a predatory biomass large enough to exert strong top-down influences on productivity and survival of zooplankton and ichthyoplankton. Furthermore, gelatinous zooplankton can exert bottom-up influences on energy transfer to fish and higher predators by altering fluxes of particles, carbon and nutrients. All of these influences remain poorly quantified due to a lack of reliable data (ICES 2003, Frost 2006).

4.2. Advantages of Deep-sea Gelatinous Zooplankton

Within the last 25 years, research into gelatinous zooplankton has revealed a list of adaptations that are believed to allow these organisms to successfully inhabit the vast, cold, dark, high-pressured, food-limited environment of the deep-sea. As compared to shallow-living organisms, depth-related physiological adaptations of deep-sea gelatinous zooplankton include size, watery tissues and flimsy bodies, decreased metabolic demands, bioluminescence as a basis for communication, and chemoreception.

According to Osborn and Barber (2004), one key to the proliferation of larger-sized gelatinous organisms in the twilight zone is the reduction of shear forces at depths below the mixed layer. Large size improves feeding success by increasing the capture rate of particles and prey. Size enhancement is achieved by producing tissue of dilute organic biomass, which offers little palatability for potential predators like fish and crustaceans. The advantage of this adaptive approach is that enhanced size is achieved without a comparable increase in metabolic demand. Thus the physics of the ocean's deep-sea encourages body forms and feeding structures that would be impractical and uncommon at shallower depths (Robison 2004). For instance, the giant siphonophores *Praya* and *Apoemia* have been witnessed to reach lengths of 30 m and 10 m, respectively. Robison (2004) describes *Deepstaria*, a semaeostome medusa, as having extremely pliant bell tissues that can stretch to four or five times its contracted diameter of a meter or more, presumably enabling it to engulf a wide range of prey types. Furthermore, *Stygiomedusa*, another large semaeostome, has bell diameters up to 1.5 m and overall lengths of 4 m or more. The girths of these medusae are large enough to provide ecological substrate for other species. In the case of the siphonophores, juvenile fishes and small amphipods (*Cystisoma*) have been known to shelter themselves along the lengths of the colonies (Robison 2004).

Owning flimsy bodies mostly comprised of water requires low levels of energy allowing gelatinous zooplankton to fast for long periods of time. Investigations into the role of lower temperatures, decreased light levels, increased pressure, and reduced food levels with greater depth ultimately suggest that the decrease in metabolic rate with increasing depth is largely due to a reduced need for locomotory skills. Childress (1995) and Seibel *et al.* (1997, 2000) have demonstrated that below 1000 m, when ambient light is absent, the decline in metabolism stops. Another energy saving tool for gelatinous zooplankton is their reliance on transparency rather than locomotion to avoid detection by their sighted predators and prey. Unlike their surface-dwelling counterparts whose predatory/prey responses are often based on locomotion triggered by vision, deep-sea gelatinous zooplankton lack image-forming eyes. Instead, they rely on other means of communication, like bioluminescence, and have evolved a sensory system to differentiate between bright and dark light intensities (Robison 2004, Nouvian 2006 and contributors therein).

Bioluminescence, a chemical process by which organisms of the deep-sea generate their own light, serves many life-sustaining functions. These functions include locating food, attracting mates and being a defense mechanism. Recently, Haddock *et al.* (2005) discovered a deep-sea siphonophore, *Erenna sp.*, using red-emitting bioluminescent appendages that act like lures for fish prey. A camouflage trick called counterillumination is used as a defense mechanism by many organisms living in the twilight depths of 200 and 1000 m. Through the use of ventral photophores, counterillumination can allow an organism to mask the opacity of its silhouette by adjusting the intensity of its light emission to that of the level of ambient light from above, protecting itself so as to go unseen by potential predators. One of the best examples of bioluminescence as a defense mechanism is the rotary disk display by the common deep-sea scyphozoan, *Atolla wyvillei*, when it is threatened. During this display, thousands of blue lights flash and can attract the attention of larger animals over a distance of 100 m in order to eat predators of *A. wyvillei*, like the mesopelagic shrimp *Notostomus robustus* (Larson *et al.* 1991, Moore *et al.* 1993, Axelsen 2005). At least 90% of deep-sea inhabitants are capable of producing their own light in one fashion or another, making bioluminescence the most widespread form of communication in the deep-sea (Robison 2004, Haddock *et al.* 2005, Nouvian 2006 and contributors therein).

Like bioluminescence, chemoreception, is another form of sensory communication that likely evolved in the deep-sea in the absence of sunlight as a visual cue. Tamburri *et al.* (2000) provides the only direct experimental evidence of chemoreception in deep-sea fauna through a study on specimens of the hydromedusa *Mitrocoma cellularia*. Hydromedusae were collected by a remote operated vehicle (ROV), transported to a laboratory, and when subjected to substrate- and solution-borne prey extract, they responded just as they would have to the smell and taste of actual prey. Naïve experimental *M. cellularia* showed no response to controls that contained no prey extract. To validate the study's findings, similar experiments were conducted in the ocean, on specimens of free-swimming *M. cellularia* that were neither collected nor restrained, yielding the same results as the laboratory findings (Tamburri *et al.* 2000; Robison 2004).

Sensory communication, like chemoreception and bioluminescence, is probably in wide use for intraspecific interactions concerning aggregation, feeding, mating, and simple recognition. Like shallow-water organisms, deep-sea soft-bodied gelatinous organisms may exploit conspicuous chemical warning signals as well as toxins as defense mechanisms against predators. Future deep-sea studies, as suggested by Robison (2004), would include molecular techniques that may allow thorough investigations into species identification, the relatedness of known taxa, and population dynamics to be made *in situ*, which would further our understanding of the adaptations and success of deep-sea gelatinous organisms. The physiological adaptations discussed above illustrate how dynamic and vigorous gelatinous zooplankton can be to a once long perceived lifeless world or, as we know it, the deep-sea.

4.3. Trophic Position

Gelatinous zooplankton consume at each level of the trophic structure within marine ecosystems. Tunicates, with special emphasis on salps, are herbivores, while members of the phyla Cnidaria and Ctenophora are almost entirely carnivores. Members of the class

Hydromedusae demonstrate patterns of omnivory, whereas members of the class Larvacea are primarily detritivores (Sommer and Stibor 2002, Robison 2004, Arai 2005).

In contrast to linearly theoretical food chains, food webs practically represent those species that do not conveniently fit into the conventional trophic levels as set by food chains. In other words, the shortcoming of food chains is that they do not recognize the complexity of interactions that comprise reality, e.g. organisms are consumed by more than one predator and consume more than one type of prey. Food webs are described as energy systems with multiple and shifting interactions between organisms because more than one predator species may consume them. As some organisms grow, they change diets and thus trophic levels as a consequence. Another example of the dynamic nature of food webs is the functional response of an organism when the relative quantity of their food item changes. Competition for food between different predators can develop when their shared food becomes limited. The biomass of top-level species may also be altered due to competition among organisms. For example gelatinous predators, including ctenophores, chaetognaths, medusae and siphonophores, and other carnivorous invertebrate zooplankton compete for copepods, euphausiids and other prey items shared by larval fish (Robison 2004). The best-known evidence of the consequence of such competitive relationships among food webs in the open ocean is the collapse of the Black Sea fishing industry by the invasion of a ctenophore, *Mnemiopsis leidyi* (Vinogradov *et al.* 1989). Tragedies like what happened to the Black Sea fishing industry have driven the scientific community to improve not only their efforts into the study of gelatinous zooplankton but also the technology with which to sample them.

The discovery of a large and complex gelatinous fauna in the deep-sea of Monterey Bay, California, USA, is one of the key ecological advances enabled by progressive technology. Robison (2004) coins the term “jelly web” and provides data from long-term studies conducted in Monterey Bay that show nutrient energy entering the jelly web through two principal pathways: crustacean and gelatinous grazers. Both groups of grazers are consumed by a variety of gelatinous predators, which are themselves consumed by other gelatinous predators. As much as a quarter of total pelagic biomass may be incorporated into the bodies of gelatinous organisms and they can seasonally dominate the second and third trophic levels of mesopelagic communities. However, the residence time and fate beyond the third and fourth trophic levels of the web are still largely unknown. Furthermore, even with a 10-year, ROV-based quantitative time series of video observations and transects in Monterey Bay, the nature and extent of the gelatinous portion of the web has been seriously underestimated and our understanding is still incomplete. Unfortunately to date, there exist few other long-term, extensive studies into deep-sea gelatinous community trophic structures as performed by the Monterey Bay Aquarium Research Institute.

4.4. Organic Matter Utilization

The occurrences of outbreaks (a.k.a. blooms) of gelatinous zooplankton, namely medusae (a.k.a. jellyfish), have the potential to yield a significant flux of organic matter to the deep-sea floor. Gelatinous zooplankton are now being recognized as playing an important role in the transfer of organic matter to the sea-floor by way of fecal aggregates and mucous sheets (Wiebe *et al.* 1979, Robison *et al.* 2005). Fecal aggregates and mucous sheets sink rapidly to the deep-sea floor, provide a labile food source for benthic organisms and make a major

contribution to oceanic biogeochemical fluxes (McCave 1975, Wiebe *et al.* 1976, Honjo 1978, 1980, Dunbar and Berger 1981, Iseki 1981, Pfannkuche and Lochte 1993, Billett *et al.* 2006). Most investigations related to fecal aggregates have been on those of crustacean origin (e.g. Fowler and Small 1972, Turner 1977, Honjo and Roman 1978, Small *et al.* 1979, Turner and Ferrante 1979, Komer *et al.* 1981, Tanoue and Hara 1986). Considerable attention, however, now targets the contribution from gelatinous zooplankton (Alldredge 1976, Wiebe *et al.* 1979, Pomeroy and Deibel 1980, Bruland and Silver 1981, Iseki 1981, Silver and Bruland 1981, Madin 1982, Matsueda *et al.* 1986, Madin *et al.* 2006). Many gelatinous zooplankton are mucus-net feeders and, during blooms, their prolific egesta (feeding nets and external houses) and degesta (feces) will constitute important components of the local particulate organic matter (POM; Morris *et al.* 1988). Still, scarcely documented is the role carcasses of jellyfish play in the downward transfer of carbon. Even less is known about rates in production and use of dissolved organic carbon (DOC) by gelatinous organisms.

NE Atlantic Ocean

Cacchione *et al.* (1978) recorded the occurrence of salp carcasses rolling along the seabed in the Hudson submarine canyon, New York, USA, at a depth of 3400 m. In the same general area, Wiebe *et al.* (1979) estimated a flux of $3.5 \text{ mg C m}^{-2} \text{ d}^{-1}$ in the carcasses of the salps in addition to $12 \text{ mg C m}^{-2} \text{ d}^{-1}$ of rapidly sinking fecal aggregates from a bloom during a mid-summer period. These findings suggest that salp carcasses may provide more than half of the daily energy requirements of the benthic microfauna. Since the longevity of the salp bloom was unknown, Billett *et al.* (2006) calculated the flux of salp feces/carcasses potentially provided a carbon input of about 1 g C m^{-2} by taking data of Wiebe *et al.* (1979) and estimating a two-month salp bloom. Their calculation is equivalent to approximately half the mean annual downward flux of organic carbon in the area as measured by near-bottom sediment traps (Biscaye *et al.* 1988). While observations made during the *Challenger* expedition indicated that salp carcasses could be transported rapidly to abyssal depths and might act as a good food source for benthic fauna (Moseley 1880), gathering supportive evidence that carcasses provide a significant transport pathway for carbon in the oceans is slow-footed. Whale carcasses have been a notable exception (Smith and Baco 2003). With regards to global significance to carbon cycling, however, fauna that occur in great abundance, like jellyfish, have a greater potential to significantly affect carbon cycling and recycling. Unfortunately, direct quantitative observations are rare.

Arabian Sea

Very few data exists on the effects of blooms of jellyfish on carbon flux and on the deep-sea fauna. Of current literature, Billett *et al.* (2006) describe large numbers of the scyphomedusan, *Crambionella orsini*, found dead on the sea floor over a wide area of the Arabian Sea off the coast of Oman at depths between 300 and 3300 m. In this study, photographic transects were used to estimate the standing stock of carbon in jelly detritus deposited on the sea-floor. These estimates ranged from 1.5 to 78 g C m^{-2} . The total annual downward flux of organic carbon as measured by sediment traps at 3100 m off the southeastern coast of Oman during the mid-1990s ranged from 4.3 to $4.8 \text{ g C m}^{-2} \text{ a}^{-1}$ (Honjo *et al.* 1999). By comparing to the highest estimates from the two studies, there is more than an order of magnitude in excess. Thus, jelly detritus in the Arabian Sea may provide a major transport pathway for organic carbon into the deep-sea (Billett *et al.* 2006).

It is uncertain what relevance the observation in the Gulf of Oman has in comparison to other oceanic areas. The authors suggest that it is possible that the jelly detritus occurred only as a result of an intense OMZ. If OMZs are key factors in delaying the rate of degradation of jellyfish as they pass through the water column, then it might be expected that the deposition of jelly detritus is more significant in OMZ regions. Jellyfish blooms, however, are widespread in the world oceans (Mills 2001). With this in mind, jellyfish carcasses, and bodies of other forms of gelatinous zooplankton, could potentially be important vectors of carbon transport to the deep-sea in all areas of the world oceans (Billett *et al.* 2006).

Mediterranean Sea

Morris *et al.* (1988) collected sediment-trap samples, which contained large amounts of organic aggregates and fecal pellets, during and after the occurrence of a salp (*Salpa fusiformis*) bloom in the Bay of Villefranche, Mediterranean Sea in April/May 1985. Salps are active herbivores, occurring in the offshore waters of the Ligurian Sea between April and June (Braconnot 1963, Choe 1985). At its maximum abundance, the salp population is distributed from the coast to at least 18 miles offshore (Nival *et al.* 1985). Sediment-trap aggregates were rich in carbohydrates and mineral grains and had similar rates of sedimentation (900-2100 m d⁻¹) to those of the fecal pellets (1000-2000 m d⁻¹). The study's results from mineralogical and organic chemical analyses indicate the potential effect of these mucus-rich aggregates on local biogeochemical fluxes.

Total organic matter (TOM; expressed as relative % dry matter) from two trap samples taken during the salp bloom measured 18% and 24%, respectively. Insoluble carbohydrate was 11% and 14%, while protein was 6% and 8%, respectively. When comparing these values to those of a trap sample taken six days post-bloom, both TOM and insoluble carbohydrate percentages were lower than those of bloom samples. The post-bloom protein percentage was 7% (Morris *et al.* 1988).

Several investigators have studied the production and sinking rates of POM created by salp blooms (Cacchione *et al.* 1978, Wiebe *et al.* 1979, Pomeroy and Deibel 1980). Salps, at low densities, are known for being ubiquitous throughout the world's oceans. Episodic blooms, however, are also known to occur at continental shelf and slope areas (Thompson 1942, Foxton 1966, Berner 1967, Binet 1976, Wiebe *et al.* 1979, Billett *et al.* 2006). Although infrequent, the pulsed nature of these blooms and the magnitude of the organic material produced can dramatically affect the local flux of surface primary production to deep-sea benthic communities and underlying sediments (Wiebe *et al.* 1979, Madin 1982, Morris *et al.* 1988).

A study by La Ferla and Azzaro (2004) highlights the metabolic carbon dioxide production of the Mediterranean Sea. Data from their case study illustrates the "peculiarity" of the deep Mediterranean waters with regards to other oceanic deep waters. Data within the case study suggests accelerated remineralization rates as having considerable importance to the Mediterranean deep layers with regards to similar oceanic depths (also in La Ferla *et al.* 2003). Of the world's oceans, the Mediterranean Sea has the highest remineralization ratio of 47% (expressed as percentages of depth-integrated deep to depth-integrated shallow), while the Indian Ocean (24.8), Pacific Ocean (21.1) and the Atlantic Ocean (14.9) follow (Packard *et al.* 1988, Naqvi *et al.* 1996, Azzaro 1997, La Ferla and Azzaro 2004). Since the Mediterranean surface water is known for its oligotrophy, this acceleration seems mainly caused by the important advective processes occurring in the Mediterranean rather than by

export production from the upper layers. Such evidence is explained partially by the availability of organic carbon suitable for remineralization and the high temperatures of the Mediterranean deep-sea (~13 °C), which aids in accelerating microbial metabolism (Seritti *et al.* 2003, Koppelman *et al.* 2004).

Pacific Ocean

Robison *et al.* (2005), highlights the importance of the mucous feeding nets of larvaceans in transporting carbon rapidly to the deep-sea floor. The authors calculated an average carbon flux to be $7.6 \text{ g C m}^{-2} \text{ a}^{-1}$ via discarded giant larvacean “houses,” which is roughly equivalent to the seafloor carbon flux at mid-slope depths in Monterey Bay, California, USA ($7.2 \text{ g C m}^{-2} \text{ a}^{-1}$; Pilskaln *et al.* 1996).

Nordic Fjords

Hansson and Norrman (1995) performed a series of incubation experiments to measure the rate of release of DOC by the scyphozoan *Aurelia aurita* that were collected in 1991-1992 in Gullmarsfjorden, Sweden. Data from those experiments showed adult medusae (9.5 to 18 cm in diameter from the Skagerrak) release DOC at a rate ranging from 0.70 to $1.6 \text{ mg C ind}^{-1} \text{ d}^{-1}$. Not only is this range similar to the amount of carbon allocated to reproduction, but also is equivalent to 2.5 and 7.1% of the carbon assimilated in one season (June to September).

In addition to determining DOC release rates by *A. aurita*, the authors found that bacterial growth was stimulated by the presence of the scyphozoan. Minerals bound in the prey items of *A. aurita* may be remineralized to the pelagic microbial community as dissolved organic matter (DOM), which can then be consumed by planktonic microbes as described by Azam *et al.* (1983). As a consequence, *A. aurita* has the potential to influence the microbial food web via the release of DOM to the microbial community (Hansson and Norrman 1995).

Mucus generated by *A. aurita*, which more easily allows prey items to adhere to the medusa, is likely the main source of the DOC observed (Schneider 1989a). Leakage of mucoid particulates associated with feeding may prove to be a key source of DOC, but it is often neglected in measurements of nutrient excretion by medusae. Some medusae excrete considerable amounts of ammonia and phosphate (Schneider 1989b), but their quantitative release and uptake of organic carbon is not well documented.

To clarify carbon use and remineralization processes in the open ocean, recent efforts point toward the understanding of the trophic role of medusae in the pelagic food web (e.g. Frost 2006, Madin *et al.* 2006). It remains unclear to what extent the carbon consumed by *A. aurita* is transferred to other planktonic organisms. One way to address the cost of losing carbon to the water-column is to relate the amount of carbon released by *A. aurita* to the total energy budget of the scyphozoan (Hansson and Norrman 1995). Consequently, more data is necessary to produce reliable correlations between carbon use and loss to the pelagic environment.

Remarks

Although a thorough search for the literature above was performed, readers should not consider it a completely exhaustive one. The examples highlighted above illustrate recent and future turns in the study of gelatinous zooplankton and their importance to the pelagic ecosystem. There is a wealth of knowledge that remains unclear, unsolved and undiscovered.

4.5. Technological Advances and What Lies Ahead

Increasing awareness and appreciation of how gelatinous zooplankton affect the health of the oceans has largely been due to *in situ* observational techniques and to rigorous investigations of trophic interactions (Hamner *et al.* 1975, CIESM 2001, Haddock 2004). In the mid-1970s, observations on the biology and distribution of gelatinous zooplankton by SCUBA divers stimulated speculation about the structure of tropical, oceanic ecosystems. It became evident that conventional sampling with plankton nets did not quantify gelatinous zooplankton accurately due to their patchy distributions, delicate construction and escape responses. Furthermore, as gelatinous zooplankton feed, they create mucous aggregates containing particulate matter that are also irregularly distributed, delicate and significantly undersampled by plankton nets (Hamner *et al.* 1975). Although blue-water SCUBA diving was one of the first methods for observing gelatinous zooplankton *in situ*, it provides a limited view of their diversity because many species occur below safe diving depths or are overlooked because they are small and transparent (Båmstedt *et al.* 2003, Haddock 2004).

Solutions to the challenges of sampling gelatinous zooplankton and the resulting lack of rigorous data include altering conventional plankton nets and developing new techniques (Figure 15). Various kinds and sizes of closed cod ends on plankton nets help minimize damage to gelatinous fauna. In addition, video, real-time image analysis, holographic sampling systems and multi-frequency acoustics offer significant promise as replacements or complements to nets (Smith and Rumohr 2005). These new techniques allow for continuous or semi-continuous sampling across a range of spatial scales. Such sampling will help decipher the infamous patchy distributions of gelatinous zooplankton and provide insights into the relationships between gelatinous zooplankton, hydrographic structures and other mesozooplankton (ICES 2003).

The question still remains, why do we need to learn more about gelatinous zooplankton? Perhaps the best, irrefutable reason for understanding their effects on the health of the ocean comes from the devastating impact that high densities can have on human activities. Local fisheries, like the tragedy of the Black Sea, are not the only victims of blooms of gelatinous zooplankton; coastal economies dependent on tourism can suffer as well. Summer is a prime season for both tourists and gelatinous zooplankton blooms. The idea of being entangled in a bloom of stinging medusae is enough to deter any beachcomber.

Research into what drives these episodic blooms can help create reliable numerical models to better predict when and where they might occur. Other “hot topics” with respect to gelatinous zooplankton include cataloging deep-sea faunal diversity and behavior and resolving the role of gelatinous zooplankton in carbon flux as part of addressing global warming. Deep-sea faunal research has revealed a number of never-before-seen or described species of gelatinous zooplankton. For example, scientists at the Monterey Bay Aquarium Research Institute (MBARI) have identified two new species of deep-sea gelatinous zooplankton, *Tiburonia granrojo* and *Stellamedusa ventana*, since 2003 (Matsumoto *et al.* 2003, Raskoff and Matsumoto 2004). These discoveries would not have been possible without such tools and techniques as described in Figure 15.

Sampling and observational techniques for gelatinous zooplankton
(modified from G. Gorsky, CIESM 2001; Frost 2006)

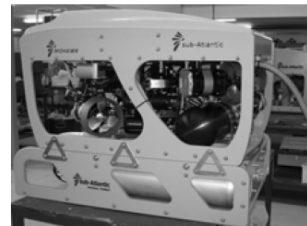
➤ **Net Sampling**

- i. *Standard WP11 nets* with mesh size larger than 200µm are used for meso-zooplankton sampling. Net sampling often destroys fragile gelatinous structures but adapted cod ends could reduce the damage.
- ii. *Large collector nets* (20-60 l) are used for sampling large gelatinous organisms. Their use is limited due to handling difficulties. When sampling dense populations of medusae, trawl nets are more appropriate.
- iii. *Multiple nets (MOCNESS, BIONESS, Hydrobios)* are poorly adapted for sampling gelatinous plankton, especially for taxonomic purposes, due to their destructive nature.



➤ **Optical Devices**

- i. *Aircraft observations* can determine the extent and spatiotemporal evolution of large outbreaks of gelatinous animals near the water's surface.
- ii. *Autonomous underwater vehicles (AUVs)* are considered the technology of the future in oceanography (Rife and Rock 2001). Eventually, these vehicles will be able to detect patches of organisms and provide images for taxonomic identification.
- iii. *Bioluminescence*, especially the patterns of bioluminescent organelles, can be used as a taxonomic descriptor and optical methods to acquire and treat these signals are in development (Mixed Light Imaging System-MLIS, Widder 1992; see also <http://www.hboi.edu/marinesci/biolum.html>).
- iv. *Submersibles*, whether manned or remotely operated vehicles (ROVs), are well suited for qualitative *in situ* studies of large gelatinous animals. They provide high-quality images and undamaged animals. As compared to manned submersibles, ROVs have narrower fields of vision, slower reaction times and more laborious manipulation.
- v. *Video profiling* promises to be an area of intensive development in the future. The Video Plankton Recorder (VPR) can visualize and quantify small zooplankton. The Underwater Video Profiler (UVP) can visualize macrozooplankton from the surface to a depth of 1000 m. With the rapid progress of imaging technologies, the quality of data collected by both instruments is constantly improving. The instruments support rapid assessment of dominant populations but do not reliably identify rare or new species.



➤ **Acoustics**

Acoustics are not well suited for the study of gelatinous animals because most of them are permeable to sound and do not produce a well-defined backscatter. Some patterns of echoes may be specific to a faunal group but variability is often high.

Figure 15. Sampling and observational techniques for gelatinous zooplankton (modified from G. Gorsky, CIESM 2001; Frost 2006). Image credits: Universität Hamburg - Institut für Hydrobiologie und Fischereiwissenschaft (IHF).

Within the events described above, we can find several ecological questions that seldom receive rigorous answers. How are patches of gelatinous zooplankton distributed across various scales in three-dimensional space? Furthermore, how does this distribution change through time and do the patches have a significant and changing substructure? What hydrographic, biological and behavioral influences create and maintain discrete patches and any associated substructure? What are the magnitudes of the top-down and bottom-up effects from such patches? What quantities of carbon and nutrients become “bound” in the gelatinous zooplankton and where do they go? At a minimum, reliable answers to such questions require combining large-scale sampling of gelatinous zooplankton, small-scale sampling and enumeration of specific taxa, and laboratory experiments and measurements on healthy animals to elucidate physiological and trophic states. Ultimately, we need sophisticated sampling techniques that support well-designed natural and manipulative experiments targeting gelatinous zooplankton if we truly want to assess their ecological role in oceanic systems.

With recent and future advances in technology, now is an opportune time for significant advances in our understanding of these enigmatic, delicate and beautiful animals (Haddock 2004).

5. CONCLUSION

Temporal and stochastic changes like increasing reproduction and abundance can be observed through the biota living in the deep-sea despite relatively stable abiotic conditions. The magnitude of these changes, however, decreases with increasing depth. It is not surprising that the animals in the well-lit surface layer of the temperate oceans are showing temporal trends, since the environmental conditions there are subject to seasonal changes like the length of daytime, temperature and the availability and mobilization of nutrients, etc. These effects also influence the animals in the twilight zone because they are closely associated with the euphotic zone via daily and seasonal migrating zooplankton and fishes within these zones. Migration into the dark zone, below 1000 m, was often postulated (Vinogradov 1968), but no direct evidence exists.

Organisms inhabiting the dark zone primarily depend on organic matter and dead corpses sinking from the surface into deeper waters. This sinking occurs in temporally changing quantities and qualities. A temporal reaction on such fluxes was observed in the zooplankton assemblage of the open ocean in the upper part of the dark zone between 1000 and 2500 m, which is also called the upper bathypelagic zone. Below these depths, temporal variations are rarely visible. Finally, when the sinking organic material reaches the bottom, where it accumulates, temporal changes again occur (Wigham *et al.* 2003, Billett *et al.* 2006). Such a “bottom effect” may impact the water-column some hundred meters above the sea bottom.

Based on the knowledge gained so far, we will open the following hypotheses for discussion:

1. There are strong indications that some faunal elements of the zooplankton community in the upper bathypelagic zone of the open ocean respond quickly to increasing availability of food by increasing reproduction. These organisms produce

high amounts of offspring so that some may survive. The reproduction strategy is *r-selected*.

2. The organisms in the lower bathypelagic realm do not show the same response. The abundance is spatially and temporally more or less stable throughout the water column (Weikert and Koppelman 1996, Koppelman and Weikert 1999, Koppelman *et al.* 2003a). Only low numbers of offspring are produced. The production strategy is *K-selected*. This is biologically a "quiet" zone, meaning that predation pressure is reduced and most of the animals are scavengers.
3. Predation by gelatinous organisms and the production of mucous alters the mode of carbon flux in the deep-sea enormously. However, due to methodological difficulties their contribution is hitherto underestimated.
4. In semi-enclosed basins with a high deep-water temperature, like the eastern Mediterranean, the "true" deep-sea fauna is impoverished and most of the animals are immigrants from shallower layers. In this environment, significant changes in abiotic parameters and an increased availability of food, as caused by the EMT (Roether *et al.* 1996, Weikert *et al.* 2001), results in long-term changes in the abundance of selected species. These changes will be memorized over an extended time-span of several years.

Knowledge of trophic changes in deep-water environments and the investigation of key taxa, including gelatinous organisms, will help us to better understand the future of deep-sea biota in a changing environment caused by CO₂ emissions and global warming. Based on increases in pH, changes in organic matter inputs both in quality and quantity, and changes in hydrography, it will become necessary to learn more about the vulnerability of deep-water ecosystems. In order to accomplish this, we have to understand the effects of climate change on the distribution and physiological capacity of the deep-sea fauna.

Investigations of deep-water animals are technologically challenging tasks (see also Figure 15) because it is hard to catch these animals alive and healthy for experiments. Pressure-retaining sampling chambers (e.g. Youngbluth 1984) and pressure aquaria, as well as *in-situ* laboratories, are necessary to gain sophisticated knowledge on the biology, physiology, and ecology of these organisms. Deep-sea laboratories can be deployed and maintained using remotely operating vehicles (ROV's). In addition, future experiments can be conducted by the use of autonomous underwater vehicles (AUV's).

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CURRICULUM VITAE

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Current Address: University of Florida
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 Gainesville, Florida, USA 32653

EDUCATION

Ph.D. Biological Oceanography, 2014

Institut für Hydrobiologie und Fischereiwissenschaft, Universität Hamburg
 Thesis: *Gelatinous Zooplankton Trophodynamics: Ecological and Biogeochemical Influences on Pelagic Food Webs*
 Advisors: Drs. Clive J. Fox, Marsh J. Youngbluth, and Myron A. Peck

M.Sc. Fisheries and Aquatic Sciences, 2003

Department of Fisheries and Aquatic Sciences, University of Florida
 Thesis: *Ecology of Lake Griffin, a hypereutrophic cyanobacteria dominated lake in central Florida*
 Advisor: Dr. Edward J. Phelps Committee: Drs. Charles Cichra and Mark Brenner

B.Sc. Environmental Science, Technology, 2001

College of Natural Resources and Environment, University of Florida
 Dean: Dr. Stephen R. Humphrey

RESEARCH INTERESTS

Trophodynamics and behavioral adaptations to environmental conditions, with special interest in gelatinous zooplankton. Additional interests include freshwater and marine ecology with emphasis on trophic state, phytoplankton composition and water chemistry.

PROFESSIONAL EXPERIENCE*(A) Positions*

Date	Employer	Position & Selected Duties
07/2010-present	University of Florida	Research Associate field sampling, laboratory analyses, data management
05-07/2009	DTU Aqua, Denmark	Visiting scientist (host: Dr. T. Kiørboe), manuscript preparation
2005-2005	Microbac Laboratories, Inc.	Laboratory Technician water quality analyses, quality control & quality assurance

2004-2004	Harbor Branch Oceanographic Institution	Research Associate cruise logistics, laboratory analyses, data management
2003-2004	University of Florida	Research Assistant field sampling, laboratory analyses, data management
2001-2003	University of Florida	Graduate Research Assistant field sampling, laboratory analyses, data management
1998-2001	University of Florida	Laboratory Technician laboratory analyses, data management

(B) Teaching Assistantships

Date	Employer	Course
2006	Universität Hamburg	Trophodynamics Interactions 14.684
2001	University of Florida	Fish and Limnology FAS 6932

(C) Other Professional Activities

Date	Activity	Duties
2014	ICES Annual Science Meeting	Participant
2014	<i>Journal of Experimental Marine Biology and Ecology</i>	Reviewer
2014	<i>Water Research</i>	Reviewer
2013	UF & Florida Sea Grant ArcGIS 10.1 workshop	Participant
2013	COSEE Florida BioCube educator workshop – Biocube – exploring backyard diversity	Participant
2013	Fourth International Jellyfish Blooms Symposium	Presenter
2012	Indian River Lagoon Symposium 2012: Looking Forward	Participant
2012	<i>Fisheries Research</i>	Reviewer
2012	University of Florida Marine Biology Symposium	Presenter
2011	CERF 21 st Biennial Conference	Presenter
2011	2 nd DTU Aqua Jelly Day- <i>Mnemiopsis leidyi</i> in European Waters: Where are they and what do we know?	Participant
2011	MESOAQUA workshop – Mesocosms in aquatic ecology: use, problems and potentials	Participant
2011	Guest co-editor <i>Hydrobiologia</i>	Editing manuscripts for special volume

2011	<i>Invertebrate Biology</i>	Reviewer
2011	<i>Journal of the Marine Biological Association of the United Kingdom</i>	Reviewer
2010	<i>Chinese Journal of Oceanology and Limnology</i>	Reviewer
2010	Third International Jellyfish Blooms Symposium	Participant
2010	ASLO Ocean Sciences Meeting	Presenter
2008	<i>Marine Biology</i>	Reviewer
2008	Eur-Oceans Final Meeting	Presenter
2008	IMBER IMBIZO Workshop “Integrating biogeochemistry and ecosystems in a changing ocean”	Participant (Mesopelagic), co- author; summary paper published in <i>Deep-Sea Research II</i>
2008	FS Maria S. Merian (MSM 07/3)	Ecological assessment of gelatinous zooplankton, Walvis Bay, Namibia
2007	FS Alkor (AL300)	Ecological assessment of gelatinous zooplankton, Dogger Bank, North Sea
2007	PICES 4 th International Zooplankton Production Symposium	Presenter
2006	FS Meteor (M71/1)	Ecological assessment of gelatinous zooplankton, Anaximander Seamount
2006	Eur-Oceans/NATO Summer School & Advanced Study Institute “Climate Change Impacts on Marine Ecosystems”	Participant
2006	Eur-Oceans Kick-off Meeting	Presenter
2005	ASLO International Meeting	Participant, co-author
2005	R/V Seward Johnson I	Midwater sampling using submersibles
2004	R/V Seward Johnson II	Midwater sampling using submersibles
2003	NALMS 23 rd International Symposium	Presenter
2003	UF FAS-Fishing For Success	Assist the public as they learn fishing ethics
2003	National Shellfish Association	Audiovisual support
1999-03	R/V Discovery	Benthic sampling
2002	Oceans Day at Florida’s Capital	University of Florida co-representative

2001-03	University of Florida Dept. Fisheries and Aquatic Sciences Graduate Student Symposium	Presenter
2001-02	R/V Bellows cruises	Otter trawls, plankton tows and dredging
2000	North American Lake Management Society	Symposium logistics

AWARDS AND HONORS

Date	Award or honor
2013	Selected for participation in COSEE Florida BioCube educator workshop – Biocube: exploring backyard diversity
2011	Selected for participation in MESOAQUA workshop – Mesocosms in aquatic ecology: use, problems and potentials
2006-08	Eur-Oceans PhD Fellowship Award (WP4-SYSMS-1101)
2006	Scholarship to the Eur-Oceans/NATO “Climate Change Impacts on Marine Ecosystems” Summer School, Ankara, Turkey
2003	North American Lake Management Society (NALMS) Student Paper Winner
2002	Florida Certificate of Boating Education

SKILLS

Laboratory:	certified QA/QC chemical analyst	nutrient enrichment bioassays
	algal culture	spectrophotometry
	<i>in situ</i> data logging	gas chromatography
	Winkler titrations	fluorometry
	inverted phase-contrast microscopy	biochemical oxygen demand
	fiber optic oxygen sensors	wet chemistry
	Beckman Coulter Counter	bacterial enumeration
Taxonomy:	cyanobacteria	phytoplankton (freshwater)
	Cnidaria & Ctenophora	mesozooplankton (limited)
Field sampling:	phytoplankton	aquatic plants
	zooplankton	benthic invertebrates
	fish	SCUBA with NITROX
	operation of boats up to 6.5 meters in length	
Software:	Microsoft Office SAS Procite MatLab (novice) ArcGIS 10.1 (novice)	

PUBLICATIONS

1. **Frost, J.R.**, F. Lombard, C.A. Jacoby (submitted) Comparative behavior of three developmental stages of *Acartia tonsa* Dana, 1849 (Copepoda: Calanoida) relative to physical gradients and biological thin layers.
2. Jacoby, C.A., **J.R. Frost**, M.J. Youngbluth, T.K. Frazer (submitted) Distribution, abundance, oxygen consumption and predatory impact of *Beroe cucumis* and

- Bolinopsis infundibulum* (Ctenophora) in the Gulf of Maine and Oceanographer Canyon.
3. **Frost, J.R.**, C.A. Jacoby, T.K. Frazer, A.R. Zimmerman (2012) Pulse perturbations from bacterial decomposition of *Chrysaora quinquecirrha* (Scyphozoa: Pelagiidae). *Hydrobiologia* 690: 247–256.
 4. **Frost, J.R.**, A. Denda, C.J. Fox, C.A. Jacoby, R. Koppelman, M. Holtegaard Nielsen, M.J. Youngbluth (2012) Distribution and trophic links of gelatinous zooplankton on Dogger Bank, North Sea. *Marine Biology* 159: 239–253.
 5. Robinson, C. *et al.* (2010) Mesopelagic zone ecology and biogeochemistry – a synthesis. *Deep-Sea Research II* 57 (16): 1504–1518.
 6. **Frost, J.R.**, C.A. Jacoby, M.J. Youngbluth (2010) Behavior of *Nemopsis bachei* L. Agassiz, 1849 in the presence of physical gradients and biological thin layers. *Hydrobiologia* 645: 97–111.
 7. Jacoby, C.A., M.J. Youngbluth, **J.R. Frost**, P.R. Flood, F. Uiblein, U. Bämstedt, F. Pagès, D. Shale (2009) Vertical distribution, behavior, chemical composition and metabolism of *Stauroteuthis syrtensis* (Octopoda: Cirrata) in the northwest Atlantic. *Aquatic Biology* 5: 13–22.
 8. **Frost, J.R.**, E.J. Phlips, R.S. Fulton III, C.L. Schelske, W. Kenney, M. Cichra (2008) Temporal trends of trophic state variables in a shallow hypereutrophic subtropical lake, Lake Griffin, Florida, USA. *Fundamental and Applied Limnology (Archiv für Hydrobiologie)* 172 (4): 263–271.
 9. Koppelman, R., **J. Frost** (2008) The ecological role of zooplankton in the twilight and dark zones of the ocean, In: *Biological Oceanography Research Trends*, ed. Mertens, LP, Nova Science Publishers, Inc., New York, pp. 67–130.
 10. Christiansen, B. *et al.* (2007) The ecology and biogeochemistry of Anaximenes Mountains, Cruise No. M71, Leg 1, 11–24 December 2006, Heraklion, Meteor-Berichte. 50 pp.
 11. **Frost, J.** (2006) Gelatinous zooplankton: evolution of sampling techniques. *Eur-Oceans Newsletter* 3. www.eur-oceans.eu
 12. Phlips, E.J., **J. Frost**, M. Yilmaz, N. Steigerwalt, M. Cichra (2004) Factors controlling the abundance and composition of blue-green algae in Lake Griffin. Final Report to the St. Johns River Water Management District, Palatka, Florida. (Project #SF669AA)
 13. Phlips, E.J., M. Cichra, **J. Frost** (2002) Assessment of Lake Griffin algal blooms. Final Report to the St. Johns River Water Management District, Palatka, Florida. (Contract#SD419AA)
 14. Phlips, E.J., E. Bledsoe, M. Cichra, S. Badylak, **J. Frost** (2002) The distribution of potentially toxic cyanobacteria in Florida, p. 22–29. In Monograph: “Proceedings of Health Effects of Exposure to Cyanobacteria Toxins: State of the Science,” August 13–14, 2002. <http://www.doh.state.fl.us/Environment/community/aquatic/cyanobacteria.htm>

PRESENTATIONS

1. Jacoby, C.A., **J.R. Frost**, M.J. Youngbluth, T.K. Frazer (2013) Distribution, abundance, oxygen consumption and predatory impact of *Beroe cucumis* and *Bolinopsis infundibulum* (Ctenophora) in the Gulf of Maine and Oceanographer Canyon. Oral Presentation Fourth International Jellyfish Blooms Symposium, Hiroshima, Japan, June 5–7, 2013.
2. **Frost, J.R.**, C.A. Jacoby, T.K. Frazer, A.R. Zimmerman (2012) Pulse perturbations from bacterial decomposition of *Chrysaora quinquecirrha* Desor, 1848 (Scypophozoa: Pelagiidae). Oral Presentation UF Marine Biology Symposium, Whitney Marine Laboratory, St. Augustine, Florida, January 19–20, 2012.
3. **Frost, J.R.**, C.A. Jacoby (2011) Jellyfish and chips. The next “It’s What’s For Dinner” in Florida? Poster Presentation CERF 2011: Societies, Estuaries & Coasts: Adapting to Change, Daytona Beach, Florida, November 6–10, 2011.
4. **Frost, J.R.**, C.A. Jacoby, M.J. Youngbluth (2010) Behavior of *Nemopsis bachei* L. Agassiz, 1849 in the presence of physical gradients and biological thin layers. Poster Presentation ASLO Ocean Sciences Meeting, Portland, Oregon, February 22–26, 2010.
5. **Frost, J.R.** (2009) Interactions between gelatinous zooplankton and discontinuities: Influence on pelagic food webs. Oral Presentation Technical University of Denmark (DTU Aqua Kaffeklubben), Charlottenlund, Denmark. June 24, 2009.
6. **Frost, J.R.**, M.A. St. John, M.J. Youngbluth, C.J. Fox (2008) Distribution and trophic role of gelatinous zooplankton over the frontal system of Dogger Bank, North Sea. Oral Presentation Eur-Oceans Final Meeting, Rome, Italy. November 25–27, 2008.
7. **Frost, J.R.**, C.A. Jacoby, G. Gust, M.H. Nielsen, R.W. Campbell, M.A. St. John (2007) Behavioral and biochemical effects of hydrostatic pressure changes on *Acartia tonsa* (Dana, 1848) (Copepoda: Calanoida): A methodological approach. Oral Presentation PICES 4th International Zooplankton Production Symposium, Hiroshima, Japan. May 28–June 1, 2007.
8. **Frost, J.R.**, M. St. John, C. Fox, M. Youngbluth (2006) Biological, chemical and physical interactions within thin layers: Resolving the trophic role of gelatinous zooplankton. Poster Presentation Eur-Oceans/NATO ‘Climate Change Impacts on Marine Ecosystems’ Summer School, Ankara, Turkey. August 14–26, 2006.
9. Youngbluth, M.J., C.A. Jacoby, **J.R. Frost**, D. Shale (2005) Distribution, metabolism and behavior of the deep-living cephalopod *Stauroteuthis syrtensis* (Suborder Cirrata). ASLO International Meeting, Santiago de Compostela, Spain. June 19–24, 2005.
10. **Frost, J.R.**, E.J. Phlips, M.F. Cichra (2003) Ecology of Lake Griffin, a hypereutrophic cyanobacteria-dominated lake in central Florida. Oral Presentation NALMS 23rd Annual International Symposium, Mashantucket, Connecticut, USA. November 5–7, 2003.