UNIVERSITY OF CALIFORNIA, SAN DIEGO

Laboratory and *In Situ* Investigations of Factors Affecting the Growth and Survivorship of the Scyphozoan Jellyfish *Aurelia* sp1

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

in

Oceanography

by

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2012

The Dissertation of Alison Michelle Cawood is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

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University of California, San Diego

2012

DEDICATION

I dedicate this dissertation to the Solana Beach Reality Changers classes of 2009 – 2016 for proving to me every day that there are very few obstacles in life that can't be overcome with hard work, determination, and the love and support of people who believe in you even when you don't believe in yourself.

EPIGRAPH

“Truth on our level is a different thing from truth for the jellyfish, and there must certainly be analogies for truth and error in jellyfish life.”

T.S. Eliot

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ABSTRACT OF THE DISSERTATION

Laboratory and *In Situ* Investigations of Factors Affecting the Growth and Survivorship of the Scyphozoan Jellyfish *Aurelia* sp1

by

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Doctor of Philosophy in Oceanography

University of California, San Diego, 2012

Professor Mark D. Ohman, Chair

Jellyfish blooms and their effects on ecosystems and humans are sources of increasing concern. In this dissertation, I examine the conditions to

which the bloom-forming jellyfish *Aurelia* sp1 are exposed in San Diego embayments and perform laboratory experiments to explore the tolerances of polyps, ephyrae, and juvenile medusae to environmentally relevant changes in salinity, dissolved oxygen, and dissolved organic matter (DOM).

In Mission Bay, *Aurelia* sp1 polyps were present year-round from 2008 - 2012. Strobilation and ephyrae production occurred in late autumn, continuing through winter. Medusae were only collected in winter and spring of 2008. In San Diego Bay, ephyrae were present each winter and medusae were present each spring. Combining my data with presence/absence records from other sources extending back to 2000, in years with high precipitation, medusae were absent in Mission Bay, but present in San Diego Bay. The timing of precipitation events coincides with the presence of ephyrae, suggesting that low salinities in Mission Bay caused high mortality of ephyrae, leading to recruitment failure and the absence of medusae.

When exposed to acute salinity changes, *Aurelia* sp1 polyps can survive for at least 72 h at salinities from 6 to 52 psu. Ephyrae are more sensitive, surviving from 17 to 40 psu. Juvenile medusae have salinity tolerances similar to ephyrae, but survive longer than ephyrae at the same salinities.

Aurelia sp1 polyps survive for at least 28 days when exposed to dissolved oxygen levels as low as 0.8 mg L^{-1}. Ephyrae survived for 10 days at similar oxygen concentrations. Ephyrae exposed to hypoxia have lower C and

N content than those exposed to air-saturated conditions, while polyps show no change.

Exposure to dissolved organic matter (DOM) had little impact on growth or survivorship of *Aurelia* sp1 polyps over 3 months. With and without DOM, fed polyps increased in abundance and starved polyps decreased in abundance. Unfed polyps in artificial sea water had lower C and N content than fed polyps in filtered sea water, but DOM made no difference within fed and unfed treatments.

Aurelia sp1 population dynamics may be particularly sensitive to survivorship of ephyrae.

CHAPTER 1:

Introduction

In recent years, headlines such as “Jellyfish blooms plague the world’s oceans” (Geere, 2011) and “Jellyfish blooms creating oceans of slime” (Vince, 2012), are showing up in newspapers and on websites from around the world. However, the science behind jellyfish (defined here as scyphozoan cnidarians) blooms is not well understood. There are large gaps in the natural history, even of groups that are considered common. In some cases, it is not known which polyps produce which planktonic medusae or where all of the life history stages are geographically located (Arai, 1997). Much of this confusion is attributable to the fact that jellyfish often have complex life cycles involving both benthic and pelagic phases. Most undergo both sexual and asexual reproduction, enabling them to adapt quickly and take advantage of changing conditions. These life history traits can lead to large seasonal concentrations of medusae, which can significantly impact local ecosystem dynamics, as well as have negative societal consequences on industries such as tourism and fisheries (Mills, 2001; Purcell et al., 2007).

Jellyfish, especially when abundant, can alter ecosystems. They can be voracious predators, and their prey can come from a variety of size classes and taxonomic groups ranging from microzooplankton to ichthyoplankton (Purcell et al., 1994; Arai, 1997; Malej et al., 2007). Prey selection can change with jellyfish size or life history stage, meaning that a wide range of prey may

be consumed simultaneously when different life history stages are present (Sullivan et al., 1994; Sullivan et al., 1997; Graham and Kroutil, 2001). Additionally, jellyfish and juvenile fish have the potential to be in direct competition for prey items (Purcell and Arai, 2001; Purcell and Sturdevant, 2001; Lynam et al., 2005).

Jellyfish can also change phytoplankton and microbial communities. Jellyfish release large amounts of dissolved organic matter (DOM), especially dissolved organic carbon (Hansson and Norrman, 1995; Condon et al., 2011). DOM can promote the growth of some microbes, such as ɣ-proteobacteria, that are often rare in ambient waters (Condon et al., 2011). DOM can also change phytoplankton composition, increasing the concentration of some phytoplankton groups, particularly 19'-hexanoyloxyfucoxanthin containing phytoplankton (generally indicative of haptophytes; Turk et al., 2008).

In addition to causing changes in ecosystems, jellyfish can have negative societal impacts on industries such as tourism, fisheries, aquaculture, and power plants (reviewed in Purcell et al., 2007). Jellyfish often occur in populated coastal areas that can be popular for recreation. Many areas depend on their coastal waters and the tourism associated with them as major sources of income. For example, in 2000, ocean and coastal tourism accounted for an estimated $22.4 billion in California, making it the largest portion of the ocean economy, with over 24 million domestic visitors to beach and waterfront areas (Resources Agency of California, 2005).

Even jellyfish with non-painful stings, such as *Aurelia* spp.*,* deter swimmers and other recreational users of coastal waters. When jellyfish were reported off of the coast of Del Mar, California, the North County Times quoted beachgoers as saying that "[they] wouldn't be dashing into the ocean for a while" and that "jellyfish made [them] hesitant to go in the water" (9 August 2005). In the Black Sea, there have been an estimated $350 million in losses to the fishing and tourism industries as a result of jellyfish and ctenophores (Whiteman, 2008).

Jellyfish populations also impact fisheries operations. Large jellyfish can clog nets and even cause boats to sink (Lynam et al., 2006; Purcell et al, 2007). Jellyfish have cost the fishing industry in one Japanese prefecture upwards of $20 million, and jellyfish blooms have been reported in 17 prefectures (Whiteman, 2008). Jellyfish can cause the death and sickness of organisms in aquaculture pens (Purcell et al., 2007). High jellyfish concentrations can clog the intakes of power plants and large ships. Interruptions of service have been reported in multiple locations in Japan, the Chesapeake Bay, and the Gulf of Oman (Purcell et al., 2007). The fact that none of these impacts are problematic when few jellyfish are present, but become so when many are found in the same place at the same time has led to an interest in large concentrations of jellyfish, or jellyfish blooms. Understanding the causal factors leading to jellyfish blooms is the underlying motivation for this dissertation.

Jellyfish Blooms

Many jellyfish live as benthic polyps that persist throughout the year, and produce ephyrae, which grow into medusae, generally once a year. Because medusae are large and easily visible, it may seem as though many jellyfish appear out of nowhere, although the smaller, less visible life history stages were likely present in the water all year. In addition to these natural pulses, there is much speculation and some largely anecdotal evidence that anthropogenic impacts, such as marine eutrophication, climate change, overfishing, and introduction of artificial substrates into marine environments may be increasing the size, persistence, and/or frequency of jellyfish blooms (e.g. Arai, 1997; Mills, 2001; Purcell et al., 2007; Richardson et al., 2009; Condon et al., 2012). Blooms are defined as in Hamner and Dawson (2009): "normal and/or abnormal seasonal abundances… directly attributable to population increase due to reproduction and growth" (a true bloom) or "increase[d]…abundance….associated with temporary or transient physical or chemical phenomena" (an apparent bloom). However, due to our current lack of knowledge regarding the ecology of jellyfish and the lack of long-term data sets containing information about jellyfish (but see Brodeur et al., 1999; Graham, 2001; Brotz et al., 2012), it is difficult to distinguish increasing jellyfish populations from natural fluctuations. Claudia Mills (2001) has said that "[i]t is unfortunate that we have so little population and ecological data about medusae and ctenophores in the field that we cannot presently distinguish between natural fluctuations and long term, possibly irreversible, change."

Additionally, it is not possible to understand the dynamics of a population without understanding all portions of the life history of the organism of interest. In the case of jellyfish, although little is known about the large medusa stage, even less is known about the ecology and population dynamics of the benthic polyps, which reproduce asexually, making it likely that they respond quickly to changing environmental conditions and play a major part in the population dynamics of these organisms.

Jellyfish blooms are not a new phenomenon. There is evidence that blooms evolved concurrently, or nearly so, with the evolution of medusae (Hamner and Dawson, 2009; reviewed in Condon et al., 2012). However, in recent years, there has been the perception that there are more jellyfish blooms, although whether more refers to changes in duration, frequency, intensity, or increased spatial extent is unclear. Popular ideas such as “fishing down the food web” (Pauly et al., 1998) and “shifting baselines” (Jackson et al., 2001) have furthered the idea that oceans full of jellyfish are the inevitable result of all of the negative influences that humans have had and are having on the oceans However, as stated above, too few data sets exist to actually make this attribution, as many data sets cover only short time periods and may only be accounting for interannual variability, not sustained increases in abundances over longer time scales (reviewed in Condon et al., 2012; Purcell, 2012).

Purported increases in jellyfish blooms are further complicated by reports of decreases in the abundance of jellyfish. Several groups of

hydromedusae have shown decreases in abundance in the northern Adriatic Sea, British Columbia, Canada, and the North Pacific (reviewed in Mills, 2001). A loss of diversity among hydromedusae, scyphomedusae, and ctenophores has been reported in St. Helena Bay, South Africa (Buecher and Gibbons, 2000). A recent meta-analysis of all available data (including newspaper articles) on changes in abundances of many gelatinous zooplankton groups (scyphomedusae, hydromedusae, cubomedusae, siphonophores, ctenophores, and salps) indicates decreases in abundances in recent times relative to 1950 in the Humboldt Current, the West Greenland shelf, and the Oyashio Current (Brotz et al., 2012). In the Central and Southern portions of the California Current Ecosystem, interannual variability was observed, but no sustained increases in abundances of hydromedusae or scyphomedusae were observed from 1951 through 2005 (Lavaniegos and Ohman, 2007).

Nearly all discussion of jellyfish blooms focuses on coastal areas and enclosed or semi-enclosed bodies of water. There is little evidence of blooms or even of the formation of large aggregations by mid-water, deepwater and open ocean jellyfish that are associated with open waters (Mills, 2001; Hamner and Dawson, 2009). This lack of bloom formation may be due to the fact that many of the life history traits more associated with bloom-forming jellies occur in coastally associated taxa (Dawson and Hamner, 2009; Hamner and Dawson, 2009), or it may simply be due to a lack of observations (Larson et al., 1991; Mills, 2001). The information that does exist does not paint a clear

picture. Using data from Continuous Plankton Recorder (CPR) samples in the North Sea, Attrill et al. (2007) concluded that there had been an increase in jellyfish from 1958 to 2000. However, there was much criticism of this conclusion (e.g. Haddock, 2008) based on the difficulty in determining species composition and abundance based on nematocysts alone, which were used to enumerate jellyfish from CPR samples, and the fact that the CPR generally collects only parts (i.e. tentacles and oral arms) from jellyfish, making it very difficult to quantify abundances. Gibbons and Richardson (2009) found seasonal and interannual variability in the abundances of gelatinous zooplankton in the North Atlantic from 1946 to 2005 based on CPR samples, but found no sustained increase in populations. They also found that most of the nematocysts belonged to holoplanktonic hydrozoans rather than meroplanktonic scyphozoans, as had been suggested by Attrill et al. (2007). Further work on the identification of nematocysts and the relationship between nematocyst abundance and medusae abundance is occurring and may be beneficial in looking at long-term changes in jellyfish populations in open ocean environments (Baxter et al., 2010).

Potential Natural Causes of Jellyfish Blooms

While most of the recent interest in jellyfish blooms has focused on their links to human activities, jellyfish blooms have been occurring for millions of years (Condon et al., 2012). There are a number of behavioral and physical factors that have the potential to cause jellyfish blooms and aggregations.

Physical Causes

A number of physical factors can cause the passive aggregation of jellyfish (reviewed in Graham et al., 2001). Other factors may cue active or behavioral responses, and those will be discussed below in the behavioral causes section. The formation of density gradients, caused by discontinuities in temperature or salinity may serve to aggregate jellyfish. Small gelatinous zooplankton, particularly hydromedusae, aggregate over salinity gradients (Arai, 1973), although large scyphomedusae, such as *Phyllorhiza punctata* traverse sharp haloclines (Graham et al., 2001). Thermoclines in Monterey Bay have been associated with layers of the large jellyfish, *Chrysaora fuscescens* (Graham, 1994).

Currents may also be important for aggregating jellyfish. Tidal currents (Zavodnik, 1987) and inshore currents (Ferraris et al., 2012) cause near shore aggregations of *Pelagia noctiluca* in the Mediterranean). Entrainment of upwelled water along coastal features may also lead to near shore aggregations of *Chrysaora fuscescens* near Monterey, California (Graham, 1994). Local circulation patterns and currents associated with semi-enclosed bodies of water such as bays and inlets have also caused aggregations of *Aurelia labiata* in Prince William Sound (Purcell et al., 2000).

Behavioral Causes

The behavioral responses of jellyfish to physical factors or to each other may cause blooms (reviewed in Albert, 2011). There is evidence of diel vertical migration (DVM) of jellyfish (Kaartvedt et al., 2007). The jellyfish *Periphylla periphylla* in a Norwegian fjord were located between depths of approximately 100 to 200 meters during the day, but formed a layer at approximately 50 meters at night (Kaartvedt et al., 2007). Laboratory studies of *Aurelia* sp. have indicated DVM (Mackie et al., 1981), but field observations have not supported this inference (e.g. Papathanassiou et al., 1987; Malej et al., 2007; Lo and Chen, 2008). Jellyfish have been shown to undergo tidally mediated vertical migrations in order to maintain their position within estuaries. *Aurelia labiata* in Roscoe Bay, British Columbia swam into still water or countercurrents on ebb tides to stay within or near the bay and rose to the flood stream to return or move further into the bay (Albert, 2007). However, *Aurelia* sp. (Van der Veer and Oorthuysen, 1985) and *Chrysaora hysoscella* and *Rhizostoma pulmo* (Verwey, 1966) were not seen to utilize vertical migration to stay within estuaries near the Wadden Sea.

Horizontal migration has been observed as well. Hamner et al. (1994) showed that the majority of *Aurelia* sp. medusae in Saanich Inlet in the summer of 1986 moved from the north end of the inlet to the south end of the inlet. Additionally, it was noted that once individual jellyfish encountered a larger group of jellyfish, their swimming direction changed from primarily horizontal to primarily vertical, enabling them to stay within the aggregation.

Daily horizontal migration was shown for *Mastigias* spp. in marine lakes in Palau. Depending on the size of the lake, the jellyfish swam up to 1 km per day (Hamner and Hauri, 1981). In the case of *Aurelia* sp. and *Mastigias* spp., the direction of swimming was thought to be influenced by the position of the sun.

Aurelia labiata have been observed actively avoiding low salinity waters. In Roscoe Bay, British Columbia, *Aurelia labiata* medusae were seen to swim away (generally in a downward direction) when they encountered water of salinities of less than 20 psu (Albert, 2008).

Potential Anthropogenic Causes of Jellyfish Blooms

In addition to these natural causes, a number of hypotheses have been put forward to explain how anthropogenic changes could be causing more jellyfish blooms, although there is little direct evidence linking any of them to sustained increases in jellyfish populations (Purcell, 2012). Here I will summarize the major hypotheses. The categories listed are broad and contain many more specific topics (some of which will be discussed here) that would need to be investigated in order to determine whether and how such factors impact jellyfish blooms.

Climate Change

Warmer temperatures may enhance the growth of jellyfish (reviewed in Purcell, 2005). Correlations between warm phases of decadal scale climate

oscillations (i.e. North Atlantic Oscillation (NAO) and Pacific Decadal Oscillation (PDO)) and increases in jellyfish abundances have been shown in the North Sea (Lynam et al., 2010), Chesapeake Bay (Purcell and Decker, 2005), Gulf of Alaska (Litzow, 2006), Bering Sea (Brodeur et al., 2008), and the northwestern Mediterranean (Molinero et al., 2005). Warming may act to speed development or growth. The number of strobila produced may increase, particularly for jellyfish that are found in polar climates (Holst, 2012). Warming may also increase stratification, which may keep food closer to the surface and therefore closer to surface-dwelling jellyfish (Purcell, 2005).

In addition to changes in temperature, changes in weather patterns leading to changes in salinity may impact jellyfish populations. Salinity changes may impact the growth or survivorship of jellyfish themselves or that of their prey items in ways that enhance bloom formation. Rainfall may also be associated with increased run-off, which could enhance jellyfish populations (this will be discussed more thoroughly in the following section; Purcell et al., 2007).

Eutrophication

Eutrophic environments have been associated with jellyfish blooms all over the world, including Elefsis Bay, Greece, Tokyo Bay, Japan, the Baltic Sea, the Black Sea, and the Gulf of Mexico (Arai, 2001). Several mechanisms for this correlation have been proposed, including hypoxia, increased nutrient availability, increased turbidity, and altered food webs.

When eutrophication occurs, the increased nutrients often cause phytoplankton blooms. As the phytoplankton die and sink out of the water column, oxygen levels can be drawn down to hypoxic (dissolved oxygen concentration of ≤ 2 mg L^{-1} or ≤ 30% saturation) or even anoxic levels . Although lethal to many animals, many jellyfish seem to do quite well under these conditions (reviewed in Purcell et al., 2001). It is believed that these differences are due to the ability of jellyfish to store oxygen within their mesoglea (Thuesen et al., 2005). Several studies have examined the impacts of low oxygen on jellyfish. *Chrysaora quinquecirrha* medusae are often associated with hypoxic waters (e.g. Purcell et al., 1994; Graham, 2001; Purcell et al., 2001; Grove and Breitburg, 2005). Neither the behavior (Breitburg et al., 1994) nor the growth rates of *C. quinquecirrha* are affected by exposure to hypoxia (Grove and Breitburg, 2005), and they can survive at oxygen concentrations as low as 0.5 mg L^{-1} for at least 48 hours (Purcell et al., 2001). Rutherford and Thuesen (2005) found that *Aurelia labiata* could survive for 15 hours under hypoxic conditions and 5 hours under anoxic conditions. *Aurelia* spp. have been found in waters with oxygen concentrations as low as 0.9 mg L^{-1} (Vinogradov et al., 1985), and are known to occur in hypoxic waters (≤ 2 mg L^{-1}) in the Gulf of Mexico (Graham, 2001), the Black Sea (Vinogradov et al., 1985; Kideys and Romanova, 2001), Denmark (Møller and Riisgård, 2007), Japan (Shoji et al., 2010), Palau (Hamner et al., 1982), and the southern Adriatic Sea (Benović et al., 2000).

However, there is less information on the survivorship of early life history stages under hypoxic conditions, which may be important in determining the number of adult medusae that are produced. *Aurelia* sp. planulae have been found at oxygen concentrations as low as 0.4 mg L^{-1} (Vinogradov et al., 1985), and laboratory experiments show enhanced planulae settlement under hypoxic conditions compared to normoxic conditions (Miller and Graham, 2012). Condon et al. (2001) examined the impact of long-term low oxygen concentrations on polyps and strobilae of *Chrysaora quinquecirrha*. During the first 5 days of the experiment, there was at least 98% survival of polyps in all treatments (air saturation, 3.5 mg L^{-1}, 2.5 mg L^{-1}, 1.5 mg L^{-1}, and 0.5 mg L^{-1} of oxygen). After 24 days, more than 40% of the polyps in all treatments were still alive. Asexual reproduction (budding and stolon formation) and strobilation occurred in all treatments; however, these processes occurred to a lesser extent in the lowest oxygen treatment (0.5 mg L^{-1}). In Tokyo Bay, *Aurelia* sp. polyps have been found at oxygen levels as low as 0.12 mg L^{-1} (Ishii and Katsukoshi, 2010). *Aurelia* sp. polyps are able to survive for more than 56 days under hypoxic (0.8 mg L^{-1}) conditions and this hypoxia tolerance enables polyps to persist in hypoxic areas that are lethal to other fouling organisms (Miller and Graham, 2012). If jellyfish of any (or all) life history stages are less susceptible to hypoxia than other predators, these tolerances may give them a competitive advantage by allowing them to persist in an environment where other predators cannot.

One of the hallmarks of a eutrophic environment is the presence of increased dissolved organic matter (DOM; Nixon, 1995). Jellyfish may benefit from DOM in two ways. Jellyfish may be able to take up DOM directly from the water as a way to supplement their diets. If this is the case, even if the biological community shifted such that their normal food sources, such as zooplankton and/or ichthyoplankton, were less readily available, the jellyfish would have a supplemental source of nutrition, which might not be available to other predators (Arai, 2001). Additionally, the presence of DOM may promote the overall productivity of the environment, providing more food for the jellyfish, thereby enhancing their growth. Using HPLC techniques, it has been shown that a number of soft-bodied marine organisms are capable of net uptake of free amino acids and glucose, and that this ability may have implications for their life histories (reviewed by Manahan, 1990 and Gomme, 2001). The ability to take up DOM may extend the larval period of some benthic invertebrates, such as the oyster, *Crassostrea gigas* (Moran and Manahan, 2004) and the bryozoan, *Bugula neritina* (Johnson and Wendt, 2007).

With respect to jellyfish, Shick (1975) showed that *Aurelia* sp. polyps were able to take up isotopically labeled glycine. However, he did not show net uptake. The importance of this issue was first addressed by Johannes et al. in 1969. They claimed that isotope methods gave evidence for influx of DOM, but not net uptake. Because there was no way to know whether isotopically labeled compounds were taken up, but non-labeled compounds

were released at the same (or higher) rates, there was no way to determine whether net uptake had occurred (Johannes et al., 1969). Shick (1975) showed that polyps that were starved, but exposed to glycine, alanine, or glucose could still be induced to strobilate, but found that they produced more abnormal ephyrae than polyps that were fed normally.

Skikne et al. (2009) examined the uptake of DOM by ephyrae of *Aurelia labiata* and *Chrysaora colorata*. They showed ephyrae of *Aurelia labiata* exposed to homogenized and filtered *Artemia* nauplii or wild-caught krill had higher carbon content after 22 days than ephyrae that had been starved, but lower carbon content than ephyrae that were fed particulate food. Additionally, many of the ephyrae that were given only DOM became abnormally shaped. They used fluorescently labeled poly-L-lysine to demonstrate uptake of the dissolved amino acid. After being incubated for 30 minutes in a relatively high concentration (3 μM) of the labeled lysine, all of the ephyrae showed fluorescence from within the radial canals.

Models by Eiane et al. (1997) have suggested that jellyfish are not susceptible to increased turbidity and light attenuation because they are tactile (non-visual) predators. However, there are few observational or experimental data to support this hypothesis (Sørnes et al., 2007). The effects of turbidity on prey capture rates and survivorship of different life stages may be important. While medusae may not be impacted by increased turbidity, earlier developmental stages (polyps and planula larvae) may experience difficulties due to increased siltation. However, polyps of coronate medusae have

protective peridermal tubes, with may protect polyps from sedimentation and allow them to survive burial for up to 5 months (Holst and Jarms, 2006). The amount of photosensitivity displayed by all stages of the life history, which would change with differing light attenuation levels, may also impact population dynamics (Sørnes et al., 2007).

It has been suggested that jellyfish may be able to take advantage of nanophytoplankton-based food webs (Greve and Parsons, 1977; Parsons and Lalli, 2002). Persistent eutrophication may lead to a switch in the major phytoplankton group from large diatoms (which become limited by silicic acid) to small flagellates (Parsons et al., 1970). This switch would create a less efficient food chain, which would make it more difficult for some higher predators to thrive, thus releasing the jellyfish from competitive pressure.

Habitat Modification

Jellyfish blooms often occur in coastal areas. These areas are often heavily modified by humans. Adding hard substrate to the environment (e.g. oil derricks, docks, artificial reefs) provides a place for polyps to attach. Studies have shown that artificial substrates including plastic, concrete, and wood can be suitable substrates for polyp settlement, and in some cases, these substrates are more preferable settlement locations than natural substrates, such as shells (Holst and Jarms, 2007; Hoover and Purcell, 2009). As polyps are the most persistent part of the life history of most jellyfish, having more suitable substrate for them to grow could allow jellyfish to

become established in an area and to keep a foothold there even under difficult conditions (Graham, 2001; Purcell et al., 2007; Lo et al., 2008). Additionally, the construction of bays and lagoons for recreation purposes can create areas of retained flow that can cause jellyfish to become entrained within an enclosed area (Purcell et al., 2007).

Species Introductions

The introduction of jellyfish into new areas can cause large blooms. The jellyfish can exploit a niche that was not previously occupied and thrive in the new environment. Examples of exotic jellyfish introductions that have led to blooms include *Rhopilema nomadica* in the Mediterranean (reviewed in Graham and Bayha, 2007), *Phyllorhiza punctata* in the Gulf of Mexico (Graham et al., 2003; Bolton and Graham, 2004), and *Sanderia malayensis* in the Yangtze River estuary (Xian et al., 2005). These blooms are generally large initially following the introduction, and taper off through time (Graham and Bayha, 2007). However, if the jellyfish have produced polyps that persist in the environment, they can be poised to bloom again if conditions become favorable (Lotan et al., 1992; Graham and Bayha, 2007; Purcell et al., 2007).

Overfishing

Overfishing can promote jellyfish blooms in two main ways. The first is by removing organisms that prey on jellyfish. As many as fifty species of fish prey on gelatinous zooplankton (Arai, 1988; Ates, 1988). Some of these fish

are even considered to be specialist predators on gelatinous zooplankton, generally organisms from the family Stromateoidei, including the commercially fished butterfish, *Peprilus triacanthus* (Ates, 1988; Arai, 2005). Other, more generalist predators that have been known to consume jellyfish include the chum salmon, *Onorhynchus keta,* and the spiny dogfish, *Squalus acanthias,* both of which are fished commercially (Purcell and Arai, 2001; Arai, 2005).

Fishing can also remove animals that compete with the jellyfish for food. There is dietary overlap between the jellyfish *Aurelia labiata* and *Cyanea capillata* and juvenile fish such as walleye pollock, *Theragra chalcogramma,* Pacific sandlance, *Ammodytes hexapterus*, Pacific herring, *Clupea pallasi,* and pink salmon, *Oncorhynchus gorbuscha* which all co-occur in Prince William Sound (Purcell and Sturdevant, 2001). It has been hypothesized that the overfishing of zooplanktivorous fishes, such as sardines, *Sardinops sagax*, and anchovies, *Engraulis encrasicolis*, have led to increased jellyfish biomass in the northern Benguela current ecosystem (Lynam et al., 2006), and in the Black Sea (Daskalov, 2002).

In nature, it is unlikely that any of these environmental factors will change in isolation. In examining the impacts of these individual factors on different portions of the life history stages of jellyfish, it will be important to look at the synergistic impacts of these factors. Furthermore, it is important to recognize that jellyfish do not occur as the sole organisms in an environment. In order to fully understand if and how these factors lead to jellyfish blooms, looking at them from a community perspective will be essential.

***Aurelia* spp.**

Some of the jellyfish most commonly associated with coastal blooms belong to the genus *Aurelia (*Mills, 2001). One member of the genus, *Aurelia* sp1, is the species that I have focused on for my dissertation research. Jellyfish from the genus *Aurelia* are semaeostome scyphozoans in the family Ulmaridae, and are commonly known as moon jellies. *Aurelia* are flat, whitish medusae with four horseshoe shaped gonads easily visible on their aboral side (Fig. 1.1). They can reach a maximum diameter of approximately 50 cm. They are common in coastal waters in many parts of the world (Wrobel and Mills, 1998). They have been known to reach high population densities as adults (Arai, 1997).

Life History

Aurelia spp. are commonly cultured in aquaria, so their life history is relatively well understood. *Aurelia* spp. generally undergo the 'typical' scyphozoan life history pattern, where development moves sequentially from a fertilized egg, to a ciliated planula larva, to an attached polyp, to a strobila (strobilating polyp), to an ephyra (early juvenile), to an adult medusa (reviewed in Lucas, 2001; Fig. 1.2). However, it is possible for a planula to develop directly into an ephyra (Kakinuma, 1975; Yasuda, 1975) or form a podocyst (a cyst that forms below the pedal disk of the polyp; Chapman, 1968). Podocyst formation was found to primarily occur in starved or near-starved polyps, and

increased temperatures increased the rate of podocyst production. Changes in salinity and dissolved oxygen concentration were not observed to cause podocyst formation (Thein et al., 2012). A polyp formed from a single planula larva is capable of different types of asexual reproduction, including budding or formation of stolons, which are elongated strands from which new polyps form (Kakinuma, 1975). The developing eggs and larvae are brooded on the oral arms or in the manubrium of the adult female medusae and young are released as fully developed planula larvae (Lucas, 2001). The ecological processes that cause these alternate pathways are not well understood.

Taxonomy

For much of the 20th century, *Aurelia aurita* was considered a cosmopolitan species with a worldwide distribution in sub-polar, temperate, and tropical waters (e.g. Russell, 1970). However, the taxonomy of *Aurelia aurita* is currently in a state of upheaval. *Aurelia* (as *Medusa aurita* Linnaeus 1758) was originally recognized by Linnaeus in the Baltic Sea. By 1910, many species of *Aurelia* had been described, but Mayer (1910) recognized only thirteen varieties in three species (*A. aurita, A. labiata,* and *A. solida*). In 1965, Kramp recognized just two species, the circumglobal *Aurelia aurita* and the arctic species *Aurelia limbata*. This classification system held until the late 1990s when Wrobel and Mills recognized *A. labiata* (1998). *Aurelia labiata* was formally redescribed by Gershwin in 2001. Gershwin argued that *A. labiata* was the species that was native to all of the Northeast Pacific, and that

any specimens that had been correctly identified as *Aurelia aurita* (e.g. San Francisco Bay; Greenberg et al., 1996) were the result of species introductions. Dawson and Jacobs (2001) conducted a molecular analysis of *Aurelia* and identified at least thirteen species, including *A. aurita, A. labiata,* and *A. limbata.* They also concluded that *Aurelia aurita* is endemic to the northeastern Atlantic Ocean, including the Baltic Sea, the location of Linnaeus' original species description. Following an analysis of macro-morphological variation and cryptic speciation in *Aurelia*, Dawson (2003) recognized at least ten molecular species of *A. aurita*, two species of *A. labiata*, and two species of *A. limbata.* Later work suggests that the species in southern California is *Aurelia* sp1, part of the *Aurelia aurita* species complex, which is also found in Japan and Australia (Dawson et al, 2005). Because it can be very difficult to distinguish the various species based on morphology and many of the older descriptions are somewhat unclear, it is difficult to determine how well the older species distinctions correspond to the genetic species that have been described by Dawson (2003). Work is being done by graduate students at the Dauphin Island Sea Lab to determine if and how the morphological descriptions correspond to genetic species (Monty Graham, personal communication).

Global Patterns in Population Dynamics

Despite the fact that *Aurelia* spp. are regarded as common in coastal waters in many parts of the world, are often associated with blooms, and are

cultured in aquaria, we know surprisingly little about patterns in their growth, reproduction, or population dynamics under environmental conditions or how changes in conditions might change those patterns. This uncertainty is especially true with regards to the earlier phases of the life history (planulae, polyps, strobilae, and ephyrae).

There are several studies that examine changes in *Aurelia* spp. medusae or medusae and ephyrae, but do not examine polyps or strobilae (e.g. Möller, 1980; Hamner et al., 1982; Papathanassiou et al., 1987; Lucas and Williams, 1994; Olesen et al., 1994; Schneider and Behrends, 1994; Omori et al., 1995; Lucas, 1996; Graham, 2001; Lo and Chen, 2008; Bastian et al., 2011; Bonnet et al., 2012). Other studies examine only benthic polyps and strobilae (e.g. Watanabe and Ishii, 2001; Miyake et al., 2002; Willcox et al., 2008; di Camillo et al., 2010). Of these studies, only five examine interannual variability (Papathanassiou et al., 1987; Lucas and Williams, 1994; Schneider and Behrends 1994; Omori et al., 1995; Graham, 2001; Lo and Chen, 2008).

These studies report a wide variety in the timing or persistence of life history stages. In many locations, polyps are present year round (e.g. Miyake et al., 2002; Willcox et al., 2008; di Camillo et al., 2010), but it seems that polyps in Tokyo Bay survive for less than one year (Watanabe and Ishii, 2001). In the Northern Hemisphere, the onset of strobilation and ephyrae production in many populations begins in the late autumn and persists through winter (e.g.; Watanabe and Ishii, 2001; Miyake et al., 2002; di Camillo et al.,

2010; Bonnet et al., 2012), but in other sites, both at high latitudes such as the Wadden Sea (Van Der Veer and Oorthuysen, 1985) and Denmark (Olesen et al., 1994) and at low latitudes such as Greece (Papathanassiou et al., 1987), strobilation and ephyrae production begins in late winter or early spring. In other locations, such as Jellyfish Lake, Palau (Hamner et al., 1982), Kiel Bight, Germany (Möller, 1980), and Horsea Lake, UK (Lucas, 1996), ephyrae are produced nearly year-round. Medusae are present in the winter and spring in the southwestern Mediterranean Sea (Bonnet et al., 2012), in the summer and autumn in Greece (Papathanassiou et al., 1987), the United Kingdom (Lucas and Williams, 1994; Bastian et al., 2011), Norway (Schneider and Behrends, 1994) and Denmark (Olesen et al., 1994), and over most of the year in Palau (Hamner et al., 1982), Taiwan (Lo and Chen, 2008), and Japan (Omori et al., 1995). These studies were conducted before the recognition of the many cryptic species of *Aurelia* spp. The newly recognized cryptic species, along with regional variability, may account for many of the reported differences in seasonal population among locations. It is not known how seasonal patterns or responses to environmental stimuli differ among species.

To my knowledge, only two studies examine all life history phases of the same population: in Gullmar Fjord, Sweden (Hernroth and Gröndahl, 1983; Hernroth and Gröndahl, 1985a; Hernroth and Gröndahl, 1985b; Gröndahl, 1988) and in the northern Adriatic Sea (Malej et al., 2012). The Gullmar Fjord studies report dense polyps during August through October and March, and intermediate polyp densities in April, May, and June. Strobilation occurred

during October, November, March, April, and May. Two types of strobilation are recognized: polydisc strobilation (five or more discs per strobila) occurred during October and November and strobila with two to four discs per strobila occurred during March, April, and May (Hernroth and Gröndahl, 1983; Gröndahl, 1988). Ephyrae were present from October through December, and again during March and April (Hernroth and Gröndahl, 1983, Hernroth and Gröndahl, 1985a). Medusae were present between June and October (Hernroth and Gröndahl, 1985b; Gröndahl, 1988). In the northern Adriatic, polyps of *Aurelia* sp8 were present year-round. Polyp densities were highest during the summer, intermediate in the winter, and lowest in the spring. Strobilae and ephyrae were seen from November through February, and a high percentage of polyps (up to 82%) were strobilating at a given time. Only polydisc strobilae were seen, with a maximum of 18 discs per strobilae. Medusae were generally observed from February through June, although a few sightings were made in January and July. *Aurelia* sp8 blooms occurred periodically in the northern Adriatic Sea from 1983 - 2001. From 2002 to 2012, bloom concentrations of *Aurelia* sp8 have occurred every year (Malej et al., 2012).

Aurelia sp1 in San Diego

In San Diego, *Aurelia* sp1 are found in Mission Bay and San Diego Bay, with occasional sightings made in coastal waters (Birch Aquarium at Scripps Institution of Oceanography, unpublished data). Polyps and medusae from

Mission Bay were identified as *Aurelia* sp1 by K. Bayha and M. Dawson (personal communication), which is consistent with the distribution predicted by Dawson et al. (2005).

Prior to 1946, Mission Bay was primarily composed of eelgrass beds, marshlands, and mudflats. After a development plan was approved, the area was dredged, jetties rerouted the flow of the San Diego River away from Mission Bay, and an "island" (originally Cabrillo Island, now Fiesta Island) was created in the center of the bay with a road that connects it to the mainland, restricting flow around the "island" (Chapman, 1963). Currently, Mission Bay is a small (approximately 18.6 km^2) estuary that is used extensively for recreation (Largier et al., 1997a; City of San Diego, 2004). It is seasonally hypersaline (Largier et al., 1997b; City of San Diego, 2004), and reaches salinities of over 40 psu (City of San Diego, 2004). Mission Bay receives freshwater input from several creeks and over 100 storm drains (Largier et al., 1997a; Largier et al., 1997b).

San Diego Bay is a long (approximately 25 km), narrow (1 -3 km) crescent-shaped bay that covers approximately 43 km^2 (Largier et al., 1997; Chadwick and Largier, 1999). Inflows into San Diego Bay have been relatively low since the San Diego River was diverted away from the bay in 1875 as part of efforts to supply drinking water to the growing San Diego population (Boone, 1912). Now, several rivers and creeks drain into San Diego Bay, although due to damming and groundwater use, less than 25% of the flow from those sources enters the bay (U.S. Army Corps of Engineers, 1973), and

water from approximately 200 storm drains enters the bay (U.S. Department of the Navy et al., 2010). San Diego Bay is also considered to be seasonally hypersaline, with salinities reaching 37 in late summer (U.S. Department of the Navy et al., 2010).

Because we know so little about natural fluctuations in *Aurelia* spp. populations or how environmental factors might alter these fluctuations, it is difficult to understand what causes blooms, to predict their occurrence, or even to truly understand the natural history of *Aurelia*. It is essential that we understand natural fluctuations, especially in light of the complications brought about by the changes in taxonomy of *Aurelia* spp. This understanding can be used to gain knowledge of the environmental conditions to which various life history stages are exposed, as well as to help identify environmental factors that might be important in controlling population dynamics. Important environmental factors can be further studied in the laboratory to understand the tolerances and responses of all life history stages, especially early life history stages for which there has been less research. This is the approach that I took for my dissertation research.

Dissertation Goals

The primary goal of this dissertation is to understand how different life history phases of *Aurelia* sp1 respond to changes in environmental conditions. In order to accomplish this goal, I attempted:

1) to gain a better understanding of the environmental conditions to which all life history stages of *Aurelia* sp1 are exposed,
2) to understand seasonal patterns of growth and abundance of the entire life history of *Aurelia* sp1, and
3) to test the effects of potentially important environmental factors on the early life history stages of *Aurelia* sp1.

This dissertation contains four research chapters. Chapter 2 examines the seasonal variation in the abundance of polyps, strobilae, ephyrae, and medusae of *Aurelia* sp1 in Mission Bay, San Diego, CA. It also characterizes the environmental factors to which each life history stage is exposed. Sampling began in February of 2008 and continued through May of 2012. *Aurelia* sp1 medusae were only seen in 2008. In all following years, polyps were present year-round and ephyrae were produced, but no medusae were seen. Combining these field observations with data from the Birch Aquarium at Scripps Institution of Oceanography, SeaCamp San Diego, and unpublished data collected by the Kaufmann lab at the University of San Diego showed that since 1999, medusae have been absent from Mission Bay in the years with the highest precipitation levels (Chapter 2). This result suggested that low salinity may be lethal to ephyrae and keep them from developing into medusae, and provided the motivation for Chapter 3.

Chapters 3, 4, and 5 involve laboratory studies to determine how the survivorship and growth of early life history stages of *Aurelia* sp1 respond to

some of the environmental factors that have been hypothesized to lead to jellyfish blooms. Chapter 3 looks at the impacts of acute salinity changes on the survivorship of polyps, ephyrae, and juvenile medusae of *Aurelia* sp1. These experiments show large salinity tolerance ranges of polyps, and smaller ranges for ephyrae and juvenile medusae. Additionally, the behavior of polyps was shown to be affected by the addition of organic osmolytes and all life history stages are able to recover after exposure to altered salinities for very short (2 or 8 hours) periods.

Chapter 4 considers the impact of different dissolved oxygen concentrations on the growth and survivorship of *Aurelia* sp1 polyps and ephyrae. Both life history stages were exposed to low oxygen concentrations (40%, 20%, and 10% dissolved oxygen (DO) saturation). Polyps survived at all DO concentrations for at least 4 weeks, but had negative growth rates under hypoxic conditions. Ephyrae survived for 10 days at 10% DO saturation and for at least 14 days under all other treatments. There was no change in the C or N content of polyps exposed to hypoxia, but polyps exposed to the lower hypoxia level had lower C and N content than those exposed to air-saturated water.

Chapter 5 examines the impact of dissolved organic matter (DOM) on the survivorship and growth of *Aurelia* sp1 polyps. In all treatments (in artificial sea water, in artificial seawater with DOM added, and in filtered sea water) polyps that were fed increased in abundance and those that were unfed decreased in abundance. Unfed polyps in artificial sea water had lower dry

mass, C, and N content than polyps that were fed in filtered sea water, but there was no difference among other treatments.

In Chapter 6, I summarize these results in the context of existing hypotheses about jellyfish blooms, and suggest important areas for further research.

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Figure 1.1: *Aurelia* sp1 medusa. Photo Credit: Vince Levesque

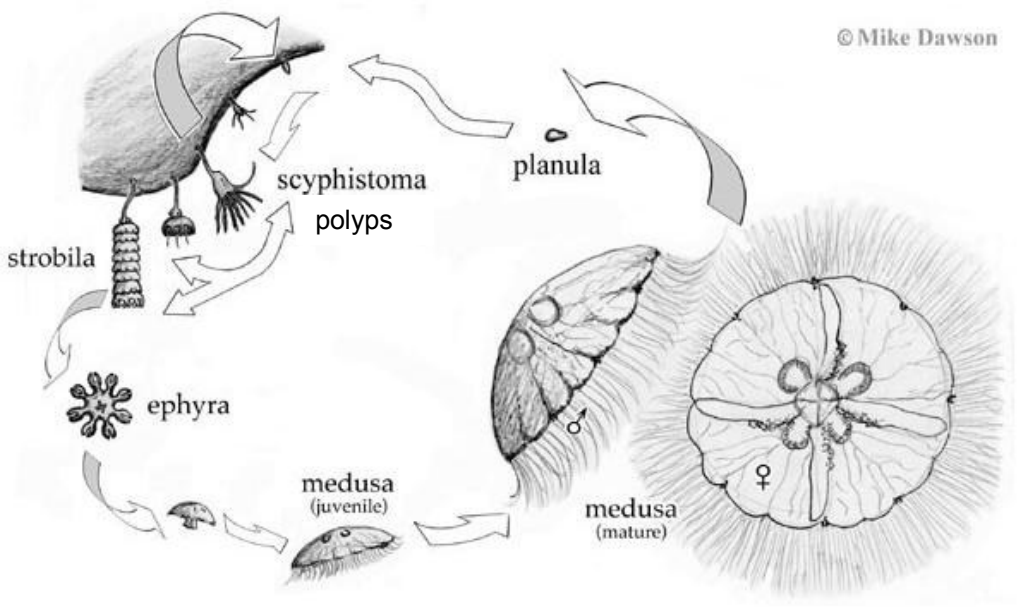

Figure 1.2: Generalized life history of *Aurelia* spp.
http://thescyphozoan.ucmerced.edu/Biol/Ecol/LifeHistory/ScyphozoaLH.html

CHAPTER 2:

Seasonal and interannual occurrence of *Aurelia* sp1 in Mission Bay and San Diego Bay, California

Abstract

Benthic and planktonic phases of *Aurelia* sp1 were examined in Mission Bay, San Diego, California from February 2008 through May 2012, and planktonic phases of *Aurelia* sp1 were examined in San Diego Bay, California from April 2009 through May 2012. Environmental variables, including temperature, salinity, dissolved oxygen, water clarity, chlorophyll *a* concentration, dissolved organic carbon, particulate organic carbon, and particulate organic nitrogen were measured concurrently. In Mission Bay, polyps were present year-round and highest polyp concentrations occurred in winter. Strobilation and ephyrae production began in late autumn and continued through winter. Medusae were present from February through May, but only sampled in 2008. In San Diego Bay, ephyrae were present in winter and medusae were present in spring. Results from the present study, combined with other sources going back to 2000, suggest that medusae were absent in Mission Bay in years with the highest precipitation, but medusae were present in San Diego Bay during those same years. Because the timing of precipitation coincides with the occurrence of ephyrae in the water column, the extreme decreases in salinity in Mission Bay may cause high mortality of ephyrae leading to recruitment failure and absence of medusae.

Introduction

In recent years, there has been increasing attention paid to the potential problems associated with jellyfish blooms (defined here as scyphozoan cnidarians; e.g. Mills, 2001; Purcell et al., 2007; Condon et al., 2012; Flynn et al, 2012; Purcell, 2012). Jellyfish blooms can have ecological impacts through direct predation (Purcell et al., 1994; Arai, 1997; Malej et al., 2007) and through competition with other organisms for food (Purcell and Arai, 2001; Purcell and Sturdevant, 2001; Lynam et al., 2005). Additionally, jellyfish blooms can have negative consequences for tourism (Purcell et al., 2007), fisheries (e.g. Lynam et al., 2006; Flynn et al., 2012), aquaculture (e.g. Doyle et al., 2008), and by clogging intakes of power plants (Purcell et al., 2007). It has been hypothesized that anthropogenic impacts, such as eutrophication, climate change, overfishing, and habitat modification, may be increasing the size, persistence, and/or frequency of jellyfish blooms (Arai, 2001; Mills, 2001; Lynam et al., 2006; Purcell et al., 2007). However, due to our current lack of understanding about the ecology of jellyfish and the dearth of relevant long-term observations, it is difficult to distinguish increasing jellyfish populations due to anthropogenic causes from natural fluctuations (Condon et al., 2012; Purcell, 2012).

One of the genera of jellyfish most commonly associated with blooms is *Aurelia*. (Mills, 2001). Blooms of *Aurelia* spp. have been noted in coastal waters around the world, including the Baltic Sea, the North Sea, the Black

Sea, Korea, India, Saudi Arabia, Australia, the Chesapeake Bay, the Gulf of Mexico, Scandinavia, and the Mediterranean Sea (Lucas, 2001; Mills, 2001). *Aurelia* spp. blooms have been attributed to a variety of anthropogenic causes including eutrophication (e.g. Papathanassiou et al, 1987; Arai, 2001), hypoxia (e.g. Miller and Graham, 2012), and habitat modification (e.g. Graham, 2001; Lo et al., 2008).

Understanding how changes in environmental conditions may lead to or prevent the formation of *Aurelia* spp. blooms requires an understanding of all portions of the life history. However, there are few data sets that address all life history phases through time. Some studies focus only on adult medusae (e.g. Schneider and Behrends, 1994; Graham, 2001; Bastian et al., 2011), only on planktonic ephyrae and medusae (e.g. Möller, 1980; Lucas and Williams, 1994; Olesen et al., 1994; Omori et al., 1995; Lucas, 1996; Papathanassiou et al., 1987; Lo and Chen, 2008; Bonnet et al., 2012), or only on benthic polyps (e.g. Watanabe and Ishii, 2001; Miyake et al., 2002; Willcox et al., 2008; di Camillo et al., 2010). These studies show a wide range of variability in the timing of appearance and the persistence of different life history phases. Studies that examine the entire life history of *Aurelia* spp. have taken place in Gullmar Fjord, Sweden (Hernroth and Gröndahl, 1983; Hernroth and Gröndahl, 1985; Gröndahl, 1988) and in the northern Adriatic Sea (Malej et al., 2012), which show different patterns in polyp densities, temperatures associated with strobilation, and timing of ephyrae and medusae presence. Most of these studies are relatively short; only eight have been

carried out for more than two years (Papathanassiou et al., 1987; Gröndahl, 1988; Lucas and Williams, 1994; Schneider and Behrends 1994; Omori et al., 1995; Graham, 2001; Lo and Chen, 2008; Malej et al., 2012).

Many of the above studies were conducted before the recognition of the many cryptic species of *Aurelia* spp. (Dawson and Jacobs, 2001; Dawson, 2003; Dawson et al., 2005). The newly recognized cryptic species, along with regional variability, may account for many of the reported differences in seasonality of population dynamics among locations. It is not known how seasonal patterns or responses to physical stimuli differ among species.

Given the wide variety of observations about the natural history of *Aurelia* spp., and their potential importance and impacts as bloom-forming jellyfish, studies that examine their entire life history are essential. Some life history stages are more sensitive or respond differently to environmental stimuli (e.g. Cargo and King, 1990; Miller and Graham, 2012; Cawood, in review), so knowing the timing and environmental conditions associated with each life history stage is an important part of understanding controls on population dynamics. Additionally, as *Aurelia* was considered to be a single species until recently, it is important to begin understanding variations between species and populations. The present study focuses on the seasonal and interannual patterns of abundance of *Aurelia* sp1 in Mission Bay and San Diego Bay, San Diego, California. I specifically address the questions: what are the timing of occurrence, persistence, and interannual variability of each

life history stage and to what range of environmental conditions is each stage exposed in these field sites.

Methods

Mission Bay Sites

Samples were collected biweekly from a floating dock in Mission Bay, San Diego, California (32.7788° N, 117.2126° W) from 8 Feb 2008 through 24 May 2012 (Fig. 2.1). Mission Bay is a small (approximately 18.6 km^2), heavily modified, seasonally hypersaline estuary (Chapman, 1963; Largier, et al., 1997a; City of San Diego, 2004; Elliott and Kaufmann, 2007). Mission Bay receives freshwater input from several creeks and from over 100 storm drains that empty into the bay (Largier et al., 1997a; Largier et al., 1997b). Mission Bay is generally well-mixed vertically (Levin, 1983; Largier et al., 1997a; Largier et al., 1997b).

Medusae and polyps from Mission Bay were identified as *Aurelia* sp1 by K. Bayha and M. Dawson (personal communication) using the molecular methods described in Dawson and Jacobs (2001). The presence of *Aurelia* sp1 in San Diego waters is consistent with distributions presented in Dawson et al. (2005).

Plankton samples were collected by hand-towing a 0.5 m diameter, 153 µm mesh ring net equipped with a General Oceanics flow meter along the dock. Sampling occurred biweekly. Four replicate horizontal surface tows were made during each sampling session. Plankton samples were fixed in

10% sodium borate-buffered Formalin. Benthic polyps were examined by out-planting ceramic tiles that had been seeded with polyps collected from the sampling dock in Mission Bay. Eighteen tiles were placed at approximately 0.25 m depth at six locations spanning the length of the dock on 6 November 2008. Because tiles were lost through time, new tiles were out-planted on 15 November 2009 and 29 October 2010. At each sampling session, tiles were photographed. Photographs were analyzed in order to determine the percent coverage of polyps and strobilae. Strobilae were generally easy to identify in photographs because they were typically redder in color than the whitish or faintly pinkish non-strobilating polyps.

Environmental samples were taken concurrently with biological samples. Temperature was measured biweekly using a YSI® model 55 dissolved oxygen probe from 8 Feb 2008 through 10 April 2009, calibrated with Winkler titrations. Beginning on 23 April 2009, continuous temperature measurements were made using a HOBO® Water Temperature Pro v2 Data Logger placed beneath the dock at approximately 0.25 m depth. Hourly measurements made by the temperature logger were averaged to obtain daily average temperatures. Water clarity was measured using a 16.5 cm diameter black and white Secchi disk. Salinity was measured using a hand-held refractometer calibrated against a Portasal™ 8410 portable salinometer.

In order to analyze dissolved organic carbon (DOC), seawater was filtered through pre-combusted GF/F filters. Forty mL of filtrate was acidified using two drops of concentrated trace-metal grade HCl and stored in

combusted borosilicate glass vials. Analysis was performed at Scripps Institution of Oceanography with a Shimadzu TOC-V_{CSN} calibrated using potassium hydrogen phthalate. DOC samples were analyzed from collections spanning 4 February 2008 through 12 January 2012.

Water was also filtered for analysis of chlorophyll *a*, particulate organic carbon (POC), and particulate organic nitrogen (PON). Separate seawater samples (250 mL) were filtered through precombusted 47 mm GF/F filters for chlorophyll analysis and for analyses of POC and PON. Filters were wrapped in pre-combusted aluminum foil and stored at -80 °C until analysis. POC/PON filters were thawed and acidified overnight in a desiccator saturated with HCl fumes. Filters were then dried at 60 °C for 48 h. Filters were weighed and approximately one-eighth of each filter was packed into a tin capsule for analysis. Samples were analyzed at the Scripps Institution of Oceanography analytical facility using a Costech Analytical Technologies model 4010 elemental analyzer calibrated with acetanilide standards. Chlorophyll *a* samples were analyzed by extracting the chlorophyll *a* from half of each filter into 90% acetone. After extraction, samples were refrigerated in the dark for 24 h. Chlorophyll *a* analysis was performed using a Turner Designs 10-AU Fluorometer. Chlorophyll *a* and POC/PON samples were analyzed from collections spanning 28 January 2010 through 24 May 2012.

On five dates (23 March 2009, 16 December 2009, 16 December 2010, 25 February 2011, 21 January 2012, and 15 April 2012) net tows were made at eight sites throughout Mission Bay (Site A 32.7889° N, 117.2472° W, Site B

32.7917° N, 117.2250° W, Site C 32.7639° N, 117.2444° W, Site D 32.7806° N, 117.2306° W, Site E1 32.7870° N, 117.2110° W, Site E2 32.7768° N, 117.2167° W, Site E3 32.7713° N, 117.2104° W, Site F 32.7681° N, 117.2241° W) to determine whether *Aurelia* sp1 ephyrae or medusae were located in parts of the bay that were not part of regular biweekly sampling. Sites were chosen using a stratified random sampling design with supplemental sampling near the site where biweekly sampling occurred (Sites E1, E2, and E3). At each site, three horizontal surface tows of 3 minute duration were made using the net used for sampling at the primary sampling site from a boat traveling at approximately 1.8 km h^{-1}. Samples were fixed in 10% sodium borate-buffered Formalin. These spatial samplings occurred within a week of sampling at the primary sampling site.

San Diego Bay Site

Samples were collected from a private dock in the Coronado Cays area of San Diego Bay, San Diego, California, USA (32.6211° N, 117.1298° W) from 23 April 2009 through 31 May 2012 (Fig. 2.1). San Diego Bay is relatively long (approximately 25 km) and narrow (1 - 3 km; Chadwick and Largier, 1999). Since San Diego Bay receives relatively little freshwater input (Largier et al., 1997b), seasonal hypersalinity can occur in the southern section of the bay (Largier et al., 1997b; Chadwick and Largier, 1999). The southern section of the bay is generally well mixed vertically (Largier et al., 1997b).

Plankton samples were collected biweekly using the same net used in Mission Bay. Four non-quantitative vertical tows were made from approximately 3 m to the surface, and samples were stored in 10% sodium-borate buffered Formalin. Because of the design of the dock, horizontal tows were not feasible at this location. As the tows were non-quantitative, ephyrae abundances were reported as presence/absence. Presence/absence visual observations of adult medusae were also made from the dock. Temperature was recorded using hourly measurements made by a HOBO® Water Temperature Pro v2 Data Logger placed beneath the dock at approximately 0.25 m depth. Hourly measurements were averaged to obtain daily average temperatures. Biweekly dissolved oxygen, salinity, water clarity, DOC, chlorophyll *a*, POC, and PON were collected and analyzed as in Mission Bay. DOC samples were analyzed from samples collected from 29 May 2009 through 31 Dec 2011. Chlorophyll *a* and POC/PON samples were collected from 23 September 2010 through the end of the study.

Historical Data

In order to put the sampling done in the present study in a broader temporal context, data from a variety of sources were combined. Data from the Birch Aquarium at Scripps Institution of Oceanography (BAS) spanned January 2000 through May 2012. This data set was comprised of observations of *Aurelia* medusae made by aquarium staff or information that was reported to BAS by the public. Negative observations were rarely

reported. BAS observations were made in Mission Bay and San Diego Bay; however, the majority of observations were from Mission Bay. Exact locations of observations were generally not reported.

SEACAMP San Diego, an educational program located on Mission Bay, provides year-round marine science camps for school groups and individuals. Photographs have been taken during the camps since February 2005. These photographs often include animals that the students observe. In many cases, photographs were taken of *Aurelia* medusae when present. The dates of photographs containing *Aurelia* medusae are used as evidence of presence. Dates when no *Aurelia* were photographed are considered evidence of absence of medusae. However, it is possible that photographs did not reveal *Aurelia* medusae when medusae were actually present in Mission Bay.

Biweekly sampling was conducted in Mission Bay from June 2001 through October 2005 by students from the University of San Diego (USD; R. Kaufmann, unpublished data). On many data sheets, students reported the presence or absence of *Aurelia* medusae. Occasions when *Aurelia* medusae were seen are considered presence observations. When it is noted that no *Aurelia* were seen or when no notations are made about *Aurelia*, medusae were considered absent.

Daily precipitation data from San Diego International Airport were obtained from the NOAA Climate Data Center for station SAN DIEGO LINDBERGH FIELD, CA US, ID: GHCND:USW00023188 (Fig. 2.1). Trace

values are considered to be 0 mm of precipitation. Data used are from 1 November 1999 through 31 May 2012.

Results

Aurelia sp1 polyps were present in Mission Bay on all sampling occasions, with the average percent cover ranging from 1.13% coverage to 47.76% (Fig. 2.2a). The densest polyp coverage occurred in December and January. The first set of outplanted polyps had the highest overall density (14.53 ± 6.4% cover, mean ± 95% confidence interval, averaged over the duration of deployment). The average percent cover of the second (2.92 ± 0.85% cover) and third (2.98 ± 0.33% cover) polyp sets was relatively low. The highest percent cover in all three polyp sets occurred in December. Open substrate was always available for polyp growth.

Strobilae were present on the tiles from 21 November 2008 – 25 February 2009, 19 November 2009 – 13 January 2010, 8 December 2010 – 28 January 2011, and 17 November 2011 – 27 January 2012. The average percent coverage of strobilae ranged from 0.0125% to 1.17% (Fig. 2.2b). The first appearance of strobilae and ephyrae in all years was observed between 17 November and 8 December (Table 2.1). The average abundance of ephyrae ranged from 0.02 ephyrae m^{-3} to 7.89 ephyrae m^{-3} (Fig. 2.2c). Ephyrae were most abundant in 2012. Medusae were only observed at the sampling dock from February through May of 2008, and the average

abundance (when present) ranged from 0.03 medusae m^{-3} to 0.27 medusae m^{-3} (Fig. 2.2d).

Spatial sampling conducted at multiple sites in Mission Bay addressed the extent to which time series sampling at a single dock was representative of the bay population. Ephyrae were seen on 16 December 2009, 16 December 2010, 25 February 2011, and 21 January 2012 as part of the spatial sampling of Mission Bay (Fig. 2.3). Average ephyrae abundances ranged from 0.026 ephyrae m^{-3} to 17.6 ephyrae m^{-3}. Ephyrae were generally present in the more inland parts of the bay, relatively close to the primary Mission Bay sampling site. No adult medusae were sampled or observed during spatial sampling.

Environmental measurements in Mission Bay (Fig. 2.4a-g) show few obvious relationships with the occurrence or abundance of any of the life history stages of *Aurelia* sp1 observed (Fig. 2.4h). There was a strong seasonal temperature cycle (Fig 2.4a). This seasonal signal was not seen in other variables (Fig. 2.4b-g). There was relatively little variability in dissolved oxygen (Fig 2.4b). Secchi depth varied between 0.6 and 3.1 m (Table 2.2, Fig. 2.4c), but these changes were not consistently related to changes in DOC, chlorophyll *a*, POC, or PON ($p > 0.1$, Spearman's rank correlation). Salinity was overall higher than in outer coast San Diego waters (Largier et al., 1997); however, sharp decreases in salinity sometimes occurred (Fig 2.4d). Peak concentrations of DOC were associated with decreases in salinity (Fig. 2.4d-c). Concentrations of chlorophyll *a*, POC, and PON show similar timing in peaks ($p < 0.1$, Spearman's rank correlation; Fig. 2.4f-g). The average

values and ranges of environmental variables from Mission Bay are given in Table 2.2.

There does seem to be a connection between the initial appearance of strobilae and ephyrae and water temperature and perhaps the water temperature gradient. Because sampling occurred only once every two weeks, strobilae and ephyrae could have appeared at any point in the two weeks leading up to the date of first observation. Therefore, the first observation of strobilae and ephyrae in Mission Bay and the two weeks preceding the first observation were used to determine the temperatures and temperature gradients. Strobilae and ephyrae occurred as temperatures were dropping, but had not yet reached their lowest levels for the year (Fig. 2.5a). The temperature at the first appearance of ephyrae and preceding days ranged from 13.8 °C - 19.83 °C. The 5-day temperature gradient (calculated from five days before the given date) was generally negative and ranged from -0.79 deg day^{-1} to 0.094 deg day^{-1} (Fig. 2.5b).

Aurelia sp1 ephyrae were sampled on only one sampling date per year in San Diego Bay in all years (Fig. 2.6a). Ephyrae were detected on 12 January 2010, 12 January 2011, and 30 January 2012. These dates may not be representative of the timing of first appearance or persistence of ephyrae in San Diego Bay because only a small volume of water was filtered in the vertical tows. Medusae were observed in San Diego Bay in all years (Fig. 2.6b).

There is no obvious relationship between the environmental variables (Fig. 2.7 a-g) and the presence of *Aurelia* sp1 ephyrae or medusae (Fig. 2.7h) in San Diego Bay. Temperature showed a strong seasonal pattern (Fig 2.7a). This pattern was not observed in other environmental variables (Fig 2.7b-g). There was little variation in dissolved oxygen or salinity (Fig 2.7b, d). Secchi disk depth varied from 1.1 to 3.5 m (Table 2.2, Fig. 2.7c), but these changes were not correlated with DOC, chlorophyll *a,* POC, or PON ($p > 0.1$, Spearman's rank correlation; Fig. 2.7c, e-g). DOC concentrations varied by a factor of 2.5 (Table 2.2, Fig. 2.7e). Concentrations of chlorophyll *a* were correlated with POC and PON ($p < 0.1$, Spearman's rank correlation; Fig. 2.7f-g). Averages and ranges of environmental variables are given in Table 2.2.

The average values of most of the environmental variables measured appear relatively similar in at the sites examined in Mission Bay and San Diego Bay (Table 2.2). However, in pairwise comparisons made on similar dates, the two bays are quite different. Temperature, dissolved oxygen, DOC, POC, and PON are all statistically higher in Mission Bay than San Diego Bay ($p < 0.05$, Wilcoxon matched-pairs signed-rank test; Table 2.2). Secchi disk depth is significantly deeper in San Diego Bay than in Mission Bay ($p < 0.05$, Wilcoxon matched-pairs signed-rank test; Table 2.2). Neither chlorophyll *a* nor salinity showed significant differences between the bays ($p > 0.05$, Wilcoxon matched-pairs signed-rank test), although the range of salinities in Mission Bay is much larger (Table 2.2, Figs. 2.4 and 2.7).

When considering presence/absence data from all sources (BAS, SEACAMP, USD, and the present study), *Aurelia* medusae were observed in Mission Bay in 2000 – 2004, 2006 – 2008, and in 2012 (Fig. 2.8a). The observations made in 2012 were made near Site C and Site D (as identified during spatial sampling, Fig. 2.3g), not near the primary Mission Bay sampling site. The data for San Diego Bay prior to 2009 are sparse, but medusae were reported in 2000, 2004, and 2009 – 2012 (Fig. 2.8b).

Mission Bay experiences large declines in salinity associated with increased rainfall. A similar decrease in salinity is not seen in San Diego Bay for the same major rainfall events (Fig. 2.9). In San Diego, the majority of rainfall occurs between November and February, which corresponds to the time when ephyrae are present in the water column. The years with rainfall above 200 mm (2005, 2009, 2010, and 2011) are the years when no *Aurelia* medusae were seen in Mission Bay (Fig. 2.10).

Discussion

Polyps occurred year-round in Mission Bay. This observation is consistent with reports from Gullmar Fjord, Sweden (Hernroth and Gröndahl, 1983; Hernroth and Gröndahl, 1985; Gröndahl, 1988), Tasmania (Willcox et al., 2008), Kagoshima Bay, Japan (Miyake et al., 2002) and the northern Adriatic Sea (di Camillo et al., 2010; Malej et al, 2012). However, in Tokyo Bay, it appears that polyps may survive for less than one year (Watanabe and Ishii, 2001). Polyps in Mission Bay showed peak percent coverage in winter

months. This pattern is contrary to other studies which show peak polyp densities in spring and summer (Hernroth and Gröndahl, 1983; Hernroth and Gröndahl, 1985; Gröndahl, 1988; Willcox et al., 2008; di Camillo et al., 2010). In other cases, polyps have been found to have no seasonal changes in density (Willcox et al., 2008), or to have high densities in summer, intermediate densities in winter, and low densities in spring (Malej et al., 2012).

At any time, only a small percentage (0% to 1.17% coverage) of polyps on the tiles were strobilating in Mission Bay. These percentages are consistent with some observations (e.g. Miyake et al., 2002; Willcox et al., 2008), but quite different from other studies which report anywhere from 19% (di Camillo et al., 2010) to nearly 100% (Watanabe and Ishii, 2001) of polyps strobilating at a time. There can be large variations in the percentage of polyps strobilating at a site between years, so it is possible that some of the discrepancy lies in interannual variability (Willcox et al., 2008). In polyp colonies originally collected from Mission Bay and kept in the laboratory, approximately 10% of polyps in the study were strobilating at a given time (personal observation). It is not known why the low levels of strobilation were observed in the field. It is possible that percentages of strobilation were higher on days in which tiles were not observed.

The first appearance of strobilae and ephyrae occurred from late November to early December in Mission Bay and ephyrae were present in San Diego Bay in January. Strobilation was observed until late January or early

February, and ephyrae were present in the water column until late February or early March in Mission Bay. Only one site was sampled regularly in Mission Bay, but the timing of occurrence was substantiated by spatial sampling of the bay. It is difficult to determine the precise timing of the appearance and persistence of ephyrae in San Diego Bay since only a small volume of water was sampled, making it possible that ephyrae were present in the water, but not detected in plankton samples. However, it appears that they do occur in winter, coinciding with the appearance of ephyrae in Mission Bay. The onset of strobilation in late fall and early winter has also been observed in places such as the northern Adriatic Sea (di Camillo et al., 2010; Malej et al., 2012), Japan (Watanabe and Ishii, 2001; Miyake et al., 2002), Thau lagoon in the southwestern Mediterranean Sea (Bonnet et al., 2012), and Gullmar Fjord, Sweden (Hernroth and Gröndahl, 1983; Hernroth and Gröndahl, 1985; Gröndahl, 1988). These times of year are generally associated with decreases in temperature and day length in the Northern Hemisphere, both of which have been proposed as factors that contribute to strobilation (Kakinuma, 1962; Custance, 1964; Spargenberg, 1968). However, there are locations, such as Jellyfish Lake, Palau (Hamner et al., 1982), Kiel Bight, Germany (Möller, 1980) and Horsea Lake, UK (Lucas, 1996) where strobilation and the production of ephyrae occur over most of the year. In high latitudes, ephyrae are sometimes not released until late winter or early spring (e.g. Van Der Veer and Oorthuysen, 1985; Olesen et al., 1994). In some warmer latitudes, such

as Elefsis Bay, Greece (Papathanassiou et al., 1987), the onset of strobilation also begins in late winter. The reasons for these differences are not clear.

Strobilae and ephyrae appeared in Mission Bay over a relatively short time window, but the range of potential temperatures when they first appeared covers a rather broad range (13.8 °C to 19.8 °C). This broad range is quite different from other studies which indicate that there is a threshold temperature or small range (1 or 2 °C) over which strobilation is initiated (e.g. Miyake et al., 2002; Willcox et al., 2008; di Camillo et al. 2010, Malej et al., 2012). Because sampling occurred biweekly, it is difficult to determine the exact temperature and temperature gradient when strobilation and ephyrae production began. There may be a more tightly constrained temperature threshold and/or gradient that cannot be resolved with a biweekly sampling resolution. The dates of observation of strobilae and ephyrae occurred in a narrower temperature range (17.0 to 18.4°C) and temperature gradient (-0.29 to -0.08° day^{-1}) when only the years 2008, 2009, and 2011 are considered. In 2010, the temperature was lower (14.3°C) and the gradient was slightly positive (0.08° day^{-1}). In 2010, there was the longest time interval between sampling events (15 days). If it is assumed that strobilae and ephyrae appeared early in the between-sampling period in 2010, the overall temperature range of first occurrence would be 15.1 to 19.8°C and the gradient would be -0.79 to 0.09° day^{-1} when considering all dates of observation and the dates between sampling sessions. Additionally, while it is possible that day length plays a role in the onset of strobilation; strobilation

can be induced in the laboratory via a temperature reduction in polyp colonies collected from Mission Bay under a 12:12 light:dark cycle (personal observation).

Aurelia sp1 medusae were present in Mission Bay from January through June and from February through June in San Diego Bay. This timing is comparable in timing and duration to populations in the northern Adriatic (Malej et al., 2012) and in the southwestern Mediterranean Sea (Bonnet et al., 2012). These areas are similar to San Diego in that all three have Mediterranean climates, which may contribute to the similarity. However, medusae in Elefis Bay, Greece are present from May through October (Papathanassiou et al., 1987). Many areas in more northern latitudes have *Aurelia* spp. present over the summer (Möller, 1980; Hernroth and Gröndahl, 1983; Hernroth and Gröndahl, 1985; Gröndahl, 1988; Lucas and Williams, 1994; Schneider and Behrends, 1994; Olesen et al., 1994; Bastian et al., 2011). A few areas, such as Horsea Lake, UK (Lucas, 1996), Tokyo Bay, Japan (Omori et al., 1995), Jellyfish Lake, Palau (Hamner et al., 1982), and Tapong Bay, Taiwan (Lo and Chen, 2008) have medusae present over most of the year.

Other studies have found that *Aurelia* spp. medusae were present in all years examined (e.g. Papathanassiou et al., 1987; Lucas and Williams, 1994; Schneider and Behrends, 1994; Omori et al., 1995; Lo and Chen, 2008; Malej et al., 2012). Some populations showed relatively little interannual variability (Lucas and Williams, 1994; Omori et al., 1995). However, other studies

documented more than an order of magnitude difference in *Aurelia* spp. abundance among years (Hernroth and Grönhdal, 1985; Schneider and Behrends, 1994; Graham, 2001; Lo and Chen, 2008). It has been hypothesized that changes in precipitation and run-off may partially explain the observed variability (Graham, 2001; Lo and Chen, 2008).

The present study shows years when no medusae were present in Mission Bay. It is believed that *Aurelia* sp1 are non-native in southern California waters (Dawson et al., 2005). It is possible that *Aurelia* sp1 in San Diego are at the periphery of their range. Peripheral distribution by itself does not explain absence of medusae, but may explain sensitivity to ambient fluctuations. Additionally, years with no medusae observations correspond to the years with the highest precipitation between November and February, the time period when ephyrae are present in the water column. During this season, the salinity in Mission Bay can drop to very low levels: 9 psu in the present study and values as low as 3 psu have been reported (City of San Diego, 2004). In addition to low salinity, high precipitation is associated with increased DOC. It is also possible that deleterious compounds are washed into Mission Bay with the rain; however laboratory studies indicate that DOM is not beneficial to *Aurelia* sp1 polyps (Chapter 5). Other environmental factors such as dissolved oxygen concentration are unlikely to cause mortality of *Aurelia* sp1 at levels reached in Mission and San Diego Bays (e.g. Shoji et al., 2008; Miller and Graham, 2012; Chapter 4). Laboratory results indicate that ephyrae are the life history phase that is most sensitive to salinity changes

(Cargo and King, 1990; Cawood, in review), and they cannot survive for more than a few hours at salinities below 17 psu (Cawood, in review). It is possible that any ephyrae present in the water during extreme drops in salinity were not able to survive. Low salinity generally exists throughout the water column in Mission Bay (Levin, 1983; Largier et al., 1997a, Largier et al., 1997b), so it would have been difficult for ephyrae to move to areas of higher salinity. The recruitment failure of ephyrae into medusae could provide an explanation for the absence of medusae.

In years when medusae were not seen in Mission Bay, they were seen in San Diego Bay. San Diego Bay experiences much smaller salinity fluctuations than Mission Bay. This is further evidence for a relationship between low salinity and the absence of *Aurelia* sp1 medusae. Lo and Chen (2008) have also hypothesized that increased precipitation is associated with times of the year when fewer medusae are present in Tapong Bay, Taiwan.

Climate change is predicted to change the amount of water delivered to coasts and estuaries, and salinity in estuaries will likely be affected. Extreme flooding and rainfall events are predicted to increase (Milly et al., 2008), and the timing and amount of precipitation and snowmelt are expected to change (Dettinger and Cayan, 1995). Human construction activities such as damming of rivers (Dynesius and Nilsson, 1994) and desalination plants (Roberts et al, 2010) also have the potential to change local salinities. The magnitude and direction of these salinity changes will vary with the estuary. The present study suggests that changes in the timing and/or severity of precipitation and

run-off, and consequent changes in salinity have the potential to impact the formation of blooms of *Aurelia* sp1. Locations with increased precipitation may experience fewer blooms while locations with decreased precipitation may experience more blooms. A greater understanding of regional population dynamics and the corresponding environmental drivers will be essential to predict and possibly mitigate responses of jellyfish populations to such climate changes.

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Table 2.1: First observation of strobilae and ephyrae in Mission Bay.

	1st Observation of Strobilae and Ephyrae
2008	21 November
2009	19 November
2010	8 December
2011	17 November

Table 2.2: Average and range of environmental variables collected in Mission Bay and San Diego Bay. Averages and ranges use all data. Matched pairs tests (in the Significance column) use only data pairs collected within one week of each other. * = $p < 0.05$ Wilcoxon matched-pairs signed-rank test.

	Mission Bay		Significance	San Diego Bay	
	Average	Range		Average	Range
Temperature (°C)	20.2	12.2 - 28.1	* n = 1127	19.8	12.5 - 27.3
% Dissolved O_2 Saturation	87.1	65.5 - 99.8	* n = 46	83.7	70.2 - 96.9
Secchi Depth (m)	1.6	0.6 - 3.1	* n = 51	2.0	1.1 - 3.5
Salinity (psu)	36.8	9.0 - 46.5	n = 46	36.8	32.0 - 40.0
DOC (mgC L^{-1})	2.5	1.1 - 11.7	* n = 29	1.9	1.3 - 2.8
Chl *a* (mg m^{-3})	8.6	2.5 - 24.4	n = 22	7.7	1.9 - 24.2
POC (µg L^{-1})	607	270 - 1977	* n = 20	418	135 - 1345
PON (µg L^{-1})	43	26 - 89	* n = 20	25	14 -49

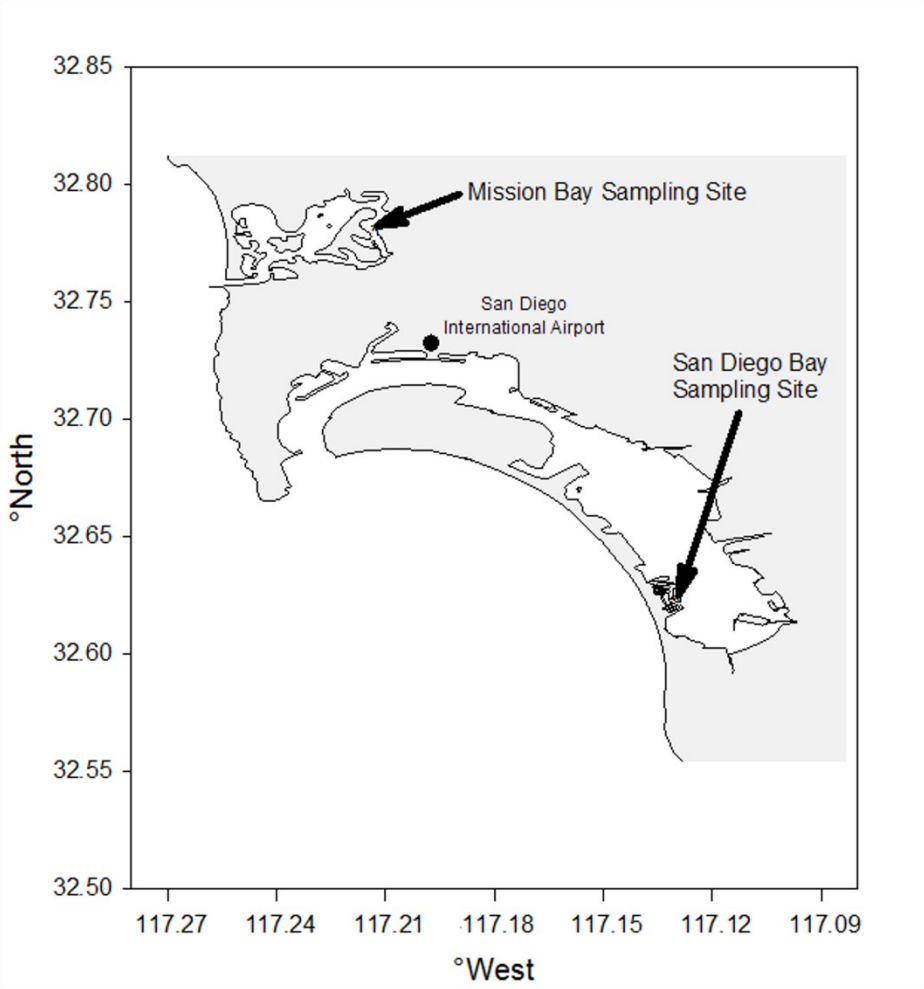

Figure 2.1: Primary sampling sites in Mission Bay and San Diego Bay, San Diego, California. Precipitation measurements were made at San Diego International Airport.

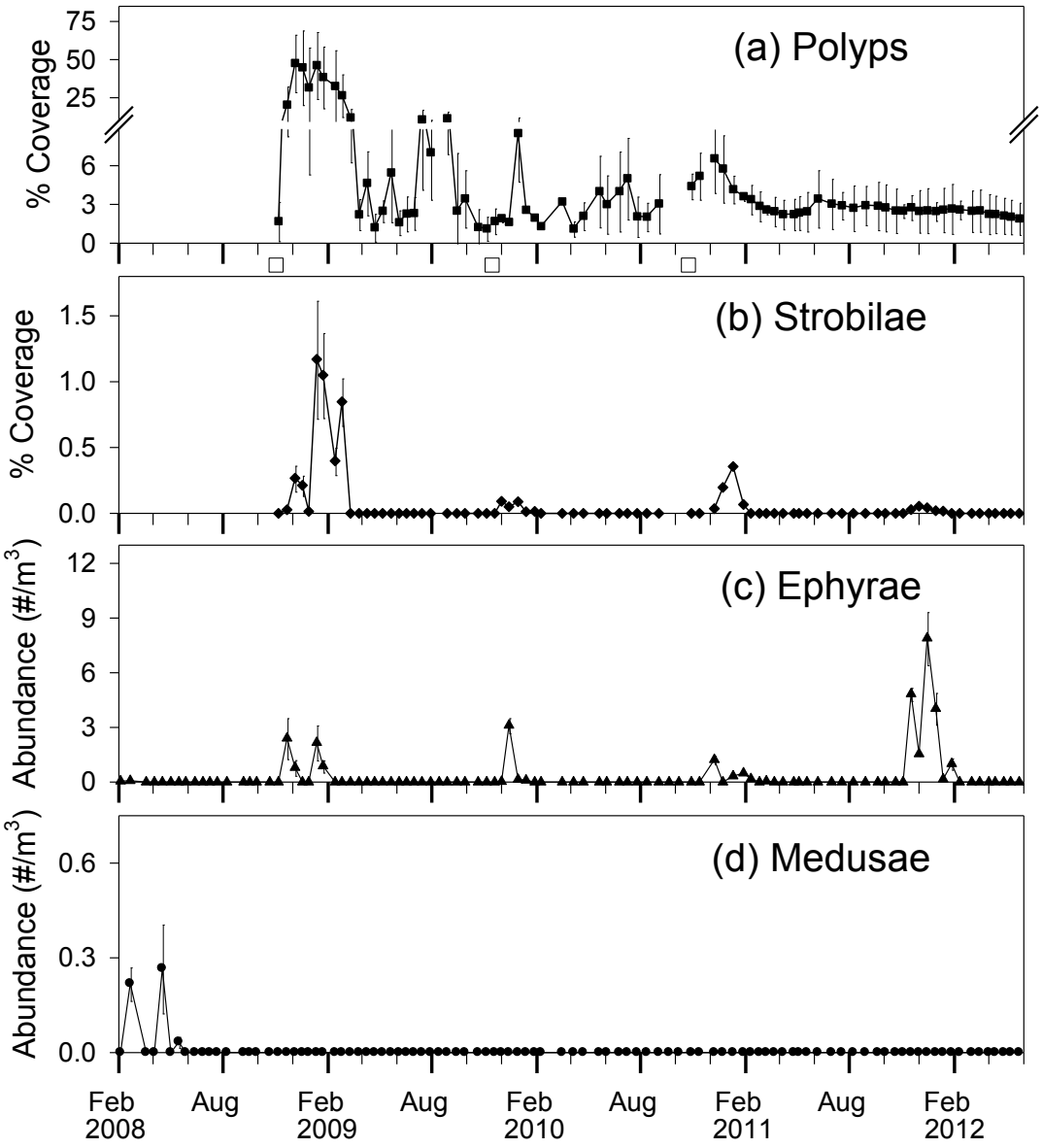

Figure 2.2: Percent coverage of (a) polyps and (b) strobilae and abundance of (c) ephyrae and (d) medusae in Mission Bay. Open squares between on (a) and (b) indicate dates when new tiles were outplanted.

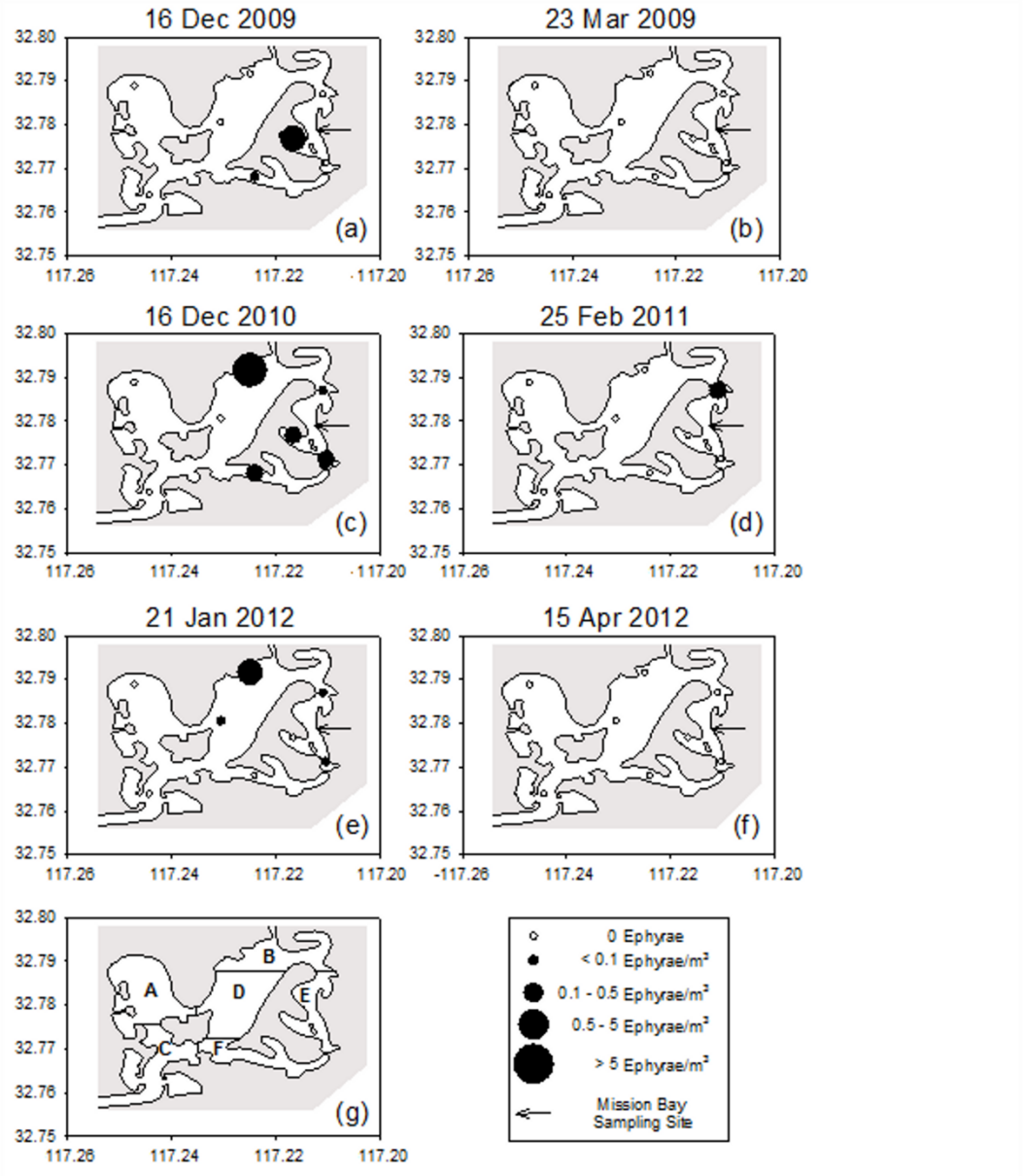

Figure 2.3: Spatial sampling for ephyrae and medusae in Mission Bay, San Diego, CA, USA. Open symbols represent sites where no ephyrae were collected. Left panels (a, c, e) indicate collections during December – January and right panels (b, d, f) collections during February – April. Arrows indicate the primary Mission Bay sampling site. (g) shows the sampling regions used in the stratified random sampling design to select sampling sites.

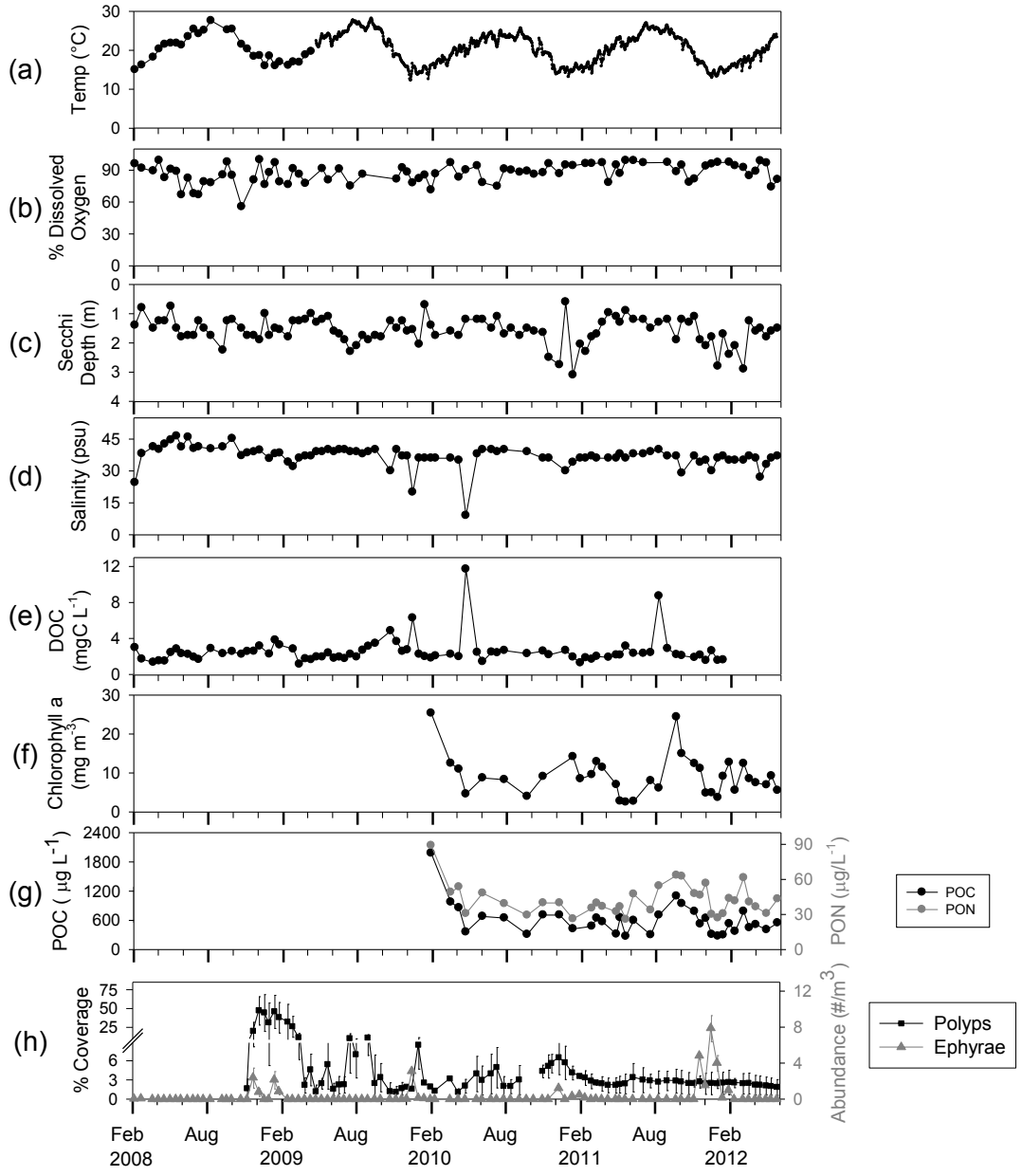

Figure 2.4: (a) Temperature, (b) percent dissolved oxygen, (c) Secchi depth, (d) salinity, (e) DOC, (f) chlorophyll *a*, and (g) POC and PON collected concurrently with (h) *Aurelia* sp1 samples in Mission Bay. (a) Prior to 23 April 2009, temperature was measured biweekly. Afterward temperatures are daily averages of hourly collected data from a temperature logger.

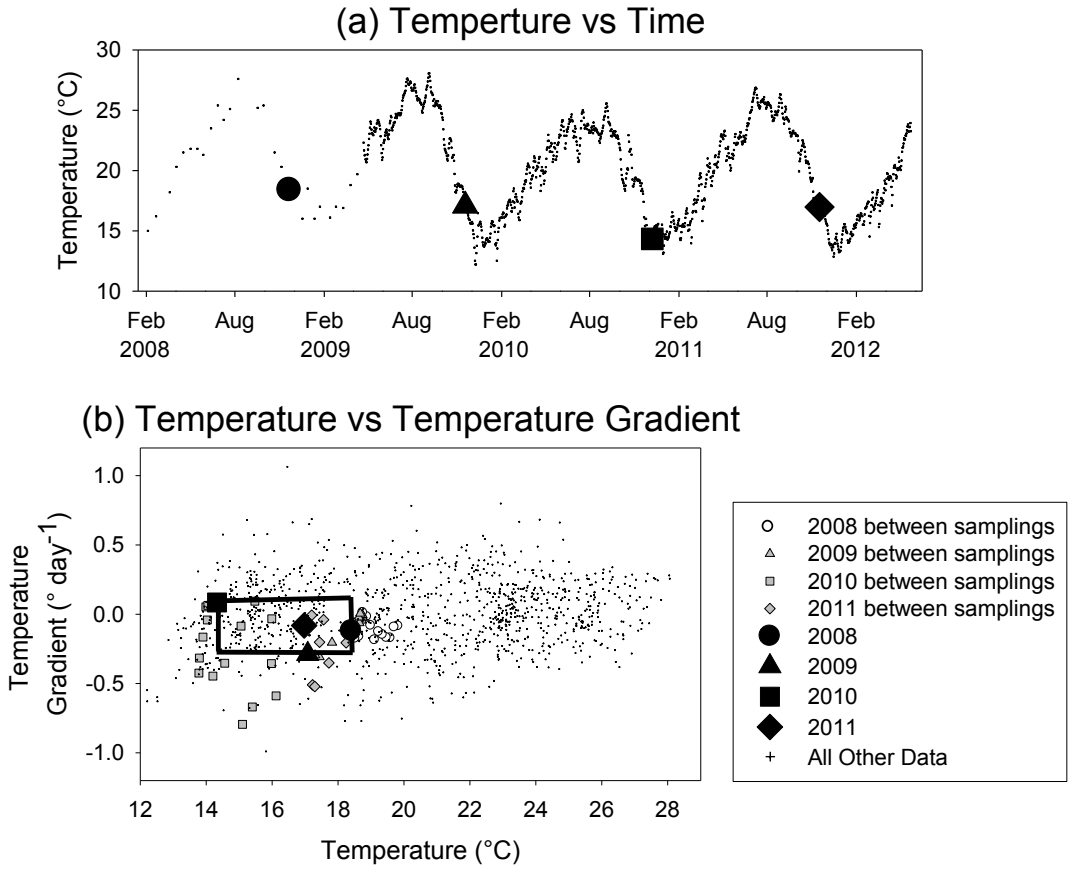

Figure 2.5: (a) Water temperature in Mission Bay from 2008 – 2011. Large symbols indicated dates of first observance of strobilae and ephyrae. Prior to 23 April 2009, temperature was measured biweekly. After that date, temperature data are daily averages of hourly collected data from a temperature logger. (b) Water temperature and 5-day temperature gradient at first appearance of strobilae and ephyrae (large black symbols). Gray symbols represent conditions on unsampled days when it is possible that strobilae and ephyrae were present but not sampled. Open symbols are interpolated because in 2008 water temperature measurements were taken biweekly. Small + symbols represent all other temperature and gradient data. The box outlines the conditions at first observance of strobilae and ephyrae.

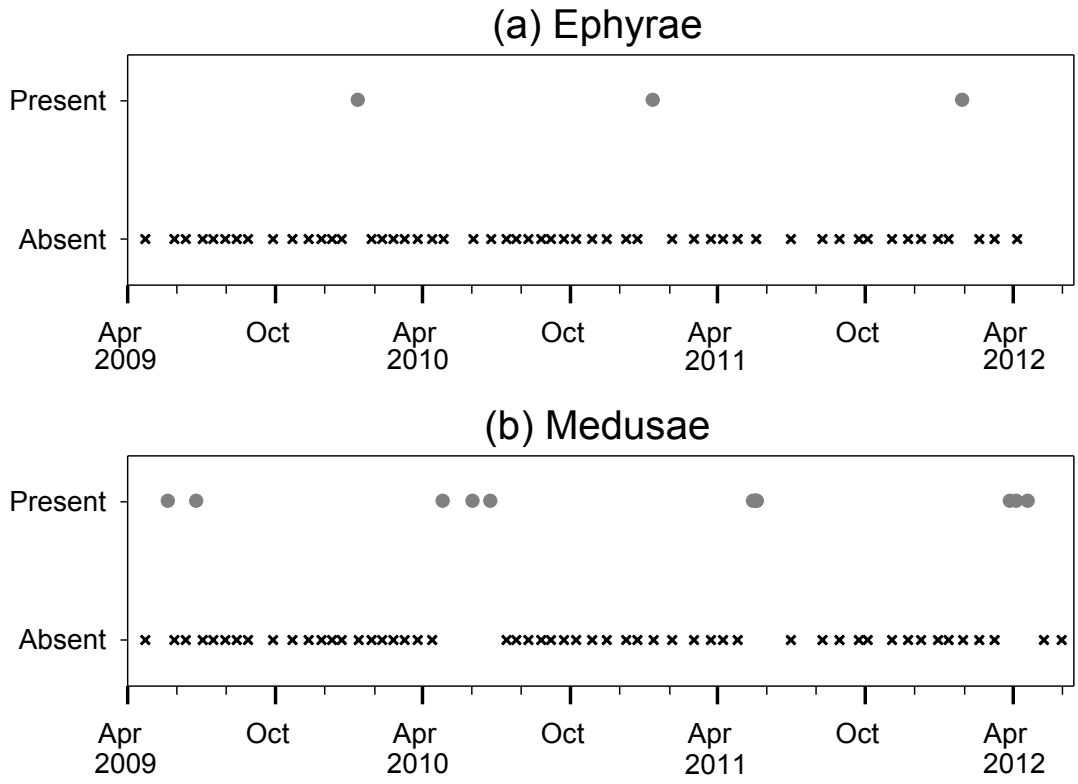

Figure 2.6: Presence (gray symbols) and absence (black symbols) of (a) ephyrae and (b) adult medusae in San Diego Bay.

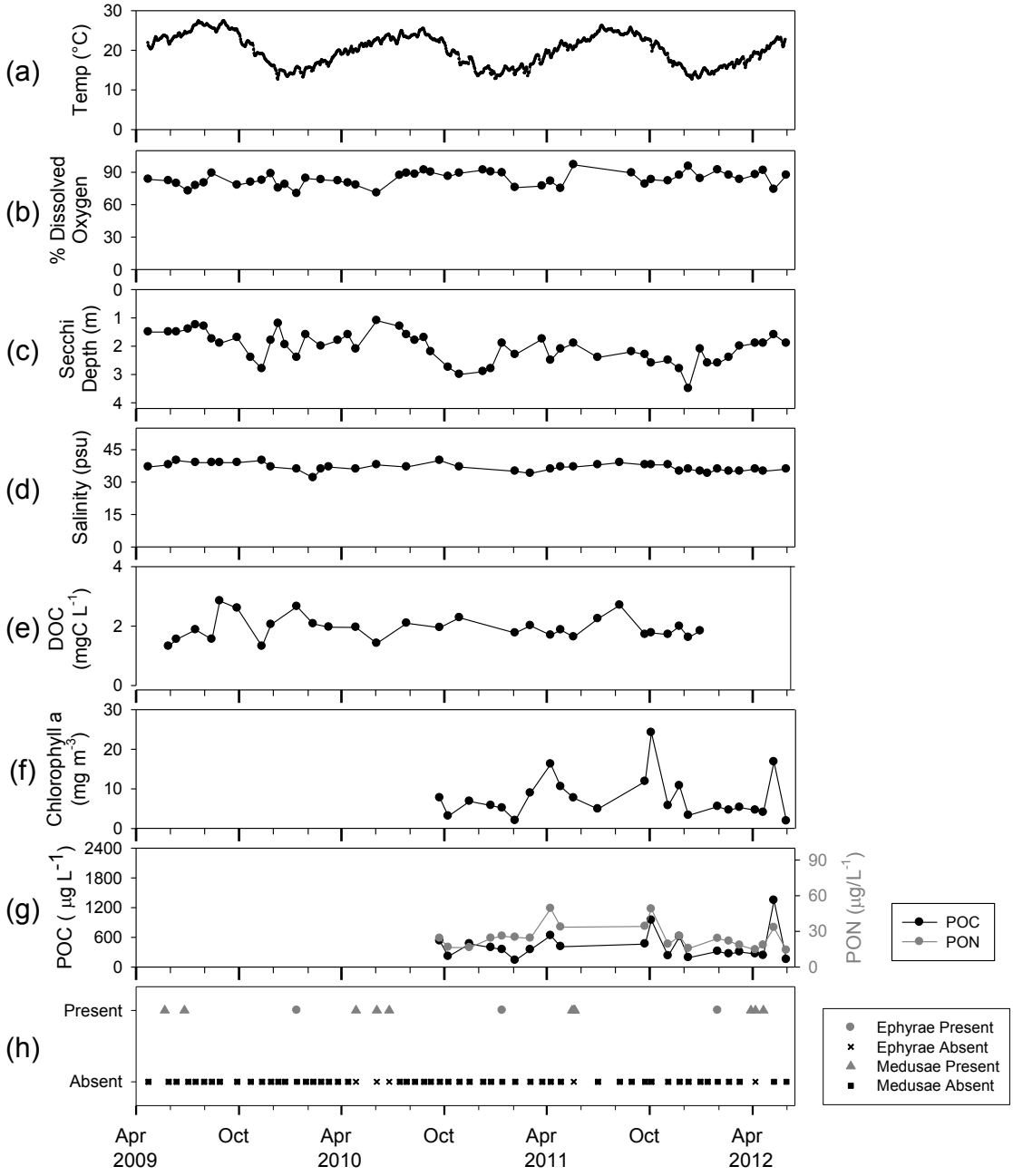

Figure 2.7: (a) Temperature, (b) percent dissolved oxygen, (c) Secchi depth, (d) salinity, (e) DOC, (f) chlorophyll *a*, and (g) POC and PON collected concurrently with (h) *Aurelia* sp1 planktonic samples in San Diego Bay.

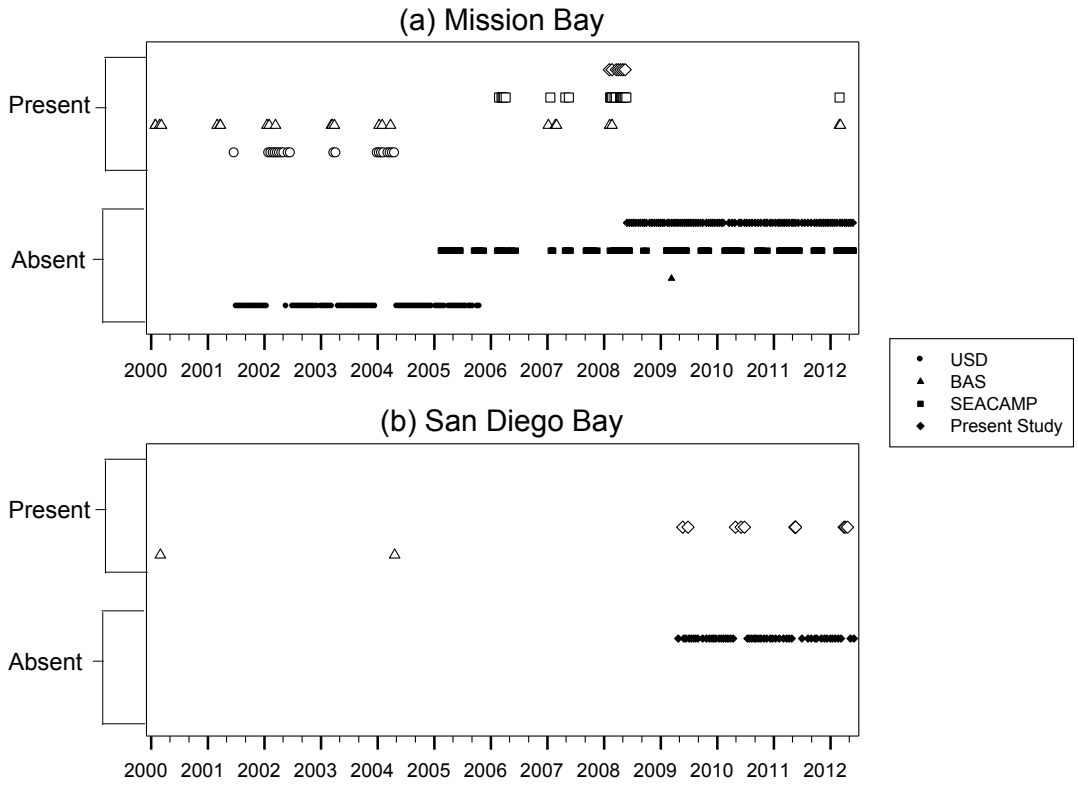

Figure 2.8: Presence (open symbols) and absence (closed symbols) of *Aurelia* sp1 medusae in (a) Mission Bay and (b) San Diego Bay. Observations made through different programs are shown with different symbols and on separate lines.

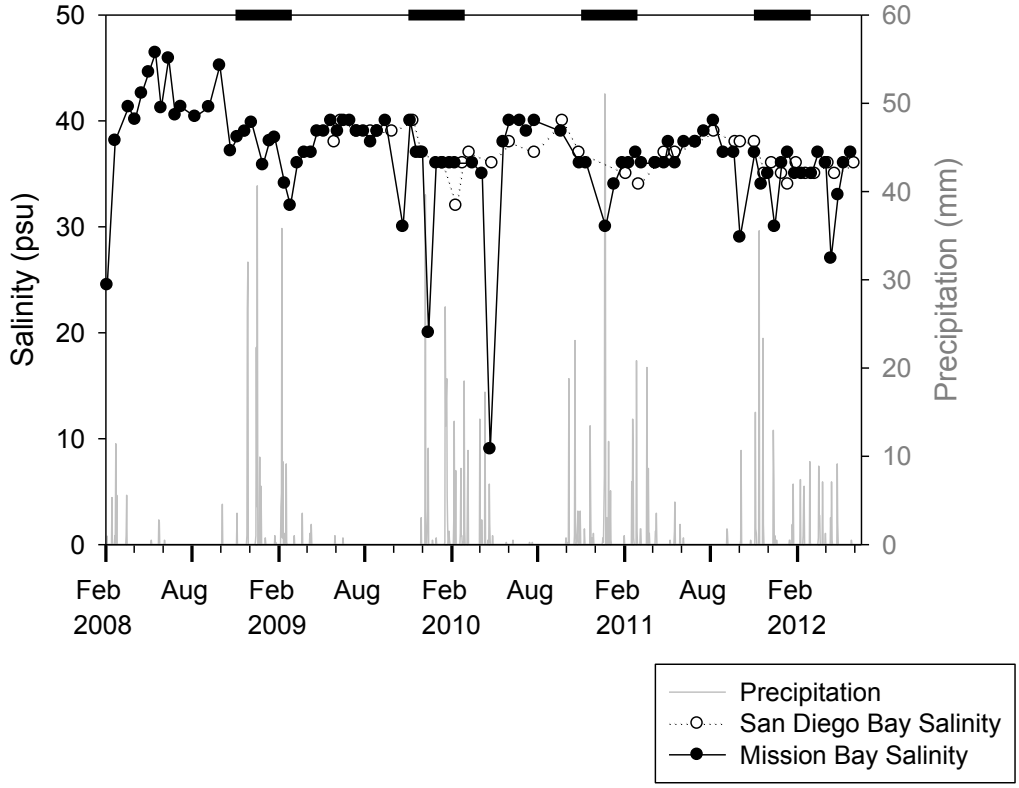

Figure 2.9: Daily precipitation recorded at San Diego International Airport (gray bars). Salinity measured once every two weeks in Mission Bay (closed symbols) and San Diego Bay (open symbols). Dark bars at the top of the graph indicate the November – February period when most precipitation occurs in San Diego.

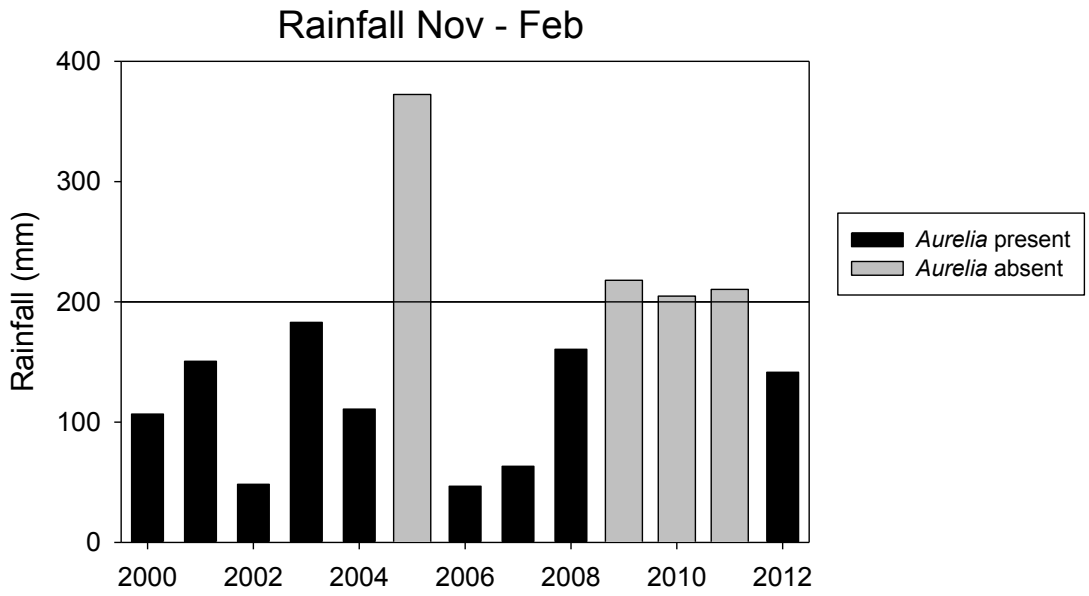

Figure 2.10: Summed rainfall from November 1 of the year before that listed on the graph through February of the year listed on the graph from San Diego International Airport. Black bars represent years in which *Aurelia* sp1 medusae were observed in Mission Bay. Gray bars represent years in which *Aurelia* sp1 medusae were not seen in Mission Bay, all of which exceeded 200 mm rainfall.

CHAPTER 3:

Impacts of acute salinity changes on the survivorship of *Aurelia* sp1 polyps, ephyrae, and juvenile medusae

Abstract

Jellyfish blooms and their effects have become sources of increasing concern in many coastal areas. One environmental factor that may influence jellyfish bloom formation is changes in salinity. Here, I examine the effects of acute salinity stress of salinities ranging from 6 to 61 psu on the survivorship of polyps, ephyrae, and juvenile medusae of *Aurelia* sp1. Ephyrae showed the most sensitivity to extreme salinities, while polyps were able to survive at salinities ranging from 6 to 52 psu for at least 72 h. The addition of an organic osmolyte, in the form of dissolved free amino acids, had no impact on the survivorship of polyps, ephyrae, or juvenile medusae, but did have an impact on the behavior of polyps. All examined life history stages showed high survivorship when exposed to extreme salinities for short periods of time (2 h) then returned to a normal salinity (29 psu). The sensitivity of ephyrae to extreme salinities may help explain the presence or absence of adult medusae in a given year. The large tolerance range of polyps would allow them to persist in an area even in years when no medusae were produced.

Introduction

Global population growth and climate change are putting ever-increasing pressure on a number of ecosystems, including wetlands, estuaries, and deltas, by changing patterns in the distribution and usage patterns of water. Climate change is expected to change the amount of water delivered to different watersheds; in some there will be increases, decreases in others. An increase in extreme rainfall and flooding events is also anticipated in some parts of the world (Milly et al., 2002), while more frequent and persistent droughts are expected in others (Sheffield and Wood, 2008). The timing of precipitation and of snowmelt is also expected to change (Dettinger and Cayan, 1995). Additionally, increased human populations will require more potable water, and this increased water usage is anticipated to reduce inflow to many estuaries (Dynesius and Nilsson, 1994). At the same time, desalination as a source of potable water is expected to increase, possibly resulting in locally increased salinities (Vörösmarty et al., 2000; Roberts et al., 2010). These changes in precipitation and inflow are likely to have a major impact on the salinity of wetlands and estuaries, which in turn will impact the abundance and distribution of estuarine organisms (Sklar and Browder, 1998; Reaugh et al., 2007). The magnitude and direction of these changes will vary with location and the initial salinity of the wetland or estuary. Changes in freshwater input, in addition to affecting salinity, will also impact dissolved oxygen concentrations, nutrient input, and may increase the

abundance of invasive species (Cloern and Nichols, 1985; Sklar and Browder, 1998).

Jellyfish are among the organisms that may be affected by these changes in salinity. In recent decades, jellyfish blooms and the problems they create have become a source of increasing concern (Mills, 2001; Purcell et al., 2007). These blooms impact local ecosystem dynamics both via direct predation and through competition with other organisms for prey (Purcell and Arai, 2001), and have negative societal impacts, affecting industries such as tourism, fisheries, and aquaculture, and clogging power plants (reviewed in Purcell et al., 2007). There is some evidence that anthropogenic impacts may be increasing the size, persistence, and/or frequency of jellyfish blooms (Purcell et al., 1999a; Mills, 2001; Purcell, 2005; Brotz et al., 2012), although others are less certain that this is the case (e.g. Condon et al., 2012). However, our current lack of knowledge regarding the ecology of jellyfish makes it difficult to understand how environmental and anthropogenic factors combine to cause (or inhibit) these blooms.

Salinity has a number of impacts on the growth and development of jellyfish in a variety of habitats. Salinity levels seem to be a major factor influencing *Chrysaora quinquecirrha* abundances and distributions in the Chesapeake Bay, and have even been used in attempts to predict and model their occurrence (Cargo and King, 1990; Purcell et al., 1999b; Purcell and Decker, 2005; Decker et al., 2007). Salinity makes a difference in the number of *Aurelia* sp. polyps actively budding in experimental cultures (Willcox et al.,

2007) and impacts the number of ephyrae produced by *Aurelia labiata* (Purcell, 2007). Adult *A. labiata* actively avoid swimming into water with low salinities (less than 20 psu; Albert, 2008) and change swimming direction when low salinity water is encountered (Albert, 2012). Salinity can also influence populations in enclosed, non-estuarine areas, such as *Pelagia noctiluca* in the Mediterranean Sea, where low rainfall corresponded to years of elevated medusae occurrence (Goy et al., 1989).

One of the jellyfish most commonly associated with bloom formation is the moon jellyfish, *Aurelia* spp. (Mills, 2001). *Aurelia* have complex life cycles involving both benthic and pelagic phases and both sexual and asexual reproduction, enabling them to take advantage of changing conditions. All portions of their life histories impact the dynamics of jellyfish populations. In most *Aurelia* populations, the benthic polyps are present year-round, meaning that they are subjected to short term, seasonal, and interannual variations in temperature, salinity, nutrient fluxes, and other environmental variables (Lucas, 2001). Strobilation and the production of ephyrae are generally cued by environmental changes (Hernroth and Gröndahl, 1983; Purcell, 2007; Willcox et al., 2008). The presence of jellyfish blooms, which are comprised of adult medusae, means there must have been large, successful populations of polyps, strobilae, ephyrae, and juvenile medusae. Therefore, it is important to understand the impacts of environmental changes on each life history stage, and not just adult medusae, which have been the focus of most previous studies on jellyfish blooms. The sensitivity of different life history stages to

changes in salinity and the timing of those changes may be important in determining whether and to what extent *Aurelia* blooms occur.

Aurelia spp. have been reported across a large range of salinities. Medusae have been observed in 14 psu in Kertinge Nor, Denmark (Olesen et al., 1994) and 38 psu in Elefsis Bay, Greece (Papathanassiou et al., 1987), although medusae have been seen in Mission Bay, San Diego, CA, USA at salinities as high as 46 psu (personal observation). Ephyrae have been reported from salinities as low as 5.5 psu in the Gulf of Finland (Palmén, 1954). Polyps have been reported in waters with salinities ranging from less than 5 psu in Tokyo Bay, Japan (Watanabe and Ishii, 2001) to 36 psu (Holst and Jarms, 2010), although polyps have been seen in Mission Bay, San Diego, CA, USA at salinities as high as 45 psu (personal observation).

Many of the studies that have been conducted on jellyfish and salinity have used relatively narrow salinity ranges and/or gradual salinity changes (e.g. Willcox et al., 2007; Holst and Jarms, 2010). These experiments are likely to correspond to seasonal or long term changes in salinity. However, in estuaries and shallow bays, salinities can change rapidly over short periods of time, generally due to storm or run-off events. Such events may cause acute changes in salinity, which are likely to persist over the scale of hours to days (Cloern and Nichols, 1985). The experiments in this study examine the impacts of such acute salinity changes on polyps, ephyrae, and juvenile medusae of *Aurelia* sp1. Specifically, these studies seek to determine the tolerances of *Aurelia* sp1 polyps, ephyrae, and juvenile medusae to acute

salinity changes, to explore the potential impacts of organic osmolytes on survivorship and behavior of polyps, ephyrae, and juvenile medusae, and to determine whether or not these life history stages are able to recover from short exposure to acute salinity perturbations.

Methods

Organisms

Aurelia sp1 polyps, ephyrae, and juvenile medusae were obtained from the Birch Aquarium at Scripps Institution of Oceanography (BAS) in La Jolla, California. The species was verified by K. Bayha and M. Dawson (personal communication) using the molecular methods described in Dawson and Jacobs (2001). The original polyps for this culture were collected from San Diego waters. The presence of *Aurelia* sp1 in San Diego agrees with the distribution presented in Dawson et al. (2005). Polyps were attached to acrylic plates. All ephyrae were two to four days old. Juvenile medusae ranged in size from approximately 1 to 6 cm bell diameter. All juvenile medusae had fully formed bells.

Salinity Tolerance

Salinity tolerance experiments were conducted at 15.6°C for 72 h. Organisms were kept on a 12:12 hour light:dark cycle. Enumerations performed during the dark part of the cycle were done using red light. Organisms were transferred from filtered sea water with salinities between 29 -

34 psu, depending on the day that the water was collected, into artificial sea water (ASW) made using MilliQ filtered water and commercially prepared sea salt mix (Coralife® scientific grade marine salt). ASW mixtures of 6, 12, 17, 28, 40, 46, 52, and 61 psu for polyps and 6, 12, 17, 21, 28, 34, 40, 46, 52, and 61 psu for ephyrae and juvenile medusae were used for the salinity tolerance incubations. Salinities were read using a hand-held refractometer, calibrated using a Portasal™ 8410 portable salinometer. All organisms were fed two-day-old *Artemia* nauplii less than 24 h before the incubations began and were not fed during the incubations.

Polyp incubations were conducted in closed glass 0.55L jars with still water. Two replicates were counted at each salinity level. Counts were performed every 8 h using a dissecting microscope. Initial polyp counts ranged from 153 to 567 polyps depending on the plate. As a behavioral metric, the state of the tentacles was noted. Polyps with tentacles that were fully extended were considered to be unstressed to mildly stressed. Polyps with tentacles partially contracted were considered to be moderately stressed, and those with tentacles completely contracted were considered to be highly stressed (Fig. 3.1). The contraction of tentacles as a response to mechanical stress was described by Johnson and Wuensch (1994). The contraction of tentacles at low salinities (≤ 12) was also noted by Holst and Jarms (2010).

Incubations of ephyrae and juvenile medusae were conducted in closed glass 0.55L jars for ephyrae and 1L jars for juvenile medusae and rotated on a plankton wheel to ensure water movement for the duration of the incubation.

For ephyrae, four replicates at each salinity treatment were enumerated; each jar contained 30 individuals. For juvenile medusae, three replicates of each salinity level were enumerated; each jar contained 15 individuals. Counts were performed every 2 h for the first 8 h, every 4 h from 8 - 24 h, and every 8 h from 24 - 72 h. As a behavioral index, ephyrae and medusae were classified as either actively swimming, interpreted as unstressed to mildly stressed individuals, or sporadically pulsing (movement was noted, but individuals were not actively swimming), interpreted as moderately to highly stressed individuals.

Amino Acid Addition

A second set of experiments was conducted in which dissolved free amino acids (DFAAs) were added to the ASW. This was done in order to provide osmolytes with which the *Aurelia* sp1 might be better able to manage osmotic stress (reviewed in Gilles, 1979; Yancey, 2005). A concentration of 250 nM of each of 7 DFAAs was added, giving a total of 1.7 µM. This concentration is somewhat higher than the concentrations of DFAAs reported in the literature (e.g. Middelboe et al., 1995; Stepanauskas et al., 2002), but as no other organic osmolytes were added to the medium, I wanted to ensure that any impacts of the addition of DFAAs would be apparent. Aspartic acid, glutamic acid, serine, arginine, glycine, threonine, and alanine were used because these have been seen to be the most common DFAAs in bays and coastal water (Yamashita and Tanoue, 2003; Aluwihare and Meador, 2008).

Amino acid addition incubations were conducted in the same manner as the salinity tolerance experiments. The ranges of salinities tested were based on the salinity tolerance experiments, with focus toward the upper and lower tolerances (6, 12, 28, 40, 46, and 52 psu for polyps and 12, 17, 21, 34, 40, and 46 for ephyrae and juvenile medusae), while avoiding the most extreme salinities where there was high mortality. Water was changed every 24 hours (with fresh amino acids added to the amino acid treatments) for all life history stages.

Recovery from Acute Salinity Changes

In order to determine whether or not *Aurelia* sp1 were able to recover from osmotic stress, acrylic plates bearing polyps, or freely swimming ephyrae or juvenile medusae were transferred from filtered sea water to ASW at altered salinities of 52 and 61 psu for polyps; 12, 17, 40, and 46 psu for ephyrae; and 12, 17, 46, and 52 psu for juvenile medusae. These experiments were intended to determine whether or not the effects of acute salinity stress are permanent or temporary. This response could be important in places where the persistence of low salinity events is very short. One set of each life history stage (two replicates with 154 - 217 individuals per replicate for polyps, four replicates of 30 individuals each for ephyrae, and three replicates of 15 individuals each for juvenile medusae) was exposed to the altered salinities for 2 h and then transferred to ASW with a salinity of 29 psu, while a second set was exposed to the altered salinities for 8 h, and then returned to 29 psu

ASW. Polyps were only tested at high salinities because there was high survivorship when exposed to low salinities in the salinity tolerance experiments. They were counted on the same schedule as the salinity tolerance experiments after they were transferred back to ASW.

Results

Salinity Tolerance

Polyps survived at salinities ranging from 6 to 52 psu for the entire 72-hour incubation (Fig. 3.2a). Some polyps survived at the highest test salinity (61 psu) for at least 32 h. The average mortality rates among salinity treatments were significantly different ($p < 0.01$, Kruskal Wallis 1-way ANOVA), with the mortality rates at 28 and 40 psu significantly lower than those at 52 and 61 psu ($p < 0.05$, Tukey range test; Fig. 3.3a). An average of 50%of surviving polyps exposed to very low salinity (6 psu) had their tentacles fully contracted during the majority of the incubation period (Fig. 3.4a). On polyp plates exposed to 12 psu, an average of 84.5% of polyps had their tentacles partially contracted.. Greater than 50% of polyps exposed to moderate salinities (17 and 28 psu) had the majority of their tentacles fully extended. Of the polyps exposed to water of 40 psu, approximately 70% of polyps had their tentacles partially contracted for the duration of the incubation. At high salinities (46 psu and higher), greater than 90% of polyps had their tentacles completely contracted (Fig. 3.4a).

Ephyrae survived at salinities ranging from 17 to 40 psu for the entire 72 h incubation (Fig. 3.2b). Ephyrae exposed to 6 psu seawater survived between 6 and 8 h. Individuals exposed to high salinities (≥ 46 psu) survived for less than 12 h. The average mortality rates among salinities were significantly different ($p < 0.01$, Kruskal Wallis 1-way ANOVA; Fig. 3.3b). In general, mortality rates at high (≥ 46 psu) and low (≤ 17 psu) salinities were significantly higher than ($p < 0.05$, Tukey range test) those at moderate salinities (21 – 34 psu; Fig. 3.3b). More than 98% of ephyrae were actively swimming for the duration of the incubation at salinities ranging from 21 to 34 psu. Above and below that range, more than 75% of the surviving ephyrae were sporadically pulsing (Fig. 3.4b).

Juvenile medusae survived at salinities of 17 to 40 psu for the duration of the experiment (Fig. 3.2c). At 6 psu, juvenile medusae survived for at least 16 h, and at least 48 h at 12 psu. At the highest tested salinity (62 psu) juveniles survived for at least 16 h and at 46 psu, they survived at least 56 h. The average mortality rates among salinity levels were significantly different ($p < 0.01$, Kruskal Wallis 1-way ANOVA, Fig. 3.3c). In general, mortality rates at lower (≤ 17 psu) and higher (≥ 46 psu) salinities were significantly higher ($p < 0.05$, Tukey range test) than at moderate salinities (21 – 34 psu; Fig. 3.3c). At lower salinities (≤ 17 psu), more than 90% of surviving medusae were sporadically pulsing. This was also the case at salinities of 52 psu and higher. More than 55% of individuals at moderate salinities (28 to 46 psu) were actively swimming (Fig. 3.4c).

Amino Acid Addition

The addition of DFAAs to ASW did not change the survivorship of polyps, ephyrae, or juvenile medusae ($p > 0.05$, Wilcoxon matched pairs test, Fig. 3.5). However, there is some indication that DFAAs changed the behavioral responses of the polyps (Fig. 3.6). When averaging all time points for a given salinity, there are significantly fewer polyps ($p < 0.05$, Wilcoxon matched pairs test) with polyps with tentacles fully extended in ASW as contrasted with ASW plus DFAAs at 12 and at 40 psu (Fig. 3.6a). There were significantly more polyps ($p < 0.05$, Wilcoxon matched pairs test) with fully contracted tentacles at 12, 40, and 46 psu in ASW only as compared to ASW with DFAAs (Fig. 3.6b).

Recovery from Acute Salinity Stress

Polyps exposed to high salinities showed high rates of survivorship (mean survivorship of 85.7% at 52 psu and 56.3% at 61 psu at 2 h of exposure and 53.6% at 52 psu and 40.4% at 61 psu at 8 h of exposure) over short time periods (Fig. 3.7a). However, the differences in survivorship at 72 h following return to moderate conditions, after 2 h, 8 h, or 72 h of exposure to modified salinities are not significantly different by a Kruskal-Wallis 1-way ANOVA ($p > 0.05$), due to small sample size.

Ephyrae showed significant differences in survivorship ($p < 0.05$, Kruskal-Wallis 1-way ANOVA) for all tested salinities, with survivorship at 2 h

exposure significantly higher than at 72 h exposure ($p < 0.05$, Tukey range test; Fig. 3.7b).

Juvenile medusae showed high rates of survivorship after exposure to all tested salinities after 2 h of exposure to altered salinities followed by a return to moderate conditions (mean survivorship of 90.0% at 12 psu, 93.9% at 17 psu, 100 % at 46 psu, and 100% at 52 psu Fig. 3.7c). Survivorship decreased, but still remained relatively high after 8 h of exposure (mean survivorship of 83.3% at 12 psu, 91.1% at 17 psu, 93.8 % at 46 psu, and 43.3% at 52 psu). There was a significant difference among percent survivorships at 52 psu ($p < 0.05$, Kruskal-Wallis 1-way ANOVA) with survivorship at 2 h and 72 h of exposure found to be significantly different from one another ($p < 0.05$, Tukey range test; Fig. 3.7c).

Discussion

Aurelia sp1 can be found in environments with a very large range of salinities. For example, observed salinities in Mission Bay, San Diego, CA, USA salinities range from 9 to 46 psu (personal observation). This study shows that their potential salinity tolerance range is even larger than that, and varies depending on which life history phase(s) are in the water. *Aurelia* sp1 ephyrae appear to be the life history stage that is most sensitive to acute salinity changes. *Chrysaora quinquecirrha* ephyrae in the Chesapeake Bay have also been shown to be the most sensitive life history stage with regard to salinity (Cargo and King, 1990). *Aurelia* sp1 polyps can survive over a large

salinity range. This means that even in cases of extreme salinity changes, at least some polyps are likely to persist. Such tolerances by polyps may be important in keeping *Aurelia* sp1 established in an area even in years where conditions are unfavorable for the production or survivorship of ephyrae and/or adult medusae. *Aurelia* sp1 are considered to be osmoconformers, meaning that their intracellular salinity varies with the salinity of the surrounding water (Arai, 1997). However, while their internal salinities may vary in the same way, the behavioral responses of all life history stages are not equal. Even the ephyrae and juvenile medusae, which would occur in the same habitats and relatively close to each other in time, do not respond identically to short, severe salinity changes.

At both high and low salinities, polyp tentacles were completely contracted. This behavior may be a response to stress, as a similar reaction is seen when polyps are mechanically disturbed (Johnson and Wuensch, 1994). However, this response does not occur with all stresses, such as long-term starvation (personal observation). In addition to being a stress response, this behavior may benefit the polyps by reducing their surface area, thereby decreasing the area over which salts can enter and leave the organism. The sporadic pulsing behavior observed in the ephyrae and the juvenile medusae may be a stress response, but it may also be beneficial to their survivorship. This behavior may cause the organisms to sink in the water column, away from low salinity layers located at or near the surface. Adult *Aurelia labiata* in

Roscoe Bay, Canada, actively swim down when they encounter low salinity layers (Albert, 2012).

Because different life history stages have different salinity tolerances, the timing and severity of acute salinity changes may impact the abundance of medusae in a given year. If salinity is dramatically lowered (below approximately 20 psu), there would likely be a high mortality of both ephyrae and juvenile medusae. However, if there were an event that dramatically raised the salinity (above approximately 40 psu), juvenile medusae are likely to survive longer than ephyrae. Therefore, the timing of the salinity perturbation events in relation to which life history stages are present may determine how many adult medusae occur later in the year. This timing in turn may impact the number of planulae that are produced, and therefore the number of new sexually produced polyps that contribute to genetic variation in the population.

These short-term, acute salinity changes occur along with longer-term salinity changes due to seasonal and interannual variability or anthropogenic changes such as damming of rivers. Polyps of *Aurelia aurita* that had been acclimated to salinities from 36 psu to salinities of 28, 20, 12, and 8 psu in a step-wise manner over the course of one month survived at these altered salinities for at least 3 months (Holst and Jarms, 2010). Salinity impacted strobilation of polyps of *Aurelia labiata*, with a lower proportion of polyps strobilating at higher salinities (34 psu) and delayed onset of strobilation at lower salinities (20 psu; Purcell, 2007). *Aurelia* sp. from Tasmanian waters

had a higher number of actively budding polyps after a 32-day exposure to higher salinities (35 psu; Willcox et al., 2008).

This study examines only part of the life history of *Aurelia* sp1. Planulae and strobilae were not tested. Planula of *Cyanea capillata, Cyanea lamarckii,* and *Chrysaora hysoscella* from the North Sea were able to survive to salinities of at least 10 psu, although planulae did not settle at salinities of less than 20 psu (Holst and Jarms, 2010). Polyps of *C. capillata, C. lamarckii,* and *Aurelia aurita* strobilated and released ephyrae at salinities from 12 - 36 psu (Holst and Jarms, 2010).

In order to predict and mitigate damage from jellyfish blooms, it is essential to understand environmental factors that cause or prevent their occurrence. Many past studies of jellyfish have focused on only the prominent medusa phase. Understanding the differential responses of all life history phases is essential to understanding jellyfish population and bloom dynamics.

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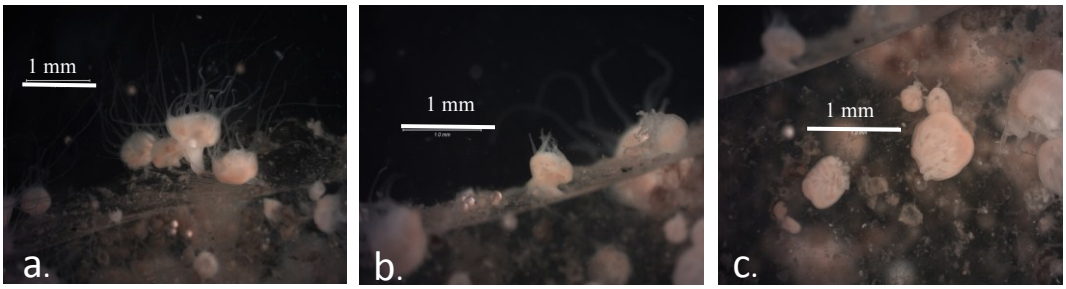

Figure 3.1: (a) *Aurelia* sp1 polyps with tentacles fully extended, (b) with tentacles partially contracted, and (c) with tentacles completely contracted. Scale bars are 1 mm.

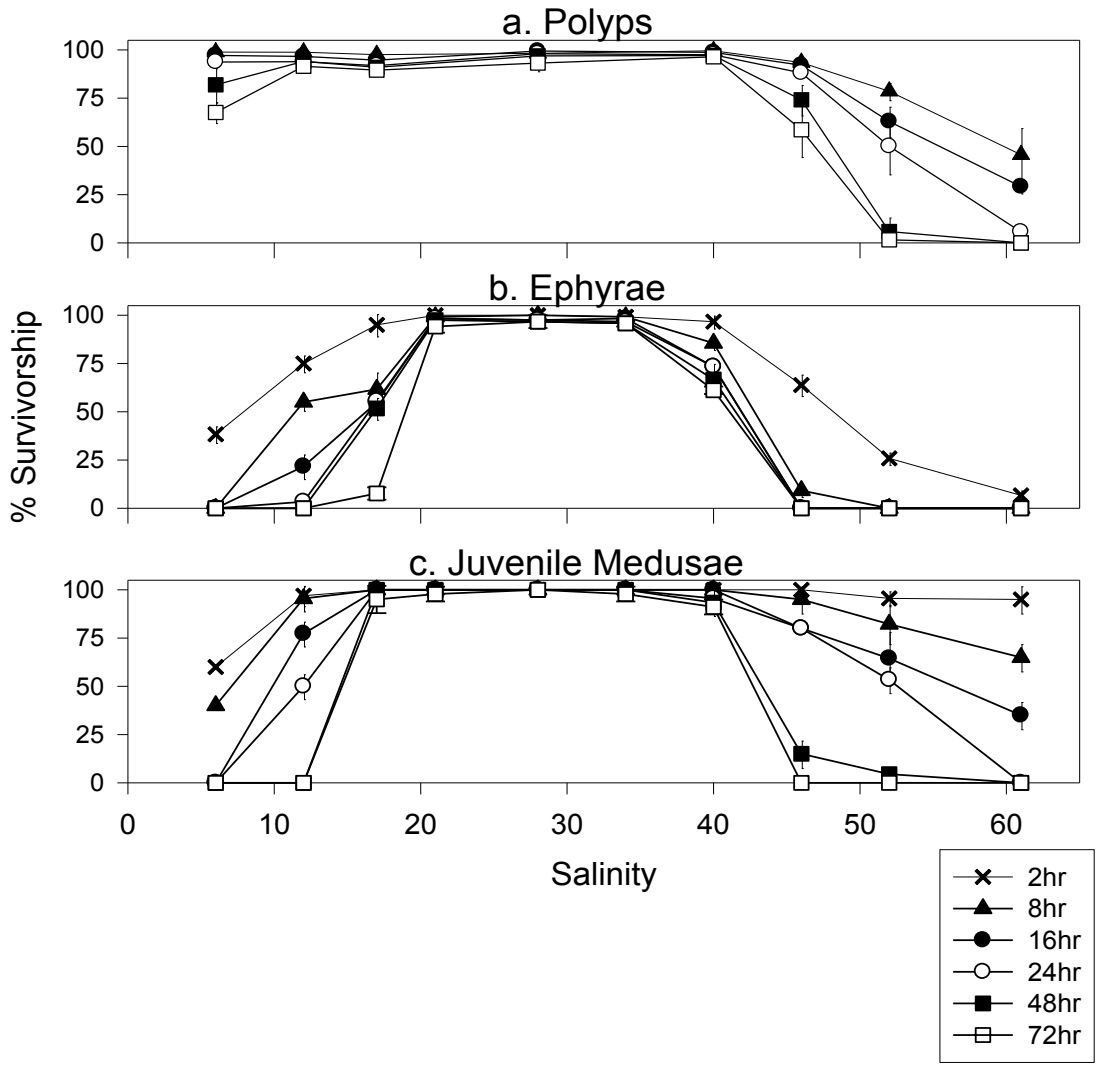

Figure 3.2: Mean percent survivorship of (a) polyps, (b) ephyrae, and (c) juvenile medusae exposed to different salinities. Each point indicates a salinity treatment and each line indicates the percent survivorship at a given time point (2, 8, 16, 24, 48, and 72 h) for all salinity treatments. Error bars indicate the range. Note that not all tested time points are plotted.

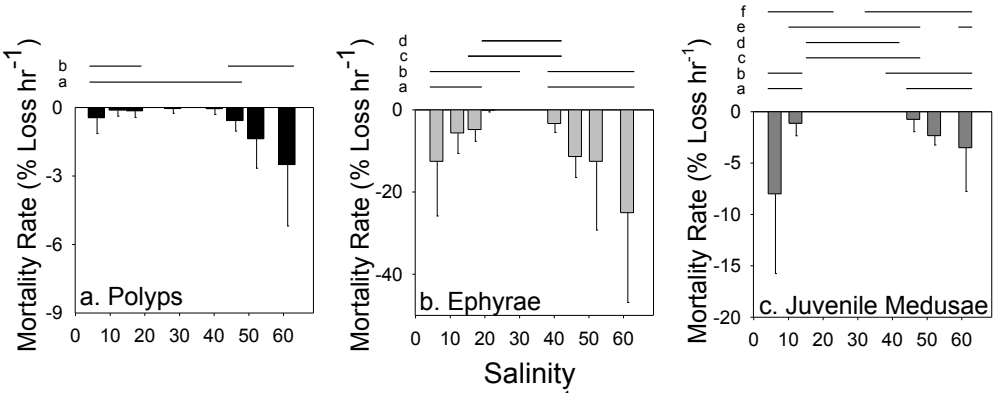

Figure 3.3: Average mortality rate (% loss hr^{-1}) for (a) polyps, (b) ephyrae, and (c) juvenile medusae. Error bars indicate ± 95% confidence intervals. Note the different y-axis scales for each subplot. Kruskal-Wallis 1-way ANOVA $p < 0.05$ for each life history stage; lines above the plots indicate the treatments are significantly different ($p < 0.05$, Tukey range test). All treatments covered by a horizontal line are statistically similar.

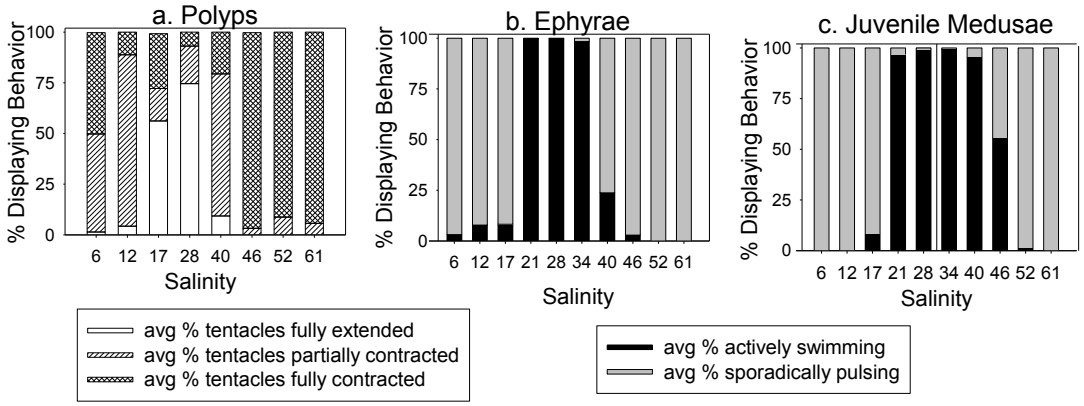

Figure 3.4: Average percent of surviving (a) polyps, (b) ephyrae, and (c) juvenile medusae displaying the specified behaviors at each salinity level.

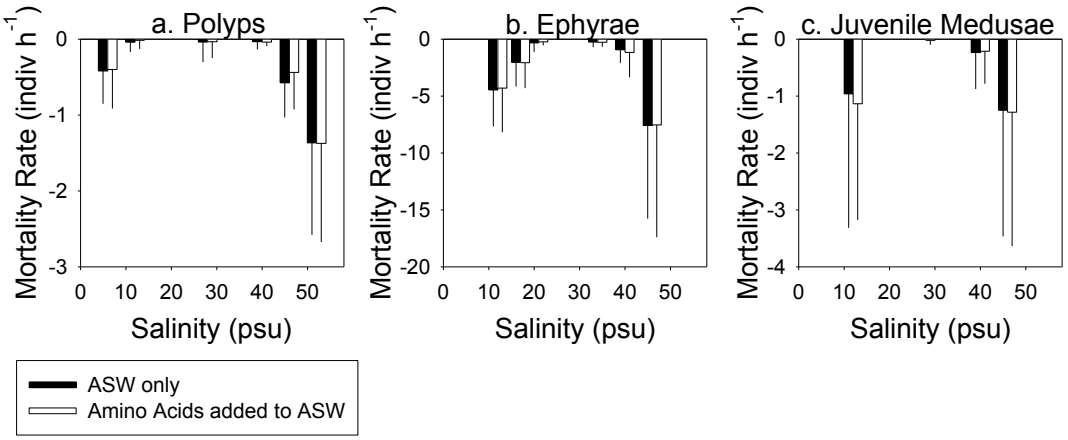

Figure 3.5: Average mortality rate of (a) polyps, (b) ephyrae, and (c) juvenile medusae exposed to artificial seawater (ASW) only or to ASW with amino acids added. Error bars indicate standard deviation. Note the different y-axis scales on each subplot.

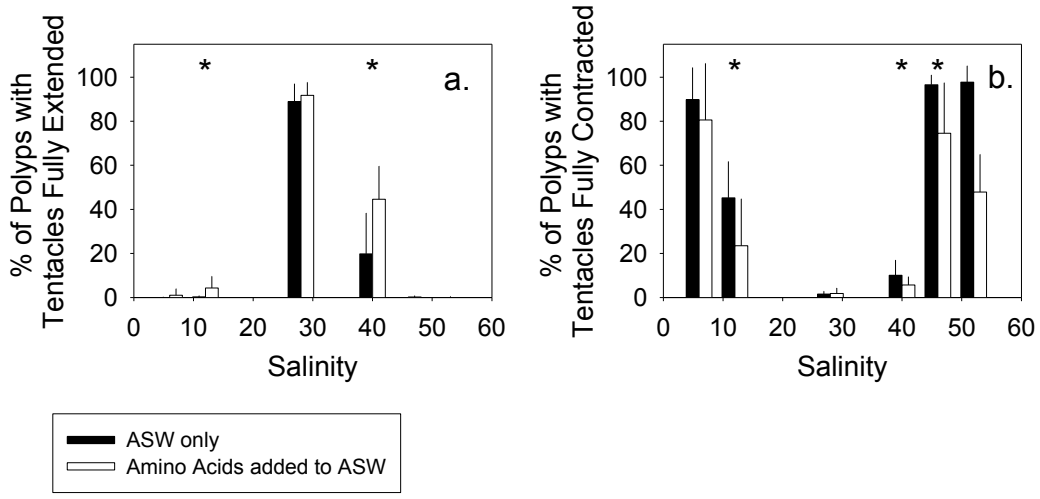

Figure 3.6: Polyps in artificial sea water (ASW) with (open bars) and without (filled bars) the addition of amino acids after 24 h of exposure to each salinity. (a) Percentage of polyps with tentacles fully extended averaged across all time points. (b) Percentage of polyps with completely contracted tentacles averaged across all time points. * = $p < 0.05$. Error bars indicate standard deviation.

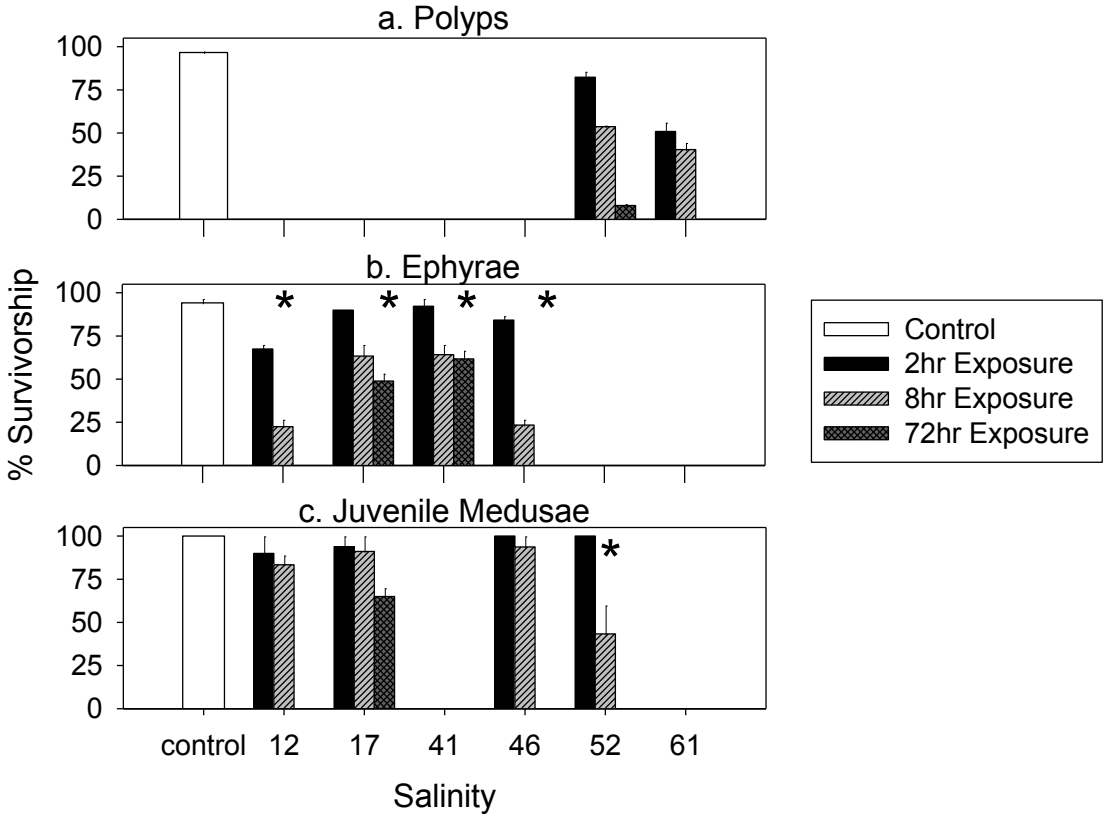

Figure 3.7: Average percent survivorship at 72 h of (a) polyps, (b) ephyrae, and (c) juvenile medusae after 2 h, 8 h, and 72 h exposure to altered salinities. The controls were exposed to 29 psu for 72 h. * = $p < 0.05$. Error bars indicate range.

CHAPTER 4:

Effects of low dissolved oxygen on the growth and survivorship of *Aurelia* sp1 polyps and ephyrae

Abstract

Coastal hypoxia is increasing around the globe. More widespread hypoxia is often cited as a possible cause of increases in the frequency and/or severity of jellyfish blooms. This study investigates the responses of the growth and survivorship of *Aurelia* sp1 polyps and ephyrae to low dissolved oxygen concentrations (3.2 mg L^{-1}, 1.8 mg L^{-1}, and 0.8 mg L^{-1}) in relation to saturated controls (7.8 mg L^{-1}). Polyps survived for four weeks at all dissolved oxygen levels, but had negative growth rates under hypoxic conditions. Ephyrae survived for 10 days at the lowest oxygen level tested (0.8 mg L^{-1}), and for the entire duration of the two week experiment at the other levels tested (7.8 mg L^{-1}, 3.2 mg L^{-1}, and 1.8 mg L^{-1}). There was no change in the C or N content of polyps at low oxygen levels compared to air-saturated levels. Ephyrae exposed to the lowest oxygen level had a lower C and N content than those exposed to air-saturated water, indicating that they do not grow normally under those conditions.

Introduction

Areas of coastal hypoxia (≤ 2.0 mg L^{-1} oxygen or ≤ 30% oxygen saturation) are increasing around the globe (Diaz and Rosenberg, 2008; Vaquer-Sunyer and Duarte, 2008; Gilbert et al., 2010). This is a cause for

concern because hypoxia can have a range of negative effects on marine life, including changes in behavior, reduced growth, reduced reproductive success and capacity, increased susceptibility to disease and infection, and at times death (Nixon, 1995; Ekau et al., 2010). Additionally, coastal hypoxia can change the way that ecosystems are structured by changing the vertical and horizontal distributions of organisms (Levin et al., 2009; Ekau et al., 2010) and altering predator/prey interactions (e.g. Breitburg et al., 1994; Breitburg et al., 1997; Møller and Riisgård, 2007).

Coastal hypoxia is often associated with anthropogenic eutrophication (Rabalais et al.; 2009; Zhang et al., 2010). However, eutrophication is not the only cause. Natural upwelling systems have been known to produce areas of hypoxia (e.g. Dugdale et al., 1977; Chapman and Shannon, 1985), which are generally associated with increased nutrient availability, elevated primary production, and subsequent decomposition. Additionally, in many locations upwelling can bring lower dissolved oxygen (DO) waters to the surface, causing hypoxia to occur at relatively shallow depths (Hoffman et al., 2011). Such effects may be particularly pronounced in locations like the Eastern Tropical Pacific (Stramma et al., 2008), the western coast of Africa (Weeks et al., 2004), and the northern California Current (Hoffman et al., 2011). Dissolved oxygen levels can become even lower in these naturally hypoxic areas when combined with the effects of anthropogenic eutrophication (Naqvi et al., 2000).

Jellyfish (defined here as scyphozoan cnidarians) are among the taxa that have the highest tolerance to hypoxia (Purcell et al., 2001; Vaquer-Sunyer and Duarte, 2008; Ekau, 2010). Jellyfish blooms and their impacts on ecosystems and human populations are sources of concern (Mills, 2001; Purcell et al., 2007). Blooms can impact ecosystems through direct predation and through competition with other organisms for prey (Breitburg et al., 1994; Breitburg et al., 1997; Purcell and Arai, 2001), and can cause negative societal impacts, such as decreasing tourism, interfering with fishing nets, killing penned fishes raised for aquaculture, and clogging power plants (reviewed in Purcell et al., 2007). There is some evidence that anthropogenic impacts, such as eutrophication, habitat alteration, and/or overfishing may be increasing the size, persistence, frequency, severity, and/or locations of jellyfish blooms (Purcell et al., 1999; Mills, 2001; Purcell, 2005; Brotz et al., 2012), although many of the time series of jellyfish that exist are too short to draw this conclusion definitively (Condon et al., 2012; Purcell, 2012).

Jellyfish have been found in hypoxic waters all over the globe. *Chrysaora quinquecirrha* medusae have been associated with hypoxic waters in Chesapeake Bay, USA (e.g. Purcell et al., 1994; Purcell et al., 2001; Grove and Breitburg, 2005), and in the northern Gulf of Mexico (Graham, 2001; Purcell et al., 2001). However, it is unclear whether or not *C. quinquecirrha* have a preference for hypoxic waters (Purcell et al., 1994; Purcell et al., 2001). *Aurelia* spp. medusae have been reported at oxygen levels as low as 0.96 mg L^{-1} in the Black Sea (Vinogradov et al., 1985), but are generally found in near-

air saturated waters (Kideys and Romanova, 2001). Other hypoxic waters where *Aurelia* spp. have been found include the northern Gulf of Mexico (Graham, 2001; Purcell et al., 2001), Skive fjord, Denmark (Møller and Riisgård, 2007), the seawater lakes of Mljet Island in the southern Adriatic Sea (Benović et al., 2000), Hiroshima Bay, Japan (Shoji et al., 2010), and Jellyfish Lake in Palau (Hamner et al., 1982). Other jellyfish, generally hydrozoans, but sometimes scyphozoans, are associated with oxygen minimum zones (OMZs) in places such as the Costa Rica Dome (Vinogradov, 1991) and Monterey Bay (Robison et al., 1998).

Laboratory studies provide further evidence of the hypoxia tolerance of jellyfish, and generally indicate that not only do jellyfish survive, but in many cases, they continue to grow and behave normally under hypoxic conditions. *Chrysaora quinquecirrha* can live for more than 48 h at a DO concentration of 0.5 mg L^{-1} (Purcell et al., 2001). Hypoxic conditions also had no impact on growth rate (Grove and Breitburg, 2005) or behavior of *C. quinquecirrha*, as defined by the rate of bell pulsation (Breitburg et al., 1994). Similarly, there was no change in the behavior of *Aurelia* sp. under hypoxic conditions (Shoji et al., 2005). *Aurelia labiata* have survived for 15 h under hypoxic conditions and up to 5 h under anoxic conditions (Rutherford and Thuesen, 2005).

Many organisms show stage-specific changes in response to low dissolved oxygen; in many cases, the early life history stages are more sensitive than the adults (Miller et al., 2002). However, in the case of jellyfish, the early life history stages may be even more tolerant of hypoxia than the

adults. Many jellyfish have complex life cycles involving benthic as well as planktonic phases and sexual and asexual reproduction (Arai, 1997). Planulae of *Aurelia* sp. have been found in waters with DO as low as 0.4 mg L^{-1} (Vinogradov et al., 1985) and have shown enhanced settlement at hypoxic levels (Ishii et al., 2008; Miller and Graham, 2012). However, at 0% oxygen saturation, *Cyanea capillata* planulae have shown abnormal settlement orientation and high mortality rates (Brewer, 1976). Benthic *Chrysaora quinquecirrha* polyps showed high survivorship at DO levels as low as 0.5 mg L^{-1} (Condon et al., 2001), but were not seen in Chesapeake Bay, USA below the depth of the persistent seasonal oxycline (Cargo and Shultz, 1966). *Aurelia* sp. polyps were found in hypoxic waters with DO concentrations as low as 0.12 mg L^{-1} in Tokyo Bay, Japan (Ishii and Katsukoshi, 2010), and laboratory studies have shown continued growth of polyp colonies exposed to DO levels as low as 0.8 mg L^{-1} for a period of nearly three months (Miller and Graham, 2012).

The present study focuses on the effects of low dissolved oxygen on the growth and survivorship of *Aurelia* sp1 polyps and ephyrae. *Aurelia* spp. are among the jellyfish most often associated with jellyfish blooms (Mills, 2001). Ephyrae are the life history stage that is often most sensitive to changes in environmental variables (e.g. Cargo and King, 1990; Cawood, in review). The potential to survive extended exposure to hypoxic conditions may be less important for ephyrae and medusae than for benthic polyps because the planktonic stages may be able to swim upwards or sink downwards into

waters with higher dissolved oxygen content. While blooms consist of medusae, in order for blooms to occur there must be sufficient populations of polyps and ephyrae to produce the adults. Understanding how early life history phases differentially respond to changes in DO concentration is an important step in understanding and predicting jellyfish blooms.

Methods

Organisms

Aurelia sp1 polyps and ephyrae were obtained from the Birch Aquarium at Scripps Institution of Oceanography (BAS) in La Jolla, California. The species identification was made by K. Bayha and M. Dawson (personal communication) using the molecular methods described in Dawson and Jacobs (2001). The polyps that started the BAS cultures were collected from waters around San Diego, California. *Aurelia* sp1 is the species predicted to be in San Diego by Dawson et al. (2005). Polyps were attached to acrylic plates. Free-swimming ephyrae used in experiments were two to ten days old. All organisms were fed two-day old *Artemia* nauplii every other day for the duration of the experiments.

Experimental Set-up

Incubations were conducted in four 50 L tanks with 2.5 cm insulation covered with clear plastic lids. Temperature was maintained at approximately 16°C by placing titanium coils attached to water baths into each tank.

Experiments were maintained under a 12:12 light:dark cycle. Raw seawater was passed through 10 µm filters and pumped into the tanks. The water within the tanks turned over approximately twice per day. The desired oxygen concentration was obtained by mixing O_2, N_2, and CO_2 using mass flow controllers. Equilibrium of the gas mixture and the filtered seawater was maintained by recirculating the temperature-controlled seawater through Liqui-Cel® membrane contactors. Two gas levels could be maintained at a time. Therefore, three separate individual experiments were conducted. In each experiment, two control tanks were maintained at near-saturated DO levels of 7.78 ± 0.35 mg L^{-1} (= 98.3% DO saturation). In Experiment 1, two tanks were maintained at a lower, but not hypoxic DO concentration of 3.24 ± 0.37 mg L^{-1} (= 41.0% DO saturation). Oxygen levels were maintained at hypoxic levels of 1.78 ± 0.29 mg L^{-1} (= 22.4% DO saturation) in Experiment 2 and 0.83 ± 0.27 mg L^{-1} (= 10.4% DO saturation) in Experiment 3. pH was approximately 8.0 in all experiments.

Temperature, salinity, pH, and dissolved oxygen concentration of each tank were measured once per day. Temperature was measured using an aquarium thermometer. Salinity was measured using a handheld refractometer calibrated with a Portasal™ 8410 portable salinometer. pH was measured using a Honeywell Durafet® pH probe. Dissolved oxygen saturation was measured using a YSI® model 55 dissolved oxygen probe calibrated using Winkler titrations.

Two acrylic plates with attached polyps were placed in each tank. Acrylic plates initially contained 136 to 362 polyps. Two 473 mL jars containing 30 ephyrae each were placed in each tank. Water was gently pumped continuously into each jar to maintain flow and keep ephyrae from sinking to the bottom of the jars. An additional jar containing 13 to 16 ephyrae was maintained in each tank, and used as a source of individuals for carbon and nitrogen analysis.

Survivorship

Polyps were enumerated twice per week for 4 weeks using a dissecting microscope. In addition to counts, a behavioral metric was noted. Polyps were classified as having tentacles fully extended, interpreted as low stress; tentacles partially contracted, interpreted as an intermediate level of stress; and tentacles fully contracted, interpreted as high stress (Cawood, in review). Ephyrae were enumerated every other day for 14 days. During Experiment 3, counts of ephyrae were made daily through day 11. The behavior of ephyrae was classified as either actively swimming or sporadically pulsing (movement was noted, but it was not a normal, active swimming motion). Survivorship includes the net effect of mortality and population growth, hence it can exceed 100%.

Carbon and Nitrogen Content

Six live polyps and ephyrae were sampled at the beginning of each incubation and a total of 12 live individuals at each oxygen level (6 from each tank) were taken at the end of the incubations. Individual organisms were rinsed with Milli-Q filtered water, then placed into tin capsules and dried for at least 48 h at 60°C. In Experiment 3, ephyrae were sampled at day 4 because of high levels of mortality. The carbon and nitrogen content of individual organisms was determined at the Scripps Institution of Oceanography analytical facility using a Costech Analytical Technologies model 4010 elemental analyzer calibrated with acetanilide.

Results

Polyps survived for 4 weeks at all dissolved oxygen treatments (Fig. 4.1a). In all control treatments (7.8 mg L^{-1}) and in the low dissolved oxygen treatment (3.2 mg L^{-1}) of Experiment 1, polyps had positive average net growth rates. In the hypoxic treatments of Experiment 2 (1.8 mg L^{-1}) and Experiment 3 (0.8 mg L^{-1}), polyps had negative average net growth rates (Table 4.1). The slopes of survivorship of the near-saturated treatments did not differ statistically ($p > 0.05$, ANCOVA). The slopes of the air-saturated controls are statistically distinct from those of the low oxygen treatment in Experiment 1 and both of the hypoxic treatments in Experiments 2 and 3 ($p < 0.05$, ANCOVA, $p < 0.05$ Tukey range test). The low oxygen treatment in Experiment 1 and the hypoxic treatments of Experiments 2 and 3 were

statistically different from one another ($p < 0.05$, ANCOVA, $p < 0.05$, Tukey range test).

Ephyrae survived for at least 14 days in all control treatments and the low oxygen treatment of Experiment 1 and the hypoxic treatment of Experiment 2. They survived for 10 days in the hypoxic treatment in Experiment 3 (Fig. 4.1b). In all treatments, there was a negative net growth rate. The mortality rate was –less than 0.4 ephyrae day^{-1} in all near-air saturated controls and in the Experiment 1 low-oxygen treatment and less than 1 ephyrae day^{-1} in hypoxic treatments in both Experiment 2 and Experiment 3 (Table 4.1). Ephyrae survivorship values were arcsine square root transformed before performing the ANCOVA analysis, in order to obtain equal variances. The slopes of the survivorship of the controls and the low oxygen treatment in Experiment 1 were not statistically different ($p > 0.05$, ANCOVA). The low oxygen treatment of Experiment 1 was also not statistically different ($p > 0.05$, ANCOVA) from the hypoxic treatment of Experiment 2 ($p < 0.05$, ANCOVA). Both of the hypoxic treatments in Experiments 2 and 3 were different from the near-saturated control treatments. The hypoxic treatment in Experiment 3 was statistically distinct from all other treatments ($p < 0.05$, ANCOVA, $p < 0.05$, Tukey range test).

In all treatments, the majority of polyps had their tentacles fully extended (Fig. 4.2a). The majority of ephyrae were swimming in all treatments except for the lowest DO concentration tested. In the hypoxia treatment of Experiment 2, an average of approximately 77% of ephyrae were actively

swimming. In all other treatments, more than 90% of ephyrae were actively swimming (Fig. 4.2b).

In order to test for an overall effect of hypoxia on C and N content, all values for a given treatment within an experiment were pooled. After four weeks, there was no difference in either the C or the N content per polyp between the control and low oxygen/hypoxic treatments of any of the three experiments ($p > 0.05$, Mann-Whitney U test; Fig. 4.3a and 4.3c). At day 4, the ephyrae from the hypoxic treatment of Experiment 3 had decreased C and N content compared to ephyrae exposed to the control treatment ($p < 0.05$, Mann-Whitney U test). There was no difference in either C or N content between control and low oxygen treatment in Experiment 1 or the hypoxic treatment in Experiment 2 (Fig. 4.3b and 4.3d). The N content of ephyrae at the beginning of the experiment was significantly lower than that of ephyrae in the low oxygen treatment of Experiment 1 ($p < 0.05$, Mann-Whitney U-test, Supp. Fig. 4.1d). There was no difference between the C or N content at the beginning of the experiment and the end of the experiment in any other treatment (Supp. Fig. 4.1a - c).

Discussion

Aurelia sp1 polyps appear to be very tolerant of hypoxia. Even at very low levels of dissolved oxygen (Experiment 3, 0.8 mg L^{-1}), approximately half of the polyps survived for four weeks. The organisms used in the present study were originally from coastal San Diego waters, where hypoxia generally

does not occur. It is possible that this subpopulation of *Aurelia* sp1 is less hypoxia tolerant than other subpopulations. *Aurelia* sp. polyps in Tokyo Bay, which is within the range of *Aurelia* sp1 (Dawson et al., 2005), survived for 10 days at DO levels as low as 0.27 mg L^{-1} (Ishii et al., 2008). Miller and Graham (2012) showed that *Aurelia* sp. polyps from the Gulf of Mexico survived and continued to reproduce asexually for at least 56 days at DO levels of 0.8 mg L^{-1}. The differences between the results of the present study and those of Miller and Graham (2012) may be explained by the fact that different species of *Aurelia* were likely used (Dawson et al., 2005). The polyps studied by Miller and Graham (2012) showed negative growth rates at day 24 and day 36 of the experiment with positive growth rates on days 48 and 56. It is possible that if the present study had been carried out for a longer time period, the polyps may have eventually shown a positive growth rate. Additionally, the polyps in the present study were much denser at the beginning of the study (approximately 9 polyps cm^{-2}) in comparison with the approximately 1 polyp cm^{-2} used by Miller and Graham (2012). Polyp density can influence growth rates (e.g. Coyne, 1973).

Ephyrae are often the most sensitive life history phase with regard to environmental variables such as salinity (Cargo and King, 1990; Cawood, in review). While ephyrae are more sensitive than polyps, it is difficult to determine how the survivorship of ephyrae directly compares with that of adult medusae. Although adult medusae have been observed at low DO concentrations in nature (e.g. Vinogradov et al., 1985; Graham, 2001; Shoji et

al., 2010), laboratory studies that involve hypoxia tolerance of medusae are generally on the order of hours to days (e.g. Grove and Breitburg, 2005; Shoji et al, 2005), so it is not possible to determine how their survivorship compares to that of ephyrae over longer time scales.

The behavior of polyps was not impacted by hypoxia. Polyps contract their tentacles in response to mechanical stress (Johnson and Wuensch, 1994) and extreme salinities (Holst and Jarms, 2010; Cawood, in review). The contrasting results with the present hypoxia experiments indicate that polyps do not respond to all stresses in the same way. However, ephyrae were not actively swimming at the lowest DO level tested (Experiment 3, 0.83 mg L^{-1}). In nature, this may mean that the ephyrae would be functionally removed from the population because they would sink out of the water column. In addition to altered behavior, the ephyrae after four days to hypoxia in Experiment 3 had a lower C and N content than ephyrae that had been exposed to near-oxygen-saturated waters, indicating that the behavioral changes were accompanied by metabolic changes. If ephyrae are not growing, or are growing abnormally, they are unlikely to recruit into healthy, viable juvenile medusae.

Depending on the timing and severity of hypoxia events, it is conceivable that low DO concentrations could either inhibit or enhance the formation of *Aurelia* sp1 blooms. In situations of severe, persistent hypoxia, it is likely that at least some portion of the *Aurelia* sp1 polyp population will be able to persist. However, if hypoxic events occur when ephyrae are present, a life history bottleneck may be created where few if any ephyrae are able to

develop into adult medusae. In that case, fewer medusae would produce fewer planulae, which in turn would impact the number and genetic diversity of polyps available to produce ephyrae in the following year. A similar pattern has been proposed with regard to salinity (Cawood, in review).

Conversely, under some circumstances, hypoxic conditions may enhance bloom formation. Hypoxia seems to promote the settlement of *Aurelia* planulae (Ishii et al., 2008; Miller and Graham, 2012). Polyps may experience hypoxia as a refuge from predation and competition with other benthic organisms (Ishii et al., 2010; Miller and Graham, 2012). Strobilation can occur at hypoxic levels (Ishii et al., 2008), so ephyrae can be produced. Some portion of ephyrae can survive for at least 10 days under severely hypoxic conditions. If the ephyrae can move to waters with somewhat higher oxygen content (even if the waters are still hypoxic), growth of the ephyrae does not seem to be affected. Adult medusae not only appear to survive in hypoxic waters (e.g. Vinogradov et al., 1985; Graham, 2001; Shoji et al., 2005), but there is evidence that they may actually benefit. Shoji et al. (2005) have shown increased predation rates by *Aurelia* sp. on larval fish under hypoxic conditions as compared to normoxic conditions. There is also evidence that *Aurelia* sp. can feed on a larger size range of larval fish under low DO conditions than at normal oxygen levels (Shoji, 2008).

Adult medusae are often viewed as the only life history phase that is significant in forming a jellyfish bloom. However, all life history stages play a part in bloom development. Ephyrae are more sensitive than polyps and

appear to be more sensitive than medusae, so their responses to hypoxia may play a major role in determining whether or not a bloom forms. Studies have shown that larval life history stages of other organisms, particularly fish and crustaceans, display higher sensitivity to hypoxia than juveniles and adults (e.g. Spicer, 1995; Miller et al., 2002; Spicer and Strömberg, 2003). Since many of these cases involve planktonic larvae and benthic juveniles and adults, it has been hypothesized that the more tolerant stages are those that are more likely to encounter hypoxic waters (Miller et al., 2002). Larvae and adults of amphipod *Echinogammarus pirloti* are found in the same habitats and show no difference in hypoxia tolerance (Spicer, 1995). The differential sensitivities of life history stages based on habitat are consistent with lower hypoxia tolerance of planktonic ephyrae than of benthic polyps. However, adult *Aurelia* sp. have been found in waters with DO concentrations that cause ephyrae to stop swimming normally and mortality if conditions persist. Alternatively, it has been suggested that higher hypoxia tolerances of early life developmental stages may reflect environmental differences during different periods evolutionary history (Herkovits, 2006). It is believed that ancestral cnidarians had polyp but no medusa stages (Collins, 2002; Park et al., 2011), so it is possible that the high hypoxia tolerance of polyps is partially based on evolutionary history. Further information on the long-term impacts of hypoxia on both immature and mature medusae, as well as information on the impacts of hypoxia on the development of ephyrae into medusae and on medusae

growth will be essential to gain a complete understanding of potential relationships between hypoxia and *Aurelia* spp. blooms.

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Table 4.1: Average survivorship and average net growth rate (± 95% confidence interval) of *Aurelia* sp1 polyps and ephyrae. Polyp experiments were 28 days long. Ephyrae experiments were 14 days long. Ephyrae survived for only 10 days in Experiment 3 (0.8 mg L^{-1}).

		Low Oxygen Treatments			Control Treatments		
		Exp 3 0.8 mg L^{-1}	**Exp 2 1.8 mg L^{-1}**	**Exp 1 3.2 mg L^{-1}**	**Exp 3 7.8 mg L^{-1}**	**Exp 2 7.8 mg L^{-1}**	**Exp 1 7.8 mg L^{-1}**
Polyps	**Survivorship**	64.3%	79.1%	106.6%	115.7%	118.6%	115.5%
	Average Net Growth Rate (polyps d^{-1})	-4.7 ± 0.56	-2.4 ± 0.21	0.9 ± 0.19	1.6 ± 0.12	1.0 ± 0.27	1.5 ± 0.21
Ephyrae	**Survivorship**	0%	47.8%	83.3%	90.0%	88.9%	88.3%
	Average Net Growth Rate (ephyrae d^{-1})	-2.78 ± 0.05	-1.21 ± 0.22	-0.36 ± 0.04	-0.21 ± 0.02	-0.24 ± 0.03	-0.25 ± 0.02

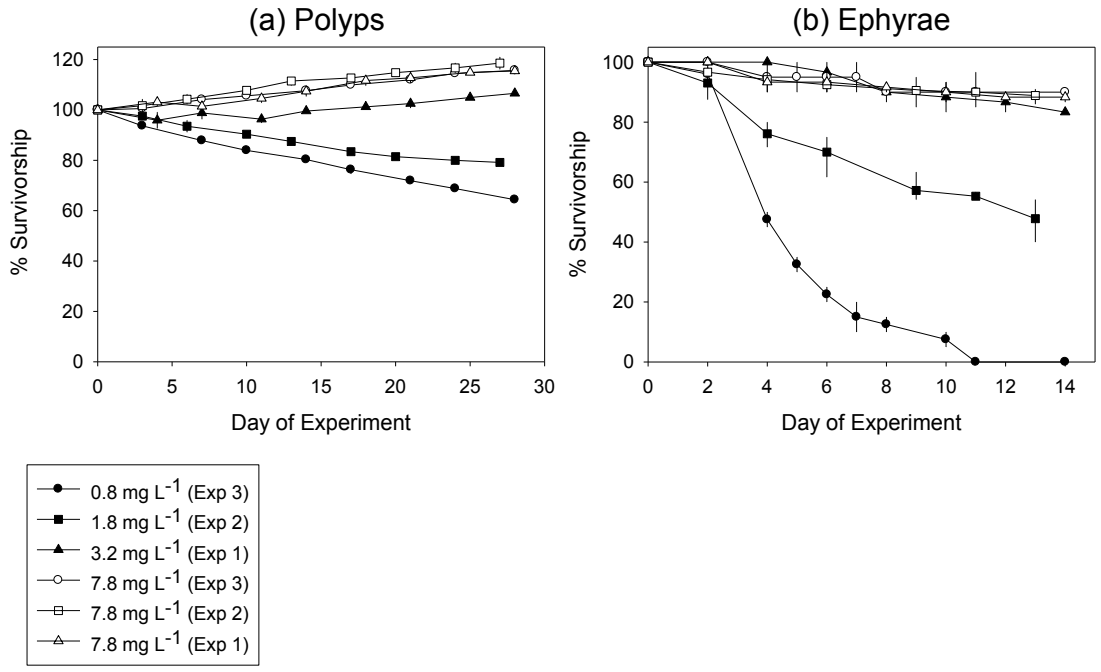


Figure 4.1: Mean percentage survivorship of (a) polyps and (b) ephyrae. Error bars indicate range.

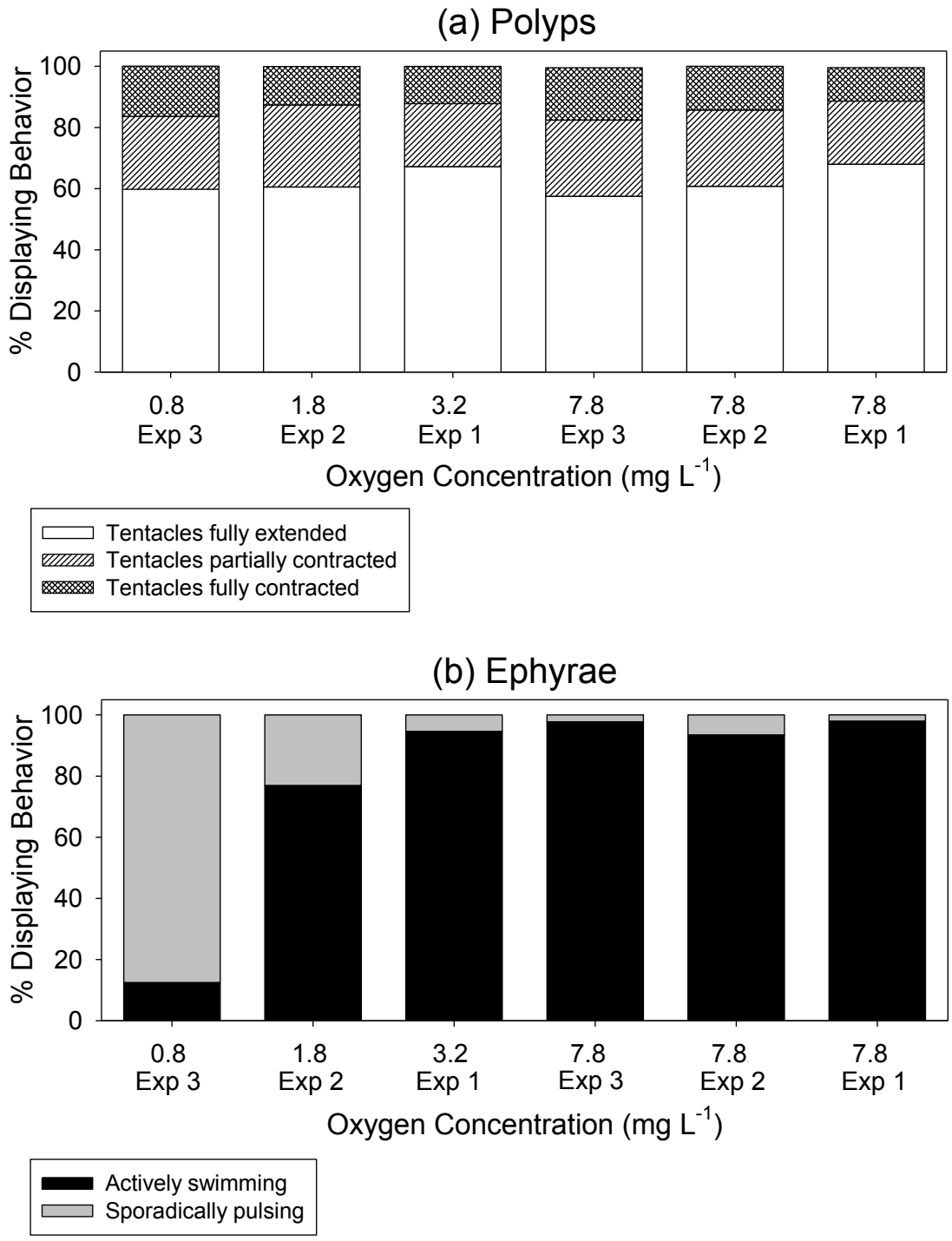


Figure 4.2: Average percentage of (a) polyps and (b) ephyrae displaying different behaviors at each oxygen level. The normoxic controls (7.8 mg L^{-1}) are shown for each experiment.

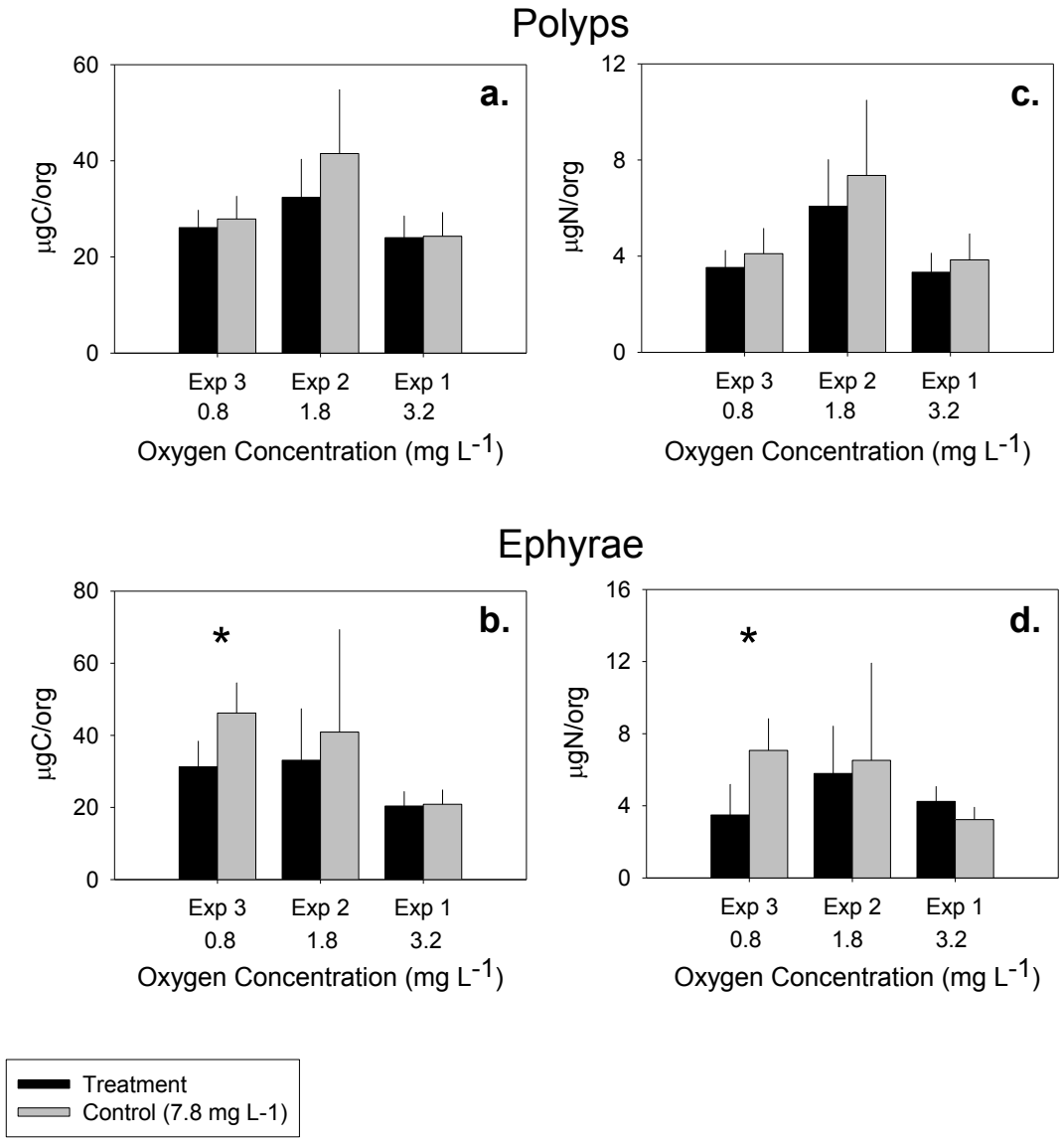
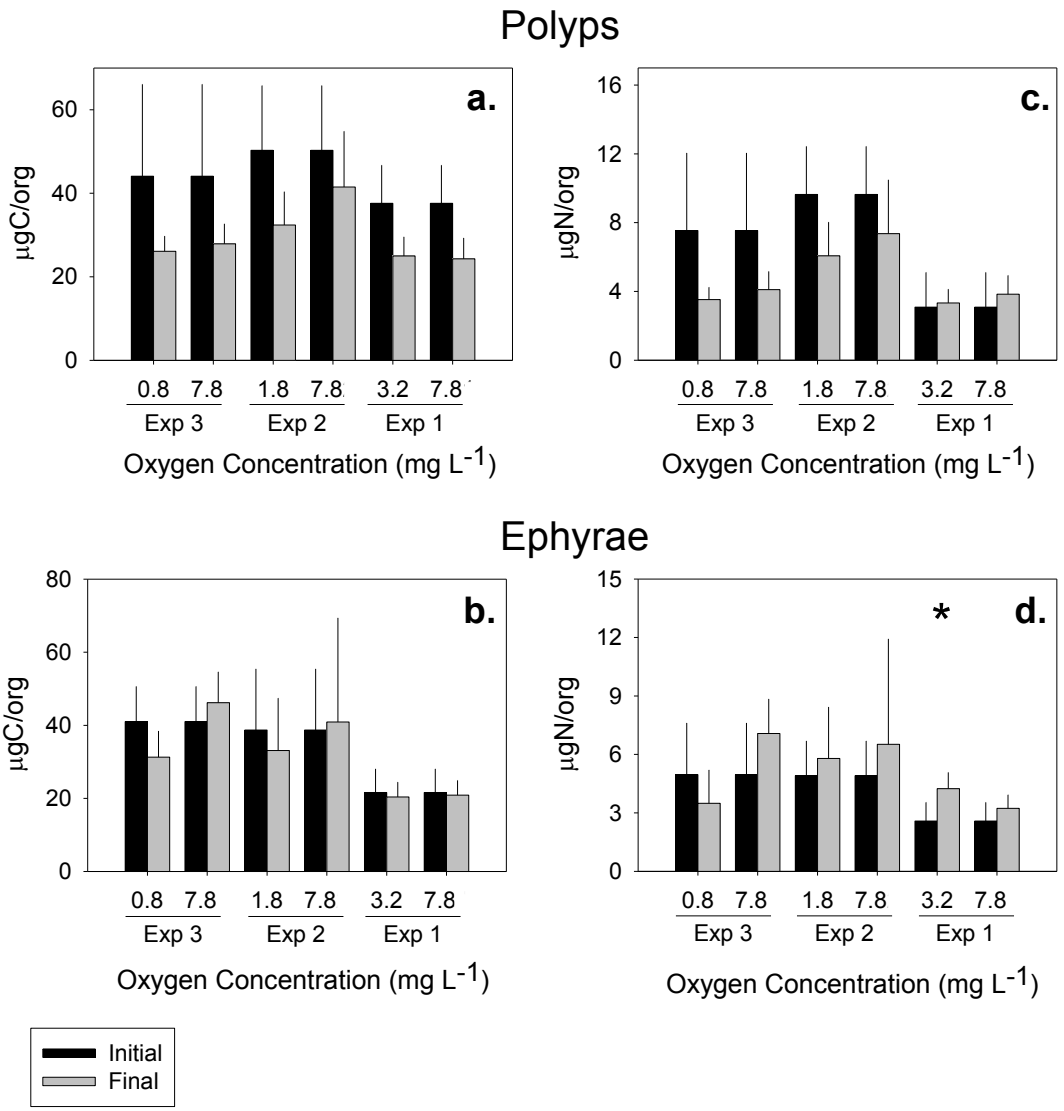


Figure 4.3: Mean final C content for a) polyps and b) ephyrae and N content for c) polyps and d) ephyrae for each experiment. Error bars indicate 95% confidence intervals. * = $p < 0.05$ Mann-Whitney U test.



Supplemental Figure 4.1: Mean initial and final C content for a) polyps and b) ephyrae and N content for c) polyps and d) ephyrae. Error bars indicate 95% confidence intervals. * = $p < 0.05$ Mann-Whitney U test.

CHAPTER 5:

Effects of dissolved organic matter on the growth and survivorship of *Aurelia* sp1 polyps

Abstract

Marine eutrophication has been invoked as an explanation for increased frequency and severity of jellyfish blooms. One of the proposed mechanisms for this connection is the potential ability of jellyfish to benefit from the increased amount of dissolved organic matter (DOM) in the water column. This study investigates the impact of DOM (in the form of dissolved free amino acids and monosaccharides) on the survivorship, dry mass, and C and N content of benthic polyps of the jellyfish *Aurelia* sp1. In all treatments where polyps were fed particulate food (in artificial sea water, in artificial sea water with added DOM, and in filtered sea water), there was an increase in the number of polyps relative to the initial counts. Conversely, unfed treatments (in artificial sea water, in artificial sea water with added DOM, and in filtered sea water) showed a decrease in the number of polyps. Unfed polyps in artificial sea water had a lower C and N content than fed polyps in filtered sea water, but there was no difference among the other treatments. This study found no ecological benefit of *Aurelia* sp1 polyps from the presence of DOM.

Introduction

Marine eutrophication is a problem that is likely to worsen in coming years as global population increases (Conley et al., 2009). It is primarily the result of run-off and coastal discharge of fertilizer and waste water (human and agricultural). As of the mid-1990s, 85% of all nitrogen fixed commercially and 80% of all phosphorus mined was used in fertilizers (Nixon, 1995). As human populations increase, there will be more fertilizer use and more human and agricultural waste run-off. Additionally, as many cultures move to a more meat-based diet, more agricultural waste will be produced (Nixon, 1995).

There are a number of consequences associated with eutrophication. Increased nutrients in the water lead to increased phytoplankton growth rates. In turn, this can cause decreased transparency, increased turbidity, and decreased invertebrate diversity (Valiela et al., 1992; Cloern, 2001). The death of phytoplankton blooms can cause bottom water hypoxia or anoxia, and reports of hypoxic areas are on the rise (reviewed in Cloern, 2001; Diaz and Rosenberg, 2008). Persistent eutrophication can also cause a shift in the resident phytoplankton community from large to small phytoplankton (Schelske and Stoermer, 1971; Smith et al., 2006). It has been argued that the size shift in phytoplankton communities is the cause of the increased frequency of harmful algal blooms in coastal waters (e.g. Dale et al., 1999).

There may be a relationship between increases in eutrophic areas and increases in the incidence and severity of jellyfish (defined here as scyphozoan cnidarians) blooms (e.g. Arai, 2001; Purcell et al., 2007).

However, it is unclear which, if any, consequences of eutrophication may account for this link (Arai, 2001). Jellyfish blooms and the ecological and anthropogenic problems they cause have been an increasing source of concern in recent years (Purcell et al., 1999; Mills, 2001; Purcell, 2005; Brotz et al., 2012). Because most existing time series of jellyfish populations are relatively short, it is difficult to determine whether the apparent increase in jellyfish blooms is real or if they are part of a natural fluctuation (Condon et al., 2012; Purcell, 2012).

One of the hallmarks of a eutrophic environment is the presence of increased dissolved organic matter (DOM; Nixon, 1995). The concept that soft-bodied marine invertebrates, including cnidarians, may be able to obtain nutrition from seawater is a long standing idea in marine ecology, mentioned as early as the 1800s (Haeckel, 1872; Thompson, 1874), and studied since the early 20th century (e.g. Pütter, 1909; Krogh, 1931). In the 1950s and 1960s, uptake of DOM was shown in a number of marine invertebrates using ninhydrin (Stephens and Schinske, 1957; Stephens and Schinske, 1961). However, this method is too insensitive to examine uptake under realistic concentrations of DOM. Later studies incorporating radiolabeling showed uptake under more realistic concentrations of dissolved free amino acids (DFAAs) and monosaccharides (e.g. Stephens, 1963; Jørgensen, 1976; Ferguson, 1988; Stephens, 1988). In 1969, Johannes et al. questioned the assumption that uptake of radiolabeled DOM could be considered net uptake. They claimed that isotope methods only gave evidence for influx of DOM. It

gave no information about net uptake because there was no way to know whether isotopically labeled compounds were taken up, but non-labeled compounds were released at the same (or higher) rates. Beginning in the 1980s, more sensitive HPLC techniques showed that a number of soft-bodied marine organisms are capable of net uptake of free amino acids and glucose, and that this ability may have implications for their life histories (reviewed by Manahan, 1990; Gomme, 2001). Many of those studies focused on the ability for uptake to occur and on the mechanisms of uptake (e.g. Manahan et al., 1982; Jaeckle and Manahan, 1989; Ambariyanto and Hoegh-Guldberg, 1999) and not on the ecological impacts of DOM uptake and utilization. However, it has been shown that the ability to take up DOM may extend the larval period of some benthic invertebrates, such as the oyster, *Crassostrea gigas* (Moran and Manahan, 2004) and the bryozoan, *Bugula neritina* (Johnson and Wendt, 2007).

Planktonic life history stages of jellyfish have been shown to utilize DOM. The zooxanthellate medusae *Linuche unguiculata* (Wilkerson and Kremer, 1992) and *Cassiopea* sp. (Welsh et al., 2009) have been shown to take up DOM. The hydrozoan *Aequorea victoria* has been shown to take up and utilize the luciferin coelenterazine dissolved in seawater (Haddock et al., 2001). Skikne et al. (2009) examined the uptake of DOM by ephyrae of *Aurelia labiata* and *Chrysaora colorata*. They showed that ephyrae of *Aurelia labiata* exposed to homogenized and filtered *Artemia* nauplii or wild-caught krill had higher carbon content after 22 days than ephyrae that had been starved,

but lower carbon content than ephyrae that were fed particulate food. Additionally, many of the ephyrae that were given only DOM became abnormally shaped.

Uptake has also been demonstrated in early portions of the life history of cnidarians. Planulae of the soft coral, *Heteroxenia fuscescens*, have been shown to be capable of net uptake of dissolved free amino acids (Ben-David-Zaslow and Benayahu, 2000). Shick (1975) showed that *Aurelia* sp. polyps were able to take up isotopically labeled glycine, however net uptake was not demonstrated. *Aurelia* sp. polyps that were starved, but exposed to glycine, alanine, or glucose showed high survivorship and could still be induced to strobilate, but produced more abnormal ephyrae than polyps that were fed normally (Shick, 1975).

The present study examines the effects of DOM on the growth and survivorship of fed and unfed *Aurelia* sp1 polyps. *Aurelia* spp. are among the jellyfish most often associated with jellyfish blooms (Mills, 2001). Polyps are often persistent year-round (Lucas, 2001), so they are exposed to the widest range of DOM concentrations. Understanding the effects of DOM on this early life history stage is important for understanding the connection between jellyfish blooms and eutrophic conditions. This study seeks to determine whether or not *Aurelia* sp1 polyps are able to utilize DOM to survive under severely food limited conditions, and if so, whether they are able to grow normally.

Methods

Aurelia sp1 polyps attached to acrylic plates were obtained from cultures started and maintained by the Birch Aquarium at Scripps Institution of Oceanography (BAS) in La Jolla, California. Acrylic plates originally contained 74 to 166 polyps with an approximate density of 5 polyps per cm^2. The polyps that originated the culture came from San Diego waters. The species was identified as *Aurelia* sp1 by K. Bayha and M. Dawson (personal communication) using the methods described in Dawson and Jacobs (2001).

Two experiments were performed. In both, polyp plates were removed from filtered seawater, rinsed with artificial sea water (ASW) made using Milli-Q filtered water and commercially prepared sea salt mix (Instant Ocean® Aquarium Systems Instant Ocean Aquarium Salt), left overnight in ASW, and rinsed again before beginning the experiment in order to reduce the presence of marine bacteria. All glassware was combusted at 500°C for at least 8 h prior to use. All tubing and other materials that could not be combusted were autoclaved when possible, rinsed and soaked for 24h in 10% HCl, and then rinsed and soaked overnight in Milli-Q filtered water before use.

Both experiments were conducted at 15.6 °C on a 12:12 light:dark cycle. Polyps were kept in 0.55 L glass jars for the duration of the experiment. Water was continuously pumped into jars in order to maintain constant DOM concentrations. Experiment 1 was conducted for 97 days and Experiment 2 was conducted for 55 days. All polyps were enumerated twice per week. For each count, a behavioral metric was noted. Polyps were classified as having

tentacles fully extended, tentacles partially contracted, or tentacles fully contracted. There were three replicates of each treatment.

There were three replicates in each treatment in both experiments. In Experiment 1, four treatments were used: ASW Only, ASW with dissolved organic matter (DOM) added (ASW DOM), ASW where polyps were fed two-day old *Artemia* nauplii (ASW Fed), and ASW with fed polyps and added DOM (ASW DOM Fed). Enumerations were the only measurements made during Experiment 1. Six treatments were used in Experiment 2: ASW Only, ASW DOM, ASW Fed, ASW DOM Fed, 0.2 µm Acropak™ filtered natural seawater (FSW Only), and FSW with fed polyps (FSW Fed). The FSW treatments were added in Experiment 2 to provide polyps with access to components of natural seawater (such as metals and more types of DOM) that may not be present in ASW. In Experiment 2, enumerations, carbon and nitrogen content analysis (CHN analysis), and bacterial counts were performed. In both experiments, because polyps are able to reproduce asexually through budding and stolon formation, the survivorship of polyps can be greater than 100%.

In both experiments, the sources of DOM were dissolved free amino acids (DFAAs) and monosaccharides. Seven DFAAs at concentrations of 200 nM each with a total concentration of 1.4 µM DFAAs were used. This concentration is comparable to natural concentrations from eutrophic, coastal areas (Middelboe et al., 1995; Stepanauskas et al., 2002). The DFAAs used were aspartic acid, glutamic acid, serine, arginine, glycine, threonine, and alanine, as these are the most common DFAAs in coastal waters (Yamashita

and Tanoue, 2003; Aluwihare and Meador, 2008). Four monosaccharides (glucose, xylose, galactose, and mannose) commonly found in seawater (Borch and Kirchman, 1997; Aluwihare and Meador, 2008) with concentrations of 1 μM each were combined to give a total concentration of 4 μM were added to each DOM treatment. This concentration is comparable to reported coastal values (Johnson and Sieburth, 1977; Borch and Kirchman, 1997). Water was constantly pumped from 5 L glass reservoir containers through acid-washed PTFE tubing into the small glass containers holding the polyps in order to maintain constant DOM levels.

Water samples were taken at days 0, 14, 28, 41, and 55 during Experiment 2 for bacterial analysis. Water samples were preserved using a final concentration of 2% sterile filtered formaldehyde for 15 minutes. 10 mL of preserved water from each treatment was filtered onto a 0.2 μm black polycarbonate filter. Duplicate filters were made for each treatment. Filters were stored at -20 ^{o}C. For staining, filters were mounted on clean glass slides and stained using Vectashield® DAPI immersion oil. Bacteria were enumerated using epifluorescence microscopy under UV excitation at 100x magnification.

In Experiment 2, six live polyps were sacrificed at the beginning of the experiment and six polyps from each treatment were sacrificed at the end of the experiment for CHN analysis. Individual organisms were rinsed with Milli-Q filtered water, placed into tin capsules, and dried at 60 °C for at least 48 h. CHN analysis was performed at the Scripps Institution of Oceanography

analytical facility using a Costech Analytical Technologies model 4010 elemental analyzer calibrated with acetanilide standards.

Results

Some polyps survived in all treatments for the durations of Experiment 1 and Experiment 2. In Experiment 1, the mean survivorship varied from 25.4% to 155.2%. In Experiment 2, mean survivorship varied from 42.2% to 186.6% (Table 5.1). Polyps in treatments that were fed (ASW Fed, ASW DOM Fed, FSW Fed) showed increases in polyp abundance relative to the initial counts (Fig. 5.1a and 5.1b). Polyps that were in unfed treatments (ASW Only, ASW DOM, and FSW Only) decreased in abundance relative to the initial count (Fig. 5.1a and 5.1b). There was a significant difference ($p < 0.05$, Kruskal-Wallis 1-Way ANOVA) between the number of polyps present at the end of both experiments relative to the initial counts. There was no statistically significant difference in the survivorship among fed treatments (ASW Fed, ASW DOM, and FSW Fed) or unfed treatments (ASW Only, ASW DOM, FSW Only; (Kruskal-Wallis 1-Way ANOVA, $p > 0.1$, Fig. 5.1a and 5.1b). In Experiment 2, the bacterial density in the water ranged from 225 bacteria mL^{-1} to 606 bacteria mL^{-1}, with an average number 392 bacteria mL^{-1}. The low bacterial concentration indicates that bacteria were not a major food source for polyps, nor did they have major impacts on DOM concentrations. In all treatments in both experiments, the more than 53% of polyps had fully extended tentacles (Fig. 5.2a and 5.2b).

There was statistically significant heterogeneity among the dry weights in Experiment 2 ($p < 0.05$, Kruskal-Wallis 1-way ANOVA), with the FSW Fed and the ASW Only treatments being significantly different from each other ($p < 0.05$, Tukey range test; Fig 5.3a). The same pattern exists with regard to the N content of polyps ($p < 0.05$, Kruskal-Wallis 1-way ANOVA), with FSW Fed and ASW Only being significantly different from one another ($p < 0.05$, Tukey range test; Fig. 5.3b). The C content of unfed treatments tended to be lower than fed treatments, however, only the FSW Fed and ASW Only treatments show a statistical difference from one another ($p < 0.05$, Kruskal-Wallis 1-way ANOVA, $p < 0.05$, Tukey range test; Fig. 5.3c).

Discussion

Aurelia sp1 polyps are very tolerant of starvation. After 97 days in Experiment 1, more than 25% of the polyps survived in the unfed treatments. The presence or absence of DOM did not appear to have an impact on growth or survivorship of *Aurelia* sp1 polyps. In all unfed treatments, there was a decreased abundance of polyps relative to the initial polyp counts, and an increase in the abundance of polyps relative to the initial polyp counts in fed treatments. The treatments with DOM added did not show increased survivorship. In the extreme case of ASW Only, there was decreased weight, C, and N content when compared to polyps under near-natural conditions (FSW Fed).

Shick (1975) conducted a series of experiments examining the relationship between *Aurelia* sp. polyps and DOM. In one experiment, 20 polyps per treatment were either fed, starved (in ASW), starved with 0.1 μM alanine, starved with 0.8 μM glycine, or starved with .27 μM glucose. In all of treatments, there was nearly 100% survivorship of polyps over 56 days. These results are quite different from those of the present study. This may be explained by some methodological differences. Shick (1975) removed all newly budded polyps as soon as they separated from the parent polyp. This means that the polyp colonies were not allowed to grow, so additional population growth cannot be accounted for. The polyps used by Shick (1975) were genetically identical clonal replicates. The polyps used in the present study were genetically heterogeneous. During Experiment 1 (97 day duration) and Experiment 2 (55 day duration), more than 25% of polyps that were in the unfed treatments survived until the end of the experiment, indicating that some portion of the population of polyps used in the present study were capable of surviving for the same duration as the polyps used by Shick (1975). It is possible that, by chance, Shick's (1975) clonal polyps began with a polyp that had a high tolerance to starvation. As all of the polyps were genetically identical, mortality would have been very low in all treatments. Additionally, the polyps used by Shick (1975) originally budded from a polyp collected near Corpus Christi, Texas, in the Gulf of Mexico. This indicates that the polyps used by Shick (1975) were likely a different species than the polyps used in the present study (Dawson et al., 2005). Different species of *Aurelia* may

respond differently to starvation, and there is a suggestion that different species of *Aurelia* polyps may have different amino acid contents (Shick, 1976).

In the present study, polyps had access to 341.1 µg C L^{-1}. The average carbon content of fed polyps was 48.9 ug C $polyp^{-1}$ and unfed polyps had an average carbon content of 15.8 ug C $polyp^{-1}$. Because there was a constant concentration of DOM, if polyps were assimilating even 30% of the carbon provided by the DFAAs and monosaccharides, there would have been sufficient carbon for polyps to maintain their carbon content. The amount of carbon provided to polyps in the present study is 94.6x greater than the amount of carbon provided in the alanine only treatment done by Shick (1975). However, in Shick's study, nearly 100% of polyps survived. The carbon provided by Shick (1975) would not have been sufficient for the polyps in the present study to maintain carbon content. Therefore, it is possible that the polyps in the Shick (1975) study had access to sources of carbon that were not accounted for. In the present study, although there was sufficient carbon, it may not have been possible for the polyps to utilize enough of it to grow and survive.

Aurelia spp. polyps respond to some stresses, such as salinity stress (Holst and Jarms, 2010; Cawood, in review) and mechanical stress (Johnson and Wuensch, 1994), by contracting their tentacles. However, the polyps in the present study did not contract their tentacles in response to starvation. Polyps that are under starvation stress may keep their tentacles fully extended

as frequently as possible in order to increase the chance of obtaining any available food particles.

Overall, polyps had lower dry weights, and CN content after 55 days compared to the initial samples, with only FSW Fed polyps showing increases. Polyps that were unfed would be expected to have lower masses, and CN content. The decreased weights and CN content may be due to the fact that polyps were in ASW. It is possible that polyps need components of natural sea water (e.g. trace metals) that are beneficial to polyp growth that are not found in ASW.

The polyps in the present study showed no ecological benefit from exposure to DOM. *Aurelia* sp. polyps that were starved or starved with the addition of DOM produced fewer ephyrae and were more likely to produce abnormal ephyrae than fed polyps (Shick, 1975). *Aurelia labiata* ephyrae exposed to DOM (derived from homogenized *Artemia* or euphausiids) gained more weight than unfed ephyrae in filtered sea water, but did not show increased survivorship (Skikne et al., 2009). However, in these studies, polyps and ephyrae were not provided both DOM and particulate food. It is unlikely that polyps or ephyrae in nature would have access to only DOM as a source of nutrition. It is more reasonable to assume that if DOM is beneficial it is as a supplement to normal diets. The present study suggests that access to sufficient particulate food is more important than the presence or absence of DOM, and that DOM, composed of common DFAAs and monosaccharides at

environmentally realistic conditions, is not sufficient nutrition for *Aurelia* sp.1 polyps.

The presence of high levels of DOM has been suggested as a mechanism that allows jellyfish to thrive in eutrophic environments (Arai, 2001). However, the present study indicates that if that is the case, polyps are not the life history phase that benefits from high levels of DOM. It is possible that ephyrae or medusae that feed and have access to DOM may have increased growth rates or reproductive capacities. It is also possible that the amount of time that planulae can spend in the water column may be enhanced by the presence of DOM, which could increase the possibility of finding a suitable settlement site.

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Table 5.1: Average survivorship of *Aurelia* sp1 polyps in Experiment 1 after 97 days and in Experiment 2 after 55 days

	Experiment 1 % Survivorship	Experiment 2 % Survivorship
ASW Fed	119.9%	141.5%
ASW DOM Fed	155.2%	170.9%
FSW Fed	N/A	186.6%
ASW Only	25.4%	42.2%
ASW DOM	33.6%	62.6%
FSW Only	N/A	57.1%

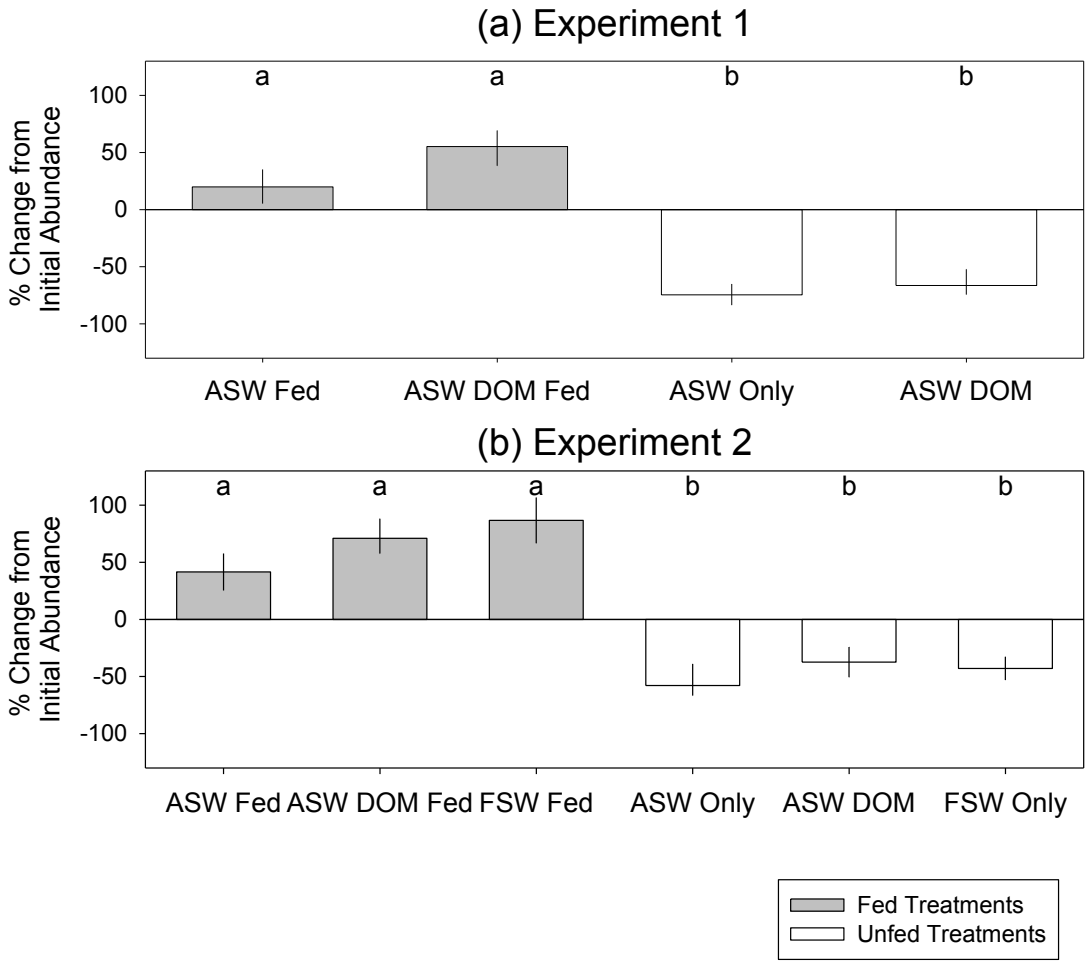

Figure 5.1: Mean change in polyp abundance compared to initial abundances in (a) Experiment 1 after 97 days and (b) in Experiment 2 after 55 days. Error bars indicate range. Bars with different letters are statistically different ($p < 0.05$, Kruskal-Wallis 1-way ANOVA).

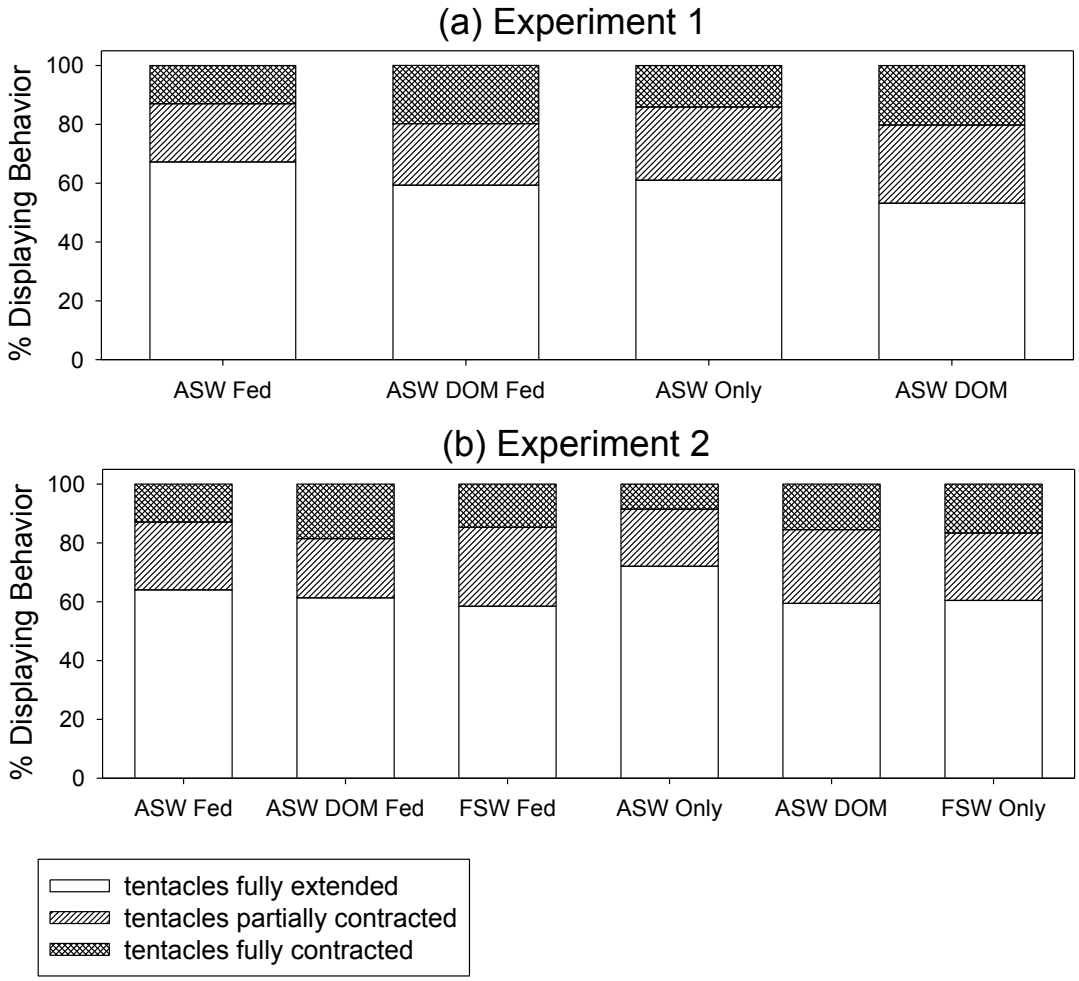

Figure 5.2: Average percent of surviving polyps displaying a specified behavior in (a) Experiment 1 and (b) Experiment 2.

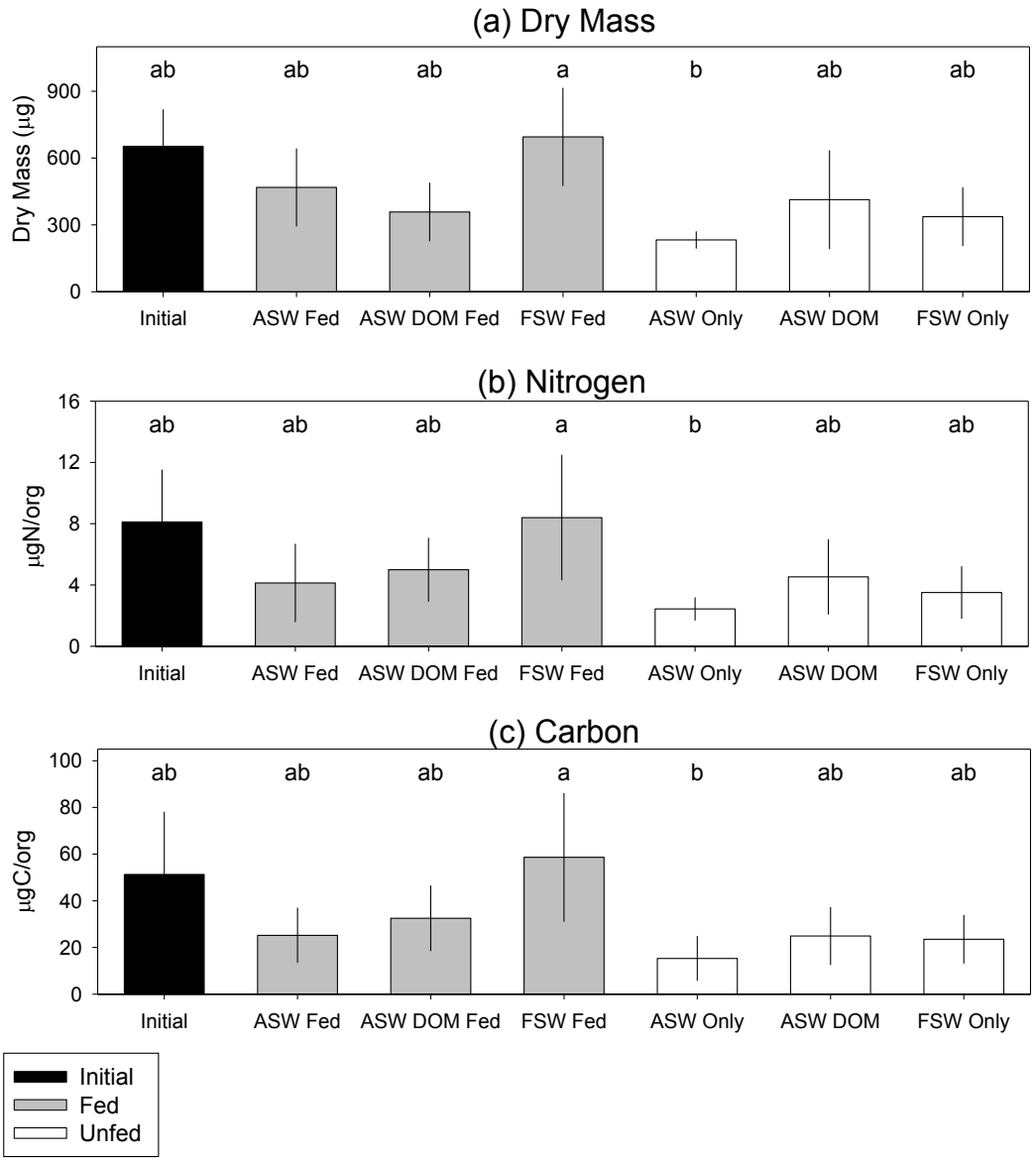

Figure 5.3: Mean (a) dry mass, (b) N content and (c) C content for polyps in Experiment 2. Error bars indicate ± 95% confidence intervals. Bars with different letters are statistically different ($p > 0.05$, Kruskal-Wallis 1-way ANOVA).

CHAPTER 6:

Summary and conclusions

The primary goal of this dissertation was to understand how different life history phases of the jellyfish *Aurelia* sp1 respond to different environmental conditions. To accomplish this objective, I first documented the environmental conditions to which *Aurelia* sp1 is exposed *in situ* during a four year field study focused principally in Mission Bay, San Diego County, with supplemental comparative work in San Diego Bay (Chapter 2). I then conducted laboratory experiments to explore the tolerances of often understudied early life history phases to potentially important environmental factors (Chapters 3 – 5). The overarching conclusion of this dissertation is that different life history phases of *Aurelia* sp1 have different sensitivities to variations in environmental conditions, which can potentially impact the population dynamics and bloom formation of *Aurelia* spp. In some ways this conclusion seems self-evident, as many organisms exhibit differences in environmental tolerance with ontogeny (e.g. Miller et al., 2002; Anger et al., 2008; Aranda et al., 2011; Pineda et al., 2012). However, much of the previous research about jellyfish has focused on only the prominent medusae phase of the life history. The results of this dissertation underscore the differential responses of different life history phases and illustrate that it is impossible to understand population dynamics or predict jellyfish blooms by focusing on only one portion of a complicated life cycle.

Benthic polyps of *Aurelia* sp1 are remarkably resistant to environmental change. Polyps persisted in Mission Bay over the approximately three and a half years examined, across a range of temperature, salinity, dissolved organic carbon (DOC), dissolved oxygen, and particulate matter conditions (Chapter 2). Polyp density varied interannually, but the cause of this variability was not clear. Strobilae formed in late November and early December. The initiation of strobilation in Mission Bay seems to be connected to a decrease in temperature, but there does not appear to be a tightly constrained temperature threshold or temperature gradient for initiation. Additionally, polyps are able to withstand acute salinity changes, with polyps surviving in salinities from 6 to 52 psu for at least 72 hours (Chapter 3). They tolerate hypoxia as extreme as 0.8 mg L^{-1} (10.4% dissolved oxygen saturation) for at least four weeks (Chapter 4), and starvation without access to dissolved or particulate organic matter for at least three months (Chapter 5). Under hypoxic conditions as well as starvation, there was little change in the C or N contents of polyps, indicating that their growth is not dramatically changed, even under extreme conditions.

The hardiness of polyps means that they are likely to persist in environments that are not habitable for many other organisms or even for other portions of the life history of *Aurelia* sp1. Therefore, it would not be possible to eradicate *Aurelia* sp1 from an area without removing benthic polyps. The presence of numerous man-made structures such as docks, marinas, oil platforms, and artificial reefs provides structure onto which polyps

can settle. Increases in suitable substrate have been proposed as a partial explanation for observed changes in *Aurelia* spp. population dynamics in the Gulf of Mexico (Graham, 2001), Japan (Miyake et al., 2002), and Tapong Bay, Taiwan (Lo et al., 2008). Additionally, it has been found that planulae of a variety of jellyfish (*Aurelia* sp., *Cyanea capillata*, *C. lamarckii*, *Chrysaora hysoscella,* and *Rhizostoma octopus*) preferentially settled on artificial substrates over natural substrates (Holst and Jarms, 2007), and polyps will grow on a variety of dock building materials (Hoover and Purcell, 2009). *Aurelia labiata* polyps settle and grow on materials such as Styrofoam and vulcanized rubber, which are often not appropriate settlement substrates for other organisms found in fouling communities (Hoover and Purcell, 2009). Therefore, polyps may be able to settle and grow on common dock building materials with little competition for space. Tolerance of difficult environmental conditions, such as hypoxia, may also create refugia where polyps can settle and grow with little competition from other fouling organisms (Miller and Graham, 2012).

On the other hand, *Aurelia* sp1 ephyrae are sensitive to changes in environmental conditions (Chapters 3 – 4). The salinity tolerance of ephyrae over 72 hours ranges from 17 to 40 psu. This is smaller than the tolerance range of polyps, and while the range is similar to that of juvenile medusae, ephyrae survive for shorter periods of time at similar salinities than juvenile medusae, especially at low salinities (Chapter 3). At hypoxia levels of 0.8 mg L^{-1} (10.4% dissolved oxygen saturation), ephyrae survive for 10 days, but do

not behave normally. Instead of actively swimming, ephyrae pulse sporadically. In nature, this may mean that the ephyrae would be functionally removed from the population because they would sink out of the water column. Additionally, at this dissolved oxygen content, ephyrae had lower C and N contents compared to ephyrae exposed to air-saturated water. This could mean that the ephyrae would not be able to grow and form healthy, viable medusae (Chapter 4). These sensitivities may mean that the ephyrae portion of the life history could serve as a life history bottleneck that keeps *Aurelia* sp1 blooms from forming.

The intolerance of ephyrae to low salinities is a possible explanation for the absence of medusae observed in Mission Bay from 2009 - 2011 (Chapter 2). The years with no medusae in Mission Bay correspond to high precipitation (and corresponding low salinity events) during the time when ephyrae are present in the water column. Salinities in Mission Bay reach values below the salinity tolerance of *Aurelia* sp1 ephyrae (Chapter 3). In these same years, medusae were present in San Diego Bay. Mission Bay and San Diego Bay are geographically close and experience similar source waters, precipitation, and air temperatures. However, the drops in salinities in San Diego Bay are less extreme than those in Mission Bay because of the increased connection to the coastal ocean. Ephyrae in San Diego Bay were not exposed to extremely low salinities, therefore they were able to develop into medusae (Chapter 2).

The response of ephyrae to salinity changes also points towards the importance of understanding the timing of life history events in relation to changing environmental conditions. If the low salinity conditions in Mission Bay occurred at a different time of the year when polyps, but not ephyrae, were present in the water, it is unlikely that the population dynamics of *Aurelia* sp1 would be severely impacted. A similar situation could exist with regard to hypoxia. Ephyrae are more sensitive than polyps (Chapter 4) and appear to be more sensitive than medusae (e.g. Purcell et al., 2001; Grove and Breitburg, 2005; Shoji et al., 2010) to severe hypoxia. If hypoxic events occur when ephyrae are present, medusae may not be produced. However, if hypoxic events occur at other times of the year, the *Aurelia* spp. population is less likely to be impacted and may actually benefit by giving polyps access to more benthic space (Miller and Graham, 2012) or allowing medusae to feed over a larger size range or on more food types (Shoji et al., 2005; Shoji, 2008). Without available information on the varying tolerances and responses of life history stages and knowledge as to when each life history phase is present, it will be impossible to determine the impacts of environmental changes on *Aurelia* spp. population dynamics.

There seems to be a growing acknowledgement of the need for studies that examine the responses of a variety of life history stages of jellyfish to environmental changes. Recent work has examined the settlement substrate preferences of planulae (e.g. Holst and Jarms, 2007; Hoover and Purcell, 2009), the hypoxia tolerance of planulae and polyps (e.g. Condon et al., 2001;

Ishii et al., 2008; Miller and Graham, 2012), the short-term hypoxia tolerance of medusae (e.g. Shoji et al., 2005; Shoji, 2008), responses of planulae and polyps to long-term salinity changes (e.g. Holst and Jarms, 2010), and the responses of polyps to sedimentation (Holst and Jarms, 2006). However, the combination of field work and laboratory work, such as conducted in the present study, is virtually absent in literature concerning jellyfish (but see Hernroth and Gröndahl, 1985a; Hernroth and Gröndahl 1985b). Additionally, few laboratory studies investigate the interactions of multiple stressors that are likely to occur in the field. Without combined studies of this type, it is difficult to develop relevant, testable hypotheses and make substantive progress towards understanding the causes of jellyfish blooms.

Despite the attention paid to jellyfish blooms in recent years in both scientific (e.g. Mills, 2001; Purcell et al., 2007; Brotz, et al., 2012; Flynn et al., 2012) and popular literature (e.g. Geere, 2011; Sala, 2011; Whiteman, 2011; Vince, 2012), much of the evidence that exists for how and why blooms form is anecdotal (Condon et al., 2012; Purcell, 2012). Understanding and eventually predicting blooms will require a mechanistic understanding of how the environment influences population dynamics of *Aurelia* spp. This goal will require a combination of laboratory studies to understand the potentially differing responses of life history phases to a variety of conditions and field studies to understand the timing and range of conditions to which each life history phase is exposed.

Blooms of *Aurelia* spp. are ecologically complicated. They involve multiple life history phases, and likely many interacting environmental factors. Gaining a full understanding of them will require much more work than can be accomplished in one dissertation. Luckily, this means that there are a variety of questions waiting to be tackled by future researchers. Such questions may include:

1) What factors contribute to the onset of strobilation, and do these factors change from one habitat to another? What controls the number of polyps that undergo strobilation or the number of ephyrae that are produced by each strobila?
2) How are populations of polyps impacted by other members of the fouling community? Are there certain assemblages in which polyps thrive and others in which their growth is inhibited?
3) How are populations of ephyrae and medusae impacted by other members of the planktonic and nektonic communities? Are there some zooplankton assemblages that are beneficial to ephyrae and or medusae and others that negatively impact ephyrae and medusae?
4) How do responses and tolerances of ephyrae to environmental conditions influence the development of ephyrae into medusae? How do the responses and tolerances of medusae change as they mature?

5) How do multiple stressors impact the growth, survivorship, and development of each life history stage of *Aurelia* sp1? Are there certain combinations of factors that promote or inhibit growth and development of one or more life history phases?
6) How do sources of mortality such as predation and pathogens impact the population dynamics of *Aurelia* spp.? Are there environments where these factors play fundamental roles in controlling population dynamics?
7) How important is genetic diversity within a polyp population? What are the impacts on the overall *Aurelia* sp. population if there are one or more years of poor recruitment of planulae?
8) In what ways are species of *Aurelia* ecologically different from one another? Are some species more prone to bloom formation?

Much of the fascination with jellyfish in popular media is related to the problems that jellyfish cause for humans. They can cause damage to industries such as tourism, aquaculture, and fisheries, as well as pose risk of injury to humans. However, at the present time, our understanding of these evolutionarily simple creatures does not allow us to predict when or where blooms will form. Gaining this knowledge is likely to become even more challenging in the face of a changing planet. Climate change is predicted to impact estuaries by causing more extreme weather events (Milly et al., 2002) and changing the timing of precipitation events (Dettinger and Cayan, 1995),

and global increases in population are predicted to alter coastal conditions by changing the flow of rivers (Dynesius and Nilsson, 1994) and through the construction of desalination plants (Vörösmarty et al., 2000; Roberts et al., 2010). These changes in freshwater inflow will likely have large impacts on salinity, dissolved oxygen concentrations, and nutrient inputs (Cloern and Nichols, 1985; Sklar and Browder, 1998). This could mean that areas that have previously experienced jellyfish blooms may experience a decrease in the frequency or severity of blooms, or they may begin to experience blooms that are even more intense. Areas that have never experienced blooms may begin experiencing blooms. The outcomes will depend on how local conditions change and how the jellyfish respond. Further investigation into the relationships between jellyfish and their environment will bring us closer to being able to make predictions, which will allow us to mitigate the negative impacts for people, while providing insight into these fascinating creatures.

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