

## ABSTRACT

Title of Thesis: EFFECTS OF ENVIRONMENTAL FACTORS ON  
DISTRIBUTION AND ASEXUAL REPRODUCTION OF  
THE INVASIVE HYDROZOAN, *MOERISIA LYONSI*

Xiping Ma, Master of Science, 2003

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The effects of temperature, salinity, food and predation on the invasive hydrozoan, *Moerisia lyonsi*, were studied in the laboratory to understand its cross-oceanic distribution patterns and the quantitative relationships between the asexual reproduction of polyp and medusa buds. Polyp mortality occurred only at some treatments of salinities 35-40. Polyps reproduced asexually at salinities 1-40 at 20-29°C, but not at

10°C. The highest asexual reproduction rates occurred at salinities 5-20 without significant difference among salinities. The scyphomedusa, *Chrysaora quinquecirrha*, was found to prey heavily on the medusae of *M. lyonsi* and may have restricted its distributions in estuaries. The initiation and proportion of medusa bud production was more responsive to environmental changes than that of polyp bud production. Unfavorable conditions enhanced polyp bud production, while favorable conditions enhanced medusa bud production. The adaptive reproduction processes of *M. lyonsi* and the significance to survival and dispersal of the populations are discussed.

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ON DISTRIBUTION AND ASEXUAL REPRODUCTION OF THE  
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by

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## CHAPTER 1

### General Introduction

## **Biotic invasions**

Invasive species have been studied for decades. Their important ecological roles and effects have been increasingly recognized by the scientific community; meanwhile, their severe economic and ecological consequences have been increasingly realized by society and government (Elton 1958; Travis 1993; U. S. Congress, OTA 1993; Parker et al. 1999). On one hand, species distributions are constantly changing over time, so we should not view species introductions as abnormal (Lodge 1993; Ruiz et al. 1997). Besides, only around 10% of all introduced species can successfully establish themselves in their new locations (the rate may vary among taxa), most of which do not have significant impacts on the native community (Williamson 1989; Vermeij 1991; Williamson and Fitter 1996). On the other hand, biological introductions are rising rapidly in number, and the rate of invasion has accelerated quickly in the last several decades due mostly to anthropogenic dispersal aggravated by commercial globalization (Ruiz et al. 1997; Cohen and Carlton 1998; Cohen 2000), which could hardly be achieved by natural processes in a similar time frame. Hence, non-indigenous species have become an important component in changing the global ecosystem (Vitousek et al. 1996; Dukes and Mooney 1999). Since the chance of the introduction of undesirable or pest alien species increases with increasing number of introductions, the ongoing rapid global-scaled biotic invasions pose a serious threat to the global ecosystem.

With the growing world trading activities, the coastal areas in the world are increasingly threatened by non-indigenous species, and the rate of species introductions is also

accelerating in coastal and marine ecosystems. For example, in San Francisco Bay and Delta ecosystem, over half of the total invasions during the past 150 years occurred in the last 35 years (Cohen and Carlton 1998; Cohen 2000). To date, about 400 alien species have been recognized along the US coastal areas, which is still believed to be an underestimate (Ruiz et al. 1997; Cohen and Carlton 1998). Although most species are not harmful to the native communities, some do turn out to be a nuisance. For example, the zebra mussel, *Dreissena polymorpha*, has invaded the Great Lakes and most of the inland waterways of eastern US, costing billions of dollars by causing dramatic changes in ecosystems, harming the native commercial species, and fouling recreational facilities and municipal or industrial water intake pipes (Mackie 1991; Ludyanskiy et al. 1993; U. S. Congress, OTA 1993).

The introductions of alien species in aquatic systems are due to mainly human activities, such as ship transportation, aquaculture activities, aquarium, and commercial organism trade (Cohen 2000; Palumbi 2001), among which ballast-water transfer by ships is a leading cause of aquatic invasions (Carlton and Geller 1993; Ruiz et al. 1997; Wonham et al. 2001). Therefore, reducing the introductions via ballast water transfer is an important step in controlling aquatic invasions. The most commonly used method to reduce ballast water induced invasions is mid-ocean water exchange. Experimentally, a 93-100% exchange of coastal water may remove approximately 80 to 100 % of coastal organisms in the tank of the ship (Smith et al. 1999; Wonham et al. 2001). Although this method is quite effective, it still can not eliminate all the problems, because the refilled

ocean water may not be lethal to some coastal taxa, and living coastal organisms are still found at the end of the ship's voyage (Smith et al. 1999; Wonham et al. 2001).

It has been increasingly recognized that the characteristics of both invaders and the target community are important in determining the invasion success and impact of an exotic species (Vermeij 1991; Lodge 1993). Good colonists usually include species capable of multiple reproductive methods (such as self-fertilization, single-sex reproduction, vegetative reproduction, asexual and sexual reproduction alternation), and species tolerant of a wide range of environmental conditions (Lodge 1993; Sakai et al. 2001). After initial colonization, the ability to compete for resources with native species, a rapid growth rate and adaptive mechanisms may be important aspects for population establishment and subsequent dispersal (Sakai et al. 2001). Some studies suggest that habitats with high disturbance, low species diversity, available niche, or absence of potential predators of invaders might be more vulnerable to invaders than otherwise (Ramakrishnan and Vitousek 1989; Case and Bolger 1991; Vermeij 1991; Lodge 1993; Johnson and Carlton 1996). Besides these, a habitat's history is also an essential factor in evaluating the susceptibility of this habitat (Vermeij 1991).

The prediction of the impacts of invasions to native community is of great scientific interest, but extremely difficult to achieve, because every potential invader and the target community, as well as their interactions, have to be intensively studied in order to do so. However, the facts often are that we know little about the ecology of both invader and community, and even less of their interactions (Lodge 1993; Ruiz et al. 1997). This

is especially true for coastal and marine ecosystems, which are much less studied and understood than fresh water or terrestrial systems. For example, the Chesapeake Bay receives over ten million metric tons of ballast water annually, which is one to two orders of magnitude more than San Francisco Bay and other Pacific estuaries do, but only about 116 alien species in Chesapeake Bay have been related to ballast water transfer, while 234 have been reported in San Francisco Bay (Ruiz et al. 1997; Cohen and Carlton 1998; Smith et al. 1999; Cohen 2000). However, we are still far from understanding this phenomenon, which needs a deep understanding of both biotic and abiotic aspects of donor and recipient systems, species interactions, and introduction pathways. Things are even more complicated because sometimes even with our best knowledge of the role of a species in its donor system, it may remain difficult to predict the impacts of this species to a recipient environment.

### **The ecological roles of gelatinous zooplankton**

Ctenophora and Cnidaria (including hydromedusae, siphonophores, scyphomedusae and cubomedusae) are two of the three major phyla that comprise gelatinous zooplankton (Purcell 1997). Despite the diversity in morphology and life cycle, species of this group share some of similarities such as fragility, gelatinous body material and ecological roles. Studies have shown that gelatinous zooplankton may reduce zooplankton populations and exert top-down control in the ecosystem. Furthermore, they can not only compete with fish for food resources efficiently but also directly prey on ichthyoplankton and



decrease fish populations (Möller 1980, 1984; Feigenbaum and Kelly 1984; Purcell 1992; Olesen et al. 1994; Purcell et al. 1994a, 1999b; Schneider and Behrends 1998).

Reportedly, gelatinous zooplankton abundances have been increasing worldwide with only some exceptions in hydrozoan species in some areas (Benovic et al. 1987; Mills 2001; Purcell et al. 2001b). One of the major results of this rising trend is the increasing occurrences and effects of non-indigenous gelatinous zooplankton species in aquatic ecosystems. For example, the German Bight in the North Sea was invaded by a siphonophore, *Muggiaea atlantica*, in July 1989, where it reached extremely high densities (up to 500 colonies m<sup>-3</sup>) and greatly affected the local ecosystem (Greve 1994). In the Mediterranean Sea, three introduced scyphomedusae, *Rhopilema nomadica*, *Phyllorhiza punctata* and *Cassiopea andromeda*, have become established and increasingly abundant in recent decades (Galil et al. 1990; Lotan et al. 1992; Mills 2001). Most recently, in summer 2000, tourists in the northern Gulf of Mexico witnessed large numbers of alien scyphomedusae, *Phyllorhiza punctata* and *Drymonema dalmatinum*, swarming in the coastal waters of the Gulf (Mills 2001).

Some studies have shown that the increase of gelatinous zooplankton in coastal and marine ecosystems may be associated with the changing global ecosystem, including increasing extent of eutrophication and anthropogenic activity (fishery exploitation, ship transportation, etc.). Meanwhile, the increasing abundances may be detrimental to fisheries in some areas, and thus aggravate ongoing global changes (Caddy and Griffiths 1990; Kideys 1994; Purcell et al. 1999b, 2001c; Arai 2001; Mills 2001). One very good

example is the invasion of the ctenophore, *Mnemiopsis leidyi*, an endemic species of the east coast of North America, to the Black Sea ecosystem. It was first sampled in the Black Sea in early 1980s, and then reached its peak abundances in the late 1980s to early 1990s, during which time most zooplankton production that usually supported fish was diverted to support a large population of this ctenophore (Vinogradov et al. 1989, 1995; Shiganova 1998; Kovalev et al. 2001; Mills 2001). Although Black Sea fisheries have been decreasing due to over-harvesting and heavy pollution, the devastating effects of *M. leidyi* were probably responsible for its final collapse, and the estimated loss of Black Sea fishery from the ctenophore was \$250 million (Zaitsev 1992; Travis 1993; Purcell et al. 2001c). This case has been viewed as one of the most notorious global biological invasion stories in the past half century (Travis 1993).

Although historically, gelatinous zooplankton have been understudied because of sampling difficulty and the lack of commercial interests for most of species in this group, things have been changing in many areas over the last several decades. The increasing massive occurrences of endemic and non-indigenous gelatinous zooplankton worldwide, especially the dramatic case in Black Sea ecosystem, strongly stimulated scientific interests and promoted numerous research efforts to study the ecology of these animals. As a result, our knowledge on the biological and ecological roles of gelatinous zooplankton community in coastal marine ecosystems has been greatly enhanced. Scientists have also explored valuable applications for the green fluorescent protein (GFP) from hydromedusae, *Aequorea victoria*, in biomedical and biochemical research areas (Tsien 1998; Schaufele 2001), which has driven a large scale annual commercial

collection activity for this species in Friday Harbor, Washington (Mills 2001).

Commercially, China and some Asian countries have a long history of using jellyfishes (several scyphomedusan species) as food resources. The current jellyfish fisheries have become a multi-million-dollar seafood business in Asia with an average annual worldwide catch of edible jellyfishes of around 321 000 metric tons (wet weight) (Omori and Nakano 2001). In some countries, such as US and Japan, jellyfishes have become attractive display items for aquariums or pets for nature enthusiasts.

### **The hydrozoan, *Moerisia lyonsi***

The hydrozoan, *Moerisia lyonsi*, first described in brackish Lake Qurun, Egypt, probably originated from the Black Sea or Middle-East areas (Calder and Burrell 1967; Calder 1971; Dumont 1994). Its first record in North America was documented in low salinity waters in the James and Pamunkey Rivers, Virginia, in 1965 (Calder and Burrell 1967). Since then, it has been reported in low salinity waters in the South Edisto River, South Carolina, Lake Pontchartrain, Louisiana, Choptank and Patuxent Rivers, Maryland, Delaware Bay (Sandifer et al. 1974; Poirrier and Mulino 1977; Purcell et al. 1999a; Dr. Mary Beth Decker, Yale University, personal communication), and probably in the low salinity areas of San Francisco Bay, California (as *Moerisia sp.* in Rees and Gershwin 2000; Mills 2001). Since it was thought to be an oligohaline species, the transoceanic distribution patterns of *M. lyonsi* are puzzling given our limited knowledge on this species at hand (Calder 1971; Dumont 1994).

*Moerisia lyonsi* does not seem to have any pronounced effects in natural systems, but it has frequently become an accidental nuisance species blooming in experimental mesocosms. It was reported as the most troublesome pest in the closed-system culture for decapod larvae in South Carolina, because it not only competed successfully with decapod larvae for food (*Artemia nauplii*) but also preyed directly on the decapod larvae and became very abundant (Sandifer et al. 1974). More recently, it occurred persistently in the mesocosms of the Multiscale Experimental Ecosystem Research Center at the Horn Point Laboratory of the University of Maryland Center for Environmental Science from 1994 to 2000, and was able to reduce copepod populations in the mesocosms (Petersen et al. 1998; Purcell et al. 1999a). The experimental mesocosms at the Academy of Natural Science Estuarine Research Center, St. Leonard, MD also encountered a similar problem in summer 2000 (Dr. Mary Beth Decker, Yale University, personal communication).

Although it is an invasive species with great colonizing potential, *M. lyonsi* has not been paid sufficient attention by researchers, and very few studies have studied the ecology of this species. The nuisance records of *M. lyonsi* in mesocosms indicated that this species may become very abundant in natural water if favorable conditions occur. Although there have been no reports of massive occurrences and destructive effects of this species in natural ecosystems yet, small hydromedusae can be very abundant and may significantly affect zooplankton or ichthyoplankton populations in natural waters (Phillips et al. 1969; Young and Chia 1987; Purcell and Grover 1990). Some studies also showed that the hydroid phase of hydromedusae may become enormously abundant

under particularly favorable conditions, and thus may play a very important role in the energy transfer between benthos and plankton (Turpaeva et al. 1977; Letunov and Marfenin 1980; Simkina 1980; Boero 1984). Purcell et al. (1999a) reported that *M. lyonsi* preferentially feeds on copepods and its predation rates increase with increasing medusa diameter and prey densities in the laboratory. The polyps of this species asexually produce both polyp buds and medusa buds. The production rates of both types of buds increased with increasing prey availability, and the measured maximum asexual reproduction rate (altogether, 146.7 buds polyp<sup>-1</sup> in 38 d when fed 8 copepods polyp<sup>-1</sup> day<sup>-1</sup> at 22°C and 9.5 salinity) was high compared with other cnidarian species (Purcell et al. 1999a). However, this is about the extent of our knowledge of the ecology of this species.

Therefore, the current study will focus on several aspects of this species that are of the greatest current interest. For example, what features enable a seemingly oligohaline species to successfully survive a transoceanic trip and distribute widely? How do environmental factors affect its polyp bud and medusa bud reproduction and what is the quantitative relationship between these two processes in responding to environmental changes? Are there any predators in Chesapeake Bay that may possibly limit the growth and distribution of its populations? Brief introductions to each of these topics follow.

## **1. Temperature and salinity tolerance ranges of *M. lyonsi***

Since temperature and salinity are fundamental physical factors in determining the potential distribution range of aquatic organisms, it is essential to study the tolerance ranges of the polyps and medusae of *M. lyonsi* to these factors to explain its discontinuous distribution pattern in the world. The Family Moerisiidae has been recorded mainly in the Middle East and the Black Sea region in the past, and most genera, including *Moerisia* in this family, have been found only in low salinity natural waters (Calder 1971; Dumont 1994; Rees and Gershwin 2000). However, genera of this family have been reported worldwide in recent decades, and *M. lyonsi* could be the first North American record of the family Moerisiidae (Calder and Burrell 1967). Some researchers suggested that the polyps of these species might be more tolerant than the medusae and might attach to the bottom of ships and survive transoceanic trips (Saraber 1962). The available reports showed that *M. lyonsi* occurs mostly in low salinity natural waters (up to 10 salinity) in summer time (Calder and Burrell 1967; Sandifer et al. 1974; Poirrier and Mulino 1977; Purcell et al. 1999a), but it seems to be able to live well in mesohaline conditions in artificial systems (Sandifer et al. 1974; Purcell et al. 1999a). Purcell et al. (1999a) documented that *M. lyonsi* occurred at high density in their experimental mesocosms with the highest salinity of 12.5. Sandifer et al. (1974) found *M. lyonsi* thriving in their decapod cultures with artificial sea water at 16 salinity. Besides, the polyps of *M. lyonsi* may encyst at unfavorable conditions, and their cysts have been observed in early spring by Dr. Purcell (personal communication). Hence, it is highly possible that *M. lyonsi* may tolerate wide ranges of temperature and salinity so

that it may survive the large salinity differences during transoceanic transportation by ships.

The literature shows that some hydrozoan species may have broad temperature or salinity ranges and be fairly tolerant of variations in these factors. The hydromedusae, *Solmundella bitentaculata*, can live in temperatures from  $-1^{\circ}\text{C}$  to  $30^{\circ}\text{C}$ , and *Rathkea octopunctata*, can be present in salinities of 2-35 (Mayer 1914; Moncaleano and Niño 1979; both cited in Arai 1992). The polyps of marine hydromedusae, *Clava multicornis*, can grow and asexually reproduce after being transferred gradually from their normal conditions ( $16^{\circ}\text{C}$ , 32 salinity) to treatments of  $12-22^{\circ}\text{C}$  and 16-40 salinities (Kinne and Paffenhöfer 1966). The polyp colonies of the hydrozoan, *Stylactic hooperi*, may grow and reproduce at  $20-30^{\circ}\text{C}$  and 25-45 salinities following a direct transfer from normal conditions of  $20-29^{\circ}\text{C}$  and 33-35 salinities to the target conditions of  $10-35^{\circ}\text{C}$  and 15-55 salinities (Nipper-Buscariolli and Moreira 1983). Mills (1984) tested the behavioral and physiological responses of nine species of marine hydromedusae to abrupt salinity changes from 30.5 to a range of 19 to 38. Most of the species could readjust their buoyancy in a range from 23-38 salinity in a few hours, but the change from salinity 30.5 to 19 was lethal to most of the species (48 hr observation). Burykin (1989) found that the colony growth rates of the marine hydroid, *Dynamena pumila*, were highest at 35 salinity, but decreased at low and high salinities (14-16, 40-46, respectively). Although this experiment was not to test survival, it did indicate that this hydroid species could at least live temporarily in a fairly broad salinity range.

Some estuarine gelatinous species may have broader temperature and salinity ranges than marine or oceanic species. The ctenophore, *Mnemiopsis leidyi*, may be present in 2-32°C and 2-38 salinities in natural waters (reviewed by Purcell et al. 2001c). The eurythermal and euryhaline scyphomedusa, *Aurelia aurita*, is found in natural waters at 0-32°C and 14-38 salinities (Lucas 2001). The scyphomedusa, *Chrysaora quinquecirrha*, occurs mostly in salinities 7-25 in Chesapeake Bay, and its asexual reproduction of polyps and ephyrae is only limited by salinities = 10 or = 25 (Cargo and Schultz 1966, 1967; Purcell et al. 1999c). The encystment of its polyp was observed at temperatures = 3°C and = 34°C and salinities = 5 and = 35 in the laboratory (Cones and Haven 1969). Therefore, *C. quinquecirrha* can probably survive in adverse conditions that are beyond the normal ranges that its medusae and polyps experience. The estuarine hydroid, *Cordylophora caspia*, can endure a wide range of salinity from fresh water to sea water (35) in the laboratory, while it normally lives in natural waters at salinities below 10, or about 10-15 (Kinne 1957; Calder 1976). Similarly, another estuarine hydroid, *Garveia franciscana*, most frequently found at salinities 10-15, can endure salinities 1-35 in the laboratory (Crowell and Darnell 1955; Calder 1976). Based on these data, I hypothesize that *M. lyonsi* may have broad ranges of tolerance to temperature and salinity. In this study, I will test the effects of different temperature and salinity on its survival and asexual reproduction activity.



## **2. The qualitative and quantitative features of asexual reproduction of *M. lyonsi***

Hydrozoan species are versatile in terms of life cycle and reproduction processes. For example, some species, such as the freshwater hydra, do not have a pelagic medusa stage; some, such as some trachyline medusae, do not have a benthic polypoid stage; some have both stages; some hydroids externally brood polyp and/or medusa buds; some spawn gametes; and still others possess some unusual reproduction strategies (Boero 1984; Brusca and Brusca 1990; Madin and Madin 1991). Despite this diversity, typical hydrozoan species, such as *Moerisia lyonsi*, have a pelagic medusa phase and a benthic polyp phase in their life cycle, and have asexual reproduction and asexual reproduction alternation (Figure 1.1), which is similar to most scyphozoan species, such as *Aurelia aurita* and *Chrysaora quinquecirrha*.

The reproduction of *M. lyonsi* is featured by high rates of asexual reproduction of both planktonic and nonplanktonic buds, short development time, single sex reproduction, and alternation of reproduction modes. A polyp of *M. lyonsi* can produce asexually both polyps and medusae in its life time, and under unfavorable conditions, the polyp may form cysts (Dr. Purcell, personal communication). Polyp buds will assume a benthic existence, whereas medusa buds will assume a free pelagic existence. Under favorable conditions, a polyp usually starts budding within 2-3 days after detaching from its founder polyp, with polyp buds produced first and medusa buds produced sometime later. The free-swimming medusa of *M. lyonsi* is transparent and usually <1 cm in diameter. The medusa reproduces sexually, and the fertilized zygotes develop into

planulae that will eventually settle and become benthic polyps (Figure 1.1). In the laboratory, medusae grow very fast and gonads can develop as early as 8 d in favorable conditions (Purcell et al. 1999a). The polyps of *M. lyonsi* not only can produce solitary polyp and medusa buds, but the stolon of the polyps can also produce secondary polyps by transverse fission of the aboral end of the stolon, which may form a primitive colony; meanwhile, the cut-off end of the stolon can also form a new polyp (Petersen 1979; Purcell et al. 1999a; personal observations).

The asexual reproduction of *M. lyonsi* makes it possible to develop a population from a single polyp, and thus, its chances of success in colonizing and secondary dispersal are greatly enhanced. Being able to reproduce by single parent is a very favorable trait for invasive species. Invasion success is enhanced if the first arrival can initiate a new population. Sexual reproduction needs the co-occurrences of both sexes at the same time, which greatly lowers the invasion success of the species. For example, the invasive Asian freshwater hydromedusa, *Craspedacusta sowerbii*, has successfully colonized most of the world's continents in the last century, but the localized populations of this species are either all male or all female outside of its home range in Asia (Ludwig et al. 1979; Rayner and Appleton 1992; Dumont 1994). However, reports indicated that both sexes of *M. lyonsi* were found in South Edisto River, South Carolina (Sandifer et al. 1974), and that the undiagnosed *Moerisia sp.* population (suspected to be the same species as *M. lyonsi*) in San Francisco Bay also had both sexes present (Rees and Gershwin 2000). The medusae of *M. lyonsi* in the current study were coincidentally all male, but this is not surprising because they were either cultured from the polyps that

eventually derived from one polyp, or collected from one experimental mesocosm where they were possibly derived from one or two polyps or cysts of the same sex by chance.

Since a polyp of *M. lyonsi* may produce both benthic polyp buds and planktonic medusa buds, the relative production of both types of bud under different environmental conditions are of great interest. On one hand, polyp bud production may enhance the survival of the offspring and maintaining of the local populations, but may have limited benefits in dispersal. On the other hand, the production of planktonic medusa buds may enhance dispersal and genetic diversity of the population, but may have limited benefits in their own survival (Boero 1984; Brusca and Brusca 1990; Madin and Madin 1991).

To my knowledge, few existing studies have tried to quantitatively describe the intrinsic relations between these two processes of the asexual reproduction of the same cnidarian species. I hypothesize that the polyp bud production and medusa bud production in *M. lyonsi* polyps may respond differently to the changing of environmental factors.

### **3. Predation on *M. lyonsi***

As previously stated, predators may play an important role in the determination of the impacts of biotic invasions. However, no predators have been known to prey on the medusae or polyps of *M. lyonsi* either in its native or new habitats. This is not surprising because gelatinous zooplankton are not preferred food for many marine species.

However, some species of gelatinous zooplankton do consume or prefer other gelatinous species (reviewed in Purcell 1991), and species of gastropod nudibranchs have been

known as the most important predators on cnidarian polyps (MacLeod and Valiela 1975; Hernroth and Gröndahl 1985; Folino 1993; Chester et al. 2000). Based on the temperature and salinity ranges of *M. lyonsi* from field and laboratory data (described previously), there is some disparity between its theoretical potential and its field occurrences in Chesapeake Bay (Calder and Burrell 1967; Purcell et al. 1999a). The theoretical salinity range of *M. lyonsi* is broader than the range of its known field occurrences. Therefore, I hypothesize that *M. lyonsi* may encounter predators in Chesapeake Bay and its distribution in the Bay may be restricted by predation rather than physical factors.

Chesapeake Bay is already known for its abundant populations of gelatinous zooplankton. The scyphomedusa, *Chrysaora quinquecirrha*, and the ctenophore, *Mnemiopsis leidyi*, are the most important gelatinous zooplankton predators and may control zooplankton populations in the Bay and its tributaries (Feigenbaum and Kelly 1984; Purcell 1992; Purcell et al. 1994b). Both can feed directly on fish eggs and larvae and may also compete with fish for copepods and other crustacean zooplankton (Cowan and Houde 1993; Purcell et al. 1994a, b). In addition, the medusae of *C. quinquecirrha* prey heavily on the ctenophore and greatly affect its abundances in the tributaries of Chesapeake Bay, and the predation relationship between these two species may reduce mortality of zooplankton and ichthyoplankton in the Bay (Feigenbaum and Kelly 1984; Purcell and Cowan 1995; Olesen et al. 1996). In the Black Sea ecosystem, the shortage of gelatinous predators of the ctenophore, *M. leidyi*, may have accounted for its devastating effects in that ecosystem (Purcell et al. 2001c).

Considering the great abundances of *C. quinquecirrha* and the ctenophore in Chesapeake Bay, if either one of them preys on *M. lyonsi*, it may have great effects on the size and distribution pattern of *M. lyonsi* populations in the Bay. The temperature and salinity ranges of the ctenophore (2-32°C, and 2-38 salinities) includes or largely overlaps with those maximum ranges known for *M. lyonsi* (18-29°C, and 1-16 salinities). Additionally, *M. lyonsi* were recorded mostly at salinities that were also favorable for ctenophore populations. Therefore, the two species may coexist well in the same habitats. The prey of the ctenophore, *M. leidyi*, mainly includes copepods, copepod nauplii and meroplankton, but no gelatinous zooplankton has been found in its diets (reviewed by Purcell et al. 2001c). Thus, I would expect that the ctenophore might not preferentially feed on the medusae of *M. lyonsi* or exert only limited effects.

By contrast, early laboratory studies found that *C. quinquecirrha* medusae selectively feed on gelatinous prey and consume copepods only when soft-bodied prey is not available (Delap 1901; Lebour 1923). Ford et al. (1997) found when *C. quinquecirrha* swims, its bell motion generates flow and eddies that can entrain zooplankton prey and greatly increase the chances of prey encounter rate on its tentacles and oral arms. Theoretically, prey with swimming speed slower than the flow speed generated by *C. quinquecirrha* is vulnerable to its capture. The predation relationship between *C. quinquecirrha* and the ctenophore is a very good evidence for this (Kreps et al. 1997). The medusae of *M. lyonsi* swim slowly (personal observations), so it is likely that they are vulnerable to the predation of *C. quinquecirrha*. Although *M. lyonsi* can live well at

salinity 16 in laboratory studies (Sandifer et al. 1974), its field records seem to have an upper bound of 10 salinity, which coincidentally is the lower bound of the optimal salinity range (10-25) of *C. quinquecirrha* (Cargo and Schultz 1966, 1967; Purcell et al. 1999c). In addition, the peak occurrences of both species are in summertime. Hence, I hypothesize that the medusae of *C. quinquecirrha* may be an important predator for medusae of *M. lyonsi*.

During my experiments, several nudibranchs (not identified to species) accidentally occurred in the *M. lyonsi* polyp culture (22°C and 10 salinity), where they fed greedily on the polyps and grew very quickly. I do not conduct further research on the predation of the nudibranchs on the polyps of *M. lyonsi* as a part of this thesis, but because nudibranchs are very important predators on cnidarian polyps. I will give a brief review of the relevant literature here, which hopefully would promote further interest in this topic.

Species of gastropod nudibranchs may heavily prey on cnidarian polyps or colonies, and the predation may be critical in controlling the benthic populations of cnidarian species (Cargo and Schultz 1967; Hernroth and Gröndahl 1985; Folino 1993). Cargo and Schultz (1967) found that a nudibranch species fed voraciously on the polyps of *Chrysaora quinquecirrha*. It was identified later as *Cratena pilata*, a nudibranch species that prefers cnidarian polyps (Cargo and Burnett 1982). Hernroth and Gröndahl (1985) showed that the predation rate of the nudibranch, *Coryphella verrucosa*, on the polyps of scyphomedusa, *Aurelia aurita*, can reach up to 200 polyps d<sup>-1</sup> in the laboratory, and

suggested that the predation may have been the main cause of a drastic decrease of *A. aurita* polyps in the field in October. Folino (1993) found that the nudibranch, *Cuthona nana*, grazes on colonies of the hydroid, *Hydractinia echinata*, and the estimated grazing intensity in the field at Gosport Harbor (New Hampshire) is about 6% of the total hydroid colony daily. As a relatively new research direction, the literature related to this topic is still growing. These studies indicated that nudibranchs, as the most important predators on hydroids found to date, may have great impacts on the benthic cnidarian populations, and thus may further affect the pelagic medusa populations as well.

Some studies showed that predator-prey associations between nudibranchs and hydroids are commonly species specific. For example, the nudibranch, *Cuthona nana*, specifically feeds on the colonial hydroid, *Hydractinia echinata* (Harris et al. 1975). Lambert (1991) found four nudibranch species coexisting in the colonies of the same hydroid species, but each of which had specific preferences on certain parts of the colony. A nudibranch species in the genus *Coryphella* feeds on a variety of cnidarian polyps, including the polyps of *Aurelia aurita* and *Cyanea sp.*, but it selectively stores specific nematocyst types from the polyps of each species (MacLeod and Valiela 1975; Day and Harris 1978; Ostman 1997).

Hydroids are typical early colonists and common members of the epifauna, or fouling communities, and they may have an important role in early community succession (Standing 1976; Boero 1984; Okamura 1986). As an example, the polyps of *M. lyonsi*

had been identified in epifauna communities in Lake Pontchartrain, LA (Poirrier and Mulino 1977). Okamura (1986) found that hydroids in the fouling community in San Francisco Bay speed up the community succession to mussel (*Mytilus edulis*) dominance. Therefore, the nudibranch-hydroid associations may indirectly affect the recruitment of later species by feeding on hydroids and preventing the restoration of the hydroids (Chester et al. 2000). Interestingly, the nudibranch, *Cuthona nana*, was found only to graze on a portion of the hydroid colonies (*Hydractinia echinata*), and then left, which enabled the polyp colony to recover quickly (Revist 1978). Recently, a caprellid amphipod (*Paracaprella tenuis*)-hydroid (*Bougainvillia rugosa*) mutualism has been found, in which the caprellid provides protection to hydroid polyps by aggressively hindering the approach of nudibranchs (Caine 1998). The species-specific associations between hydroids and nudibranchs or other species make the overgrowth of hydroid colonies by other successive colonists a complex issue.

In summary, the interactions of nudibranchs and cnidarian polyps represent a research direction with rising interests. Further quantitative studies on this topic with the hydroids, whose medusa forms are of regional or ecological importance, are especially desirable and may yield fruitful results.

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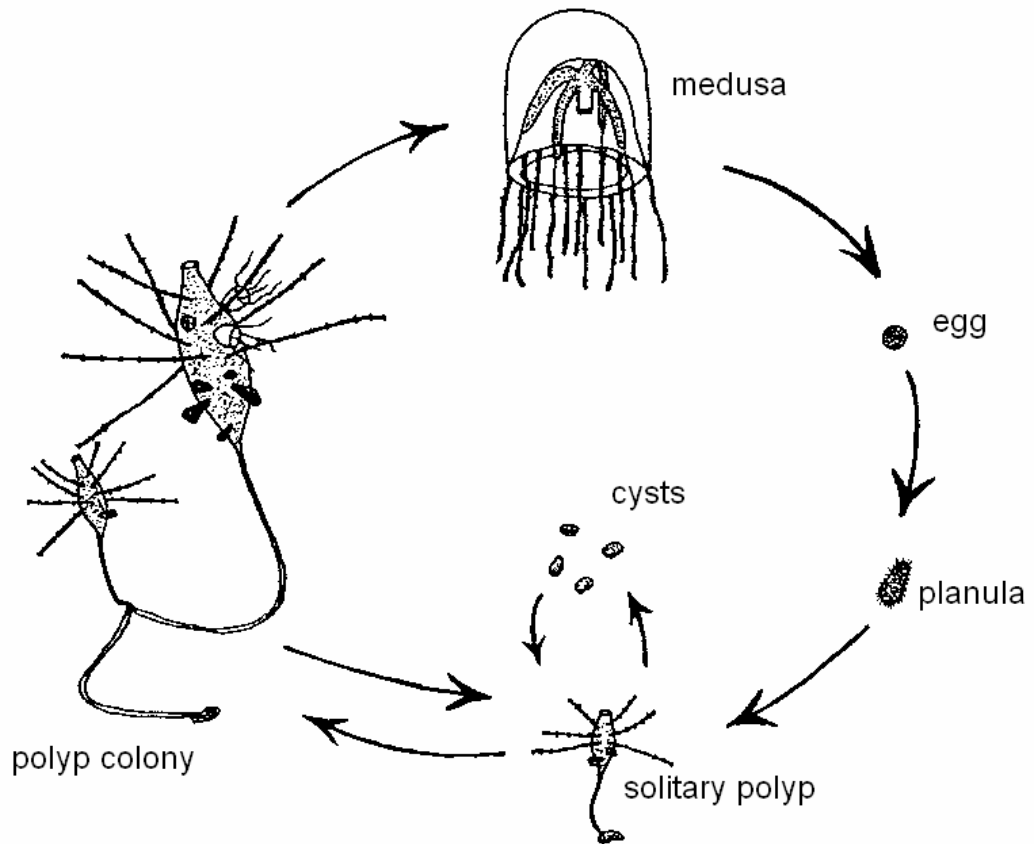
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Figure 1.1. *Moerisia lyonsi*. Life history.



## CHAPTER 2

Effects of Environmental Factors on Distribution and Asexual  
Reproduction of the Invasive Hydrozoan, *Moerisia lyonsi*

## **Introduction**

Non-indigenous species have become an important component in changing the global ecosystem (Vitousek et al. 1996; Dukes and Mooney 1999; Sakai et al. 2001). Some invasive species have caused severe economic disruptions costing billions dollars, or resulted in unexpected and undesired changes in native ecosystems (Mackie 1991; Travis 1993; U. S. Congress, OTA 1993; Parker et al. 1999; Mack et al. 2000). Species introductions are still rapidly rising in number, and the rate of introductions has accelerated in the last several decades (Ruiz et al. 1997; Cohen and Carlton 1998; Cohen 2000). As a result, the coastal areas in the world are increasingly threatened by non-indigenous species. About 400 alien species have been recognized along the US coastal areas, but this is still believed to be an underestimation (Ruiz et al. 1997; Cohen and Carlton 1998). On the other side, roughly only 10% of all introduced species can successfully establish themselves in their new locations (the rate may vary among taxa), and among the 10%, most do not have significant impacts on the native communities (Williamson 1989; Vermeij 1991; Williamson and Fitter 1996). However, since the chance of undesired or pest alien species becoming established increases with increasing number of introductions, the ongoing rapid biotic invasions pose a serious threat to the global ecosystem.

The characteristics of both invaders and the target community are important in determination of the invasion success and the impacts of an exotic species (Vermeij 1991; Lodge 1993). Generally, good colonists usually include species capable of

multiple reproductive methods (such as self-fertilization, single-sex reproduction, vegetative reproduction, asexual and sexual reproduction alternation), and species tolerant to wide ranges of environmental conditions (Lodge 1993; Sakai et al. 2001). The ability to compete for resources with native species, a rapid growth rate, and suitable adaptive mechanisms, may be important for population establishment and subsequent dispersal (Sakai et al. 2001). Some studies suggest that habitats with high disturbance, low species diversity, empty niches, or absence of potential predators of invaders might be more susceptible to biotic invasions than otherwise (Ramakrishnan and Vitousek 1989; Case and Bolger 1991; Vermeij 1991; Lodge 1993; Johnson and Carlton 1996). However, the prediction of the impacts of invasions to native communities is extremely difficult. Accordingly, every potential invader and the target community, as well as their interactions, has to be intensively studied to understand the impacts (Lodge 1993; Ruiz et al. 1997).

The concerns about non-indigenous gelatinous zooplankton have increased rapidly since the late 1980s, because gelatinous zooplankton abundances have been largely increasing worldwide (Mills 2001; Purcell et al. 2001b). Some studies have suggested that the increasing of gelatinous zooplankton in coastal and marine ecosystems may be associated with the changing global ecosystem, such as the increasing extent of eutrophication, fishery exploitation and shipping activity, and so on (Caddy and Griffiths 1990; Kideys 1994; Purcell et al. 1999b; 2001c; Arai 2001; Mills 2001). Meanwhile, the increasing abundances of gelatinous zooplankton population may be harmful to fisheries in some areas, thus aggravate the ongoing global change (Purcell et

al. 1999b, 2001c; Mills 2001). One very good example is the devastating effects of the ctenophore, *Mnemiopsis leidyi*, an endemic species of the east coast of North America, on the Black Sea ecosystem. It was probably brought to the Black Sea by ballast water in early 1980s, reaching its peak abundances in the late 1980s to early 1990s, when most zooplankton production, that previously had supported fish, became diverted to support a large population of the ctenophore (Vinogradov et al. 1989, 1995; Shiganova 1998; Kovalev et al. 2001; Mills 2001). Although the fisheries of the Black Sea had been decreasing due to over-harvesting and heavy pollution, the massive effect of *M. leidyi* was probably responsible for its final collapse, and the estimated economic loss in the Black Sea fishery from the ctenophore was about \$250 million (Zaitsev 1992; Travis 1993; Purcell et al. 2001c). It has been viewed as one of the most notorious global biological invasion stories in the past half century (Travis 1993) and greatly stimulated research interest in gelatinous species.

The invasive hydrozoan, *Moerisia lyonsi*, a native of the Black Sea or Middle-East areas, was first recorded in North America in low salinity waters in the James and Pamunkey Rivers, Virginia, in 1965 (Calder and Burrell 1967; Calder 1971; Dumont 1994). Since then, its presence has been reported in low salinity estuarine waters (up to 10) in the South Edisto River, South Carolina, Lake Pontchartrain, Louisiana, Choptank and Patuxent Rivers, Maryland, Delaware Bay (Sandifer et al. 1974; Poirrier and Mulino 1977; Purcell et al. 1999a; Dr. Mary Beth Decker, Yale University, personal communication), and probably in San Francisco Bay, California (as *Moerisia sp.* in Rees and Gershwin 2000; Mills 2001). The characteristics of the reproduction of *M. lyonsi*

include asexually producing both polyp buds and medusa buds, high rate of asexual reproduction, short development time, and alternation of asexual and sexual reproduction (Purcell et al. 1999a). Therefore, *M. lyonsi* might be an ideal colonist. Although there has been no reports of massive occurrences and destructive effects of this species in nature yet, small hydromedusae species can be very abundant and have significant impacts on zooplankton or ichthyoplankton populations in natural ecosystems (Phillips et al. 1969; Young and Chia 1987; Purcell and Grover 1990). Several other studies have shown that hydroids of hydromedusae can become enormously abundant under particularly favorable environmental conditions, and suggest that they may play a very important role in the energy transfer between benthos and plankton (Turpaeva et al. 1977; Letunov and Marfenin 1980; Simkina 1980; Boero 1984). Therefore, it would be wise to monitor this species with vigilance.

Very few studies have addressed the ecology of *M. lyonsi*, so our knowledge about its role in any ecosystem is still very limited. This study will focus on three topics. First, *M. lyonsi* was thought to be an oligohaline species (Calder 1971; Dumont 1994), so its transoceanic distribution pattern is puzzling based on our limited knowledge. Because temperature and salinity are fundamental physical factors in determining the potential distribution range of aquatic organisms, knowledge of the tolerance ranges of the polyps and medusae of *M. lyonsi* to temperature and salinity will be essential to address this question. Second, as mentioned previously, a polyp of *M. lyonsi* may asexually produce both polyp buds and medusa buds in its lifetime, which is not common in coastal and marine invertebrates. However, few existing studies have described the quantitative

relationship between the processes of polyp bud production and medusa bud production. I hypothesize that these two processes in the same species may respond differently to environmental changes. If so, the quantitative relationship between these two processes could play an important role in regulating the population dynamics and overall advantages achieved by the species from two different types of populations (benthic and pelagic). I will test the hypothesis in the current study. Finally, I suspect that the distributions of *M. lyonsi* in Chesapeake Bay may be restricted by predation pressure, but no predators have yet been documented to prey on this species. I will study two potential predators of *M. lyonsi*, the scyphomedusa, *Chrysaora quinquecirrha*, and the ctenophore, *Mnemiopsis leidyi*. Both of these species are very abundant and play important roles in Chesapeake Bay ecosystem (Feigenbaum and Kelly 1984; Purcell 1992; Purcell et al. 1994b).

## **Materials and Methods**

### **Experimental animals**

Polyps of *M. lyonsi* were initially collected from settling plates held at 25°C (on average) and 10 salinity in experimental mesocosms of the Academy of Natural Science Estuarine Research Center (ANSERC), St. Leonard, MD on August 9, 2000. Thereafter, the polyps were cultured at room temperature (22°C) and 10 salinity at Horn Point Laboratory (HPL), Cambridge, MD. All polyps used in this study were derived from one single polyp. Polyps grew on the bottom of shallow cylindrical plastic beakers filled



with ~200 ml water. Individual cultures were fed daily with either natural zooplankton (mainly *Acartia tonsa* copepods and nauplii) collected by a plankton net with 64  $\mu$ m mesh off the HPL dock, or *A. tonsa* cultured in the mesocosms of the Multiscale Experimental Ecosystem Research Center (MEERC) at HPL. Water was changed daily and the leftover food items were removed daily.

Medusae of *M. lyonsi* to be used for salinity tolerance range test (Experiment 1) were collected from the MEERC mesocosms maintained at 25°C and 12 salinity on September 28, 2000. Medusae of *M. lyonsi* to be used for predation experiments (Experiment 3) were cultured from the polyps that were eventually derived from one single polyp. The medusa cultures were maintained at 22°C and 10 salinity in 8 L plastic containers and fed with natural zooplankton.

The scyphomedusae, *Chrysaora quinquecirrha*, and ctenophores, *Mnemiopsis leidyi*, used in the predation experiments, were collected with a dip net off the HPL dock and gently transferred to experimental containers with a bucket. *Chrysaora quinquecirrha* medusae were collected at 22±24°C and 10.6-13.1 salinity, and *M. leidyi* were collected at 24°C and 10.6 salinity.

### **Salinity preparation and measurements**

Waters of different salinities were generated by mixing 5 $\mu$ m filtered Choptank River water with deionized water to lower the salinity or by adding Instant Ocean sea salt

solution to raise the salinity. Salinity and temperature were measured with a YSI Salinity/Conductivity/Temperature meter (Model# 30/10 FT, Yellow Springs, Ohio). Counts and measurements of the polyps and medusae of *M. lyonsi* were achieved using an Olympus dissecting microscope.

### **Experiment 1: Temperature and salinity tolerance ranges of *M. lyonsi***

To test the effects of salinity on medusae of *M. lyonsi*, 16 similarly sized medusae collected at 25°C and 12 salinity from the MEERC mesocosms were arbitrarily divided into four groups, and then each group of 4 medusae were kept at 22°C and 12 salinity with the same number of *A. tonsa* copepods (40 copepods per 200 ml beaker) for 1 d to allow them to recover from handling. Afterwards, each group were transferred with a wide-mouth pipette to another 200 ml beaker filled with modified Choptank river water at 22°C and at one of four salinities, 1, 5, 20 and 26, with 40 pre-added *A. tonsa*, and held there for 24 hrs. The swimming behavior of the medusae was observed 5-10 minutes every hour for the first 6 hours, then again at 24 hr.

A preliminary non-replicated experiment was done before the main experiment to test the approximate salinity range of *M. lyonsi* polyps. Groups of 6 immature polyps (new buds had not started to appear) were transferred without any acclimation from salinity 10 to 0 (deionized water), 1, 5 to 40 in 5 unit intervals, and each group was kept in a 60 ml open glass jar at that salinity for 8 d, fed daily with same amounts of *A. tonsa* copepods (60 copepods jar<sup>-1</sup> d<sup>-1</sup>). The experiment was conducted at 20°C. The number

of surviving polyps and newly detached buds were counted daily. Newly detached buds and leftover food items were removed from the jar after counting, followed by a water change and feeding.

A main temperature and salinity experiment (T-S experiment) was conducted to test the combined effects of temperature and salinity on *M. lyonsi* polyps. The experimental design was similar as a Randomized Complete Block design (RCB). There were 5 temperature levels (10, 15, 20, 25,  $29\pm 1^\circ\text{C}$ ), with each maintained in a walk-in constant temperature chamber as a block without replication. Nine salinity levels (1, 5, 10, 15, 20, 25, 30, 35 and 40) were randomized within each temperature room. Each salinity level had three replications (at jar level) assigned completely at random to each salinity group within temperature blocks. Each 60 ml glass jar held 2 polyps. The polyps used for this experiment were born on the same day and cultured at  $20^\circ\text{C}$  and salinity 10. At the beginning of the treatment, all the selected polyps had developed 1-5 new polyp buds attached on their bodies but had not yet started to produce solitary buds. These polyps were transferred without any acclimation from holding conditions at  $20^\circ\text{C}$  and 10 salinity to one of the 45 treatments of temperature and salinity and maintained at that condition for 7 d. Thirty *A. tonsa* copepods were added to each jar once daily ( $15 \text{ polyp}^{-1} \text{ d}^{-1}$  on average). The light regime, provided by overhead fluorescent lights, was controlled as 12 h light/12 h dark for all treatments. I counted the numbers of surviving polyps and of newly detached polyp or medusa buds daily. Newly detached buds and uneaten food were removed from the jar after counting. Water was changed daily after counting. The Asexual Reproduction Rate (ARR, the number of new buds  $\text{polyp}^{-1} \text{ d}^{-1}$ )

for each replicate was the total number of newly detached polyp and medusa buds in each jar from day 2 to day 7 averaged per polyp per day (day 1 was treated as acclimation time due to the abrupt transfer).

I tested the effects of temperature and salinity treatments on polyp survival (categorized survival data) over the 7 d duration using a Mantel-Cox test (Stokes et al. 1991). The asexual reproduction rate (ARR) estimates were tested for normality as assumption prior to analysis. ANOVA was used to test temperature, salinity and the interaction effects on ARR. In this test, because there were no temperature replications and salinity treatments were not completely randomized within temperature blocks, the effects of temperature and salinity were tested by using the type III mean square for T\*S as an approximate error term. I did a Spearman Rank correlation test to check the relationships between temperature or salinity (1-30) and ARR. To further analyze the relationship between ARR and temperature at each salinity level, I checked normality assumptions and then used a simple linear regression test for ARR versus temperature at each salinity (since temperature had no replicates, the ARR at each temperature and salinity level was the average value from salinity replicates within each temperature). I also did multiple regressions by R-square Selection Method and Stepwise Selection Method to find the best predicting model for ARR from independent variables, temperature and salinity, and the square or square root transformations of the independent variables (to capture the nonlinearity). Unless otherwise stated, all statistics methods above and below are introduced in Zar (1999) and conducted with SAS statistical software (SAS 8.1), and statistical significance was assessed at the  $p = 0.05$  level.

**Experiment 2: The effects of environmental factors on the asexual reproduction of *M. lyonsi* polyps (T-S-F experiment)**

The experiment design was similar to a split-split plot design with two temperature levels (20, 29±1°C), each maintained in a water bath as a block, with three salinity treatments (5, 15, 25) as plots randomly arranged within each water bath and 4 food levels (4, 8, 12, 16 *A. tonsa* copepods polyp<sup>-1</sup> d<sup>-1</sup>) as split plots randomly assigned within each salinity plot. There were three replications (at jar level) completely randomized within each food split plot. Each jar held 2 polyps in a 60 ml open glass jar. The experiment started with a salinity acclimation for polyp cultures, in which polyps were transferred from 23°C and 10 salinity to salinities 5, 15 and 25 at the same temperature and maintained for 2 d. Newly detached polyp buds in these cultures were removed daily, while on the third day, the newly detached polyps at each salinity were selected for the experiment. The new polyps at each salinity were assigned to different temperature and food treatments without changing salinity. Food (copepods) was placed in each jar at assigned levels once daily. Light was provided by a ceiling fluorescent light without any dark period. During the experiment, any secondary polyps growing from the original polyp were cut off with a dissecting knife or scissor under a dissecting microscope. The experiment ran 31 d for the 29°C treatment and 34 d for the 20°C treatment.

During the experiment, I measured two types of development time for each replicate: the Development Time for polyp buds ( $DT_p$ ) was defined as the time from the day that a polyp detached from its founder polyp (which was the same as the starting time of the experiment) to the day that its first polyp bud detached; the Development Time for medusa buds ( $DT_m$ ) was defined as the time from the day that a polyp detached from its founder polyp to the day that its first medusa bud detached. I counted the numbers of unconsumed copepods and of newly detached polyp and medusa buds for each replicate jar daily. After counting, I removed them from the jars and changed water. The Asexual Reproduction Rate of the polyps in 31 d (ARR, the number of new buds  $\text{polyp}^{-1} \text{d}^{-1}$ ) for each replicate was the total number of newly detached polyp and medusa buds in 31 d averaged per polyp per day. Another dependent variable,  $R_m$ , was constructed for each replicate as the total number of newly detached medusa buds in 31 d divided by the total number of newly detached medusa and polyp buds in 31 d.

The food treatments was designed as four fixed levels ( $F_0$ ,  $A. tonsa \text{ polyp}^{-1} \text{d}^{-1}$ ), but the actual food consumption ( $F$ ,  $A. tonsa \text{ polyp}^{-1} \text{d}^{-1}$ ) for each replicate was estimated by the given number of copepods minus the unconsumed number averaged per polyp per day. Therefore, in this aspect, the food consumption ( $F$ ) was also a dependent variable with continuous values. I tested the dependency of food consumption ( $F$ ) on the temperature, salinity and assigned food levels ( $F_0$ ) by a similar test to a split-split plot design (<http://www.tfrec.wsu.edu/ANOVA/RCBspsp.html>). As described for the T-S experiment previously, because temperature treatments had no replication, and because salinity and food treatments were not completely randomized within temperatures, the

effects of temperature and salinity were tested using the type III mean square for T\*S (error for main plots) as an error term (SAS statement: test h=T S e=T\*S;), while the effects of F and F\*S were tested using the type III mean square for S(T\*F) (the error for subplots) as an error term (SAS statement: test h=F F\*S e=S(T\*F);). Thereafter, upon testing normality for residuals of dependent variables, I used temperature and salinity as independent variables, and food consumption (F) as a covariate, to do ANCOVA tests for the dependent variables including  $DT_p$ ,  $DT_m$ , ARR and  $R_m$ , respectively. For the same reason as above, the same approximation of error terms was used in the ANCOVA tests to test the effects of temperature and salinity (SAS statement: test h=T S e=T\*S;). I also conducted multiple regression analysis (similar to T-S experiment described previously) to find the best predicting model for ARR by temperature, salinity, food consumption, and the square or square root transformations of these variables (to capture the nonlinearity).

### **Experiment 3: Pilot study on predation on *M. lyonsi***

A preliminary experiment was used to explore the interactions between the medusae of scyphozoan, *Chrysaora quinquecirrha*, or the ctenophores, *Mnemiopsis leidyi*, and the medusae of *Moerisia lyonsi*. *Chrysaora* (3-4 cm in diameter) and the ctenophores (4-5 cm in length), collected at 24°C and 10.6 salinity, were transferred separately to 8 L containers containing 5 µm filtered Choptank River water at 22°C and the same salinity. They were fed with natural zooplankton and held for 1 d. At the same time, two groups of 30 *M. lyonsi* medusae (2.0-3.0 mm in diameter) from the cultures at 22°C and 10

salinity were transferred to 22°C and 10.6 salinity with natural zooplankton (same conditions as for *Chrysaora* and the ctenophores), and held for 2 d. Then, 3 ctenophores and 1 *Chrysaora* were separately placed in two 8 L containers at the same conditions without food and held for 1 d. On the third day, I transferred each group of 30 *Moerisia* into the containers, one with 3 ctenophores and another with 1 *Chrysaora*. Then, for the *Chrysaora* container, I directly observed interactions for 1 h and ended the experiment. For ctenophores, I watched their behavior for the first 2 h, and left them in the containers for another 4 h. Subsequently, I picked out the ctenophores and examined their gut contents under a dissecting microscope. The *Moerisia* were left in the container over night (16 h) since they were tangled by mucous and sank to the bottom. I observed their behavior again in the morning and then retrieved and counted them.

To quantify the size effects of *Chrysaora* medusae on their predation rate on *Moerisia* medusae, I examined the feeding of 8 different sized *Chrysaora* (3-10 cm in diameter, each in a different tank) on 30 *Moerisia* (all about 2.0-3.4 mm in diameter). Each *Chrysaora*, collected off HPL dock, was transferred to a 100 L cylindrical tank containing 5 µm filtered Choptank River water adjusted to the capture salinity (10.6-13.1), and acclimatized without any food for 1 d. Temperatures in the tanks were 22-23°C throughout the experiment. *Moerisia* medusae from the cultures (at 22°C and 10 salinity) were transferred to the same temperature and salinity conditions as for *Chrysaora*, and held separately for 1 d with natural zooplankton as food. One hour before the feeding experiment, *Moerisia* were moved to a container with a sieved bottom (64 µm) positioned in the same tank with *Chrysaora* for acclimation without



food. Then, *Moerisia* were gently released from the sieved container into the tank, and *Chrysaora* were allowed to feed for 1 h in the dark. *Chrysaora* were then removed from the tank, rinsed and their diameter measured. A control tank without *Chrysaora* was run separately with only 30 *Moerisia* (1.5-3.8 mm in diameter) for 1 h. *Moerisia* remaining in the tank with and without *Chrysaora* were collected by draining the water slowly through a 64  $\mu\text{m}$  sieve, and counted. The predation rate (no. *Moerisia* medusae predator<sup>-1</sup> h<sup>-1</sup>) for each *Chrysaora* was calculated by the equation  $P = (N_0 - N_t)/t$ , where P is the predation rate of *Chrysaora* on *Moerisia*,  $N_0$  and  $N_t$  are the number of *Moerisia* medusae at the beginning and end of the feeding experiment respectively, t is the time of feeding (= 1 h), respectively. I did a normality test for the data and then used linear regression to describe the relationship between predation rate and predator size.

To study the effect of size and density of *Moerisia* medusae on the predation rate by *Chrysaora* medusae, I examined the feeding of *Chrysaora* in the same size range (4-5 cm diameter) on *Moerisia* at 5 different densities (8, 14, 18, 28 and 52 *Moerisia* per *Chrysaora*, each in a tank) with three replications. Each density was comprised of two sizes of *Moerisia* in equal proportion (1.4-2.2 mm diameter as small group, and 2.6-3.4 mm diameter as large group). The result of the control tank used in the previous experiment was also taken as a control for this experiment. Other experimental procedures were the same as described in the previous paragraph, except that after feeding, unconsumed *Moerisia* in this experiment were also measured for sizes. The predation rates (P) were calculated the same way as above for each sized prey, and for the prey data with two sizes combined. I did normality tests on the predation rates and

then used a nonparametric paired t-test to compare the difference between large and small *Moerisia*. Because no significant difference was detected for the two groups, I used simple linear regression to get the regression equation for the predation rate with two prey sizes combined.

## **Results**

### **Experiment 1: Temperature and salinity tolerance ranges of *M. lyonsi***

The medusae of *M. lyonsi* were tolerant of salinity change. After being directly transferred from 12 to 1, 5, 20 and 26 salinity at 22°C, the medusae immediately sank to the bottom at 1 and 5 salinity, but floated on the surface at 20 and 26 salinity. After 2 h, 2 out of 4 medusae at 5, 20 and 26 salinity started swimming in the water column, and after 4 h, all 4 medusae at these salinities were swimming in the water column and feeding. At 1 salinity, all the medusae remained motionlessly on the bottom since the transfer began until the end of 24 h experiment, but they were still alive.

The 8 d preliminary experiment showed that the salinity tolerance range of *M. lyonsi* polyps was broad and they were also tolerant of dramatic salinity change. After the abrupt transfer from 20°C and 10 salinity to a range of salinity from 0 to 40, no polyps survived at 0 salinity; some mortality occurred at 35 and 40 salinities at the end of experiment (2 of 6 polyps died at 35 salinity, 3 of 6 died at 40 salinity). Polyp development and new bud production occurred at all other salinity levels from 1 to 30,

and even the surviving polyps at 35 salinity showed some development and produced new buds. The production rate of new buds was highest at 10 salinity (4.5 new buds polyp<sup>-1</sup> d<sup>-1</sup>).

In the 7 d T-S experiment, after direct transfer from 20°C and 10 salinity to the 45 temperature (10-29 °C) and salinity (1-40) treatments, mortality of polyps occurred only in 6 treatments that were all at 35 and 40 salinity with temperature from 10 to 25°C; no mortality was observed at any treatment of salinity 1 to 30 (Figure 2.1). One hundred percent mortality of polyps occurred in two temperature treatments (10°C and 15°C) at 40 salinity (Figure 2.1, 2.2B). No polyp death was noticed at any tested salinities (1-40) at 29°C during the experiment (Figure 2.1). The results of a Mantel-Cox test showed that temperature and salinity treatment had significant effect on the number of surviving polyps over time (Cochran-Mantel-Haenszel Statistics based on table scores,  $p < 0.0001$ ), with lower survival rate being associated with higher salinities and/or lower temperatures (Figure 2.1; Table 2.1). From the time series comparison for those treatments where mortality occurred, there was greater and earlier mortality at 40 salinity than at 35 salinity, and at lower temperatures than at higher temperatures (Figure 2.2A, B).

The asexual reproduction rate (ARR) in the T-S experiment differed among temperature and salinity treatments ( $p < 0.0001$ ) (Figure 2.3; Table 2.2). The highest ARR occurred at the warmest temperatures and intermediate salinities (5-20), meanwhile, no or limited asexual reproduction occurred at the coolest temperatures (10-15°C) and the highest

salinities (35-40) (Figure 2.3). At 29°C, polyp asexual reproduction occurred at all the tested salinities 1 to 40, while at 10°C, no polyp development and asexual reproduction occurred at any tested salinity (Figure 2.3). The original numbers of buds prior to the treatments were not significantly different among all the temperature and salinity treatments ( $p > 0.15$ ) (Table 2.2). Therefore, the observed difference in ARR was not due to the difference in initial conditions prior to the treatments, but most probably due to the treatment effects. There was a significant linear correlation (Spearman Correlation Coefficient equal to 0.84) between ARR and temperature ( $p < 0.0001$ ), but not between ARR and salinity ( $p = 0.15$ ). Further tests (simple linear regressions) for the relationship between ARR and temperature at each salinity level showed that ARR increased linearly with increasing temperatures at salinities 1-25, but no linear relationships were detected at salinities 30, 35 and 40 (Table 2.3). Hence, at lower salinities 1-25, temperature effects were robust and 29°C was probably the most favorable temperature for the polyps, while at higher salinities 30-40, the effects of salinity became strong enough to counter temperature effects.

The least square means (LSM) comparisons among different salinity treatments indicated the optimal and suboptimal salinity ranges for *M. lyonsi* polyps. The least square means Asexual Reproduction Rate (ARR) were not significantly different among salinities 5-20, where the highest ARR occurred (Table 2.4). Besides, the least square means ARR among salinities 1, 25-35 were not significantly different from each other, where the relative lower ARR values occurred (Table 2.4). Therefore, salinities 5-20 may be the optimal salinity range for *M. lyonsi* polyps, while salinity 1, 25-35 may be

suboptimal for the polyps. Salinity 40 was not included in this comparison due to many missing values caused by high mortality of the polyps, but high mortality at this condition indicates that 40 salinity is suboptimal for the polyps. The least square means of ARR were not significantly different among any three adjacent salinity levels (difference = 10) except between salinities 1 and 5, as well as between salinities 1 and 10 (Table 2.4). Hence, the salinity effects varied more dramatically among lower salinities (1-10) than among higher salinities.

During the 7 d T-S experiment, both polyp bud production and medusa bud production were observed for some treatments with medusa bud production always sometime later than polyp bud production. Polyp bud production occurred at 1-40 salinities at 20-29°C, and at 1-25 salinities at 15°C, but not at any salinity at 10°C. Secondary polyp growth was not observed during this relatively short experiment. Medusa buds were observed at 1-35 salinities at 25°C, and at 5-40 salinities at 29°C, but not at 10-20°C at any salinity. The maximum daily polyp bud production, 20 polyp buds polyp<sup>-1</sup>, occurred at 29°C and 15 salinity. The maximum daily medusa bud production, 6 medusa buds polyp<sup>-1</sup>, was recorded at 29°C and 10 salinity. The highest total asexual reproduction rate (ARR), 12.6±1.7 (mean ± stdev) new buds polyp<sup>-1</sup> d<sup>-1</sup>, occurred at 29°C and 15 salinity (with 15 copepods polyp<sup>-1</sup> d<sup>-1</sup>).

## **Experiment 2: The effects of environmental factors on the asexual reproduction of *M. lyonsi* polyps**

During the T-S-F experiment, the polyps always started polyp bud production first; medusa bud production, if it occurred, started sometime later than polyp bud production (Figure 2.4). In other words, the Development Time for polyp buds ( $DT_p$ ) was always earlier than the Development Time for medusa buds ( $DT_m$ ). The experiment started with all newly detached polyps, so the development time was equal to the number of days before the first bud of either type was produced. The experimental results showed that the difference between  $DT_p$  and  $DT_m$  was much greater at 20°C than at 29°C (Figure 2.4), which was about  $19 \pm 6$  d (mean  $\pm$  SD,  $n=36$ ) difference at 20°C, and only  $8 \pm 3$  d ( $n=36$ ) at 29°C. Both types of development time ( $DT_p$  and  $DT_m$ ) were shortened to some extent with increasing food consumptions, but both were longer at 25 salinity than at 5 or 15 salinities, and at 20°C than at 29°C (Figure 2.4).

Other than these, the Development Time for polyp buds ( $DT_p$ ) was apparently less affected by changing experimental conditions than the Development Time for medusa buds ( $DT_m$ ). Based on the results from the T-S experiment previously, the conditions for the T-S-F experiment, temperatures from 20°C to 29°C, salinities from 25 to 5 or 15, and feeding rates from 4 to 15 copepods polyp<sup>-1</sup> d<sup>-1</sup>, represent a range from the relatively less favorable conditions to the more favorable conditions for the polyps of *M. lyonsi*. Under very favorable conditions in which all three factors were suitable, polyps started to produce new polyp buds asexually in as little as 2 days after their own detaching from

the founder polyps, and to produce medusa buds in about 8-10 days (Figure 2.4B). Under the least favorable conditions for all three factors, the polyp bud production started in about 7-9 days, but medusa bud production was delayed beyond the 34 d experimental period (Figure 2.4A). On average,  $DT_p$  was only about 3-5 d longer at 20°C than at 29°C, while  $DT_m$  was more than two weeks longer at 20°C than at 29°C. Therefore, the significantly bigger gap between  $DT_p$  and  $DT_m$  at 20°C than at 29°C (Figure 2.4) was mainly caused by the delay of medusa bud production, rather than a change in polyp bud production. In addition, the between salinity difference was also larger for  $DT_m$  than for  $DT_p$  (Figure 2.4). At 20°C and 25 salinity, most of the treatments never produced medusa buds during the 34 d experiment regardless of food consumption (Figure 2.4A). Hence, the conditions at 20°C and 25 salinity would be considered the least favorable conditions for medusa bud production even with high food consumption in this study.

The results of ANCOVA tests generally agreed with the observations described in the previous paragraph. Temperature and food consumption both had significant effects on  $DT_p$  and  $DT_m$ , whereas salinity had significant effects on  $DT_m$  only ( $p=0.036$ ) (Table 2.5). Food consumption (F) was negatively and linearly related with both  $DT_p$  and  $DT_m$  (Figure 2.4; Table 2.5, F:  $p<0.0001$ ). The effects of food consumption on  $DT_p$  were similar at different temperatures or salinities (Figure 2.4; Table 2.5, F\*T:  $p=0.241$ ; F\*S:  $p=0.925$ ). By contrast, the effects of food consumption on  $DT_m$  were similar at different temperatures, but not the same at different salinities (Figure 2.4; Table 2.5, F\*T:  $p=0.340$ , F\*S:  $p=0.030$ ). The least square means comparison between temperature

treatments showed that both  $DT_p$  and  $DT_m$  were significantly shorter at 29°C than at 20°C ( $p < 0.01$  in both cases). The least square means for  $DT_m$  were 15.0, 15.9 and 22.9 d at salinity 5, 15, and 25, respectively, and there was no significant difference between salinity 5 and 15 ( $p = 0.336$ ), but there were significant differences between 25 salinity and 5 or 15 salinity ( $p = 0.01$  for both). This means that  $DT_m$  of the polyps was significantly shorter at 5 and 15 salinity than at 25 salinity. Since  $DT_p$  were not significantly different among salinities ( $p = 0.188$ ), there were only two factors (temperature and food) affecting  $DT_p$ , but all three factors affected  $DT_m$ .

The test of dependency among the treatment variables, in which food consumption (F) was treated as a dependent variable, showed that food consumption was significantly influenced by temperature, salinity, and the assigned food level ( $F_0$ ) (Table 2.6). The least square means of food consumption of the polyps were not significantly different between 5 and 15 salinity ( $p = 0.168$ ), but were significantly less at salinity 25 than at 5 ( $p = 0.039$ ), and at salinity 25 than at 15 ( $p = 0.019$ ). The polyps consumed fewer copepods at 20°C than at 29°C ( $p = 0.065$ ), which was considered to be significant here because the degree of freedom for temperature comparison was only 1. Due to the dependency of food consumption on temperature and salinity, the interpretations of ANCOVA test results will be different with respect to the situations in which no significance was detected for temperature and salinity effects. Because food consumption had significant effects on all dependent variables in the ANCOVA tests, no significance for temperature or salinity effects on certain dependent variables in the ANCOVA tests would only mean that no direct effects were detected statistically, but



temperature or salinity may still have effects on the dependant variables by affecting food consumption of the polyps. Therefore, in terms of salinity effects on the development time for polyp buds ( $DT_p$ ), the results of the ANCOVA test described in the previous paragraph (Table 2.5) mean that salinity itself had no direct effects on  $DT_p$  after counting in the food effects as a covariate, and that salinity effects on  $DT_p$  were mostly through affecting food consumption of the polyps.

The total asexual reproduction rate of the polyps of *M. lyonsi* in 31 d (ARR) increased linearly with the increasing food consumption at all the temperature and salinity treatments in the T-S-F experiment (Figure 2.5). The results of the ANCOVA showed that food consumption had significant direct effects on ARR, but temperature and salinity both had no significant direct effects on ARR ( $p < 0.0001$ ,  $p = 0.071$ , and  $p = 0.429$ , for F, T, and S effects, respectively) (Table 2.7). Hence, food consumption was an essential factor in controlling the total asexual reproduction. However, due to the significant dependency of food consumption on temperature and salinity as described previously, the ANCOVA result really means that temperature and salinity affected ARR indirectly by affecting food consumption of the polyps. The results also showed that the rates in which ARR increased with increasing food consumption were statistically different among temperature or salinity treatments (F\*T:  $p = 0.006$ ; F\*S:  $p = 0.029$ ) (Table 2.7).

The daily asexual reproduction of the polyps of *M. lyonsi* consists of two parts, the daily polyp bud production and the daily medusa bud production, both of which changed with

time and experimental conditions. Figure 2.6 showed the variations of the daily polyp bud and medusa bud production in some selected representative treatments. The quantities of both were the highest under the best conditions (for example: Figure 2.6A;  $T=29^{\circ}\text{C}$ ,  $S=5$ ,  $F=13.4$  copepods  $\text{polyp}^{-1} \text{d}^{-1}$ ), and the lowest under the least favorable conditions in the T-S-F experiment (for example: Figure 2.6B;  $T=20^{\circ}\text{C}$ ,  $S=25$ ,  $F=2.2$  copepods  $\text{polyp}^{-1} \text{d}^{-1}$ ), while intermediate values occurred under other conditions between the extremes (for example: Figure 2.6C, D, E, F). In the best conditions in the experiment, the daily polyp bud production quickly peaked in the first week after detaching from a founder polyp, then dropped rapidly in the second week, and almost completely disappeared when medusa bud production reached a similar or higher peak during the third week (Figure 2.6A). Hence, there seemed to be a shift between the peaks of polyp and medusa bud production under the best conditions. While under the least favorable conditions in this experiment ( $T=20^{\circ}\text{C}$ ,  $S=25$ ), polyp bud production occurred and persisted at low levels, but medusa bud production was almost zero throughout the 34 d experimental period (for example: Figure 2.6B, C). Hence, the asexual reproduction of the polyps at these conditions consisted of only polyp bud production. In other intermediate situations, polyp bud production reached its peak first, then dropped as the medusa bud production began, but never completely stopped during the course of the experiment (for example: Figure 2.6D, E, F). Instead, polyp production persisted at a much lower level than its peak value after the medusa bud production began, while the medusa bud production was at a somewhat or much lower level than at the best conditions (For example: Figure 2.6D, E, F).

The average daily polyp bud and medusa bud production over 31 d varied differently under the similar experimental conditions (Figure 2.7). A compensational mode between polyp and medusa bud production of *M. lyonsi* was observed. Firstly, at the unfavorable temperature of 20°C, medusa bud production was low and did not increase much with increasing food consumption, while polyp bud production still occurred and increased with increasing food consumption, just as at higher temperature (Figure 2.7A, C). This situation was exacerbated when temperature and salinity both were unfavorable (20°C and 25 salinity), where medusa bud production was not observed at all for most of the polyps, while the trend of polyp bud production did not change much in these conditions compared with other tested conditions (Figure 2.7A, C). Secondly, at the most favorable temperature of 29°C, medusa bud production increased rapidly with increasing food consumption while polyp bud production did not show the same trend, and even dropped to some extent at the highest food consumption when medusa bud production accelerated (Figure 2.7B, D). As a result, the total of both productions, which was the asexual reproduction rate (ARR), could always be increasing with increasing food consumption at all temperature and salinities (Figure 2.5). Meanwhile, the reproduction energy was distributed as different proportions of the two types of offspring under different experimental conditions.

The quality compositions of the asexual reproduction (ARR) may be better described by the variable,  $R_m$ , the ratio of the total medusa bud production to the total asexual reproduction of the polyps in 31 d.  $R_m$  had more complex variations than ARR (described previously) in responding to the changes of environmental factors (Figure 2.5,

2.8). First, at 20°C (Figure 2.8A), there was an apparent difference of  $R_m$  of 5 and 15 salinities with 25 salinity, and  $R_m$  was almost zero at any food consumption value at 25 salinity. Second, by comparing the two panels of Figure 2.8, it can be easily seen that the response of  $R_m$  to food consumption at 20°C (Figure 2.8A) was different from that observed at 29°C (Figure 2.8B). Finally, almost half of the replicates at 29°C (17 out of 36) had  $R_m > 0.5$  (Figure 2.8B), which means that the proportion of medusa buds was greater than the proportion of polyp buds at this temperature, while no replicate at 20°C exceeded  $R_m = 0.5$  (Figure 2.8), so polyp bud production was the major form of the asexual reproduction at 20°C.

The results of the ANCOVA agreed with most of the observations described above (Table 2.7), in which food consumption and salinity all had significant direct effects on  $R_m$  ( $p < 0.0001$ ,  $p = 0.010$ , for F and S effects, respectively), and the patterns of food effects were different at 20°C and at 29°C (F\*T,  $p = 0.001$ ). The least square means of  $R_m$  at salinities 5, 15 and 25 were all significantly different from each other ( $p < 0.01$  for all pairs). Temperature only had indirect effects on  $R_m$  mostly by changing food consumption ( $p = 0.553$ ). Combining the previous results for ARR, it may be concluded that both the partitioning of the asexual reproduction (represented by  $R_m$ ) and the quantity of the total asexual reproduction (represented by ARR) were directly affected by food consumption, while not directly affected by temperature, but salinity had direct effects on  $R_m$ , but not on ARR (Table 2.7).

Finally, the polyps of *M. lyonsi* in the T-S-F experiment had the highest asexual reproduction rate at similar temperature and salinity conditions to the T-S experiment previously. The highest total asexual reproduction rate in this experiment,  $5.9 \pm 0.3$  buds polyp<sup>-1</sup> d<sup>-1</sup> (mean  $\pm$  SD, for three replicates), occurred at 29°C and 15 salinity at an average daily food consumption of  $12.7 \pm 0.6$  copepods polyp<sup>-1</sup> d<sup>-1</sup>. The highest polyp bud production in a single replicate, 4.1 polyp buds polyp<sup>-1</sup> d<sup>-1</sup>, occurred at 29°C and 15 salinity with an average daily actual food consumption of 10.5 copepods polyp<sup>-1</sup> d<sup>-1</sup>. The highest medusa bud production in a single replicate, 4.4 medusa buds polyp<sup>-1</sup> d<sup>-1</sup> (altogether 135.5 medusa buds polyp<sup>-1</sup> in 31 d), occurred at 29°C and 15 salinity with an average daily actual food consumption of 14.3 copepods polyp<sup>-1</sup> d<sup>-1</sup>.

Predictive equations for the asexual reproduction rate of *M. lyonsi* polyps

The data from the 7 d T-S experiment and the one month (31-34 d) T-S-F experiment provide foundation of predictive equations for the asexual reproduction rate (ARR). To determine the independent factors that would be included in the best predictive model for ARR, besides experimental factors (T, S or F), I tested the square and square root of temperature and salinity ( $T^2$ ,  $S^2$ ,  $T^{\frac{1}{2}}$ ,  $S^{\frac{1}{2}}$ ), and the multiple of temperature and salinity (TS) for their relative importance in the predictive model for both experiments.

The best predictive model from the T-S experiment,

$$\log_{10}(ARR + 1) = -1.022 + 0.049T - 0.069S + 0.446S^{\frac{1}{2}} \dots\dots\dots$$

(1)

includes three variables, temperature (T), salinity (S), and the square root of salinity ( $S^{\frac{1}{2}}$ ), which would yield a total model R-square of 90% (Table 2.8). In this equation, temperature contributed the highest partial model R-square of 63%, while salinity contributed a total of 28% model R-square (16% from  $S^{\frac{1}{2}}$ , and 11% from S) (Table 2.8). Therefore, temperature accounted more for predicting ARR than salinity from the equation (1), especially because there were fewer degrees of freedom for temperature (DF = 4) than for salinity (DF = 8) in the T-S experiment.

The best predictive model for ARR from the T-S-F experiment

$$\log_{10}(ARR + 1) = -0.319 + 0.043F - 1.955 \times 10^{-4}TS - 0.045S + 0.334S^{\frac{1}{2}} \dots\dots\dots (2)$$

includes four variables, food consumption (F), salinity (S), temperature\*salinity (TS), and the square root of salinity ( $S^{\frac{1}{2}}$ ). A total model R-square of 92% was achieved by these four variables, among which food consumption alone constitutes 83% of the partial model R-square, and temperature and salinity (TS, S,  $S^{\frac{1}{2}}$ ) together contributed 9% of partial model R-square (Table 2.8). Hence, food consumption was much more important for predicting ARR than temperature and salinity in equation (2). However, since the degree of freedom for temperature was 1, and salinity 2, while food consumption had 72 measured values in the T-S-F experiment, the role of temperature and salinity may have been underrepresented in this equation.

### Experiment 3: Pilot study on predation on *M. lyonsi*

The preliminary experiment showed that no medusa of *Moerisia lyonsi* was captured or preyed on by the ctenophore, *Mnemiopsis leidy*, but the medusae of *Chrysaora quinquecirrha* preyed heavily on *M. lyonsi* medusae. All 30 *M. lyonsi* medusae were retrieved after being held in one 8 L container with 3 ctenophores for 6 h and the following night without ctenophores. During the experimental period, I found that ctenophores secreted mucus that trapped *M. lyonsi* medusae. Subsequently, the medusae sank to the bottom of the container. I left the medusae without ctenophores overnight, and found that the medusae were able to escape from the mucus and then swim in the water column freely. By contrast, *C. quinquecirrha* fed voraciously on *M. lyonsi* medusae. Most of *M. lyonsi* medusae that came into contact with the tentacles of *C. quinquecirrha* were unable to escape. Only 6 out of 30 *M. lyonsi* medusae remained in the container after being placed together with 1 starved *C. quinquecirrha* for 1 hr. It was easy to see the *M. lyonsi* medusae in the stomach of *C. quinquecirrha* through its transparent bell tissue.

Further pilot predation experiments in 100 L containers showed that the predation rate of *C. quinquecirrha* medusae on *M. lyonsi* medusae increased linearly with increasing predator diameter ( $p=0.001$ ;  $F=30.7$ ) (Figure 2.9A). The regression equation ( $R^2 = 0.744$ ) is:  $y = 0.226x$ , where  $y$  is the predation rate (number of *Moerisia* predator<sup>-1</sup> h<sup>-1</sup>) and  $x$  is predator diameter in millimeters. During the 1 h feeding, 10 to 21 *M. lyonsi* were eaten by different sized *C. quinquecirrha*. The predation rate dropped at the largest

predator size, where 16 *M. lyonsi* were eaten by the 101 mm *C. quinquecirrha*, about the same number as eaten by the 62 mm *C. quinquecirrha* (Figure 2.9A).

The predation rate of *C. quinquecirrha* medusae ( $45.6 \pm 2.8$  mm,  $n=15$ ) on *M. lyonsi* medusae with two *M. lyonsi* sizes, 1.4-2.2 mm as small sized group and 2.6-3.4 mm as large sized group, were not significantly different from each other (nonparametric paired t-test;  $p = 0.117$ ) (Figure 2.9B). The predation rate increased linearly with increasing prey density when two sizes of *M. lyonsi* were combined ( $p < 0.0001$ ,  $F=158.1$ ) (Figure 2.9C). The regression equation ( $R^2 = 0.908$ ) with two sizes combined is:  $y = 0.496x$ , where  $y$  is the predation rate (number of *Moerisia* predator<sup>-1</sup> h<sup>-1</sup>) and  $x$  is the density of *M. lyonsi* per 100 L. The predation rate of *C. quinquecirrha* on *M. lyonsi* was  $5.2 \pm 1.2$  predator<sup>-1</sup> h<sup>-1</sup> ( $n=3$ ) at the lowest prey density of 8 *M. lyonsi* per 100 L, and  $25.3 \pm 4.0$  predator<sup>-1</sup> h<sup>-1</sup> ( $n=3$ ) at the highest prey density of 52 *M. lyonsi* per 100 L. There was no satiation noted for the available prey densities (Figure 2.9C).

## **Discussion**

### **Temperature and salinity tolerance ranges of *M. lyonsi***

My experiments demonstrated that the medusae and polyps of *M. lyonsi* may have broad temperature and salinity ranges and be tolerant of fairly dramatic changes in salinity.

*Moerisia lyonsi* could not live in fresh water, but it may be present in, or at least tolerate for an extended period of time, salinities ranging from 1 to 40 given suitable



temperatures. This is surprising for a species that is thought previously to be oligohaline (Calder and Burrell 1967; Sandifer et al. 1974; Poirrier and Mulino 1977; Dumont 1994). My study showed that *M. lyonsi* is instead a euryhaline species physiologically, which is defined as a species that can tolerate salinity ranges of 10 to 30 (reviewed by Kinne 1971). Studies have shown that animals are generally more susceptible to a dramatic change in environmental condition than to a gradual change. For example, in the laboratory, copepods (*Acartia tonsa*) exhibited high mortality when the instantaneous salinity change was greater than 10-15, but the maximum range they could survive by gradual changes of salinity was from <1 to 72 (Cervetto et al. 1999). However, the methods that I used in the current study were abrupt transfer without acclimation, so the temperature and salinity ranges of *M. lyonsi* found in my experiments should be still considered as conservative estimates. Furthermore, it is well known that the temperature or salinity range for reproduction in euryhaline species is usually narrower than that for other life processes (such as survival) (Kinne 1970, 1971). However, in my experiments, the asexual reproduction of *M. lyonsi* polyps occurred at salinities 5-25 at 15°C, and at salinities 1-40 at 20-29°C. Hence, the salinity tolerance range of *M. lyonsi* polyps derived from my experiments was similar to the range for asexual reproduction, while the tolerance range may be even broader.

The results of the experiments indicated that *M. lyonsi* medusae were more tolerant to a change toward higher salinity (from 12 to 26) than to a change toward lower salinity (from 12 to 1) in terms of the absolute difference. A similar tendency was detected for the polyps, where salinity effects changed more dramatically among lower salinities (1-

10) than among higher salinities (Table 2.4). However, the change toward higher salinity was only about twice the original salinity, while the change toward the lower salinity was about 10 times lower than the initial salinity, so it might be more reasonable to compare the change in terms of times rather than differences. In this sense, the change of salinity from 10 or 12 to 5 would be roughly the same magnitude as the change from 10 or 12 to 25 salinity, while the change from 10 or 12 to 1 salinity was the most dramatic change compared with all other salinity changes in the experiments. And thus, the behavioral response of *M. lyonsi* medusae and the relatively low asexual reproduction rate of its polyps at 1 salinity may indicate their susceptibility to such a dramatic change in salinity, and 1 salinity may not be suboptimal to the species only based on these experimental results alone. Poirrier and Mulino (1977) reported that the polyps of *M. lyonsi* were found in epifaunal communities at 18°C and 2.8 salinity in Lake Pontchartrain, Louisiana, before but not after a flood when the salinity dropped sharply to 0.5 in less than a week; the temperature during that event was relatively low (below 20°C). From the results of my study, the polyps of *M. lyonsi* could not only tolerate an abrupt change from 12 to 1 salinity and live there for at least 1 week (the experimental duration), but also grow and reproduce at 1 salinity at above 20°C after the abrupt transfer.

Based on the results of my experiments, the distribution of *M. lyonsi* in Chesapeake Bay may not be limited by temperature, although it seemed that low temperatures (10-15°C) and extreme salinities (1, 35-40) may limit the distribution and survival of *M. lyonsi* polyps. The polyps may encyst under unfavorable conditions. Their cysts have been

observed in early spring (Dr. Purcell, personal communication). Encystment in adverse conditions would enhance the success of distribution and survival of invasive species. Encystment of the polyps of *C. quinquecirrha* occurs at high and low temperatures (= 3°C or = 34°C) and salinities (= 5 or = 35) in laboratory studies (Cargo and Schultz 1966, 1967; Cones and Haven 1969). There have been no studies on the encystment of *M. lyonsi* polyps. However, encystment may greatly broaden their temperature and salinity tolerance ranges, and thus may help them survive low winter temperatures in Chesapeake Bay, where the average surface and bottom temperatures are usually well below 10°C. Hence, temperature may not be able to restrict its field distribution in the Bay.

The results of my experiments also suggest that salinity may not be a limiting factor for the field distribution of *M. lyonsi* in Chesapeake Bay over most of its area. Salinity differences exist horizontally and vertically in estuaries due to fresh water inflow and tidal activities, etc. Hence, estuarine species, especially sessile benthic animals, are frequently subjected to salinity variations throughout their lifetimes, and the ability to adapt to salinity changes is very important for both individual survival and population maintenance. However, the variations of salinity in a large estuary such as Chesapeake Bay that an individual animal may encounter are generally less extreme than the abrupt changes used in my experiments. The general ranges of temperature and salinity in Chesapeake Bay primarily fall between 0-30°C, and from 0-33 salinity over a distance of hundreds of kilometers in all seasons. Therefore, the seemingly restricted field

occurrences of *M. lyonsi* in waters at salinities up to 10 are not likely due to salinity restrictions.

The ability of *M. lyonsi* polyps to tolerate wide ranges of temperature and salinity, as well as the ability to form cysts, may help the species survive transoceanic transport either by ballast water transfer or by attaching to the bottom of the ships. In aquatic systems, ballast-water transfer is a leading means of introduction of alien species, and the most widely used method to reduce such invasions is via mid-ocean water exchange (Carlton and Geller 1993; Ruiz et al. 1997; Wonham et al. 2001). Experimental studies showed that a replacement of 93-100% of coastal water with ocean water can lead to a salinity shock that may remove 80-100 % of coastal organisms; however, some coastal taxa were able to survive such exchange and were found at the ships' destinations (Smith et al. 1999; Wonham et al. 2001). However, the effects of other factors, such as food or light limitation in the ballast tank, were unable to be quantified in those studies. If we assume the salinity of ocean water is about 35, the salinity shock resulted from such an exchange is well within the magnitude of salinity change that *M. lyonsi* polyps can tolerate if temperature is not stressful. Hence, this method may not be able to completely prevent the spreading of *M. lyonsi* via waterways. Other than this, knowing when and in what conditions the encystment of *M. lyonsi* polyps occurs would be helpful for a better understanding of this process.

The impressive adaptations of *M. lyonsi* to salinity variations are not commonly seen among other cnidarian species, especially marine species, which generally tolerate a

narrower salinity range than brackish water species (Kinne 1971). Available studies on marine hydroid species rarely showed any species having a similar wide salinity range as that found in *M. lyonsi*. The polyps of *Clava multicornis* could grow and asexually reproduce in most of the treatments after being transferred gradually from their normal conditions (16°C, 32 salinity) to treatments of 12-22°C and 16-40 salinities (Kinne and Paffenhöfer 1966). Another marine hydrozoan, *Stylactic hooperi*, has been subjected to a similar experiment with similar magnitude of changes in temperature and salinity by Nipper-Buscariolli and Moreira (1983) as *M. lyonsi* polyps in the current study. They tested the combined effects of temperature and salinity on the colonies of *S. hooperi* over a 19 d period beginning with a direct transfer from normal conditions (20-29°C and 33-35 salinities) to the target conditions (10-35°C, 15-55 salinity) without acclimation. They found that high mortality (mostly 100%) of polyp colonies occurred at the extremes of temperature (10°C and 35°C) with all tested salinities, and at the extremes of salinity (15 and 55) with all tested temperatures. Besides that, partial mortality (up to 100%) still occurred under all other intermediate conditions except in two combinations (15°C & 25 salinity, and 20°C & 45 salinity). Mills (1984) tested the behavioral and physiological responses of nine species of marine hydromedusae to abrupt salinity change from 30.5 to a range of 19-38 salinities, in which most of the species could recover from the salinity shock ranging from 23 to 38 salinity in a few hours, which represented approximately 75% to 127% of their normal salinity. The change from salinity 30.5 to 19 was lethal to most of the species (48 hrs observation). Burykin (1989) found the colony growth rate of marine hydroid, *Dynamena pumila*, was highest at salinity 35, but decreased at both low and high salinities (14-16, 40-46, respectively). It

indicated that this hydroid species may have a fairly broad salinity tolerance range. Compared with these marine cnidarian species, the adaptability of *M. lyonsi* to temperature or salinity variations is impressive. It should be noted that the presence of prey in my experiment may have increased the survival of *M. lyonsi* medusae.

Studies have shown that salinity fluctuation or instability in natural waters may act as a “brake” on speciation and evolution, and the numbers of species endemic to brackish and estuarine waters are considerably fewer than that in oceans (reviewed by Kinne 1971). This is especially true at salinities from 5 to 8, known as the “eco-physiological boundary”, where the least number of species occur among all the salinities from fresh to sea water (Khlebovich 1968, 1969). A dramatic change in ionic ratios or hydrochemical characteristics occurs in this salinity range compared with the salinities below or above, so ionic species composition rather than salinity change may be behind this phenomenon (reviewed by Kinne 1971). I did not monitor ionic composition in my experiment. However, the range of the field occurrences for *M. lyonsi* was from above fresh water to 10 salinity, crossing through the eco-physiological boundary. Such impressive adaptations to both salinity change and ionic change are rare in estuarine species.

Similar to the general tendency mentioned above, there are only a small number of euryhaline cnidarian species including hydrozoans that occur in estuarine or brackish habitats, and the diversity of cnidarian species decreases rapidly with decreasing salinity (Calder 1976; Dumont 1994). Most of these euryhaline estuarine cnidarians can be

found over a wide range of salinities, but very few can cross the ecophysiological line as described above. The medusae and polyps of *C. quinquecirrha* are found mostly at salinities 7-25 in Chesapeake Bay, and the medusae can not live at salinity below 5 (Cargo and Schultz 1966, 1967; Wright and Purcell 1997). Its asexual reproduction of polyps and ephyrae is limited by salinities = 10 or = 25 (Purcell et al. 1999c). The ctenophore, *Mnemiopsis leidyi*, may be present in estuarine waters at salinities 2-38 (Purcell et al. 2001c), However, it is not known experimentally if the ctenophore can survive a dramatic change in salinity with the similar magnitude as that found for *M. lyonsi*. The eurythermal and euryhaline scyphomedusae, *Aurelia aurita*, are found in 0-32°C, and 14-38 salinities worldwide (Lucas 2001). However, recent studies by molecular methods suggested that this cosmopolitan ecological generalist may actually consist of many locally adapted species, each of which may have only limited ability to exploit new locations (Greenberg et al. 1996; Dawson and Jacobs 2001; Dawson and Martin 2001).

By contrast, in addition to *M. lyonsi*, two other estuarine hydroids, *Cordylophora caspia* and *Garveia franciscana*, can tolerate a salinity range of at least 1-35 in laboratory studies, while they normally live in salinities below 10, or about 10-15 (Crowell and Darnell 1955; Kinne 1956, 1957; Calder 1976). The similarity among these three estuarine hydromedusan species is interesting. The difference between their ecological potential (represented by field occurrences) and physiological potential (represented by maximal tolerance ranges to physical factors in the laboratory) indicates that other

factors, probably predation or interspecies competition etc., rather than physical factors, may have contributed to their restricted distribution patterns (Calder 1976).

Other factors, such as hypoxia, may be important in determining field distributions of *M. lyonsi* in the Bay. Moderate to severe hypoxia or anoxia occurs seasonally in tributaries and mainstem of the Chesapeake Bay (Breitburg 1990, 1992; Sanford et al. 1990; Purcell et al. 2001a). Condon et al. (2001) found that the polyps of *C. quinquecirrha* may survive about 5 d in severe hypoxia ( $0.5 \text{ mg l}^{-1}$ ) in laboratory experiment, and that the survival rate dropped rapidly thereafter, but in moderate hypoxia ( $= 1.5 \text{ mg l}^{-1}$ ), >80% of the polyps survived for at least 24 d. However, Purcell et al. (2001a) suggested that long term exposure to low dissolved oxygen may kill the benthic stages of hydromedusan and scyphomedusan species, and therefore may limit their distribution in ecosystems experiencing hypoxic conditions. In the northern Adriatic Sea, the diversity of hydromedusan species with benthic hydroids has decreased from over 40 species in the 1910s to about 10 species in the 1980s, and the decline of hydrozoan diversity was believed to be related to the increasing extent of oxygen depletion in bottom waters during those years (Benovic et al. 1987). The impacts of low oxygen on the medusae and polyps of *M. lyonsi* have not been studied, but it is possible that summertime hypoxia in some areas might act as one of the limiting factors that restrict the distribution of benthic polyps of *M. lyonsi* in Chesapeake Bay.



## **The effects of environmental factors on the asexual reproduction of *M. lyonsi* polyps**

Because there is a lot of information revealed by the results of the T-S-F experiment, to be organized and easily understood, I compiled the most important statistical results for factors (T, S, and F) and parameters ( $DT_p$ ,  $DT_m$ , ARR, and  $R_m$ ) from ANCOVA tests in one table (Table 2.9). For a quick reference,  $DT_p$  and  $DT_m$  were the development times (also referred to as starting time, initiation time, or the first budding time, in this discussion) for polyp buds and medusa buds, respectively. ARR was the asexual reproduction rate averaged over 31 d, which is also referred as total quantity of the asexual reproduction in this study.  $R_m$  was constructed as the ratio of total medusa bud production to the total asexual reproduction in 31 d, and often referred as partitions or quality compositions of asexual reproduction in the context to differentiate with ARR. Comparison of the rows in Table 2.9 shows the differences among the effects of environmental factors become clear, while the different responses among the reproduction characteristics become clear by comparison of the columns, as follows.

### Temperature effects

It is well established that temperature is a primary factor, though not the only factor, in regulating, initiating, and synchronizing reproduction activities of aquatic invertebrates, given that other conditions are not stressful (Kinne 1970). This is generally true for asexual reproduction in most cnidarian species studied, probably with only few

exceptions. Many studies have shown that changing temperature is a critical factor in initiating strobilation or determining the reproductive seasons of most scyphomedusan species (Calder 1974; Hofmann et al. 1978; Brewer and Feingold 1991; Kikinger 1992; Lotan et al. 1994; Lucas and Lawes 1998; Purcell et al. 1999c). However, Hernroth and Gröndahl (1985a) suggested that light may trigger the strobilation for *Aurelia aurita*. For hydromedusan species, many studies also showed evidence that temperature has significant effects on the initiation time of polyp bud or medusa bud production (Werner 1956, 1958, 1963; Bierbach and Hofmann 1973; Hecker and Slobodkin 1976; Nipper-Buscariolli and Moreira 1983; Kato and Hirabayashi 1991). The results of my experiment showed that temperature had significant direct effects on the development times of polyp buds and medusa buds by *M. lyonsi* polyps (summarized in Table 2.9), with special notice that the same magnitude of decreasing in temperature created a much longer delay in the onset of medusa bud production than that of polyp bud production (Figure 2.4).

The results of the T-S-F experiment also showed that temperature affected the total quantity, as well as the partitioning of the asexual reproduction of *M. lyonsi* (ARR and  $R_m$ ), mostly through changing food consumption (Table 2.9). Therefore, its effects on ARR and  $R_m$  may not be as strong as on the initiation times described above. However, since there were only two levels of temperature tested in the experiment, its effects might have been underestimated. Even this, given the significant direct effects of temperature on the starting time of medusa bud production described previously, these

results showed important indications that temperature may be critical in controlling the asexual reproduction and sexual reproduction alternation of this hydroid species.

Available studies show that temperature may not only affect the rate of the asexual reproduction, but also the onset times and partitioning of polyp bud and medusa bud production, which thus may play an important role in controlling the shift between different reproduction modes in some cnidarian species. Werner (1956, 1958, 1963; all cited in Kinne 1970) demonstrated a critical temperature (6-8°C) for asexual and sexual reproduction alternation in hydromedusae, *Rathkea octopunctata*, the medusa of which can reproduce asexually by budding medusa from its manubrium and also sexually by producing gametes. He found that the medusa reproduces asexually below 6-8°C, but sexually above 6-8°C. Another colonial hydroid, *Coryne tubulosa*, grows asexually in a colony forming attached polyps asexually and grow stolons above 14°C, but the mode changes to asexually budding medusae after being transferred to 2°C, and the two processes are reversible (Werner 1963; cited in Kinne 1970). These two cases showed a complete alteration between the modes of asexual and sexual reproduction, or between the modes within asexual reproduction (polyp bud or medusa bud production) at certain temperatures.

The populations of many cnidarian species (those with multiple reproductive modes) may simultaneously produce both medusa and polyp buds, or produce both sexually and asexually, over a large range of temperature. Hence, the quantitative relationships between different reproduction modes in a wide temperature range are of more interest

from the population perspective (this is also true for the effects of salinity and food). Purcell et al. (1999c) tested temperature (15-25°C), salinity, and food effects on the asexual reproduction of the polyps of *C. quinquecirrha*, and found that decreasing temperature can delay strobilation time. However, temperature did not significantly affect the total production of ephyrae or polyp at lower salinities 5-20 (note that 10-25 was about the optimal range for *C. quinquecirrha*), although ephyra production increased significantly with increasing temperatures at higher salinities 20-35 (Purcell et al. 1999c). Purcell et al. (1999c) did not compute a parameter similar to  $R_m$  in my experiment, but their results indicated that not only the total quantity, but also the partitions of its asexual reproduction, varied with environmental changes. However, since the food treatments in their studies were given as zooplankton densities, rather than as actual consumption, the effects of temperature and salinity on food consumption could not be accounted for. Thus the temperature effects at lower salinities 5-20 might have been underestimated; in other words, the temperature effects on the asexual reproduction of *C. quinquecirrha* at the lower salinities might have been indirect rather than having no effect.

### Salinity effects

Just as for temperature, my results showed important regulation by salinity of the asexual reproduction of *M. lyonsi*, indicating that salinity is an important factor in determining the population sizes distributed into asexual and sexual stages. Salinity had significant direct effects on medusa bud production ( $DT_m$  and  $R_m$ ), while it affected the

initiation time for polyp bud production and the total asexual reproduction rate ( $DT_p$  and ARR) mostly through changing food consumption of the polyps (Table 2.9). The most evident changes were that a change from salinity 5 and 15 to salinity 25 (from optimal to unfavorable) at 20°C caused significant delay in the initiation time of medusa bud production (Figure 2.4), and that medusa bud production decreased significantly or disappeared (Figure 2.8). However, polyp bud production still occurred at low rates under the least unfavorable conditions.

The effects of salinity on many aspects of reproduction activities may be less than those of temperature and light due to less rhythmic variations, especially in areas with fairly constant salinity or a narrow range. However, some studies have suggested that salinity changes may play an important role in timing and rate of asexual reproduction, or in the alternation or shift between different reproduction modes in some cnidarians (Segerstråle 1957; Kinne and Paffenhöfer 1966; Spangenberg 1968; Kinne 1971; Nipper-Buscariolli and Moreira 1983; Purcell et al. 1999c). Segerstråle (1957) found reduced reproductive capacities of *Aurelia aurita* in Baltic Sea, in that its medusae still reproduced sexually at salinities below 6, but its scyphistoma stage (asexual reproduction stage) stopped developing. The polyps of *C. quinquecirrha* were very similar to the polyps of *M. lyonsi* in terms of salinity effects on asexual reproduction. Cargo and Schultz (1967) found that an elevation in salinities from 20 to 25 caused substantial shortening in the initiation time of strobilation in the polyps of *C. quinquecirrha*. The results of Purcell et al. (1999c) indicated that the total quantity and partitioning of the asexual production of *C. quinquecirrha* were affected significantly by

salinity. Also, ephyrae were not produced at salinity 5 with all tested temperatures (15-25°C), although polyp production still occurred at a low rate at that salinity. The similarity between the results of Purcell et al. (1999c) and my study is that at unfavorable salinity conditions, the production of free-swimming medusa offspring via asexual reproduction stopped in both species, but polyp bud production still persisted at relatively low rates.

Interestingly, both my T-S and T-S-F experiments showed that the highest asexual reproduction rates of *M. lyonsi* occurred at salinities from 5 to at least 15 (5-20 in the T-S experiment). Thus the salinity range at which the highest asexual reproduction of its benthic polyps occurred was much broader than that of its reported field occurrences (below 10 salinity). Similarly, the brackish colonial hydroid, *Cordylophora caspia*, has the highest colonial growth rate at salinity 15 in laboratory, but occurs most frequently in natural water at lower salinities 5-10 (Kinne 1956, 1957). By contrast, the marine colonial hydroid, *Clava multicornis*, has its highest colonial growth rate at salinity 24 in the laboratory (colony growth rate in the order of salinity: 40<16<24>32), while it is found primarily at about 32 salinity in the field (Kinne and Paffenhöfer 1966). Overall, the discrepancy between the primary field occurrences and the physiological potential for these hydroid species is puzzling. Other factors such as predation may be more decisive for these species than physical factors discussed here.

## Food effects

Food consumption by the polyps had significant direct effects on all the selected features of the asexual reproduction of *M. lyonsi*; meanwhile, food consumption was significantly affected by temperature and salinity. Studies have shown that temperature and salinity directly affect feeding activity, nutrition and assimilation in some hydroids (Kinne 1957; Kinne and Paffenhöfer 1965; Hecker and Slobodkin 1976; Boero 1984). The physiological reason behind the effects of temperature and salinity on growth or reproduction is because changes in activity and metabolism happen in the first place, and then these changes again affect growth or reproduction.

Several studies are particularly relevant to my study in terms of food effects on polyp asexual reproduction. Chen et al. (1985) found that ephyra production by the scyphozoan, *Rhopilema esculenta*, was positively related to food availability in the laboratory. Purcell et al. (1999c) tested food effects on the asexual reproduction of the polyps of *C. quinquecirrha* at 20 salinity (optimal) and 15-25°C, and found that high food levels significantly increased ephyra production, while polyp bud production was not much affected. More interestingly, their results indicated a shift from primarily polyp bud production to primarily medusa bud production as food ranged from low (0.2 prey ml<sup>-1</sup>) to high concentration (4.4 prey ml<sup>-1</sup>), which were equivalent to a change in  $R_m$  of about 20% to 60%, 18% to 88%, and 56% to 95%, at 15°C, 20°C, and 25°C, respectively. This is similar to the compensational mode found in *M. lyonsi* polyps in my experiments.

Purcell et al. (1999a) tested the effects of prey level on the asexual reproduction of *M. lyonsi* (at 22 °C and 9.5 salinity) and found that greater food availability markedly increased both polyp bud and medusa bud production while shortening the initiation time of both kinds. However, they also found that the ratio of medusa to polyp bud production decreased from 28:1 to 2-3:1 as food changed from 1 to 2-8 copepods polyp<sup>-1</sup> d<sup>-1</sup> (equivalent to  $R_m$  from 97% to 68-74% approximately). Under similar conditions (22 °C, 5-15 salinity, and 4-8 copepods polyp<sup>-1</sup> d<sup>-1</sup>, in Figure 2.8A),  $R_m$  was relatively lower in my study (mostly below 50% with large variations in data) than that (68-74%) in Purcell et al. (1999a). One possible reason for this difference may be due to the longer experimental period (38 d) in Purcell et al. (1999a), so that there was more time for medusa bud production (which always occurred later than polyp bud production) in their study than in my experiment. Since the lowest food consumption by the polyps was about 4 copepods polyp<sup>-1</sup> d<sup>-1</sup> in my experiment, it is impossible to compare the results at 1 copepods polyp<sup>-1</sup> d<sup>-1</sup>. However, from the tendency showed in figure 2.8A in my experiment, I would expect  $R_m$  at this extremely low food condition might be lower than at higher food conditions in my study. Hence, the extremely high  $R_m$  at extremely low food in Purcell et al. (1999a) is puzzling. Many similar studies indicated that formation of pelagic medusa buds is not an indication of unfavorable environmental conditions, and that an enhancement in medusa bud production along with decreasing food availability has not been seen in these studies (Kinne and Paffenhöfer 1966; Hofmann et al. 1978; Nipper-Buscariolli and Moreira 1983; Chen et al. 1985; Madin and Madin 1991; Purcell et al. 1999c).



The exact reason for the difference between my study and that of Purcell et al. (1999a) in  $R_m$  at extremely low food is not known. Another detectable difference between these two studies was the difference in the size of the experimental containers, which was 60 ml jar used in my study and 15 ml well used in their study. It is already known that the polyps of *M. lyonsi* can not only produce solitary polyps, but also can form a primitive colony by forming attached polyp (Petersen 1979; Purcell et al. 1999a; personal observations). However, in both my study and Purcell et al. (1999a), polyps were only allowed to be solitary, and the secondary polyps were cut off and removed from the containers. Many benefits are associated with coloniality, such as space, structure, aggregation and communication (Shelton 1979), and thus, space and structure are important issues for colonial hydroids. Some studies have found that overcrowding in space may cause the hydroid colony to reabsorb the overgrown part, while food variations within the colony can result in adaptive growth of the colony toward the area of better food availability, even natural distribution of colonial hydroid may be regulated by space competition (Knight-Jones and Moyses 1961; Shelton 1979; Calder 1991; Jormalainen et al. 1994; Blackstone 2001). Hence, it may be an interesting research direction to study the relationship between overcrowding or extreme food scarcity and medusa bud production by hydroid colony.

The asexual reproduction rates of *M. lyonsi* polyps in the current study were very high compared with the results by Purcell et al. (1999a) and others. The highest daily asexual reproduction rate from both the T-S and T-S-F experiments in this study ranged from

about 6 to 13 new buds polyp<sup>-1</sup> d<sup>-1</sup> (at 29°C and 15 salinity with a food supply of 13-15 copepods polyp<sup>-1</sup> d<sup>-1</sup>). The polyps of *C. quinquecirrha* can produce 0.7 polyps and 13 ephyrae polyp<sup>-1</sup> in 42 d (at 25°C, 20 salinity with high food concentration of 4.4 prey ml<sup>-1</sup>) (Purcell et al. 1999c). The highest total asexual reproduction rate of *M. lyonsi* (at 22°C, 9.5 salinity, 8 copepods polyp<sup>-1</sup> d<sup>-1</sup>) was 3.9 new buds polyp<sup>-1</sup> d<sup>-1</sup> measured by Purcell et al. (1999a), who concluded that the asexual reproduction rate of *M. lyonsi* polyps is impressively high in comparison with other studied cnidarian species discussed therein. Therefore, my results provide further evidence that *M. lyonsi* polyps are highly productive among studied cnidarians.

Comparisons among different characteristics of the asexual reproduction of *M. lyonsi*

One of the key concepts of reproduction and development in biology is that separation into sexes is more expensive than asexual reproduction, because it requires developing and maintaining more sophisticated or complex reproductive structures and mating requires the encounter of one or more of its same kind. However, sexual reproduction bears a selective advantage by promoting generic variety in offspring, which may in turn promote survival chances in the next generation under unfavorable conditions even both parents could not survive (Solomon et al. 1996; Starr and Targart 1998). The advantages of asexual reproduction would be that they do not need to search for mate, and it makes it easier for animals having a very low population density to maintain population size (Solomon et al. 1996; Starr and Targart 1998). *Moerisia lyonsi* has a life cycle with asexual and sexual reproduction alternation, and can produce both polyp buds and

medusa buds during asexual reproduction. The medusa form, produced by asexual reproduction, is the sexual form that will develop gonads. Hence, medusa bud production of *M. lyonsi* through asexual reproduction is on the way toward the sexual reproduction mode in respect to its life cycle.

The results from my experiments indicated that *M. lyonsi* medusae tolerated less environmental change than its polyps. This may also hold for *C. quinquecirrha* or other similar cnidarian species (Cargo and Schultz 1966, 1967; Hofmann et al. 1978; Madin and Madin 1991; Purcell et al. 1999c). Additionally, the temperature and salinity ranges for sexual reproduction may be narrower than those for asexual reproduction of the same species (Kinne and Paffenhöfer 1966). And thus, medusa bud production is more expensive in two aspects. Firstly, it may be more costly for the polyps physiologically since this production involves developing different structures. Secondly, it may be more costly for the population since the medusae may be subjected to greater danger and greater mortality, as well as less reproductive success in unfavorable environments. Hence, the production of medusa buds is a high price paid by the polyp of the species to trade for the benefits of sexual reproduction (generic diversity, greater survival chances for the later generations) for the species or population as a whole, rather than the individual itself. Therefore, it would be best to be most conservative in spending energy on this type of offspring in terms of timing and quantity. Otherwise, if there is no difference between the production of the delicate medusa and the production of the more tolerant polyp in responding to environmental changes, it would be disadvantageous for the species or the population in the course of natural selection.

The different responses to environmental changes among the tested reproductive features of *M. lyonsi* become clear by comparing the different columns in Table 2.9. Firstly, medusa budding time ( $DT_m$ ) was most affected by all three environmental factors compared with polyp budding time ( $DT_p$ ), and the quantity and partitions (ARR and  $R_m$ ) of the asexual reproduction of *M. lyonsi*. Secondly, the total quantity of the asexual reproduction (ARR) of *M. lyonsi* was less affected by the environmental conditions than all other characteristics, especially, the medusa bud partitioning in asexual reproduction ( $R_m$ ) was more responsive to environmental changes than ARR (Table 2.9). Polyp bud production occurred at all the tested conditions, while medusa bud production varied greatly with different conditions, completely stopping in unfavorable conditions, and rapidly increasing in quantity and partitioning at particularly favorable conditions (Figure 2.7, 2.8). There is also a possibility that under extremely low food availability while other conditions are not very stressful, the polyps of *M. lyonsi* may exclusively produce medusa buds to aid in dispersal away from the stress (Purcell et al. 1999a). Purcell et al. (1999c) suggested that the production of polyp buds by *C. quinquecirrha* may be an adaptation to maintain the populations, but ephyra production is more flexible, allowing the population to quickly respond to changing food conditions. My study provided more evidence and detail of how this may happen in one species through its adaptive asexual reproduction processes.

Overall, *M. lyonsi* population may produce both types of offspring via asexual reproduction in a fairly large range of temperature, salinity and food conditions, while

the quantitative relations between these two processes may vary with different conditions. The two processes were quantitatively “tuned” with each other at any given conditions within its tolerance range, rather than random or parallel relation. The adaptive reproduction processes may play a significant role in regulating the population size, composition, distribution, as well as generic advantages of the species for a long run. Hydromedusae and some other cnidarian species were often called “opportunists”, since they are able to take advantage of a wide range of environments and outbreak in large numbers in favorable conditions. The results of my study suggested that *M. lyonsi* is indeed a great opportunist.

#### **Pilot study on predation on *M. lyonsi***

The medusa of the scyphomedusae, *C. quinquecirrha*, is the first predator that has been documented to prey on the medusae of *M. lyonsi*. The medusae of *C. quinquecirrha* are large predators that swim almost continuously in the water column (Ford et al. 1997). When they swim, the bell motion generates flow and eddies that can entrain zooplankton prey and greatly increase the chances of encounter of the prey with their tentacles and oral arms of the medusae (Costello and Colin 1994; Ford et al. 1997). Theoretically, prey with a swimming speed slower than the flow speed generated by the bell motions are vulnerable to capture. Thus, relatively slow-moving hydromedusae and ctenophores may have better chances to be captured by *C. quinquecirrha* than fast swimming copepods. Indeed, *C. quinquecirrha* is known to be a major predator of the ctenophore, *Mnemiopsis leidyi*, and it may control their population in the tributaries of Chesapeake

Bay (Purcell and Cowan 1995; Kreps et al. 1997). Olesen et al. (1996) found that the growth rate of ephyrae of *C. quinquecirrha* is greatest when they feed on the ctenophore larvae in laboratory, and suggested that the ctenophore may be a critical contributor to the rapid growth rate of *C. quinquecirrha* ephyrae in springtime in Chesapeake Bay. My finding of its predation on the slow swimming *M. lyonsi* is further evidence for *C. quinquecirrha* feeding on soft-bodied prey.

The prey of the ctenophore, *Mnemiopsis leidyi*, mainly includes copepods, copepod and barnacle nauplii, and bivalve veligers, which together may account for as much as 99% of its August diet in Chesapeake Bay, but gelatinous zooplankton have not been reported in its diet anywhere (reviewed by Purcell et al. 2001c). Gerritsen and Strickler's (1977) plankton foraging models predict that a slow-moving or stationary predator would encounter mainly fast-moving prey. The ctenophore, *Mnemiopsis leidyi*, is a slow-swimming (relatively to adult copepods in general) cruising predator that may have complex feeding mechanisms (Waggett and Costello 1999). On one hand, it can catch fast-moving adult copepods that collide on the inner surface of the oral lobes with a capture efficiency as high as 74% (no. of captures divided by no. of encounters) (Costello et al. 1999). Compared with the swimming speed of adult copepods, the medusae of *M. lyonsi* are a slow swimmer that either hover neutrally buoyant or swimming slowly through the water column (personal observations), so this type of feeding mechanism of the ctenophore may not fit *M. lyonsi*. On the other hand, the ctenophore can also catch small copepod nauplii that are entrained by the fluid currents generated by its auricular cilia with high efficiency (94% of encounters) (Waggett and

Costello 1999). Compared with the general sizes of copepod nauplii, *M. lyonsi* medusae are too large (<1 cm in bell diameter), so the fluid motions generated by the auricular cilia of the ctenophore may not be strong enough to entrain the medusae. Therefore, it is not surprising the feeding of the ctenophore on the medusae of *M. lyonsi* did not occur during my observations. However, more extensive experiments are necessary to demonstrate this convincingly.

The results of my predation experiments indicates that predation of *C. quinquecirrha* medusae on *M. lyonsi* medusae is a typical type I foraging response, in which feeding increases linearly with increasing prey density without satiation (Figure 2.9). In type I response of the simple Lotka-Volterra model, the predators cannot control the prey's population because the proportion of the prey population consumed by the predators would remain a constant value, so the prey population would still go unchecked (Gotelli 1995). However, the predation rates of *C. quinquecirrha* on *M. lyonsi* in my study may have been largely underestimated due mostly to the restrictions exerted by experimental tanks. Purcell and Cowan (1995) used mesocosms to measure the predation rate of *C. quinquecirrha* on the ctenophore. Their results showed that about 6 ctenophores (average 14 ml in volume) were eaten by each *C. quinquecirrha* (average 80 mm in diameter) daily with a prey density of 6 ctenophores  $\text{m}^{-3}$  in 3.2  $\text{m}^3$  mesocosms, and the numbers were significantly lower in 1  $\text{m}^3$  mesocosms. Several other studies also reported the restriction effects of experimental container on feeding of *C. quinquecirrha* (Cowan and Houde 1993; Purcell et al. 1994a). Hence, the 100 L cylindrical tank used in my predation experiments might have restricted the predation of *C. quinquecirrha* on

*M. lyonsi*. The results showed a significant drop in predation rate when *C. quinquecirrha* diameter reached 100 mm (Figure 2.9A), which may simply indicate that large *C. quinquecirrha* were more restricted by the container size than the smaller ones. Therefore, the predation rates of *C. quinquecirrha* on *M. lyonsi* could be much greater than those I observed. In addition, the field densities of *M. lyonsi* in Chesapeake Bay have never been documented anywhere, it was not possible to choose a realistic density range of *M. lyonsi* for my experiments, so the relevance of these data to the field populations should be judged with caution.

This and previous studies revealed that *M. lyonsi* is an ideal colonist from many aspects, but as previously described, it was most frequently found in oligohaline waters in the field. My predation experiments may have provided a clue for the apparent conflicts between the ecological potential and physiological potential of this species in terms of distribution ranges. Table 2.10 provides comparisons of important ecological data between *C. quinquecirrha* and *M. lyonsi*. Their theoretical ranges of temperature and salinity largely overlap with each other, especially in summertime and mesohaline salinities. However, the optimal salinity range of *M. lyonsi* in the laboratory started from oligohaline waters at 5 salinity, while *C. quinquecirrha* are most abundant from salinities above 10 in tributaries or mainstem in Chesapeake Bay (Cargo and Schultz 1966, 1967; Purcell et al. 1999c), which coincides with the upper bound (10 salinity) of the field salinity range for *M. lyonsi*. These data suggest that predation pressure might be one of critical factors in regulating the field distribution ranges of *M. lyonsi* populations in Chesapeake Bay, especially given the high predation rate of *C. quinquecirrha* on *M.*



*lyonsi* I found and the high field density of *C. quinquecirrha* (may exceed  $10\text{ m}^{-3}$ ) in some tributaries (Purcell 1992; Purcell and Cowan 1995).

During my experiments, I also found that an unidentified nudibranch species in the polyp culture ( $22^{\circ}\text{C}$  and 10 salinity) feeding on *M. lyonsi* polyps and growing very fast. Species of gastropod nudibranchs have been known as the most important predators on benthic cnidarian polyps or colonies. Existing studies have shown that the predation rate of nudibranchs on hydroids can be very high and may be critical in controlling the benthic populations of cnidarian species (Cargo and Schultz 1967; Hernroth and Gröndahl 1985b; Folino 1993). For example, the predation rate of the nudibranch, *Coryphella verrucosa*, on the polyps of *Aurelia aurita* can reach up to  $200\text{ polyps d}^{-1}$  in the laboratory, which may greatly contribute to the decrease of the field populations of *A. aurita* polyps in October (Hernroth and Gröndahl 1985b). The nudibranch species, *Cratena pilata*, has been found feeding voraciously on the polyps of *C. quinquecirrha* (Cargo and Schultz 1967; Cargo and Burnett 1982; Sagasti et al. 2000). It is not clear if this is the same nudibranch species as I found in my polyp culture. However, as with *C. quinquecirrha*, this nudibranch predominantly lives in upper mesohaline range (Cargo and Schultz 1967; Cargo and Burnett 1982; Sagasti et al. 2000). Hence, it is possible that this nudibranch species, the scyphomedusan, *C. quinquecirrha*, and probably still other predators, might have prohibited the distributions of the populations of *M. lyonsi* toward mesohaline or sea waters in the estuaries.

## Overall conclusions

1. The polyp of *M. lyonsi* may tolerate broad ranges of temperature and salinity, and field distributions of this species in Chesapeake Bay may not be restricted by temperature or salinity. Mortality of the polyps occurred only in treatments associated with highest salinity levels 35-40 (with a temperature ranging from 10-25°C) after direct transfer from 22°C and 10 salinity to a variety combinations of temperature (10-29°C) and salinity (1-40). No mortality occurred at 1-40 salinities at 29°C. The salinity range of the medusae, about 5-26 at least, may be narrower than the range of the polyps.
2. The asexual reproduction rate of *M. lyonsi* polyps was very high compared with other cnidarian species. Asexual reproduction of the polyps occurred at all tested salinities from 1-40 at 20-29°C, with the highest rates occurred in the range of 5-20 salinities and 25-29°C with high food availability. No bud production occurred at 10°C at any salinity during the 7 d experimental duration.
3. Temperature effects were more robust on initial times of the asexual reproduction than the on total asexual reproduction rate and the partitioning of medusa bud production. While salinity effects were more robust on the features related to medusa bud production than otherwise. Food consumption significantly affected all the selected reproductive parameters of *M. lyonsi*.

4. The initial times, total quantity and partitioning of the asexual reproduction of *M. lyonsi* were all significantly affected by environmental factors but with some subtle differences. The initial time of medusa bud production was the most strongly affected feature, while the total asexual reproduction was the least responsive feature. The medusa bud and polyp bud production compensated each other to some extent under different conditions.
  
5. The scyphomedusan, *Chrysaora quinquecirrha*, was shown to be a potentially important predator of *M. lyonsi* medusae. The physiological optimal salinity range (5-20) for the asexual reproduction of *M. lyonsi* was well above the salinity range of its field occurrences (<10). The result of my experiments indicated that the field distributions of *M. lyonsi* in Chesapeake Bay may be restricted by predation pressures from predators in mesohaline region.

### **Ending remarks**

To end my study, I would like to use some personalized words in describing this lovely creature, *M. lyonsi*, who lent it to me for this study, or I hope, probably to others for more future studies. It is certainly a charming creature with many impressive features that other seemingly big and awesome guys may dream to own a couple, such as euryhaline adaptability with almost all band of salinities, high growth rate and productivity, early development time, coloniality, adaptive reproduction processes, benthic and pelagic alternation life cycle, etc., etc. In my eyes, *M. lyonsi* is the greatest

opportunistic. Yes, it can take advantage of favorable conditions and rapid increase in numbers. However, this is resulted from a careful and fairly advanced “budgeting” process involving multiple parameters, such as “pregnancy” time, offspring types, material and energy, spending and gain, space and structure, benefit of short run and long run, benefits of individual and “society”, and so on. As a whole, in the range of its strength, it never gives a single chance to be in “red”, or extinction. So no wonder it can take favorable chances, it is always prepared!

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Table 2.1. *Moerisia lyonsi*. Results generated by Mantel-Cox test via SAS on temperature and salinity treatment effects on survival of *Moerisia lyonsi* polyps in the T-S experiment. The stacked data in the cells are frequency on the top, row percentage in the middle, and column percentage on the bottom.

<b>Sal. treatments</b>	Death	Survival	Row total	<b>Temp. treatments</b>	Death	Survival	Row total
<b>1</b>	0	205	205	<b>10°C</b>	56	317	373
	0.0%	100.0%			15.0%	85.0%	
	0.0%	11.7%			52.3%	18.0%	
<b>5</b>	0	210	210	<b>15°C</b>	31	347	378
	0.0%	100.0%			8.2%	91.8%	
	0.0%	11.9%			29.0%	19.7%	
----- Sal. 10-30 were omitted since the result for each of them was exactly the same as for 5 salinity in the row above -----				<b>20°C</b>	11	367	378
					2.9%	97.1%	
					10.3%	20.9%	
<b>35</b>	22	184	206	<b>25°C</b>	9	365	374
	10.7%	89.3%			2.4%	97.6%	
	20.6%	10.5%			8.4%	20.7%	
<b>40</b>	85	111	196	<b>29°C</b>	0	364	364
	43.4%	56.8%			0.0%	100.0%	
	79.4%	6.3%			0.0%	20.7%	
Column total	107	1760	1867	Column total	107	1760	1867

Table 2.2. *Moerisia lyonsi*. Statistical results for temperature (T, 10-29°C), salinity (S, 1-40) and their interaction effects on the number of the original number of buds prior to treatments (Original) and the asexual reproduction rate (ARR, new buds polyp<sup>-1</sup> d<sup>-1</sup>) in the T-S experiment. DF = degrees of freedom. MS is mean square in type III ANOVA table. *p*-values above 0.05 mean no significance. The DF value marked with an asterisk symbol (\*) was reduced because 100% percent polyp mortality occurred in two treatments.

Dependent Variable	Source	DF	MS	<i>F</i> -value	<i>p</i>
Original	T	4	0.22	1.78	0.156
Original	S	8	0.11	0.90	0.529
Original	T*S	32	0.12	0.24	1.000
ARR	T	4	255.26	29.32	<0.0001
ARR	S	8	60.77	6.98	<0.0001
ARR	T*S	*30	8.70	13.55	<0.0001

Table 2.3. *Moerisia lyonsi*. Simple linear regression tests for temperature (10-29°C) and asexual reproduction rate (ARR, new buds polyp<sup>-1</sup> d<sup>-1</sup>) at different salinities (S, 1-40) in the T-S experiment. The intercept and slope estimations are listed only for those salinities of significance (p<0.05). *p*-values above 0.05 mean no significance.

Salinity levels	Intercept estimate	Slope estimate	<i>p</i>
S=1	-2.456	0.198	0.039
S =5	-6.908	0.622	0.007
S =10	-7.318	0.650	0.002
S =15	-7.076	0.601	0.023
S =20	-6.382	0.518	0.024
S =25	-4.388	0.370	0.019
S =30			0.073
S =35			0.058
S =40			0.367



Table 2.4. *Moerisia lyonsi*. Least Square Means (LSM) comparisons for the asexual reproduction rate (ARR, new buds polyp<sup>-1</sup> d<sup>-1</sup>) among different salinity treatments for the T-S experiment. The numbers except in the last column are *p*-values against the hypotheses: LSM(i)=LSM(j). ARR lsm at salinity j was omitted since it was the same as ARR lsm at salinity i in the last column. *p*-values above 0.05 mean no significance.

Salinity i/j	5	10	15	20	25	30	35	ARR lsm at sal. i
1	0.001	<0.001	0.004	0.032	0.182	0.642	0.622	1.47
5		0.903	0.596	0.167	0.029	0.003	<0.001	5.41
10			0.515	0.134	0.016	0.002	<0.001	5.54
15				0.385	0.089	0.013	0.002	4.83
20					0.387	0.086	<0.016	3.88
25						0.377	0.091	2.94
30							0.361	1.97
35								0.88

Table 2.5. *Moerisia lyonsi*. Statistical results of ANCOVA tests on the effects of temperature (T) and salinity (S) on the development time for polyp buds ( $DT_p$ ) and medusa buds ( $DT_m$ ) in the T-S-F experiment, with food consumption (F, copepods  $\text{polyp}^{-1} \text{d}^{-1}$ ) as a covariate. DF = degrees of freedom. MS is mean square in type III ANOVA table.  $p$ -values above 0.05 mean no significance. The DF value for  $DT_p$  marked with an asterisk (\*) is due to the deletion of one abnormal data point. The  $F$ -values marked with asterisks (\*) in the data columns were computed using the error term for T\*S to better fit the experimental design.

Source	$DT_p$				$DT_m$			
	DF	MS	$F$ -value	$p$	DF	MS	$F$ -value	$p$
Model	11	17.05	15.88	<0.001	11	471.63	100.82	<0.001
Error	*59	1.07			60	4.68		
T	1	8.34	*28.79	0.033	1	391.95	*68.12	0.014
S	2	1.25	*4.33	0.188	2	153.22	*26.63	0.036
F	1	6.70	6.24	0.015	1	108.65	23.23	<0.001
T*S	2	0.29	0.27	0.765	2	5.75	1.23	0.300
F*T	1	1.51	1.40	0.241	1	4.33	0.92	0.340
F*S	2	0.08	0.08	0.925	2	17.26	3.71	0.030
T*S*F	2	0.06	0.06	0.945	2	7.96	1.70	0.191

Table 2.6. *Moerisia lyonsi*. Statistical results of the Split-split plot test on the effects of temperature (T), salinity (S) and assigned food level ( $F_0$ , copepods  $\text{polyp}^{-1} \text{d}^{-1}$ ) on the actual food consumption (F, copepods  $\text{polyp}^{-1} \text{d}^{-1}$ ) in the T-S-F experiment. DF = degrees of freedom. MS is mean square in type III ANOVA table.  $p$ -values above 0.05 mean no significance for the particular source, while the  $p$ -value for T marked with two asterisks (\*\*) was taken as significant in consideration of its very low DF value and actual data distributions. The  $F$ -values marked with one asterisk (\*) in the data columns were computed by testing T and S effects against the T\*S error term, and  $F_0$  and S\*  $F_0$  effects against S(T\*  $F_0$ ) error term, as those in a split-split plot design.

Source	DF	MS	$F$ -value	$p$
Model	23	33.68	172.86	<0.001
Error	48	0.19		
T	1	21.23	*13.90	**0.065
S	2	40.19	*26.31	0.037
$F_0$	3	213.16	*152.91	<0.001
T*S	2	1.53	7.84	0.001
S* $F_0$	6	3.00	*2.15	0.145
S(T* $F_0$ )	9	1.39	7.15	<0.001

Table 2.7. *Moerisia lyonsi*. Statistical results of ANCOVA tests on the effects of temperature (T) and salinity (S) on the asexual reproduction rate (ARR, new buds  $\text{polyp}^{-1} \text{d}^{-1}$ ) and the ratio of the total medusa bud production to the total asexual reproduction ( $R_m$ ) in the T-S-F experiment, with food consumption (F, copepods  $\text{polyp}^{-1} \text{d}^{-1}$ ) as a covariate. DF = degrees of freedom. MS is mean square in type III ANOVA table.  $p$ -values above 0.05 mean no significance for the particular sources. The  $F$ -values marked with asterisks (\*) in the data columns were computed using the error term for T\*S to better fit the experimental design.

Source	DF	ARR			$R_m$		
		MS	$F$ -value	$p$	MS	$F$ -value	$p$
Model	11	11.36	73.02	<0.001	0.2753	19.33	<0.001
Error	60	0.16			0.0142		
T	1	1.29	*12.65	0.071	0.0003	*0.50	0.553
S	2	0.14	*1.33	0.429	0.0544	*104.78	0.010
F	1	58.43	375.4	<0.001	0.3300	23.18	<0.001
T*S	2	0.10	0.66	0.523	0.0005	0.04	0.964
F*T	1	1.28	8.20	0.006	0.1923	13.50	0.001
F*S	2	0.59	3.77	0.029	0.0033	0.23	0.793
T*S*F	2	0.23	1.51	0.223	0.0097	0.68	0.511

Table 2.8. *Moerisia lyonsi*. Summary of statistics of Multiple Regression (by R-selection Method and Stepwise Selection Method) for predicting the Asexual Reproduction Rate (ARR, new buds  $\text{polyp}^{-1} \text{d}^{-1}$ ) in the T-S experiment and the T-S-F experiment, based on temperature (T), salinity (S), or food consumption (F, copepods  $\text{polyp}^{-1} \text{d}^{-1}$ ). The predicted variable is  $\text{Log}_{10}(\text{ARR}+1)$  for both experiments.  $p$ -values above 0.05 mean no significance.

Experiments	Variables	Partial R-Square	Model R-Square	C(p)	F-Value	$p$
T-S	T	0.628	0.628	346.0	211.1	<0.0001
	S	0.114	0.742	204.5	54.7	<0.0001
	$S^{\frac{1}{2}}$	0.161	0.902	4.0	202.5	<0.0001
T-S-F	F	0.831	0.831	70.9	343.9	<0.0001
	TS	0.036	0.867	43.6	18.4	<0.0001
	$S^{\frac{1}{2}}$	0.008	0.875	38.7	4.56	0.0364
	S	0.044	0.918	5.0	35.7	<0.0001

Table 2.9. *Moerisia lyonsi*. Overview of statistical significance from ANCOVA tests for the T-S-F experiment.  $DT_p$ : the development time for polyp buds;  $DT_m$ : the development time for medusa buds; ARR: the asexual reproduction rate (new buds  $\text{polyp}^{-1} \text{d}^{-1}$ );  $R_m$ : the ratio of the total medusa bud production to the total asexual reproduction; One asterisk symbol (\*): significance with a  $p$ -value between 0.01 and 0.05; Two asterisk symbol (\*\*): significance with a  $p$ -value less than 0.001; N: no significance (but having indirect effects by affecting food consumption).

	$DT_p$	$DT_m$	ARR	$R_m$
Temperature	*	*	N	N
Salinity	N	*	N	*
Food consumption	*	**	**	**

Table 2.10. *Chrysaora quinquecirrha* and *Moerisia lyonsi*. Habitat requirement of the scyphomedusan, *C. quinquecirrha*, and the hydromedusan, *M. lyonsi* from laboratory or field data in Chesapeake Bay, USA.

	<i>C. quinquecirrha</i>	<i>M. lyonsi</i>
Salinity range in lab.	5-35 salinity	1-40 salinity
Optimal salinity range	10-25 salinity	5-20 salinity
Salinity range in field	7-25 salinity	From above 0 to 9.3 salinity
Temp. range in lab.	3-34°C	Not limited in 10-30°C
Seasonal range	May-Oct. generally	May-Oct. theoretically
Initial temp. for reproduction	15°C for strobilation	15°C for budding polyp buds, 20°C for budding medusa buds
Encystment	= 3°C or = 34°C; = 5 or = 35 sal.	Observed, but no available data
Field records	Mainstem and many tributaries	James & Pamunkey Rivers, VA Choptank & Patuxent Rivers, MD.
Field density	From <0.01 up to >10 m <sup>-3</sup>	No data available
Cited from	Cargo & Schultz 1966, 1967; Cones & Haven 1969; Purcell & Cowan 1995; Purcell et al. 1999b	Calder & Burrell 1966; Purcell et al. 1999a; Decker MB, Purcell JE, personal communication; This study

Figure 2.1. *Moerisia lyonsi*. The total percent mortalities of the polyps in each temperature and salinity treatment at the end of 7 d (with all three replicates combined, altogether 6 polyps for each treatment) in T-S experiment.

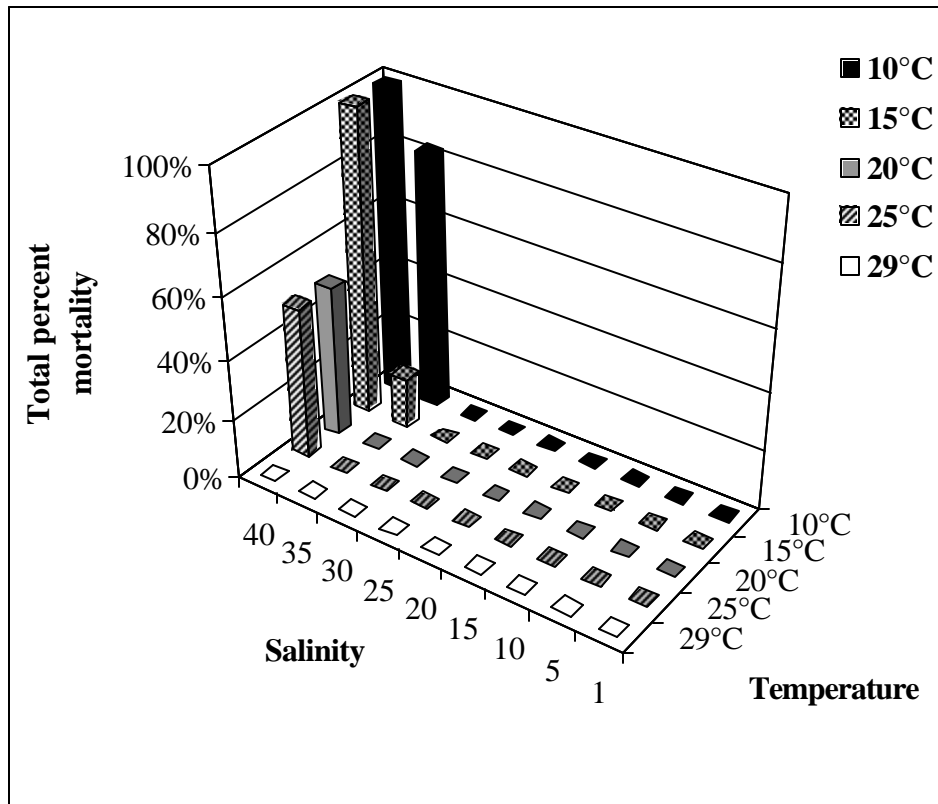




Figure 2.2. *Moerisia lyonsi*. Cumulative percent mortality of the polyps over time for treatments where mortality occurred during the 7 d T-S experiment. (A) at 35 salinity; (B) at 40 salinity. Note: the data points in the figure are three replicates combined with a total of 6 polyps.

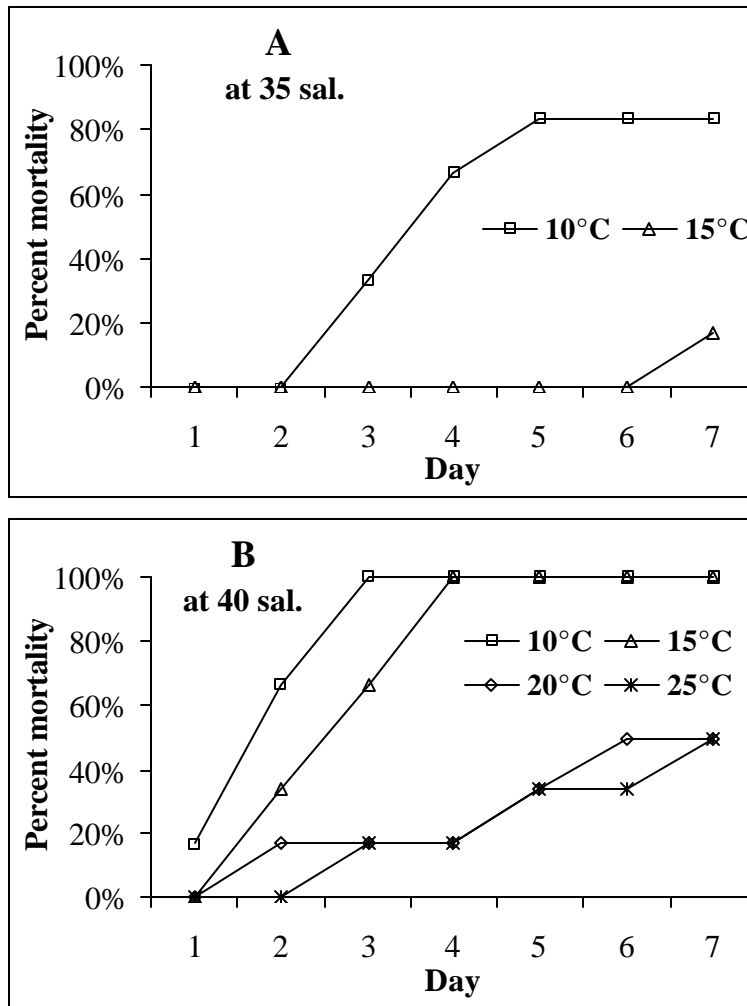


Figure 2.3. *Moerisia lyonsi*. Temperature (10-29°C) and salinity (1-40) effects on the asexual reproduction rate (new buds polyp<sup>-1</sup> d<sup>-1</sup>) of the polyps in the 7 d T-S experiment. The blank columns at 40 salinity were because all the polyps died. Number is mathematics mean of three replicates ± SD.

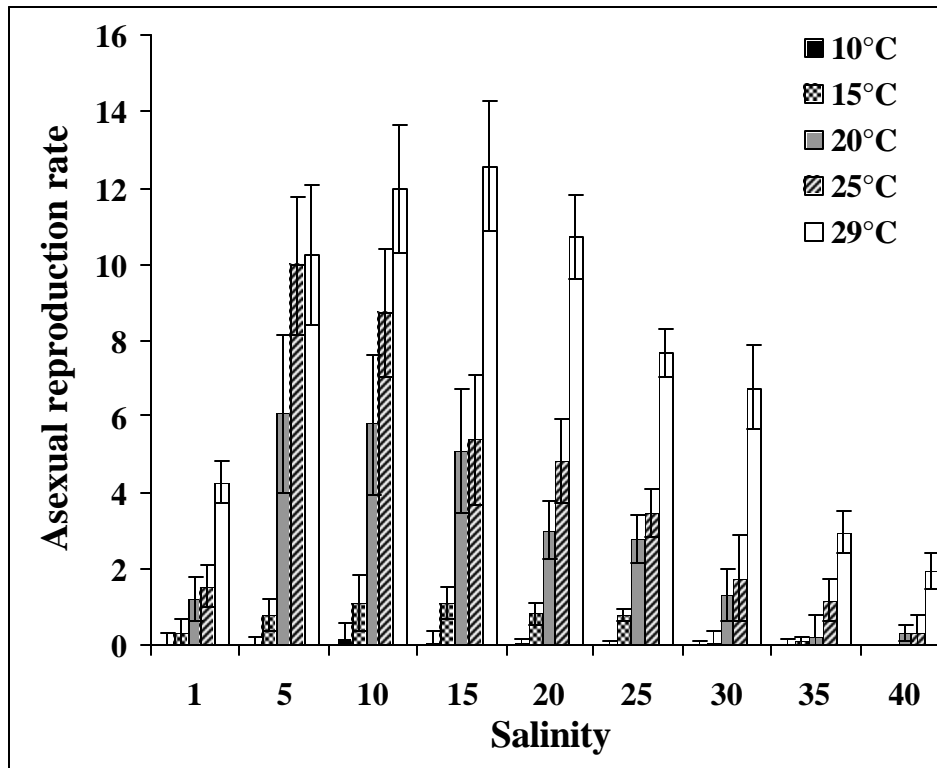


Figure 2.4. *Moerisia lyonsi*. Development Time for polyp buds ( $DT_p$ ) and medusa buds ( $DT_m$ ) in relation to temperature, salinity and food consumption (copepods  $\text{polyp}^{-1} \text{d}^{-1}$ ) in the T-S-F experiment. (A) at 20°C; (B) at 29°C. All the open symbols are for  $DT_m$  at different salinities, and all the solid symbols are for  $DT_p$  at different salinities. Note: data points with a value of 35 d are not actual measurements, but indicate that the time was longer than the 34 d experimental period.

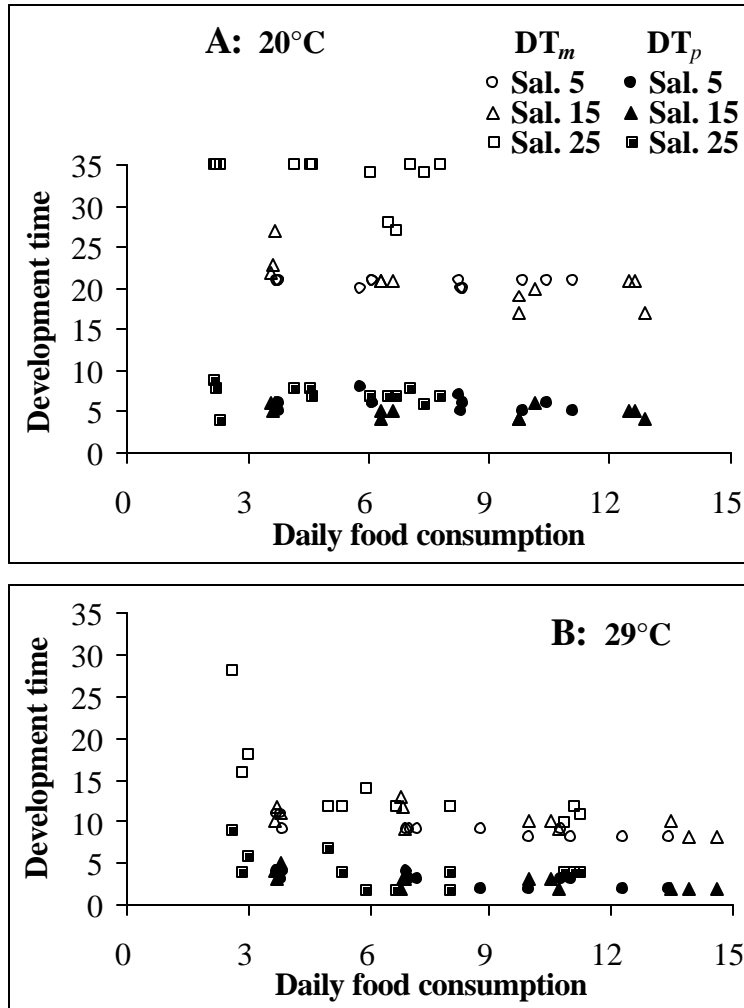


Figure 2.5. *Moerisia lyonsi*. Asexual reproduction rate (ARR, new buds polyp<sup>-1</sup> d<sup>-1</sup>) of the polyps in relation to temperature, salinity and daily food consumption (copepods polyp<sup>-1</sup> d<sup>-1</sup>) in the T-S-F experiment. (A) at 20°C; (B) at 29°C.

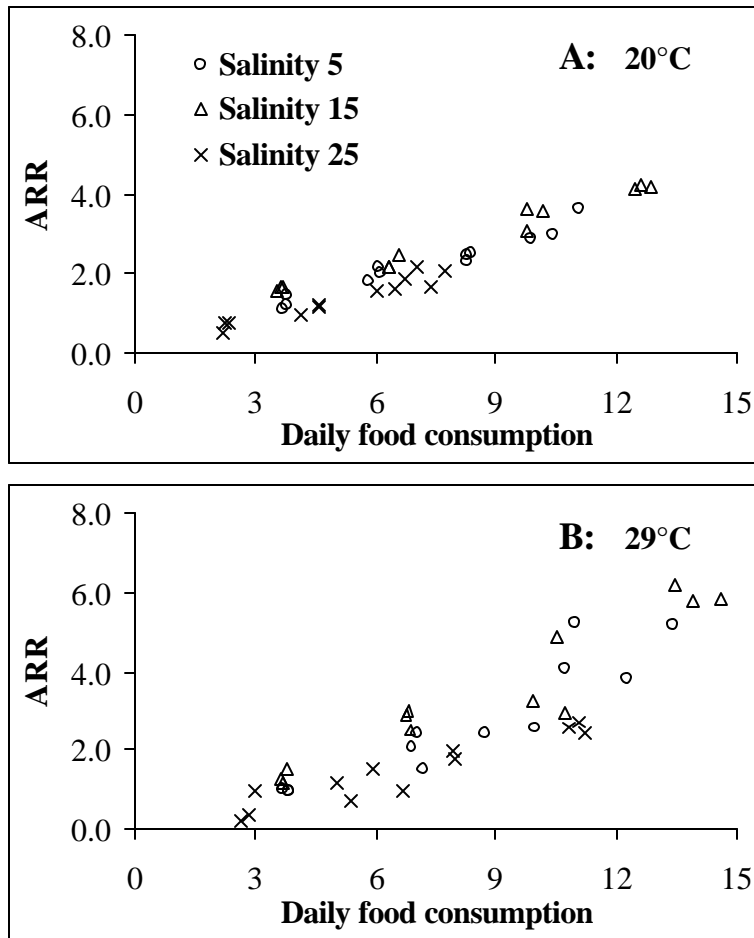


Figure 2.6. *Moerisia lyonsi*. Time series of daily polyp bud production (new polyp buds  $\text{polyp}^{-1} \text{d}^{-1}$ ) and medusa bud production (new medusa buds  $\text{polyp}^{-1} \text{d}^{-1}$ ) in relation to temperature (T), salinity (S) and food consumption (F, *Acartia tonsa* copepods  $\text{polyp}^{-1} \text{d}^{-1}$ ) for some selected treatments in the T-S-F experiment. The conditions of this experiment, temperature from 20°C to 29°C, salinity from 25 to 5 and 15, and food levels from 4 to 16, represent a range from the relatively less favorable to favorable conditions for *M. lyonsi* polyps. (A) T, S and F all favorable; (B) T, S and F all less favorable; (C) T and S less favorable; (D) T and F less favorable; (E) T less favorable; (F) S less favorable.  $R_m$  is the ratio of total medusa bud production to the total asexual reproduction in 31 d.

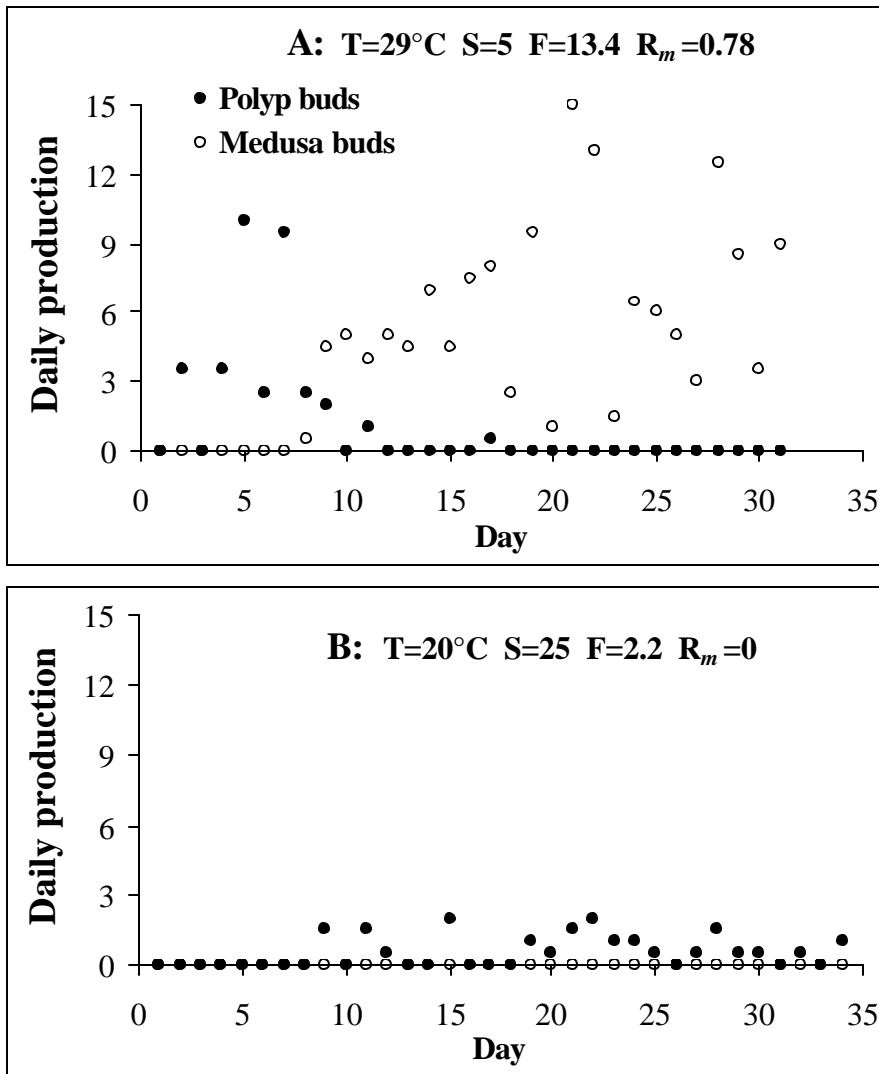


Figure 2.6 Contd.

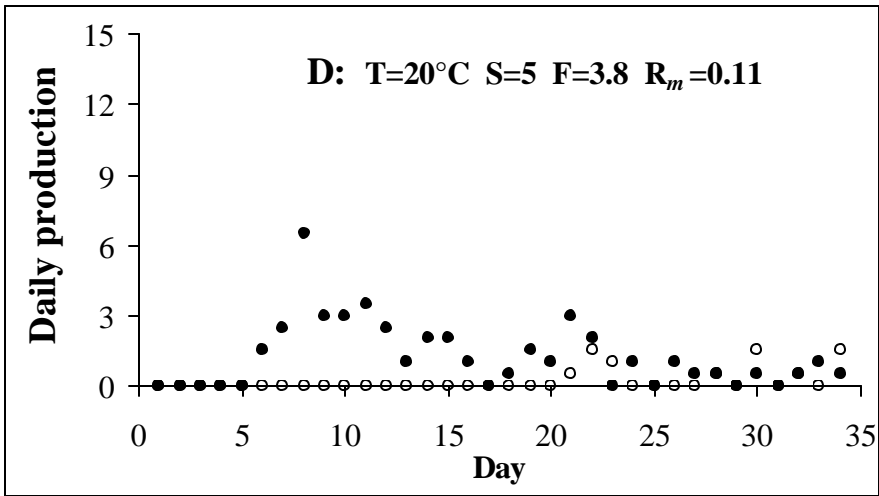
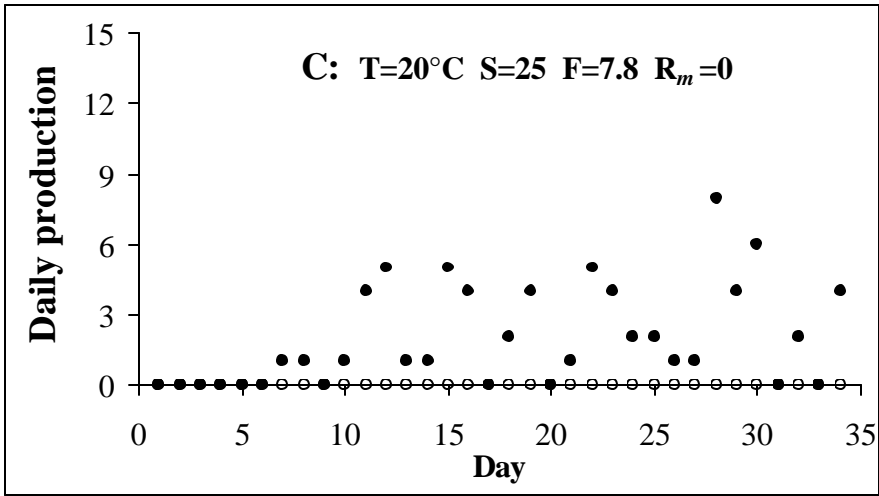


Figure 2.6. Contd.

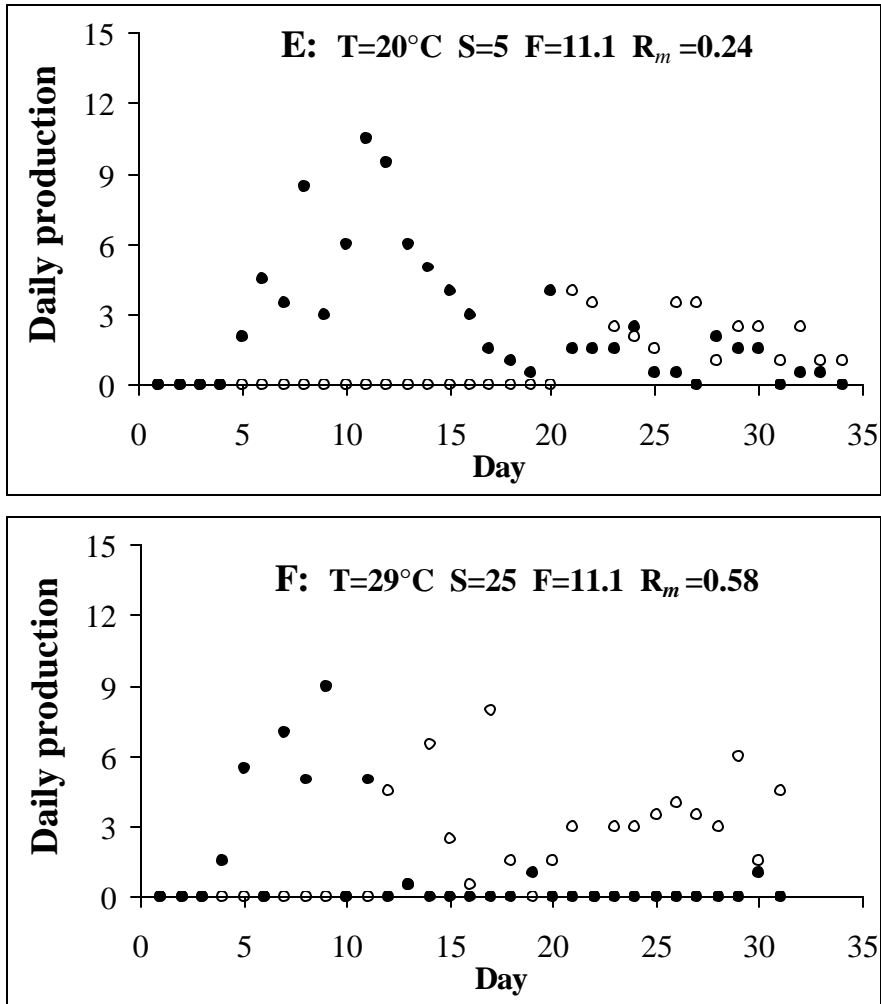


Figure 2.7. *Moerisia lyonsi*. Daily polyp bud production and medusa bud production (No. new buds  $\text{polyp}^{-1} \text{d}^{-1}$ ; Data points were 31 d average) in relation to temperature, salinity and food consumption (copepods  $\text{polyp}^{-1} \text{d}^{-1}$ ) in the T-S-F experiment. (A) polyp bud production at 20°C; (B) polyp bud production at 29°C; (C) medusa bud production at 20°C; (D) medusa bud production at 20°C.

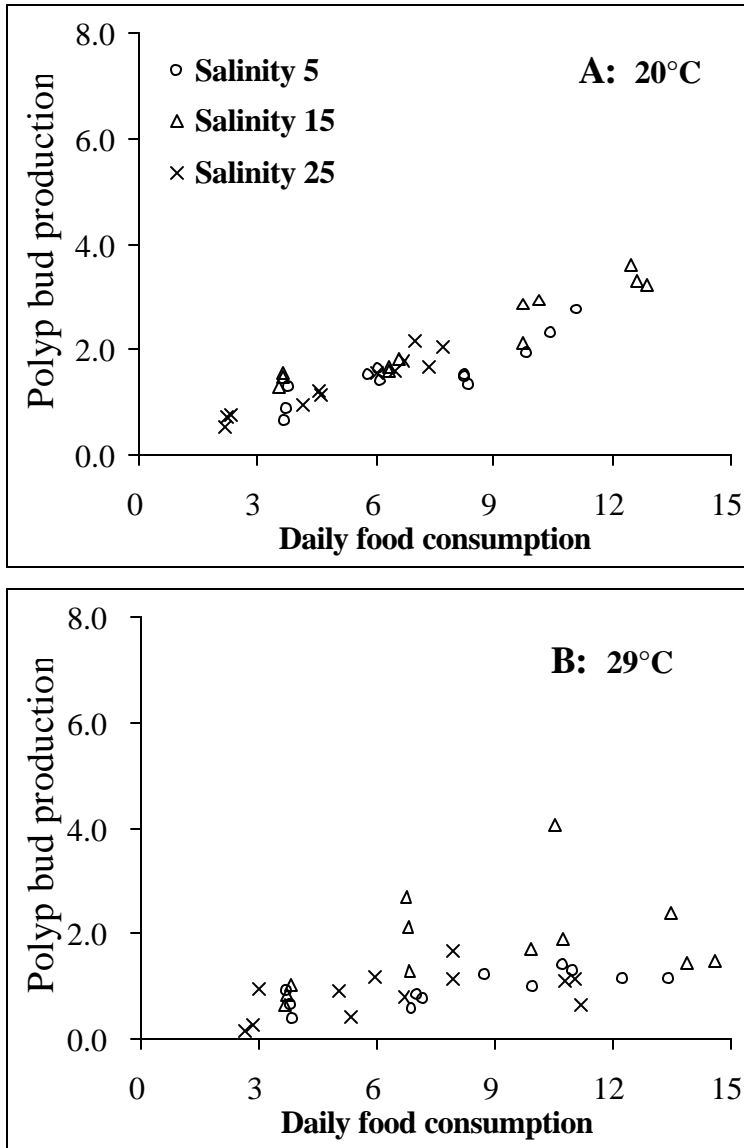




Figure 2.7 Contd.

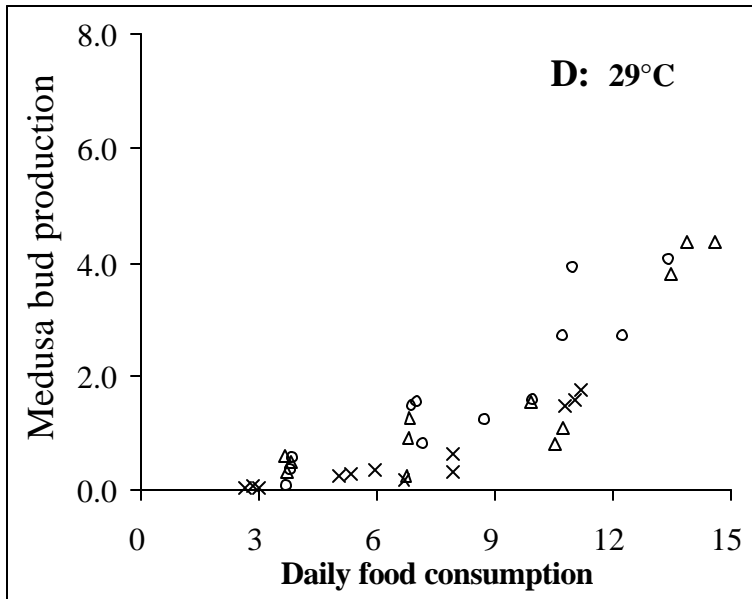
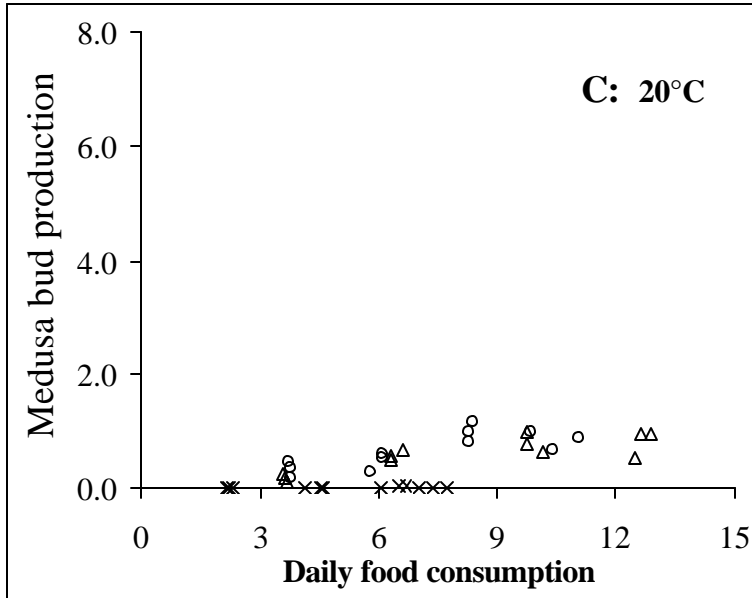


Figure 2.8. *Moerisia lyonsi*. Ratio of the total medusa bud production to total asexual reproduction of *M. lyonsi* polyps in 31 d ( $R_m$ ) in relation to temperature, salinity and daily food consumption (unit: *Acartia tonsa* copepods polyp<sup>-1</sup> d<sup>-1</sup>) in the T-S-F experiment. (A) at 20°C; (B) at 29°C.

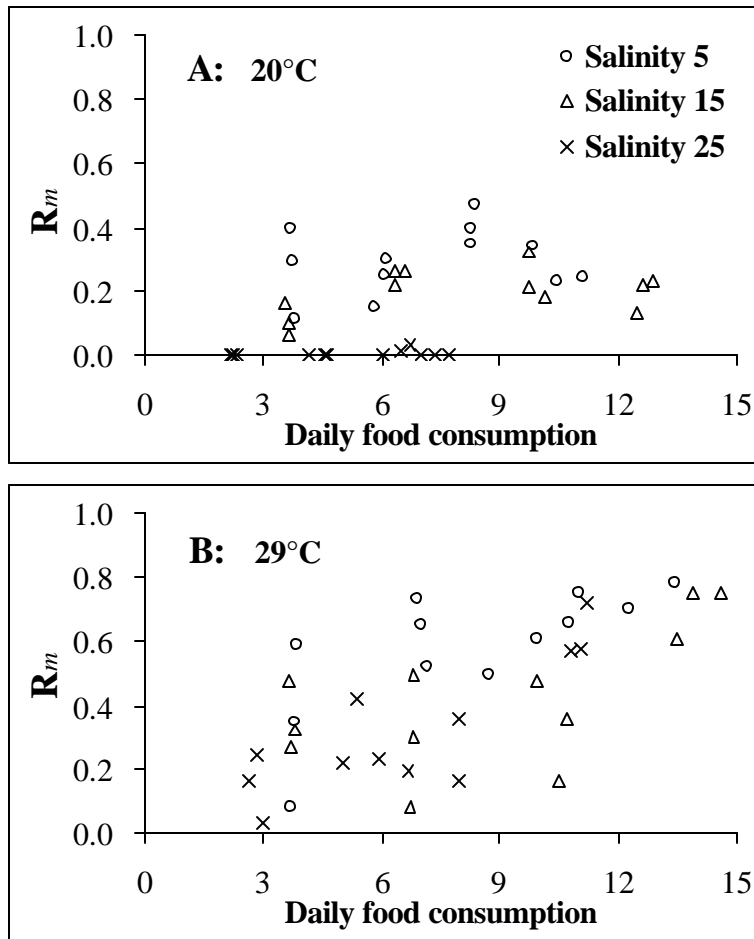
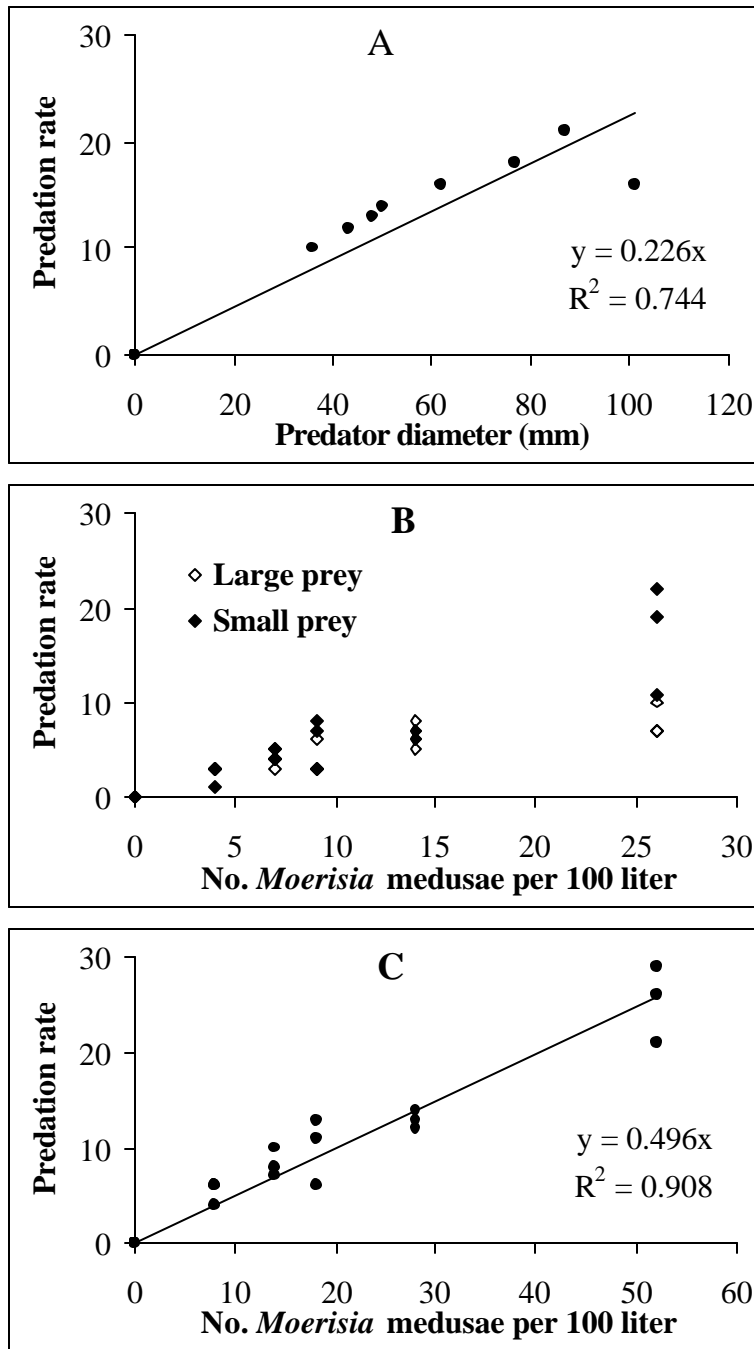


Figure 2.9. *Chrysaora quinquecirrha* and *Moerisia lyonsi*. Predation rate (No. *Moerisia* predator<sup>-1</sup> h<sup>-1</sup>) of *C. quinquecirrha* on *M. lyonsi* medusae. (A) in relation to predator sizes; (B) in relation to two sizes of *Moerisia*, 1.4-2.2 mm diameter (small prey) and 2.6-3.4 mm diameter (large prey), at different densities; (C) in relation to prey densities with two sizes of *M. lyonsi* combined.



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