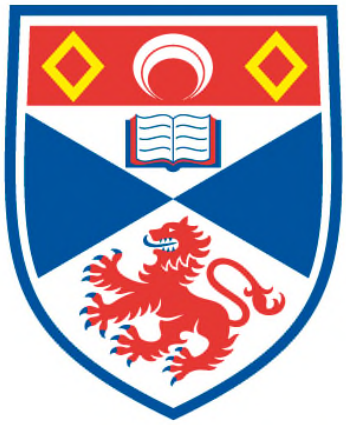
# INFLUENCES OF TEMPERATURE AND SALINITY ON ASEXUAL REPRODUCTION AND DEVELOPMENT OF SCYPHOZOAN JELLYFISH FROM THE BRITISH ISLES

**Chad L. Widmer**

**A Thesis Submitted for the Degree of PhD**
**at the**
**University of St Andrews**



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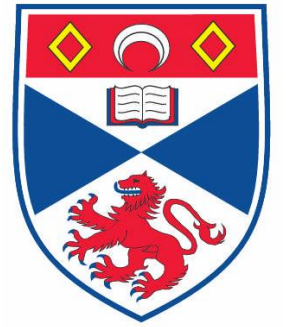

A thesis submitted to
The University of St Andrews
for the degree of
Doctor of Philosophy

July 2014

# Thesis Declaration

I, Chad L. Widmer, hereby certify that this thesis, which is approximately 43,000 words in length, has been written by me, and that it is the record of work carried out by me, or principally by myself in collaboration with others as acknowledged, and that it has not been submitted in any previous application for a higher degree.

I was admitted as a research student in September 2010 and as a candidate for the degree of Doctor of Philosophy in September 2011; the higher study for which this is a record was carried out in the University of St Andrews between 2010 and 2014.

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# Abstract

**General abstract.** Jellyfish (Phylum Cnidaria, Class Scyphozoa) play important roles in pelagic ecosystems as predators and prey. Seasonally they form blooms facilitating reproductive success, but that are at times problematic for human enterprise. Medusa abundance has been correlated with environmental variables in several instances. However, the direct mechanisms for changes in medusa abundance are unclear. As global sea surface temperatures continue to change there is increasing concern that warming may enhance conditions favourable for the generation of jellyfish medusae. It is important to understand the ways in which temperature affects all life history stages of jellyfish if we are to begin to understand factors associated with jellyfish bloom formations, but how temperature and salinity affects life history stages of scyphozoan jellyfish from British waters remains largely unknown. In Chapter 1 I provide a general introduction to some key issues important to the formation of jellyfish blooms. In Chapter 2 I present results for experiments testing the effects of temperature on settlement and metamorphosis of planulae larvae of *Cyanea capillata*, *Cyanea lamarckii*, *Chyrsaora hysoscella*, and *Aurelia aurita*. Chapter 3 reports on the effects of temperature and salinity on survival, and asexual reproduction of scyphistomae of the same species. Chapter 4 reports on the effects of temperature and salinity on growth of newly released ephyrae of each of the above mentioned species, as well as the effects of starvation on survivorship on ephyrae of *A. aurita* originating from two distinct populations of scyphistomae. In Chapter 5 I provide a brief summary of significant findings for each life history stage, their theoretical implications when taken together, and next steps for future research. I also offer recommendations for ecosystem managers with an eye toward affecting the numbers of near-shore jellyfish medusae generated each season in the waters surrounding the British Isles.

**Chapter 2.** Planula larvae of *Aurelia aurita*, *Cyanea capillata* and *Cyanea lamarckii* were exposed to temperature regimes likely to be currently encountered in summer-autumn (15 and 20°C), and conditions predicted to possibly occur 100 years from now (23°C) as well as two additional lower temperatures (5 and 10°C). Planula larvae of *Chrysaora hysoscella* were exposed to (12, 16, 19 and 23°C). Settlement of planulae was faster at higher temperatures, and temperature had significant effects on mortality and stages of development reached by the ends of the experiments for all species tested with deleterious effects only being manifested at the highest and lowest temperature extremes. Planulae were shown to have a remarkably wide range of thermal tolerances and so impacts of warming on planulae may not act as a bottleneck compared with effects of warming on other life history stages.

**Chapter 3.** In order to better understand how climate variability may affect the timing and magnitude of jellyfish blooms laboratory incubator experiments were conducted testing the effects of either 4 or 5 temperatures (4, 9, 14, 19, 23°C) and 2 or 3 salinities (21, 27, and 34) on British scyphistomae of *Cyanea capillata*, *Cyanea lamarckii*, *Chrysaora hysoscella*, and *Aurelia aurita*. Two different populations of *A. aurita* scyphistomae were tested; one originating from Orkney, Scotland and the other from Southampton, England. Temperature and salinity significantly affected asexual reproductive output for all species tested, with temperature being the more important driver of the two factors. As temperature increased the mean number of podocysts, and budded progeny produced per scyphistomae varied with species and populations

tested. Conversely, as temperature increased the probability of strobilation, and therefore mean number of ephyrae produced, decreased for all species tested. Since scyphistomae asexually reproduce more benthic life history stages in warmer temperatures summer through early autumn are probably important periods for benthic colony expansion and maintenance in natural populations. In contrast, most ephyrae are produced during colder periods of the year. If sea temperatures in the North Sea continue to increase at the current rate the ranges of *C. capillata*, *C. lamarckii* and *Ch. hysoscella* may begin to shift northward. The current range of British *A. aurita* may remain unaffected.

**Chapter 4.** Newly released ephyra larvae of four species of British scyphomedusae, *Aurelia aurita*, *Cyanea capillata*, *Cyanea lamarckii* and *Chrysaroa hysoscella*, were exposed to short-term laboratory experiments for 7 day periods to test the effects of temperature (4, 9, 14, 19 and 23°C) and one to three salinities (34, 27, 21) on growth. Additionally, ephyrae of *A. aurita* from two different populations (Southampton, England and Orkney, Scotland) were maintained for a period of eight weeks without food in order to determine the effects of starvation on survivorship. Ephyrae of *C. capillata* had the highest maximum growth rate observed in the study, 22.79% $d^{-1}$ at 4°C salinity 21, and ephyrae of *Ch. hysoscella* had the lowest maximum growth rate, 14.11% $d^{-1}$ at 19°C and a salinity of 34. These results suggest that newly released ephyrae of British scyphomedusae may be adapted for enhanced growth at scyphistomae strobilation temperatures. Survivorship in starvation experiments was higher for *A. aurita* ephyrae from the Orkney population than the Southampton population. Orkney *A. aurita* ephyrae may be better able to survive for extended periods with little to no particulate food which may be important for overwintering in a state resembling diapause.

# Acknowledgements

**Supervision**
I would like to thank both of my supervisors for hosting me, and for their unwavering support during this project. Specifically, I appreciate the candour, and guidance of Professor Andrew Brierley. Cheers for allowing be to build a little jelly lab on your estate. I am also very grateful to Dr. Clive Fox for sharing his wisdom, and professional insight. Thank you, Clive for the scyphistoma adventures. I look forward to working with you both in the future.

**Technical**
I also wish to gratefully acknowledge the technical support I received whilst conducting this work. In particular I would like to thank Mr. Iain Johnston, Scottish Oceans Institute, Mr. Thomas Knowles, Monterey Bay Aquarium, and Dr. Andrew Whiston, St Andrews Aquarium, for lending materials that enabled me to construct a jellyfish culture facility. I also wish to thank Mr. Jamie Craggs, Horniman Museum, and Dr. William Sanderson, Heriot-Watt University, for initial scyphistoma collections. I heartily thank Mr. Donald Malone for his indomitable enthusiasm. He really tied things together.

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**Personal**
Most importantly, I wish to thank my wife Alicia for her eternal support. She has inadvertently learned more about scyphistomae ecology than any innocent person probably should have. She helped me plan this scheme during a caravan trip around the UK, so perhaps she isn't so innocent after all. I am looking forward to many more fine adventures with her.

# Contents

# Chapter 1

## General Introduction

Part of the work described here has been published as:

Lucas CH, Graham WM, Widmer CL. 2012. Jellyfish life histories: role of polyps in forming and maintaining scyphomedusa populations. Advances in Marine Biology 63: 133–96.

### Introduction

Medusae belonging to the phylum Cnidaria, hereafter referred to as jellyfish, play key roles in healthy ecosystems acting as zooplanktic predators (Arai 1997), prey for a small host of organisms (Arai 2005), and homes for hitchhiking symbiotic organisms such as barnacles and juvenile crabs (Pages 2000, Towanda and Thuesen 2006). Some jellyfish species seasonally occur in large groups consisting of thousands of individuals. These groups are known to many specialists as blooms and are a normal occurrence in pelagic ecosystems (Graham et al. 2001, Hamner and Dawson 2009). Blooms facilitate reproductive success, and may also be a consequence of common behaviour that keep medusae within physiological tolerances through directed swimming as medusae move en masse in order to avoid deleterious conditions, or move towards favorable ones (Graham et al. 2001). Jellyfish blooms can however, be problematic for human activities, and in the last few decades the idea has arisen that the magnitude and frequencies of jellyfish blooms are changing, occurring more frequently in some areas and less often in others (Mills 2001, Brotz et al. 2012, Condon et al. 2012). The notion that jellyfish numbers are rising in response to global climate change has been grasped by the popular press (Condon et al. 2012). However, the ways jellyfish abundances change in response to climate variability may not be universal, and are for the most part unknown.

### 1.1 Jellyfish blooms and industry

1.1.1 *Negative effects of jellyfish blooms*

Jellyfish blooms have the potential to negatively affect a number of marine based industries (Dong et al. 2010). Large numbers of jellyfish have clogged the seawater intakes of power plants (Mills 2001, Purcell 2005, Purcell et al. 2007), diamond mining operations (Lynam et al. 2006) and annually crush the intake pre-filter screens at the Monterey Bay Aquarium in Monterey, California (personal observation, Fig. 1C).

Figure 1. Northeast Pacific sea nettles, *Chrysaora fuscescens.* A. Medusae in Monterey Bay, California; B. Medusae that have been advected into Monterey Harbor; C. Seawater intake pre-filter screen crushed by a bloom of medusae during summer 2010 at the Monterey Bay Aquarium, Monterey, California, USA. The pre-filter screen was 1m wide x 1.25m tall (Photos by C. Widmer).

Jellyfish can also impact commercial fishing by clogging and sometimes breaking fishing nets (Mills 2001, Kawahara et al. 2006), or fouling entire catches leading to what is known by some fishermen as "slime hauls." Jellyfish can sting fish gills and eyes, and have also led to mass mortalities in caged farmed fish (Mills 2001, Boero et al. 2008, Doyle et al. 2008). Blooms of small jellyfish can also lead to decreased feeding rates of farmed fish, whilst blooms of larger jellyfish can clog net pen walls leading to oxygen depletion inside the rearing pens (Nickell et al. 2010). Jellyfish also act as competitors with commercially important fish for zooplankton prey (Purcell and Sturdevant 2001, Brodeur et al. 2002, Gorbatenko et al. 2009, Lilley et al. 2009, Shoji et al. 2009), affecting overfished ecosystems in particular (Lynam et al. 2006). Potentially large numbers of fish eggs and larvae can be consumed by gelatinous predators and in some cases this has been hypothesized as having significant impacts on fish early life survival (Purcell et al. 1987, Purcell and Arai 2001, Lynam et al. 2005c, Titelman and Hansson 2006). Additionally, some species of jellyfish can sting or injure swimmers, sometimes fatally, (Fenner and Williamson 1996, Fenner et al. 2010, Sando et al. 2010) with adverse effects on tourism (Heggie 2009).

### 1.1.2 *Positive effects of jellyfish blooms*

Despite publications describing negative impacts of jellyfish blooms on marine ecosystems and human activities, they do also play many positive roles (Doyle et al. 2014). People are generally fascinated by jellyfish because they are often portrayed by the media as both beautiful and a bit scary. However, not all jellyfish stings are harmful to humans. In Palau harmless spotted lagoon jellies, *Mastigias spp.*, are a huge draw for snorkeling tourists (Dawson et al. 2001). Jellyfish are also one of the most popular display animals at public zoos and aquariums and new jellyfish exhibitions are often constructed when managers wish to increase their attendance (Widmer 2008a). Jellyfish have been eaten by people in Asia for more than a 1000 years (Hsieh et al. 2001) and there remains an active and lucrative fishery for edible jellyfish (Omori and Nakano 2001, You et al. 2007, Dong et al. 2009). Medusivorous species may also help to regulate the abundance of other more harmful species (Strand and Hamner 1988, Purcell 1991, Titelman et al. 2007). Additionally, green fluorescent protein originally isolated from the hydrozoan jellyfish, *Aequorea victoria*, has been widely used by molecular biologists for marking proteins earning the Nobel Prize in 2008 for the workers who discovered it (Zimmer 2005).

## 1.2 Anthropogenic factors possibly affecting jellyfish blooms

A number of anthropogenic factors including overfishing, habitat modification, eutrophication, and climate change have been all been proposed as enhancing conditions favorable to the formation of jellyfish blooms (Arai 2001, Mills 2001, Purcell 2005, Purcell et al. 2007, Richardson et al. 2009). Much of what has been put forward is speculative, but convincing evidence is beginning to emerge.

### 1.2.1 *Overfishing*

Removal of species that compete with jellyfish for zooplanktic prey may be favourable for jellyfish medusae and scyphistomae. The growth of jellyfish medusae increases, to a point, with increased prey availability (Bamstedt 1990, Bamstedt et al. 1994). Therefore decreasing the number of zooplanktivorous competitors such as fishes could provide additional prey for jellyfish (Purcell et al. 2007). Increased prey availability would benefit scyphistomae since asexual reproduction is enhanced in well fed scyphistomae, and well fed scyphistomae produce more ephyrae than poorly nourished ones during strobilation (Spangenberg 1967, Purcell et al. 1999, Ishii and Watanabe 2003, Wiesenthal 2012). Medusa blooms produced by well-nourished scyphistomae colonies could be substantially larger than blooms generated by poorly fed colonies.

### 1.2.2 *Coastal construction*

The proliferation of human-made coastal constructions has been suggested to provide ideal habitat for the benthic life history stages of some scyphozoan jellyfish. Planula larvae of some species have been shown to settle preferentially on the undersides of floating surfaces (Holst and Jarms 2007, Hoover and Purcell 2008), and such an orientation is thought to be advantageous to developing scyphistomae (Grondahl 1988a, Watanabe and Ishii 2001). Floating aquaculture rafts, marina pontoons, and docks are thus potential scyphistoma habitat. For example, and estimated 100 million scyphistomae of *Aurelia labiata* live on the undersides of floating docks in Cornet Bay, Washington (Purcell et al. 2009). A further example followed the removal of aquaculture rafts from Tapong Bay, Taiwan after which water quality improved and the abundance of *Aurelia aurita* blooms ceased. It was suggested that this occurred as a result of removal of habitat for the scyphistomae (Lo et al. 2008).

### 1.2.3 *Eutrophication*

Terrestrial run-off from populated areas or agriculture can increase the amount of nutrients within coastal ecosystems. This in turn can lead to eutrophication which is an un-natural increase in primary production, and depending on the nature of the phytoplankton bloom, this may cause increases in zooplankton providing additional food for jellyfish (Arai 2001). Increased eutrophication was linked to long term increases in the abundance of *Nemopilema nomuri*, in the Yellow and East China Seas however, their abundance was not significantly linked with chlorophyll *a* (Xu et al. 2013). Eutrophication may also lead to the formation of oxygen depleted zones which may be harmful to some fish larvae (Breitburg 1994) and copepod nauplii (Stalder and Marcus 1997), but that jellyfish medusae (Purcell et al. 2001) and planula larvae (Ishii et al. 2008, Miller and Graham 2012) are able to tolerate.

1.2.4 *Climate change*

Average global sea surface temperatures have been increasing at a rate of about 0.13°C each decade since 1979 (Solomon et al. 2007). This trend may be masked by substantial regional variation, but by the end of the 21st century UK seas are predicted to be 1.5 – 3.5°C warmer than they are at present (Hughes et al. 2010). Salinity surrounding the British Isles is variable (Hughes et al. 2010) and can be affected by anomalies in oceanographic conditions (Belkin et al. 1998), and changes in the North Atlantic Oscillation (NAO) due to increased storm water run-off during warm wet years when the NAO index is in a high phase (Drinkwater et al. 2003). Temperature and salinity are known to influence the growth of jellyfish ephyrae (Bamstedt et al. 1999, Widmer 2005), settlement of planulae (Holst and Jarms 2010, Webster and Lucas 2012) and the asexual reproduction of scyphistomae (Arai 1997, Holst and Jarms 2010, Lucas et al. 2012). Increasing sea surface temperatures over time are likely be favorable for some species of jellyfish while being deleterious to others (Dawson et al. 2001, Mills 2001, Purcell 2007).

## 1.3 Locating and predicting jellyfish blooms

1.3.1 *Locating and understanding patterns of abundance*

Due to their potential for rapid growth and susceptibility to being transported by currents, jellyfish medusae seem to suddenly appear and then disappear (Graham et al. 2001). Size, frequency, timing and locations of blooms can be different each year, and variations may also occur over longer time scales (Purcell 2005). It is difficult to know whether or not blooms are actually occurring more frequently now than they were in the past due to the lack of accurate long term jellyfish monitoring data (Purcell et al. 2007). A number of approaches have been employed in order to try to better understand jellyfish abundance patterns. These techniques include monitoring of beach stranding events (Houghton et al. 2007, Fleming et al. 2013), acoustic surveys (Brierley et al. 2005, Colombo et al. 2009), monitoring from ships of opportunity (Doyle et al. 2007, 2008, Nickell et al. 2010), aerial surveys (Houghton et al. 2006, Magome et al. 2007, Nickell et al. 2010), underwater video cameras (Graham et al. 2003), remotely operated underwater vehicles (Raskoff 2001), recording of jellyfish in fisheries research trawl surveys (Hay et al. 1990a), and remote sensing with satellites (Nickell et al. 2010). All of these methods have advantages and disadvantages, but there is at present no truly cost effective single method for detecting and monitoring jellyfish blooms at the ecosystem scale.

1.3.2 *Correlative associations of medusa abundance in the North Sea*

In the North Sea, abundances of some jellyfish species in fisheries trawl data have been correlated with changes in the NAO. When the NAO index was in a negative phase medusae of *Cyanea capillata*, *C. lamarckii* and *Aurelia aurita* were highly abundant whilst when the NAO was in a positive phase the abundance of the medusae were reduced (Lynam et al. 2004, 2005b). Medusa abundance patterns were not however, uniform. Medusa abundance in the northern North Sea was more strongly influenced by oceanic inflows which may mask any influence of the NAO, but in the southern North Sea medusa abundance was more strongly linked with changes in the NAO (Lynam et al. 2010). However, the underpinning mechanisms leading to the observed correlations were unknown. In order to better understand those mechanisms experiments on the influence of changing environmental factors on the asexual reproductive output of benthic life history stages of jellyfish are required since the benthic stages determine whether or not medusae are generated (Arai 1997).

### 1.4 Background of study species

In the waters surrounding Britain, *Cyanea capillata*, *Cyanea lamarckii*. *Chyrsaora hysoscella*, and *Aurelia aurita* are the largest and most often observed semaeostome scyphomedusae (Russell 1970). Medusae of *C. capillata* are northern boreal and are not observed as far south as the English Channel, *C. lamarckii* and *Ch. hysoscella* are southern boreal and *A. aurita* occurs all around the British Isles (Russell 1970, Hay et al. 1990b, Barz and Hirche 2007, Houghton et al. 2007). In addition to preying upon zooplankton in general, some jellyfish prey upon medusae of other species (Strand and Hamner 1988, Arai 1997, 2005, Titelman et al. 2007). Of the abovementioned species, *C. capillata* is at the top of the gelatinous food chain (Russell 1970) followed by *C. lamarckii*, *Ch. hysoscella* and *A. aurita* respectively (Russell 1970). Jellyfish higher on the gelatinous food chain may help to regulate the abundance of species below them (Hansson 1997a), and may also help to regulate potentially problematic non-native ones (Hosia and Titelman 2011). Changes in the abundance of a particular medusa species can affect ecosystems through their direct and indirect effects on the gelatinous food chain, zooplankton abundance, and as prey for other organisms.

### 1.5 Life cycle of near-shore Scyphozoan jellyfish

Most, but not all, jellyfish species possess a biphasic life history alternating between benthic and planktonic stages (Arai 1997, Lucas et al. 2012). The life cycle of the majority of members of the class Scyphozoa involves sexually reproductive medusae (Fig. 1A and B; Fig. 2A) and cryptic benthic scyphistomae (Fig. 2B) that reproduce asexually (Arai 1997, Widmer 2008b). Fertilized eggs develop into tiny free-swimming planula larvae (Fig. 2B, 1) that often settle on the undersides of shaded surfaces in laboratory studies (Holst and Jarms 2007). After settlement, the planulae metamorphose into scyphistomae capable of feeding as soon as they develop tentacles and a mouth (Widmer 2006).


Figure 2. Life cycle of near-shore jellyfish belonging to the Class Scyphozoa. A. Mature *Cyanea capillata* medusa; scale bar = 5cm. B. 1 planula larva, 2 scyphistoma, 3 strobila, 4 ephyra; scale bar = 2mm (Photos by C. Widmer). This figure was included in (Lucas et al. 2012).

The long-lived scyphistomae produce new progeny scyphistomae by budding them from their bases, by fission (Fig. 3), and by stolon budding (Arai 1997, Lucas et al. 2012). Stolons are temporary pseudopod-like extensions that sometimes extend from the bases of scyphistomae and attach to the nearby substrate (Fig 3, 1). From these stolons new buds are also formed (Adler and Jarms 2009). Many species produce protective podocysts from which new scyphistomae emerge (Fig. 4A, B) in a process known as excystment (Arai 2009). Viable podocysts can persist for years enabling colonies to survive periods of adverse conditions, and also play a role in colony expansion (Arai 2009, Kawahara et al. 2012, Thein et al. 2012a).

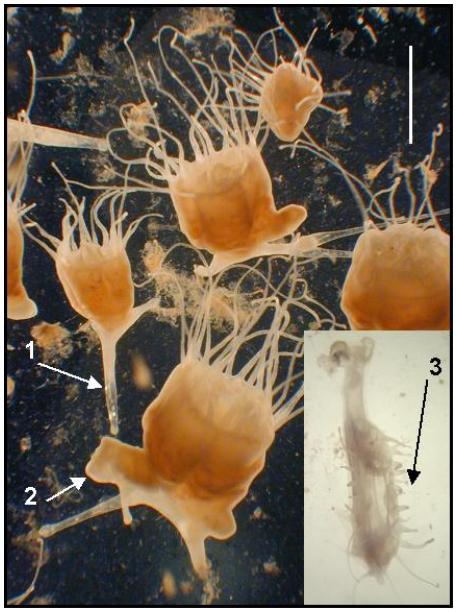


Figure 3. Common asexual reproductive modes scyphistomae. 1. Stolon, 2. Side budded progeny scyphistoma, 3. fission; scale bar = 2 mm (photos by C. Widmer). This figure was included in (Lucas et al. 2012).

Scyphistomae undergo the process of strobilation and metamorphose into strobilae (Fig. 2B, 3) that generate and release free-swimming ephyrae (Fig. 2B, 4) with the metamorphosis often being triggered by a change in environmental conditions (Lucas et al. 2012). The planktonic ephyrae then go on to develop into medusae. Depending on conditions each strobila may release dozens of ephyrae. After the last ephyra is released the strobila metamorphoses back into a scyphistoma although this will be smaller than it was before strobilating. A period of feeding and growth usually occurs before the scyphistoma can strobilate again. Jellyfish blooms begin to develop when large numbers of strobilae release ephyrae during the same period.

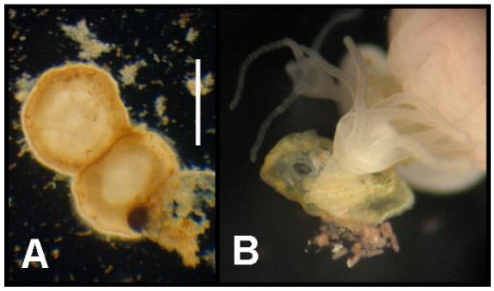


Figure 4. Podocysts. A. Two podocysts of *Chrysaora fuscescens*. B. A scyphistoma that has recently excysted from the podocyst; scale bar = 1mm (Photos by C. Widmer). This figure was included in (Lucas et al. 2012).

## 1.6 Conclusion and aims:

### 1.6.1 *Conclusion*

Medusa abundance is dependent upon success at all stages of the jellyfish life cycle (Colin and Kremer 2002). Determining how life history stages of jellyfish respond to changing environmental conditions may thus lead to an enhanced understanding of mechanisms driving medusa abundance patterns, and may ultimately improve our ability to predict when and where blooms of medusae occur. Improvements in predictability of blooms could have potential benefits to a wide range of human

activities including power utility companies, fisheries, and tourism. Such information is also essential for modelling the potential impacts of climate change on the frequency and intensity of jellyfish blooms. This fact has not gone unnoticed by the jellyfish research community and such studies have been suggested by several authors as an important area for future research (Lucas 2001, Mills 2001, Boero et al. 2008, Arai 2009, Richardson et al. 2009). One of the challenges associated with understanding medusa abundance is that research to date has often focused on spatial-temporal correlations between climate variables and medusa abundance e.g., (Goy et al. 1989, Lynam et al. 2004, 2005b, Robinson and Graham 2013) without linking this to the abundance, location and strobilation patterns of their scyphistomae (Decker et al. 2007). The ultimate aim of the present study was to move from correlative associations between field observations of medusa abundance and climate indices to improved understanding of the mechanisms driving such relationships in areas such as the North Sea.

### 1.6.2 *Specific aims*

To learn more about how changing environmental variables affects the abundances and distributions of British jellyfish, this PhD research focused on how temperature and salinity affect different life history stages of British jellyfish. The specific aims of the study were to:

Chapter 2: To test the effects of temperature on survivorship, settlement, and subsequent development of planula larvae into scyphistomae of *Cyanea capillata*, *Cyanea lamarckii*, *Chrysaora hysoscella*, and *Aurelia aurita*.

Chapter 3: To test the effects of temperature and salinity on asexual reproductive output of scyphistomae of *C. capillata*, *C. lamarckii*, *Ch. hysoscella*, and two different populations of *A. aurita* (one originating from Orkney, Scotland, and the other from Southampton, England).

Chapter 4: To test the effects of temperature and salinity on growth of newly released ephyrae larvae of *C. capillata*, *C. lamarckii*, *Ch. hysoscella*, and *A. aurita* to determine thermal conditions optimal for growth, and to determine their growth rates during the first seven days of development in different environmental regimes; and to test the effect of starvation on ephyrae of two different populations of *A. aurita* (Orkney and Southampton).

The thesis concludes with a summary of experimental findings, and a discussion of their theoretical and practical implications. In particular, I discuss causative mechanisms associated with correlations linking medusa abundance in the southern North Sea with changes in the NAOI, the ways in which benthic colonies of scyphistomae may maintain themselves during different seasons *in situ*, and how jellyfish populations may respond to gradually increasing sea surface temperatures predicted to occur over time. I also suggest directions for future research that might aid in the development of predictive models that could provide actionable information for resource managers.

# Chapter 2

## The effects of temperature on settlement and development of British scyphozoan jellyfish planula larvae

### 2.1 Introduction

Dispersal, site selection and successful metamorphosis are important functions of meroplanktic marine invertebrate larvae (Cameron 1986, Müller and Leitz 2002). Species with slow settlement rates will remain as plankton for extended periods allowing them to disperse over greater distances, whereas species with fast settlement rates may have lower overall dispersal potential (Nishikawa et al., 2003; O'Connor et al., 2007). However, a potential drawback to increased planktic duration may be increased exposure to predation (Grondahl 1988b, O'Connor et al. 2007) or dispersal to unsuitable benthic habitats. Factors affecting larval settlement have implications for distribution of adult stages (Thorson, 1950). For jellyfish, successful settlement and metamorphosis of planula larvae is required in order to establish new colonies of scyphistomae (Brewer, 1976; Dolmer & Svane, 1993; Grondahl, 1988b) which ultimately go on to produce medusae.

The vast majority of scyphozoan jellyfish are r-strategists (Lucas 2001) producing thousands of independent lecithotrophic planula larvae. The larval settlement and metamorphosis period may represent a potential bottleneck for jellyfish life histories (Colin and Kremer 2002). Therefore, it is important to understand factors influencing successful settlement of planulae in order to understand where colonies of scyphistomae are likely to become established, which may then contribute to a better understanding of medusa distributions and bloom formation potential. With some exceptions, global sea surface temperatures have been increasing at a rate of about 0.13°C each decade since 1979 (Solomon et al. 2007). Although inter-annual variability is high, UK seas are predicted to be about 1.5 – 3.5°C warmer year round than they are now by the end of the 21$^{st}$ century (Lowe et al. 2009, Hughes et al. 2010). How increasing sea surface temperature trends may affect settlement and development of jellyfish planulae inhabiting UK seas is largely unknown.

Planulae settle on nearly any natural substrate covered in biogenic films including rocks, algae, barnacles and ascidians (Grondahl 1989), as well as artificial substrates (Holst and Jarms 2007, Hoover and Purcell 2008). Mechanosensory and chemosensory cells (Müller and Leitz 2002) enable planulae to inspect a site prior to settlement and then re-enter the plankton if the site is not suitable (Brewer, 1976, 1978, 1984). Many scyphozoan planula larvae show a preference for settling on the undersides of surfaces (Brewer, 1976, 1978; Holst & Jarms, 2007; Svane & Dolmer, 1995) resulting in scyphistomae that hang, with their mouths pointed downward with dangling tentacles (Brewer, 1978; Fitt & Costley, 1998; Gilchrist, 1937). Being so oriented is thought to be beneficial to survival (Grondahl 1988b, Watanabe and Ishii 2001) and acts as a mechanism for avoiding siltation, enhancing waste removal, and increasing prey capture efficiency. Planulae of *Aurelia aurita* and *Cyanea capillata* have also been shown to settle preferentially in the presence of conspecifics

(Grondahl 1989, Dolmer and Svane 1993) which ensures that larvae settle in appropriate habitats, presumably capitalizing on the success of previous generations.

A number of abiotic factors affecting planula settlement have been investigated. Hypoxia enhanced settlement rates of *A. aurita* in Tokyo Bay, Japan (Ishii et al., 2008). Planulae of *C. capillata* preferentially settled in low light levels (Svane and Dolmer 1995), and also on substrate with roughened surface textures (Brewer, 1976, 1978). Water currents also affected planula settlement rates and distributions of *C. capillata* (Brewer, 1976; Dolmer & Svane, 1993) with planulae settling faster in still water than in moving water. Experiments have also shown that planulae of some species from the North Sea have wide salinity tolerances (Holst and Jarms 2010) enabling them to potentially establish scyphistomae colonies in the southern Baltic Sea.

While several investigations have focused on the effects of various factors on settlement of scyphozoan planulae, relatively few have focused directly on the effects of temperature. This limits our understanding of how scyphozoan planulae may respond to increasing sea surface temperatures due to climate change. To date there has been only one published study on the effects of temperature on settlement of *A. aurita* planulae from UK waters (Webster and Lucas 2012). Those planulae were produced by mature medusae that were collected near the Isle of Wight in southern England. Nothing is published to our knowledge on how temperature may affect planulae settlement for other large scyphomedusae from more northerly UK waters. This Chapter reports results for laboratory incubator experiments conducted to investigate two specific hypotheses in order to determine the ways in which planula larvae of four species of scyphozoan planulae larvae from British waters may respond to increasing sea temperatures over time. (1) Temperature affects settlement rates of planulae larvae, and (2) temperature affects survivorship and development of post settlement larvae.

## 2.2 Methods

Planula larvae of *Cyanea capillata*, *Cyanea lamarckii* and *Aurelia aurita* were incubated at 5 different temperatures for 14 days, and planulae of *Chrysaora hysoscella* at 4 temperatures for 7 days. During the experiments the number of planulae that had settled each day was counted, and the stage of development recorded. At the ends of the experiments the number of surviving individuals was also recorded.

### 2.2.1 *Collection of planulae*

Medusae brooding planulae were collected as beach stranded specimens on East Sands beach, St. Andrews, Scotland at low tide during summers 2011 and 2012 with the exception of *Chrysaora hysoscella* medusae which were collected by SCUBA divers near Dalefort, Wales, UK in August, 2011 and posted to the Scottish Oceans Institute. The numbers of mature medusae used for harvesting planulae and their collection locations are shown in Table 1. Beach stranded medusae were all checked for signs of life, i.e. pulsing, before being immediately transported inside insulated boxes filled with seawater from the collection sites to the Scottish Oceans Institute and placed in 20 L buckets, filled with 18 L of 5 µm-filtered North Sea water. When the *C. hysoscella* medusae arrived in the post, the same protocol was implemented. Mature medusae were left in the buckets for two hours during which time they

released planulae. After two hours the medusae were removed and the planulae allowed to accumulate on the bottoms of the buckets for 30 minutes. Planulae were collected from the bucket bottoms with a pipette and immediately transferred to gently aerated 500 ml beakers filled with 5 µm filtered North Sea water at salinity 34, which was confirmed using a calibrated hand held refractometer (Bellingham and Stanley, Kent, UK). Planulae collected from all mother medusae of each respective species were mixed together in the aerated 500 ml beakers.

2.2.2 *Transferring planulae to replicate wells*

In order to begin each treatment with similar concentrations of planulae, a calibrated "Pipet 4u" brand pipette (Nordhausen, Germany) was used to place an aliquot of known volume of bubbling planulae solution into each well of 6-well polycarbonate culture plates (Thermo Scientific, Walthom, MA) filled with 12 ml of 5 µm-filtered sea water. To ensure that similar numbers of planulae were present in each well at the start of the experiments a digital camera was mounted to the top of a dissecting stereomicroscope and swimming planulae were photographed and then counted. If the numbers of planulae were not similar, the experimental well was cleaned and repopulated with a new aliquot of bubbling planulae solution.

Table 1. Collection locations for medusae and approximate starting numbers of planulae used in each treatment replicate for each of the experiments.

| Species | Medusae collection locations | Number of mother medusae | Initial mean number of planulae per well | Std. Dev. of the mean | Std. Error of the mean |
|---|---|---|---|---|---|
| *Aurelia aurita* | East Sands, St. Andrews, UK | 5 | 66.7 | 10.52 | 1.11 |
| *Cyanea lamarckii* | East Sands, St. Andrews, UK | 5 | 60.2 | 17.82 | 2.52 |
| *Cyanea capillata* | Broughty Ferry, Dundee, UK | 3 | 62.5 | 8.41 | 1.19 |
| *Chrysaora hysoscella* | Dalefort, UK | 3 | 48.0 | 20.87 | 2.13 |

2.2.3 *Pre-experiment acclimation*

After planulae were transferred to their respective 6-well culture plates they were gradually acclimated to target temperatures ±1°C over a period of 3 days in a stepwise manner inside darkened temperature controlled incubators (Lucky Reptile Herp Nursery II incubator, Waldkirch, Germany, Fig. 1) where they remained for the duration of their respective experiments. Temperatures were measured and checked daily throughout the acclimation and experimental periods with USB data loggers **(**Lascar EL-USB-1, Wiltshire, UK) to ensure desired experimental conditions were being met**.**

Figure 1. Lucky Reptile Herp Nursery II incubators utilized during experiments.

### 2.2.4 *Experimental protocols*

After the three day acclimation period was completed experiments were initiated and planulae in each replicate were checked each day in order to determine whether or not they had settled, and if they had settled to which stages they had developed. Not all species tested underwent the same sequence of development. For example, planulae of *C. lamarckii* immediately encysted upon settlement forming planulocysts, whereas none of the other species tested exhibited this behaviour. The normal progression of developmental stages for each species tested is shown in Table 2, and examples of each stage of development are shown in Figure 2. The number of replicates per treatment, temperatures and durations of each experiment are shown in Table 3. Most experiments were allowed to continue for 14 days. This duration was chosen because scyphistomae formed by earlier settling planulae preyed upon remaining swimming planulae and may have had enough energy to begin asexual reproduction. This would lead to erroneous counts of asexually reproduced progeny as successful settlers. Water in the treatment wells was not changed during the experiment, and developing scyphistomae were not purposefully fed.

Table 2. Early life history stages and their sequences of development for each species tested.

| | Early life history stages of respective species | | | |
|---|---|---|---|---|
| Species | Stage 1 | Stage 2 | Stage 3 | Stage 4 |
| *Aurelia aurita* | Not settled (NS) | 0-tentacles (OT) | 4-tentacles (4T) | 8-tentacles (8T) |
| *Cyanea lamarckii* | Not settled (NS) | Planulocyst (PC) | 4-tentacles (4T) | 8-tentacles (8T) |
| *Cyanea capillata* | Not settled (NS) | 0-tentacles (OT) | 4-tentacles (4T) | 8-tentacles (8T) |
| *Chrysaora hysoscella* | Not settled (NS) | 0-tentacles (OT) | 2-tentacles (2T) | 4-tentacles (4T) |

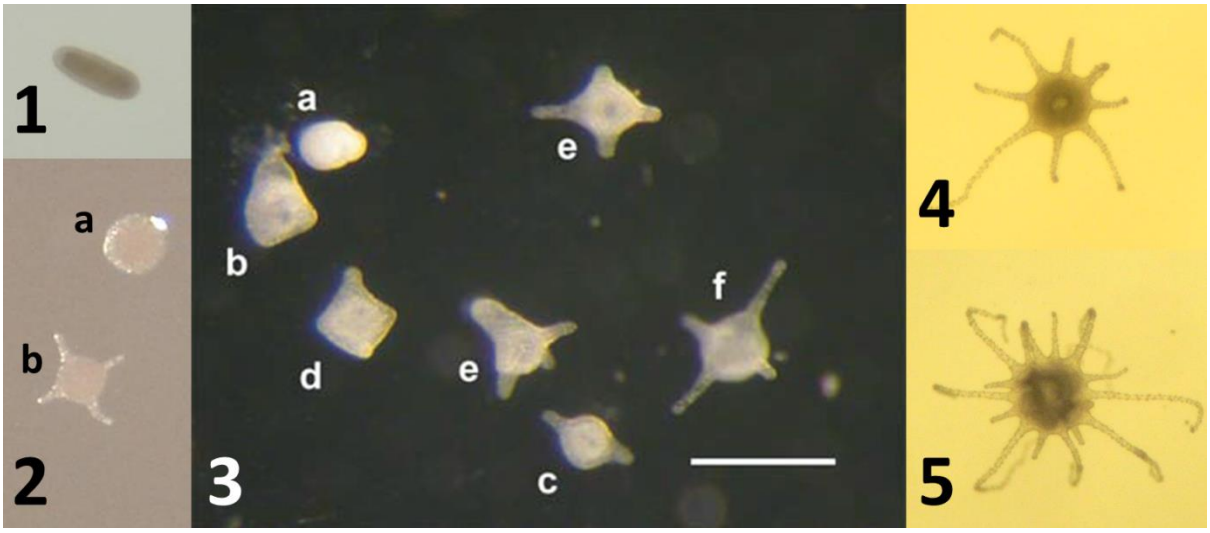

Figure 2. Early stages of scyphistoma development. (1) *Aurelia aurita* planula larva. (2) a. *Cyanea lamarckii* planulocyst, b. 4-tentacles stage scyphistoma. (3) after Holst and Jarms (2007) a. *Chrysaora hysoscella* settled planula, b. 0-tentacles stage scyphistoma, c. 2-tentacles stage scyphistoma, d. 2-tentacles stage with rudiments of additional tentacles forming, e. Early 4-tentacles stage scyphistomae, f. Later 4-tentacles stage. (4) *A. aurita* 8-tentacles stage scyphistoma. (5) *A. aurita* 16-tentacles stage scyphistoma. *Scale bar* = 0.5 mm.

Medusae in UK waters generally brood their planulae from midsummer to early autumn (Russell 1970), so the temperatures tested were chosen to reflect ones planulae are likely to encounter during their settlement attempts, with the addition of a high temperature treatment, 23°C to assess how planulae may respond in a future climate change scenario with increased sea surface temperatures.

Table 3. Summary of experiments testing the effects of temperature on settlement and metamorphosis of planula larvae.

| Species | Temperatures tested (±1°C) | Number of replicates per treatment | Duration (Days) |
|---|---|---|---|
| *Aurelia aurita* | 5, 10, 15, 19, 23 | 18 | 14 |
| *Cyanea lamarckii* | 5, 12, 16, 20, 23 | 10 | 14 |
| *Cyanea capillata* | 5, 10, 15, 20, 23 | 10 | 14 |
| *Chrysaora hysoscella* | 12, 16, 19, 23 | 24 | 7 |

### 2.2.5 *Statistics*

All data were analysed using the statistical software IBM SPSS version 21. Survivorship of planulae was determined by finding the difference between the number of planulae at the start of the experiment and the number that could be accounted for and were in viable, good condition at the end in each of the replicate wells. A viable surviving planula was considered to be one that was either still swimming and appeared competent to settle, or one that had settled and begun to develop normally without deformities. Data for the number of planulae surviving was converted into arcsine square root transformed percentages before further analysis since percentages, or proportions are binomially distributed and this transformation often makes the distribution normal (Ahrens et al., 1990). After evaluating the assumptions of normality and homoscedasticity with Shapiro-Wilk and Levene's tests respectively, one-way ANOVA or Kruskall-Wallis tests were performed as appropriate, followed by respective Tukey's HSD or Mann-Whitney U post hoc tests. For all of the experiments and species investigated the following was the first null hypothesis tested:

$H_{o1}$: The mean percentage of planulae that survived was independent of temperature.

One-way MANOVAs were conducted to test whether stages of development reached by the ends of experiments by planulae of all species examined was independent of temperature. Prior to analysis, the percentages of planulae at each stage of development at the end of the experiments were arcsine square root transformed. One-way MANOVAs were first performed on the aggregated dependent variables, stages of development, in order to avoid inflating the type I error rate in follow up ANOVA or Kruskal Wallis tests (Cramer and Bock 1966). Further, before conducting MANOVA tests, a series of Pearson correlations were performed between the dependent variables in order to test the MANOVA assumption that dependent variables would be correlated with one another in the moderate range (i.e. .20 - .60) (Meyers et al. 2006). For all experiments and species investigated the following was the second null hypothesis tested:

$H_{o2}$: The aggregate dependent variable (stages of development) was independent of temperature.

Before conducting the series of following on tests from significant MANOVAs results, data for stages of development were first tested for normality and homoscedasticity with Shapiro-Wilk and Levene's tests respectively. When the above assumptions were met one-way ANOVAs were conducted followed by a series of Tukey's HSD post-hoc tests to examine individual mean difference comparisons against temperature levels and stages of development subscales. When the above assumptions were not met, nonparametric Kruskal-Wallis tests were performed followed by post hoc Mann-Whitney U tests. For all experiments and species investigated the following additional null hypotheses were tested following on from statistically significant MANOVA results:

$Ho_3$: The mean percentage of planulae in Stage 1 at the end of the experiment will be independent of temperature (see Table 2 for respective stages of development).
$Ho_4$: The mean percentage of planulae in Stage 2 at the end of the experiment will be independent of temperature.
$Ho_5$: The mean percentage of planulae in Stage 3 at the end of the experiment will be independent of temperature.
$Ho_6$: The mean percentage of planulae in Stage 4 at the end of the experiment will be independent of temperature.

**2.3 Results**

2.3.1 *Planula settlement and development of* Chyrsaora hysoscella

Temperature had a significant effect on the mean percentages of planulae that survived until the end of the experiment (Table 4) therefore $H_{o1}$ was rejected. Post hoc comparisons showed significant differences in survivorship between each pair of treatments with 16°C > 19°C > 12°C > 23°C. Three sources of planula mortality were identifiable; being preyed upon by developing scyphistomae, dissolving due to unsuitable conditions, or running out of energy reserves and stopping all activity without metamorphosing into scyphistomae.

Temperature also had a significant effect on the mean percentages of planulae that stopped swimming and sank to the bottoms of their replicate wells without metamorphosing (Table 4). Post hoc comparisons showed that the mean percentage of planulae that stopped swimming without metamorphosing was significantly highest in the 12°C treatment with 12°C > 16°C = 19°C = 23°C (Table 4).

Table 4. One-way ANOVAs for effects of temperature on survivorship of *Chrysaora hysoscella* planulae. Means for stage of development that were shown not to be significantly different with Tukey's HSD test share a letter.

| | ANOVA | | 12°C | | 16°C | | 19°C | | 23°C | |
|---|---|---|---|---|---|---|---|---|---|---|
| Fate | $F_{(3,92)}$ | p | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| Survived | 28.83 | < 0.001 | 0.216 C | 0.151 | 0.521 A | 0.190 | 0.384 B | 0.162 | 0.136 D | 0.105 |
| No metamorphosis | 13.83 | < 0.001 | 0.237 A | 0.233 | 0.050 B | 0.084 | 0.035 B | 0.111 | 0.050 B | 0.073 |

Note N = 96, SD = standard deviation.

This experiment was run for 7 days because all of the planulae fates could be established at the end of that time. Most planulae settled on the undersides of the surface of the water / air interface in replicate wells and there was no evidence for gregarious settlement. Planulae that had not settled, been eaten, or dissolved within seven days simply stopped swimming, sank to the bottoms of the wells and did not metamorphose into scyphistomae. In the 16°C and 19°C treatments planulae began to settle by day two and continued settling until the end of the experiment (Figure 3). Planulae were slower to settle in the 12°C and 23°C treatments with an initial settlement beginning by day three and significantly lower total settlement by day 7 (Figure 3, Table 5).

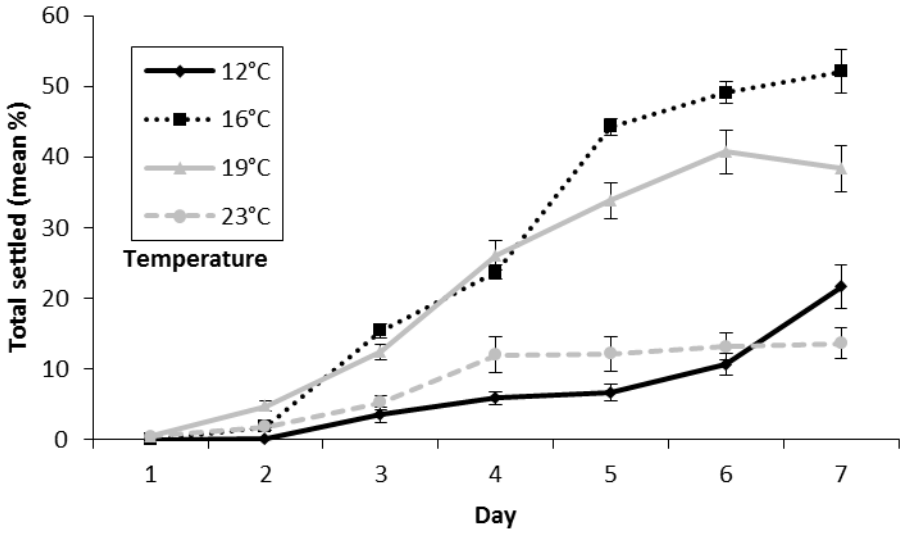


Figure 3. *Chrysaora hysoscella* total mean % planula settlement over seven days; Error bars = SE.

The result from MANOVA test was statistically significant (Pillais' Trace = .886, $F_{(12, 273)} = 9.528$, $p < .001$) therefore null hypothesis $H_{o2}$ was rejected. The multivariate effect size was estimated at 0.295, which implies that 29.5% of the variance in the aggregated dependent variable was accounted for by temperature. A series of one-way ANOVAs were performed on each of the four dependent variables as a follow-up to the significant MANOVA. All of the follow-up ANOVAs were statistically significant (Table 5) therefore null hypotheses $Ho_{3\text{-}6}$ were rejected.

Table 5. Follow on from significant MANOVA results. One-way ANOVAs for effects of temperature on stages of development reached by *Chrysaoara hysoscella* planulae at the end of the experiment. Means for stage of development that were shown not to be significantly different with Tukey's HSD test share a letter.

| | ANOVAs | | 12°C | | 16°C | | 20°C | | 23°C | |
|---|---|---|---|---|---|---|---|---|---|---|
| Stage | $F_{(3,92)}$ | p | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| NS | 28.83 | < 0.001 | 0.784 B | 0.151 | 0.479 D | 0.190 | 0.616 C | 0.162 | 0.864 A | 0.105 |
| 0T | 9.72 | < 0.001 | 0.144 A | 0.141 | 0.141 A | 0.083 | 0.095 A | 0.095 | 0.027 B | 0.036 |
| 2T | 20.91 | < 0.001 | 0.035 C | 0.047 | 0.100 A | 0.057 | 0.048 B | 0.039 | 0.015 D | 0.028 |
| 4T | 31.87 | < 0.001 | 0.037 D | 0.031 | 0.280 A | 0.134 | 0.241 B | 0.138 | 0.094 C | 0.085 |

Note N = 96, SD = standard deviation; NS = not settled, 0T = settled without tentacles, 2T = 2-tentacles stage, 4T = 4-tentacles stage.

Planulae were able to successfully settle and metamorphose into scyphistomae in all of the temperatures tested. More planulae settled and were viable in the 16°C and 19°C treatments, than in the 12°C and 23°C treatments respectively. Planulae that settled in the 12°C treatment were mostly in the 0-tentacles stage but believed to be viable.

The optimal temperatures in terms of settlement and development after 7 days for *C. hysoscella* in this experiment were 16°C and 20°C. Fewer numbers of planulae were able to successfully settle at 12°C and 23°C, and those that did not settle had different fates. Planulae that did not settle at 12°C simply sank to the bottom of the experimental wells and failed to metamorphose. Planulae that did not settle at 23°C were either eaten by resultant scyphistomae of earlier settlers, or dissolved as evidenced by small piles of debris on the bottoms of replicate wells.

2.3.2 *Planula settlement and development of* Cyanea capillata

Temperature had a significant effect on the mean percentages of planulae that survived until the end of the 14 day experiment (Table 6) therefore $H_{o1}$ was rejected. Post hoc comparisons showed significant differences in survivorship between pairs of treatments with 5°C > 10°C = 15°C = 20°C > 23°C. Two sources of mortality were identifiable; being preyed upon by developing scyphistomae starting on day 4, or dissolving due to unsuitable conditions beginning on day 6.

Table 6. Kruskal-Wallis test and descriptive statistics for effects of temperature on survival of *Cyanea capillata* planulae during a 14 day experiment, M = median, IQR = Inter Quartile Range

| | | | | 5°C | | 10°C | | 15°C | | 20°C | | 23°C | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fate | df | H | p-value | M | IQR | M | IQR | M | IQR | M | IQR | M | IQR |
| Survived | 4 | 32.37 | < 0.001 | 0.708 A | 0.007 | 0.423 B | 0.007 | 0.168 B | 0.005 | 0.028 B | 0.002 | 0.001 C | 0.00 |

N=50; medians that share a letter were shown not to be statistically significant with Mann-Whitney post hoc tests.

Planulae in all temperature treatments settled relatively quickly, and the general trend was that planulae in warmer water settled more quickly than planulae in cooler water. Nearly 80% of planulae in the three highest temperatures (15, 20, and 23°C) settled within 2 days (Figure 4) followed by planulae in the 10°C treatment in which 80% of planulae had settled within 3 days. In the 5°C treatment 80% of the planulae had

settled within 6 days, and they had significantly higher total viable settlement (Table 7) at the end of the experiment.

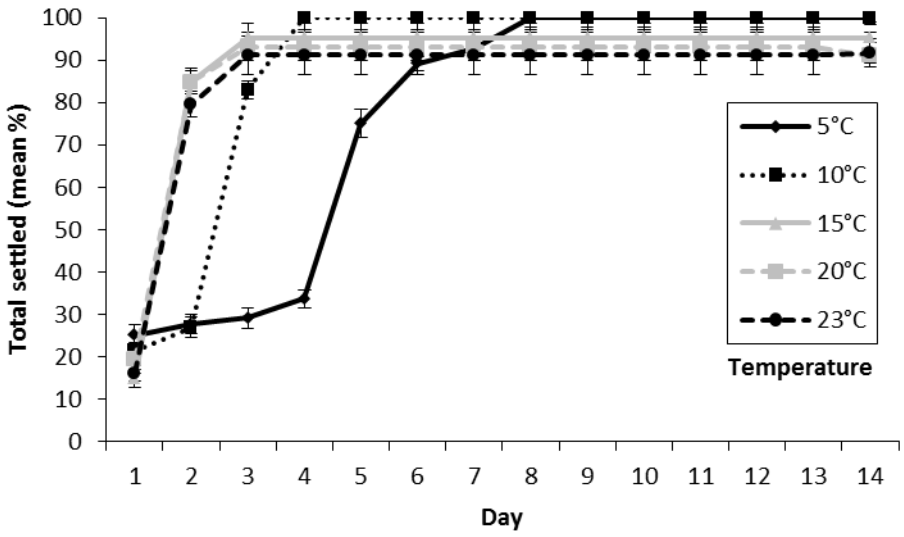


Figure 4. *Cyanea capillata* planulae settlement at 5 different temperatures over a 14 day period; error bars = SE.

A statistically significant MANOVA effect was obtained (Pillais' Trace = 1.969, $F_{(16, 180)} = 10.9$, $p < .01$) and the multivariate effect size was estimated at 0.492 implying that 49.2% of the variance in the aggregated dependent variable was accounted for by temperature. All of the follow-up Kruskal-Wallis tests were statistically significant (Table 7) therefore null hypotheses $Ho_{3\text{-}6}$ were rejected because temperature significantly affected all four stages of development reached. A series of Mann-Whitney U post hoc tests were performed to examine individual mean difference comparisons against temperature levels and stages of development, results are shown in Table 7.

Table 7. Follow on from significant MANOVA *Cyanea capillata* planulae results, Kruskal-Wallis tests with stages of development as dependent variables at the end of a 14 day experiment testing effects of temperature on planulae fates. Means for stages of development that were shown not to be significantly different with Mann-Whitney U tests from each other share the same letter.

| | Kruskal-Wallis tests | | | 5°C | | 10°C | | 15°C | | 20°C | | 23°C | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Stage | H | df | p-value | M | IQR | M | IQR | M | IQR | M | IQR | M | IQR |
| NS | 10.78 | 4 | <0.05 | 0.0 A | 0.007 | 0.052 B | 0.091 | 0.048 B | 0.08 | 0.002 B | 0.006 | 0.0 B | 0.0 |
| 0T | 42.91 | 4 | < 0.001 | 0.541 A | 0.352 | 0.0 B | 0.027 | 0.0 B | 0.004 | 0.0 B | 0.0 | 0.982 C | 0.191 |
| 4T | 34.07 | 4 | < 0.001 | 0.151 A | 0.079 | 0.048 B | 0.037 | 0.06 B, C | 0.045 | 0.07 C | 0.031 | 0.0 D | 0.0 |
| 8T | 39.58 | 4 | < 0.001 | 0.301 A | 0.393 | 0.897 B | 0.106 | 0.902 B | 0.061 | 0.827 B | 0.063 | 0.0 C | 0.0 |

Note N=50; NS = not settled, 0T = settled without tentacles, 4T = 4-tentacles stage, 8T = 8-tentacles stage.

Planulae were not able to successfully settle and metamorphose into scyphistomae in all of the temperatures tested. By the end of the experiment planulae in the 5°C treatment had significantly greater viable settlement than in all other treatments (Table 6), but did not have the significantly greatest mean percentage of planulae that

had developed to the 8-tentacles stage which was the last stage of development reached without having fed (Table 7). The 23°C treatment had the greatest mean percentages of 0-tentacle stage post settled planulae (Table 7), followed by planulae in the 5°C treatment. Planulae in the 0-tentacles stage at 5°C were in good condition and remained viable until the end of the experiment whereas none of the planulae in the 0-tentacles stage maintained at 23°C were viable at the end of the experiment. Planulae that had not yet settled in the 23°C treatments were misshapen, and ones that had settled began to disintegrate on day 6 and continued to do so until the experiment was terminated.

2.3.3 *Planula settlement and development of* Cyanea lamarckii

Temperature significantly affected survivorship of *Cyanea lamarckii* planulae at the end of the 14 day study (Table 8). Post hoc tests showed that greatest survivorship was observed in the 23°C treatment, with 23°C > 19°C = 16°C = 12°C > 5°C. None of the planulae in the 5°C treatment appeared viable at the end of the experiment. Instead, their cilia stopped beating and they all sank to the bottoms of their replicate wells failing to metamorphose into planulocysts. To check whether planulae in the 5°C treatment would metamorphose given more time, planulae in that group were observed for an additional 7 days. After 21 total days none of the 5°C planulae resumed swimming or had metamorphosed.

Table 8. *Cyanea lamarckii*. Kruskal-Wallis test and descriptive statistics for effects of temperature on survivorship of *C. lamarckii* planulae during a 14 day experiment.

| | | | | 5°C | | 12°C | | 16°C | | 19°C | | 23°C | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fate | df | H | p-value | M | IQR | M | IQR | M | IQR | M | IQR | M | IQR |
| Survived | 4 | 30.77 | < 0.001 | 0.0 C | 0.0 | 0.41 B | 0.245 | 0.541 B | 0.341 | 0.696 B | 0.229 | 0.677 A | 0.353 |

N=50, IQR = Interquartile range. Medians that share a letter were shown not to be statistically significant with Mann-Whitney post hoc tests.

Settlement did not occur in any of the five treatments during the first seven days of the experiment, but planulae in the four highest temperatures began settling between days seven and eight (Figure 5). The settlement rate was similar for the 4 highest temperature treatments from days 8 – 14 and post hoc tests revealed that the total mean percentages of planulae that had viably settled for those treatments were not significantly different on day 14 (Table 9).

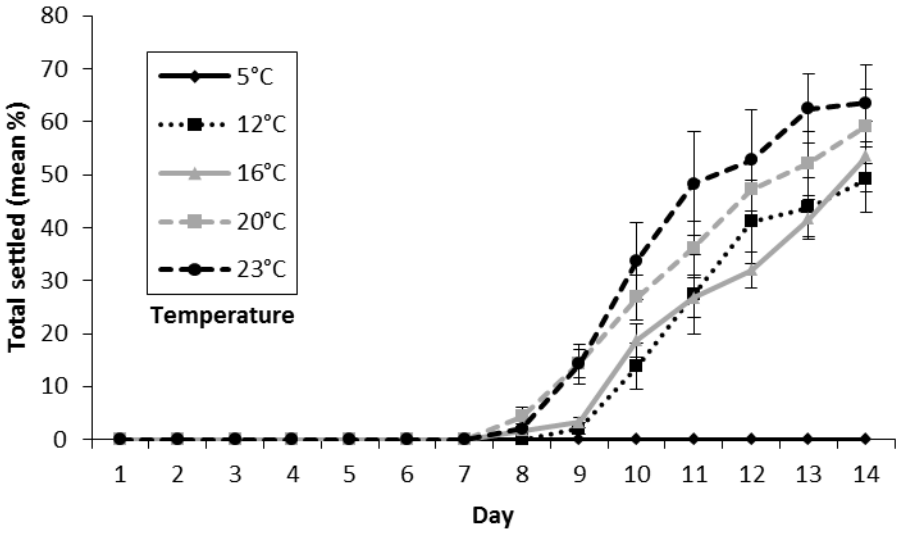


Figure 5. Total mean percentages of *Cyanea lamarckii* planulae settled on each day of a 14 day experiment; error bars = SE.

A statistically significant MANOVA effect was obtained (Pillais' Trace = 2.094, $F_{(16, 180)} = 12.35$, $p < .001$) indicating that temperature had a significant effect on stage of development, the aggregated response variable. The multivariate effect size was estimated at .523, implying that 52.3% of the variance in the aggregated dependent variable was accounted for by temperature. The mean percentage of planulae that had not settled (i.e. stage 1) was statistically significant (Table 9), therefore null hypothesis $H_{o3}$ was rejected. Post hoc tests showed that the mean percentages of planulae that had not settled was highest in the 5°C treatment, with none of the mean percentages of non-settling planulae from 12 – 23°C being significantly different from one another. The mean percentages of planulae in stages 2 – 4 were also shown to be statistically significant (Table 9), therefore null hypotheses $H_{04\text{-}6}$ were rejected.

Table 9. Follow on from significant MANOVA *Cyanea lamarckii* planulae results. Kruskal-Wallis tests with stages of development as dependent variables at the end of a 14 day experiment testing effects of temperature on planulae fates. Means for stages of development that were shown not to be significantly different with Mann-Whitney U tests from each other share the same letter.

| | Kruskal-Wallis tests | | | 5°C | | 12°C | | 16°C | | 20°C | | 23°C | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Stage | H | df | p-value | M | IQR | M | IQR | M | IQR | M | IOR | M | IQR |
| NS | 26.4 | 4 | < 0.001 | 1.0 A | 0.0 | 0.59 B | 0.245 | 0.459 B | 0.0.341 | 0.304 B | 0.229 | 0.322 B | 0.354 |
| PC | 30.8 | 4 | < 0.001 | 0.0 D | 0.0 | 0.38 A, B | 0.133 | 0.336 B, C | 0.21 | 0.237 C | 0.212 | 0.609 A | 0.331 |
| 4T | 36.3 | 4 | < 0.001 | 0.0 C | 0.0 | 0.039 B | 0.137 | 0.189 A | 0.082 | 0.214 A | 0.114 | 0.097 B | 0.108 |
| 8T | 39.1 | 4 | < 0.001 | 0.0 B | 0.0 | 0.0 B | 0.0 | 0.0 B | 0.0 | 0.082 A | 0.121 | 0.0 B | 0.0 |

Note N=50, NS = not settled, PC = planulocyst, 4T = 4-tentacles stage, 8T = 8-tentacles stage.

Some planulae failed to successfully settle and metamorphose into scyphistomae in all of the temperatures tested. There was a downward trend with increasing temperature for the mean percentages of planulae that had not settled by the end of the experiment. None of the planulae settled at 5°C therefore the mean percentage for settling planulae in that group was 0.0% with the remaining treatments having successful settlement rates ranging from 49 – 63%.

Temperature also had significant effects on planulae in each of the other three stages of development with perhaps the most interesting result being the mean percentages of planulae in the planulocyst stage. Post hoc tests showed that there were significantly more planulocysts in the highest and lowest successful settlement temperatures tested with 12°C = 23°C. The mean percentages of planulae that had developed to the 4-tentacles stage were also significant with 16°C = 20°C > 12°C = 23°C > 5°C. Planulae in the 20°C treatment had significantly higher mean percentages of larvae that had developed to the 8-tentacles stage with 20°C > 5°C = 12°C = 16°C = 23°C therefore 20°C was the optimal temperature for quickly developing healthy late stage scyphistomae in this experiment.

2.3.4 *Planula settlement and development of* Aurelia aurita

Temperature significantly affected survival of *Aurelia aurita* planulae at the end of the 14 day experiment, and post hoc tests revealed that survival was greatest for planulae maintained at 5°C (Table 10). Two sources for larval mortality were identified with both involving predation. First, planulae that settled quickly and metamorphosed into scyphistomae went on to prey upon remaining non-settled planulae. Second, planulae that had gregariously settled and metamorphosed into small scyphistomae near established larger scyphistomae were sometimes preyed upon by their neighbours.

Table 10. Kruskal-Wallis test and descriptive statistics for effects of temperature on survival of *Aurelia aurita* planulae during a 14 day experiment.

| | | | | 5°C | | 10°C | | 15°C | | 20°C | | 23°C | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Fate | df | H | p-value | M | IQR | M | IQR | M | IQR | M | IQR | M | IQR |
| Survived | 4 | 30.19 | < 0.001 | 0.592 A | 0.208 | 0.428 B | 0.243 | 0.421 B, C | 0.102 | 0.351 C | 0.102 | 0.416 B, C | 0.102 |

N=90; medians that share a letter were shown not to be statistically significant with Mann-Whitney U post hoc tests.

Planulae maintained at different temperatures began to settle on different days with those maintained at 10, 15 and 20°C beginning to settle sooner than those maintained at 5 and 23°C. Planulae in the 10, 15 and 20°C treatments began to settle on day 2 and gradually continued to settle at similar rates to one another until the end of the experiment (Figure 6). They were followed by planulae in the 5°C treatment which began to settle on day 5 and then rapidly continued to settle until day 8 and then leveling off on day 9. The pattern of settlement in the 23°C treatment was similar to those in the 5°C treatment however planulae did not begin to settle in the 23°C treatment until day 6. The gradual decline in the mean percentages of planulae that had settled in some treatments was due to earlier established larger scyphistomae preying upon smaller scyphistomae resulting from gregarious later settling planulae.

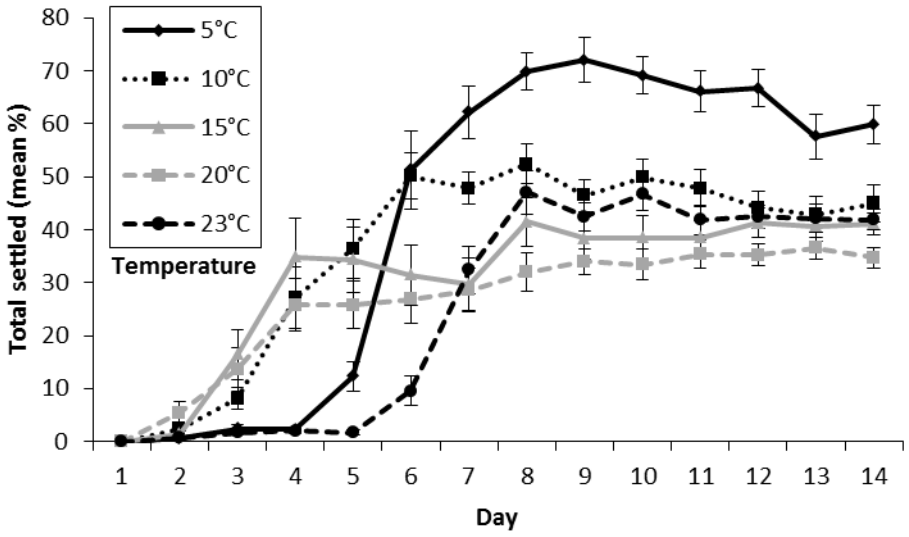


Figure 6. Total mean percentages of *Aurelia aurita* planulae settled on each day of a 14 day experiment.

A one-way MANOVA was conducted to test the hypothesis that there would be one or more mean differences between the aggregated dependent variable (stages of development) and temperature. A statistically significant MANOVA effect was obtained (Pillais' Trace = 1.027, $F_{(20, 336)} = 5.8$, $p < .001$). The multivariate effect size was estimated at .257, implying that 25.7% of the variance in the aggregated dependent variable was accounted for by temperature. All of the follow on Kruskal-Wallis tests for the effects of temperature on mean percentages of larvae observed in each stage of development at the end of the experiment were significant (Table 11).

Table 11. Follow on from significant MANOVA *Aurelia aurita* planulae results. Kruskal-Wallis tests at the end of a 14 day experiment testing effects of temperature on planulae fates. Means for stages of development that were shown not to be significantly different with Mann-Whitney U tests from each other share the same letter.

| | Kruskal-Wallis tests | | | 5°C | | 10°C | | 15°C | | 20°C | | 23°C | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Stage | H | df | p-value | M | IQR | M | IQR | M | IQR | M | IQR | M | IQR |
| NS | 28.86 | 4 | < 0.001 | 0.434 B | 0.195 | 0.571 A | 0.256 | 0.583 A | 0.123 | 0.649 A | 0.102 | 0.586 A | 0.105 |
| 0T | 44.84 | 4 | < 0.001 | 0.271 A | 0.107 | 0.161 B | 0.149 | 0.211 B | 0.149 | 0.041 C | 0.054 | 0.195 B | 0.059 |
| 4T | 23.01 | 4 | < 0.001 | 0.131 A | 0.133 | 0.059 B | 0.043 | 0.049 B | 0.046 | 0.038 B | 0.045 | 0.046 B | 0.052 |
| 8T | 12.06 | 4 | < 0.05 | 0.17 A, B | 0.087 | 0.222 A | 0.101 | 0.154 B | 0.101 | 0.186 A, B | 0.109 | 0.163 B | 0.101 |
| 16T | 34.34 | 4 | < 0.001 | 0.0 C | 0.0 | 0.0 B, C | 0.017 | 0.017 B | 0.042 | 0.031 A | 0.047 | 0.0 B, C | 0.018 |

Note N=90, NS = not settled, 0T = settled without tentacles, 4T = 4-tentacles stage, 8T = 8-tentacles stage, 16T = 16-tentacles stage.

Some planulae of *A. aurita* failed to successfully settle and metamorphose into scyphistomae in all of the temperatures tested. Post hoc tests (Table 11) showed that planulae in the 5°C treatment had the lowest mean percentages of planulae that had not settled by the end of the experiment with 5°C < 10°C = 15°C = 20°C = 23°C. The 5°C treatment also had the significantly largest mean percentages of larvae in the 0-tentacles stage of development with 5°C > 10°C = 15°C = 23°C > 20°C, and similarly

the 5°C treatment had the largest percentages of planulae in the 4-tentalces stage of development with 5°C > 10°C = 15°C = 20°C = 23°C (Table 11). While the mean percentages of planulae that had reached the 8-tentacles stage of development was significant clear trends were not observable. There was however a clear trend for the number of planulae that had developed to the 16-tentacles stage. The 20°C treatment had the largest mean percentages of planulae that had reached the 16-tentacles stage with 20°C > 23°C = 15°C = 10°C > 5°C (Table 11). None of the planulae in the 5°C treatment had reached the 16-tentacles stage of development by the end of the experiment, but they probably would have given more time.

**2.4 Discussion**

Jellyfish planula larvae are important in establishing new colonies through dispersal yet the ways in which temperature affected their settlement rates, and more importantly post-settlement fates, for most species of jellyfish are largely unknown. In this study temperature affected survivorship, settlement rates and ultimately the stages of development reached for all four species tested. Planulae of all species were able to successfully settle by the ends of their respective experiments within a wide range of temperatures, and deleterious effects were only manifested at the highest and lowest temperatures. Possible reasons for this are explained below.

2.4.1 *Mortality due to exceeding thermal tolerances*

Temperature had negative effects on survivorship when planulae were maintained at temperatures beyond their thermal tolerances which were wide ranging for most of the species tested. However, these effects were not immediately observable and were only manifested when experiments were allowed to run for appropriate durations. Some planulae in low temperature treatments sank to the bottoms of their respective replicate wells and failed to metamorphose into scyphistomae. This type of mortality was observed in the *Cyanea lamarckii* and *Chrysaora hysoscella* experiments, and was also observed for planulae of *Cotylorhiza tuberculata* from the Mediterranean sea (Prieto et al., 2010) and *Aurelia aurita* from southern England (Webster and Lucas 2012). Some planulae maintained at high temperatures settled quickly and later dissolved without developing into competent scyphistomae as for example in the *C. capillata* and *Ch. hysoscella* experiments. Mature scyphistomae of the tropical *Cassiopea xamachana* have also been observed to disintegrate in high temperatures (Fitt and Costley 1998), but the planula experiment they conducted had a duration of 72 hours so it is not possible to compare the effect of the elevated temperature on post settlement larvae.

2.4.2 *Mortality due to predation of scyphistomae*

Two additional predation-based sources of mortality were identified during the study. Firstly, planulae were preyed upon by replicate-mates that had settled earlier and metamorphosed into scyphistomae. This type of mortality was observed in all of the experiments. Such behaviour has been observed in other studies. For example, scyphistomae of *A. aurita* in Sweden have been shown to prey upon their own planulae and on the planulae of *C. capillata* (Grondahl 1988b). A later pilot study conducted in St. Andrews confirmed that developing scyphistomae of all species tested preyed upon planulae of all other species including their own. In natural populations predation by dense aggregations of scyphistomae may be able to negatively affect recruitment of other species of planulae (Grondahl 1988b) as well as other species of benthic invertebrates (Thorson 1950, Mileikovsky 1974). Developing

scyphistomae probably have a wide diet and are opportunistic preying upon anything they are physically capable of capturing and ingesting. Being able to eat a wide variety of prey items, including siblings, would ensure that developing scyphistomae are able to acquire required energy for fast growth into mature scyphistomae.

The next source of mortality was again due to post-settlement cannibalism, but this time influenced by gregarious settlement. Young scyphistomae in close proximity to one another often preyed upon neighbouring scyphistomae resulting in a steady decrease in the total number of settled planulae that had survived as exemplified with *A. aurita*. This type of mortality continued until all neighbouring scyphistomae were eaten with the end result being scyphistomae that were evenly distributed across the available settlement area. A similar trend was observed with post settlement specimens of *Chrysaora plocamia* by (Riascos et al, 2013). Reasons for the decreasing survivorship trend with *C. plocamia* were not given but predation by neighbouring scyphistomae would be a potential explanation. Gregarious settlement has been shown for planulae of *C. capillata* (Dolmer and Svane 1993) and *A. aurita* (Grondahl 1989), and this tendency has two major implications. First, settling in the presence of established scyphistomae colonies ensures that planulae settle in an appropriate habitat for successful development. However, settling near other scyphistomae increases the chances of being preyed upon. Post settlement predation by neighbouring scyphistomae may be an important factor in determining initial distributions of juvenile scyphistomae in the field.

### 2.4.3 *Possible shortcomings of methods*

One problem with studies on the settlement of planulae consisting of several replicates with many planulae in each experimental well are the confounding effects of predation which have been largely ignored by most authors. Encounter rates within the wells may be artificially inflated and larval behaviour may be altered (Cowden et al., 1984). The general protocol for conducting experimental planulae settlement studies in the past has been to use percentages (Fitt and Costley 1998, Holst and Jarms 2007, 2010, Ishii et al. 2008) or counts (Nishikawa et al. 2003, Webster and Lucas 2012, Riascos et al. 2013) of settled planulae as response variables. In the future a different and perhaps better way to conduct planulae studies without the confounding effects of predation might be to follow results for individual planulae placed in individual wells.

### 2.4.4 *The influence of temperature on settlement rates*

Temperature had different effects on the settlement rates of different species. One might expect that the general trend would be for planulae maintained in cold temperatures to have lower settlement rates, meaning longer planktic durations, than planulae maintained in warmer temperatures as found for example with *Nemopilema nomurai* from the Sea of Japan (Kawahara et al. 2012) or *Cotylorhiza tuberculata* from the Mediterranean Sea (Prieto et al. 2010). This was the case for *C. capillata* in the experiments described here, and also true in part for *A. aurita* and *Ch. hysoscella*. Planulae of *C. lamarckii* did not settle at 5°C, but the other temperatures tested did not appear to have any effect on settlement rates (Figure 7). At 23°C, the potential climate change scenario summer temperature, settlement was also delayed for *Ch. hysoscella* and *A. aurita*. I interpret this to mean that 23°C might not be an optimal temperature for settlement of these species. Planulae may not find this temperature entirely suitable, but they may eventually settle given no other option. Results for *A.*

*aurita* from St. Andrews are partially in agreement with those of Webster & Lucas (2012) who found that settlement was delayed in cooler temperatures in *A. aurita* from southern England. However, their experiment only considered three temperatures (6, 12, 18°C) which did not include 23°C so a comparison of results at that temperature is not possible.

The effects of temperature on settlement rates are important because they will affect larval dispersal, gene flow and survivorship ultimately affecting the wider distribution of the species. The general trend for scyphozoan planulae from UK seas is that within physiological tolerances there will be greater dispersal potential in cooler waters which is in agreement with findings for a wide range of other invertebrates with planktonic larvae (O'Connor et al. 2007). Greater dispersal is also associated with potentially greater gene flow, or the transportation of genes from one population to another (Bohonak 1999, Nishikawa et al. 2003). However, spending more time in the plankton can reduce survival (Moloney et al. 1994, Hare and Cowen 1997). Dispersal into unsuitable habitats, for example sinking below the thermocline in the northern North Sea would be deleterious to *C. lamarckii* and *Ch. hysoscella* and may be one reason these species are said to have more southerly distributions (Russell 1970). In Chapter three other reasons for the more southerly distribution of *Ch. hysoscella* are presented. Planulae are also subject to predation (Grondahl 1988b, 1989), and in cooler waters with longer planktic durations planulae are subject to if for longer (Rumrill 1990). Predation on planulae has the potential to affect the distribution of scyphistomae which can then go on to affect the locations of jellyfish blooms since scyphistomae are responsible for generating medusae.

2.4.5 *The influence of temperature on settlement fates*

Generally speaking, within thermal tolerances temperature affected development rates but not necessarily the ability to settle and metamorphose which is in accordance with the findings for *A. aurita* from southern England (Webster and Lucas 2012) and *C. plocamia* near Chile (Riascos et al., 2013). Outside of physiological tolerances planulae maintained at low temperatures sank to the bottoms of their replicate wells, stopped swimming and then failed to metamorphose as exemplified by *C. lamarckii* and *Ch. hysoscella*. Planulae of *C. capillata* maintained at 23°C, the sea surface temperatures predicted to possibly occur in a future climate change scenario (Hughes et al. 2010), settled quickly but failed to metamorphose and began to disintegrate by day 6 of 14. In an experiment testing the effects of salinity on settlement of *C. capillata* planulae Holst and Jarms (2010) maintained planulae at room temperature 22°C ± 3°C for 6 days. They recorded the amount of settlement, but did not report on the condition of the larvae. Had they allowed the experiment to run for longer it is highly likely that they would have observed the same phenomenon which may have had implications for the interpretation of their results.

The most interesting results regarding settlement fates were observed in *Cyanea* species. In nonlethal temperatures more planulocysts were formed by *C. lamarckii* at 12 and 23°C than at 16 and 20°C. The presence of more planulocysts at 12°C can be explained by slower developmental rates at lower temperatures. Given one or two more weeks it is expected that scyphistomae would have excysted and developed normally. Planulocysts may act as protection against predation (Brewer & Feingold, 1991) and deleterious abiotic factors (Arai 1997). The planulocysts formed at 23°C appeared to be viable, and those that had excysted developed into healthy 4-tentacles

stage scyphistomae. In natural populations planulocysts of *C. lamarckii* would probably excyst and develop into scyphistomae as temperatures dropped in early autumn, and survive in this stage throughout the winter (Chapter 3) as shown for planulocysts of *C. capillata* from the Niantic River in eastern Connecticut (Brewer & Feingold, 1991). This strategy may allow scyphistomae to mature in time to contribute to medusa blooms the following summer.

A difference exists in the life cycles of *C. capillata* from the Niantic River, Connecticut, USA and *C. capillata* from Broughty Ferry, Scotland, UK. Planulae of *C. capillata* from the Niantic River formed planulocysts upon settlement (Brewer, 1976) whereas those from Broughty Ferry did not. It is highly likely that these populations are molecularly distinct each bearing the same name (Dawson 2005). Planulae of *C. capillata* from Broughty Ferry settled within about 5 days and quickly developed into 8-tentacle stage scyphistomae. Perhaps the relatively fast settlement and development negates the need for a planulocyst stage in North Sea *C. capillata*.

2.4.6 *General conclusions*

Tolerances of planula larvae to heat and cold stresses may be a physiological limiting factor defining latitudinal range. Of the four species of medusae studied here, *Cyanea capillata* is northern boreal, *Cyanea lamarckii* and *Chrysaora hysoscella* are southern boreal and *Aurelia aurita* occurs all around the British coasts (Russell 1970). The temperatures considered in these experiments were within the range of temperatures likely to be encountered by planulae with the addition of a global climate change scenario temperature (Hughes et al. 2010). It would be expected that northern species would have higher survivorship in cooler temperatures whilst southern species would have better survivorship in warmer temperatures, and *A. aurita* would be expected to have high survivorship in all temperatures tested. The data from the experiments described in this chapter suggest that this was the case.

The results presented here suggest that warmer temperatures may lead to greater post settlement mortality for planulae of species like *C. capillata* and *Ch. hysoscella* at the southern extremes of their ranges which could lead to a gradual shift northward. If planulae are unable to successfully establish or supplement existing colonies of scyphistomae which are subject to competition (Watanabe and Ishii 2001, Colin and Kremer 2002, Ishii et al. 2008) and predation (Hernroth and Grondahl 1985a) eventually those southern populations will disappear. Increasing temperatures may allow *C. lamarckii* which may have been thermally restricted by cool temperatures to move farther northward and increase their range. Predicted warming should have little effect on the range of *A. aurita* as influenced by effects on the planula stage because they were able to successfully settle in all of the temperatures tested.

Planulae in this study were shown to have a remarkably wide range of thermal tolerances and so impacts of increased temperatures may not constitute an important a bottleneck point in the life cycle. Temperatures appeared to have more importance in determining rates of development rather than affecting the ability to develop. Increasing sea temperatures may restrict dispersal potential by decreasing the duration of the planktonic phase however, the longer-lived medusae are also dispersed in the plankton. Therefore, the amount of dispersal restriction caused by thermal effects on the planulae may be minimal.

# Chapter 3

**The effects of temperature and salinity on asexual reproductive output of scyphistomae**

## 3.1 Introduction

Jellyfish blooms have been chronicled in various ways since prehistoric times. Specimens are present in the fossil record, and jellyfish were also depicted on pottery by the ancient Minoans *ca.* 4000 BCE (Condon et al. 2012). Over the last few decades it has been hypothesised that the frequency and magnitude of jellyfish blooms has been changing, but the direct causes for these perceived changes are unclear. In many locations blooms appear to be occurring more often than they used to (Mills 2001, Richardson et al. 2009, Dong et al. 2010, Brotz et al. 2012) while in others jellyfish seem to be disappearing (Dawson et al. 2001, Mills 2001). The magnitude, frequency, and locations of blooms can be different each year, and variations may also occur over longer time scales (Purcell 2005). Whether blooms are occurring more frequently now than they did in the past is challenging to answer because of the lack of accurate long-term monitoring (Purcell et al. 2007, Nickell et al. 2010). Presently, there may not be enough data to support the paradigm that global jellyfish populations are increasing (Condon et al. 2012), and available evidence appears to suggest that jellyfish abundances fluctuate with long-term climate cycles (Condon et al. 2013).

Whilst human activities in some locations enhance conditions favourable for the formation of larger jellyfish blooms than would naturally occur (reviewed in Chapter 1), studies linking climate variability with medusa abundance indicate that environmental variables are important in determining population sizes. Examples include blooms of *Pelagia noctiluca* in the western Mediterranean which have been correlated with warm temperature, low rainfall and high atmospheric pressure (Goy et al., 1989); *Chrysaora quinquecirrha* medusa abundances in the Chesapeake Bay USA estuary which have been linked with low stream flow and warm temperatures during May (Cargo and King 1990); and increased medusa abundances of *Chrysaora* spp. and *Aurelia* sp. in the Gulf of Mexico which have been linked with warm winters, cool dry springs, and warmer than average summers (Robinson and Graham 2013). In the North Sea jellyfish medusa abundance has been linked with the NAO (Lynam et al. 2004, 2005b, 2010).

The winter NAO index alternates between positive and negative phases and this affects the frequencies and magnitudes of storms leading to variations in sea temperature and salinity (Visbeck et al. 2003). Changes in sea water parameters due to the influence of the NAO have been shown to influence the abundance, distribution, and growth rate of organisms at various trophic levels (Drinkwater et al. 2003). From 1977 – 1979 the NAO was in a negative phase and medusae of *Cyanea capillata, C. lamarckii* and *Aurelia aurita* were highly abundant in the southern North Sea, whilst medusae of *C. lamarckii* and *A. aurita* were less abundant when the NAO was in a positive phase (Lynam et al. 2004, 2005b, 2010). Medusa abundance in the northern North Sea was more strongly linked with oceanic inflow, where the

influence of NAO on medusa abundance may be masked, whilst in the southern North Sea medusa abundance was more strongly linked with the NAO index (Lynam et al. 2010). Whilst studies have linked medusa abundance with climate variability, the underlying causative mechanisms behind these correlations are unclear.

In order to better understand how climate variability may affect the timing and abundance of medusae it is important to study the effects of environmental conditions on all the life history stages of jellyfish. It is especially important to study the scyphistomae since they determine whether or not a bloom of medusae will form via the process of strobilation. Scyphistomae also play a vital role in the life cycle of many jellyfish because they sustain and expand the benthic colonies via asexual reproduction. The locations and habitat for scyphistomae colonies of British jellyfish are largely unknown with the exception of *A. aurita* (e.g., Fig. 1). Some authors have gone so far as to speculate about scyphistoma locations, and timing of strobilation events based upon presence of ephyrae found in near shore waters (Verwey 1942, Hernroth and Grondahl 1985b, Grondahl 1988a, Lucas and Williams 1994). Until scyphistoma populations are found and studied long-term *in situ* it will be necessary to rely on laboratory experiments to learn more about how benthic life history stages may respond to different climate scenarios.

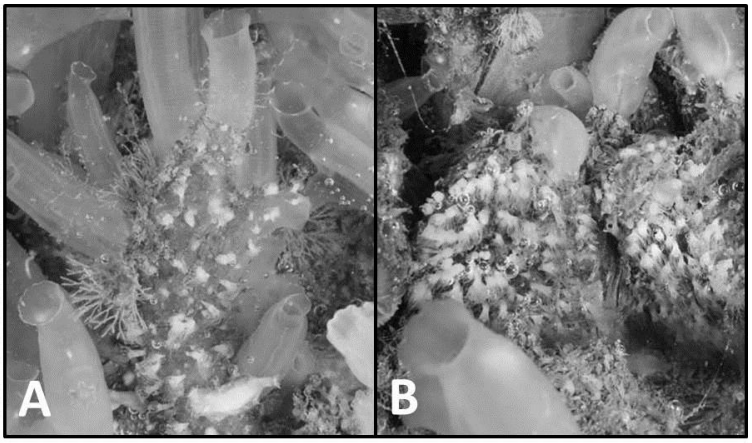


Figure 1. Natural colonies of *Aurelia aurita* scyphistomae found living on (A) ascidians, *Ciona intestinalis*, and (B) mussels, *Mytilus edulis*, on the underside of floating docks at Craobh Haven harbour, Scotland 31 July 2013.

Laboratory experiments were conducted using incubators to investigate the effects of changed temperature and salinity conditions on different species and populations of jellyfish scyphistomae native to British waters in order to investigate the role of changing environmental conditions on regulating medusa and scyphistoma abundance. Specific hypotheses were that changes in both temperature and salinity significantly affected (1) mortality, and (2) asexual reproductive output of scyphistomae, as well as (3) timing of release, and (4) abundance of juvenile medusae.

## 3.2 Methods and materials

### 3.2.1 *Founding stock cultures*

Experiments were conducted with scyphistomae of *C. lamarckii*, *C. capillata*, *Ch. hysoscella* and two different populations of *A. aurita*; one from Orkney, Scotland and the other from Southampton, England. Scyphistomae of *A. aurita* (Southampton)

were obtained from Jamie Craggs, Aquarium Curator, from the Horniman Museum in London, England. They were grown from planulae produced sexually by jellyfish originating near Southampton, England during summer 2010. Scyphistomae of *A. aurita* from Orkney were provided by Dr. William Sanderson, Reader, from Herriot-Watt University, Edinburgh. In 2010 Dr. Sanderson discovered the scyphistomae whilst SCUBA diving in Scapa Flow. The *A. aurita* (Orkney) scyphistomae were growing on the tests of ascidans, *Ascidia mentula*, which were attached to the wrecks of the WW II escort vessel F2 and WW I light cruiser SMS Karlsruhe in 14 – 17 and 10 – 27 meters deep water respectively. The ascidians, with scyphistomae attached, were subsequently transported to the Scottish Oceans Institute. Individual scyphistomae were carefully removed with a fine tipped forceps from their host ascidians and then placed inside plastic culture plates filled with 5µm-filtered North Sea water where they attached naturally.

To establish stock cultures of *C. capillata* and *C. lamarckii* scyphistomae, planulae were collected from the brood pouches on the oral arms of five beach-stranded female medusae of each species. Planulae from all five specimens were mixed together. The *C. capillata* medusae originated from Dunstaffnage Castle beach, near Oban, Scotland, and the *C. lamarckii* medusae were collected on East Sands beach, St. Andrews, Scotland. Planulae of *C. capillata* were settled and raised to the scyphistoma stage at the Scottish Association for Marine Science, Oban, during summer 2011, and planulae of *C. lamarckii* were settled and raised into scyphistomae at the SOI, St. Andrews, during summer 2012. Mr. Craggs from the Horniman Museum also collected planula larvae of *Ch. hysoscella* that were released by 3 sexually mature female medusae he collected whilst SCUBA diving near Dalefort, Wales, in August, 2011. Mr. Craggs posted the *Ch. hysoscella* planulae to the SOI where they were allowed to settle on plastic culture dishes and subsequently cultivated, ultimately reaching the scyphistoma stage. Once established, all stock cultures of scyphistomae were maintained at 10°C in the SOI and fed *Artemia franciscana* (Kellog) nauplii once per week.

3.2.2 *Selecting temperatures and salinities to test*

In order to select appropriate temperatures to test, ranges commonly reported for stations in the North Sea by the Centre for Environment, Fisheries and Aquaculture Science (Cefas) were employed (e.g., Fig. 2). A lower case of 4°C was selected as reflecting typical late winter temperatures. A warming trend has been observed in the North Sea over the last 25 years and this is predicted to continue (Belkin 2009, Hughes et al. 2010). Therefore, 23°C was selected as an upper case to examine the possible effects of extreme summer temperatures which might occur in the southern North Sea during the 2080s (Hughes et al. 2010). Salinities were chosen to reflect ranges potentially experienced by North Sea and other European scyphistomae (Grondahl 1988a), and were within the ranges reported for successful planulae settlement and development for *C. capillata*, *C. lamarckii*, *Ch. hysoscella* and *A. aurita* from Helgoland, German Bight, North Sea (Holst & Jarms, 2010).

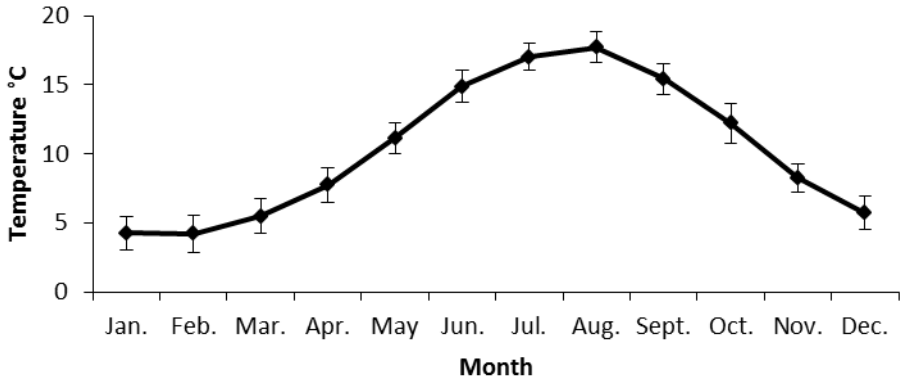


Figure 2. Monthly average sea surface temperatures at Cromer, Norfolk England, located at 52° 56'N, 1° 18'E covering the period 1971 – 2000; bars = SD. The data used to produce this chart were obtained from http://www.cefas.defra.gov.uk.

The temperatures and salinities tested for each species, in addition to sample sizes in each experiment, are shown in Table 1.

Table 1. Summary of temperatures and salinities tested for each species in laboratory incubator experiments testing the effects of temperature and salinity on asexual reproductive output of scyphistomae.

| Species | Temperature ±1 °C | Salinity | n |
|---|---|---|---|
| *Cyanea capillata* | 4, 9, 14, 19, 23 | 21, 27, 34 | 18 |
| *Cyanea lamarckii* | 4, 9, 14, 19 | 27, 34 | 18 |
| *Chrysaora hysoscella* | 4, 9, 14, 19, 23 | 27, 34 | 18 |
| *Aurelia aurita* (Orkney) | 4, 9, 14, 19, 23 | 21, 27, 34 | 15 |
| *Aurelia aurita* (Southampton) | 4, 9, 14, 19, 23 | 21, 27, 34 | 18 |

3.2.3 *Equipment and acclimations*

Experiments were conducted inside darkened temperature controlled incubators (Lucky Reptile Herp Nursery II incubator, Chapter 2, Fig. 1). The incubators were darkened to illuminate the potentially confounding effects of light on asexual reproduction. The temperature in each incubator was continuously measured throughout the acclimation and experimental periods with USB data loggers **(**Lascar EL-USB-1**).** North Sea water at salinity 34 was adjusted by mixing with distilled water to make sea water of salinities 21 and 27. Salinity was measured with a calibrated hand held Bellingham and Stanley refractometer. One scyphistoma from the stock cultures described above was placed in each well of 6-well polycarbonate culture plates filled with 12 ml of 5µm-filtered North Sea water, and then gradually acclimated to target salinities at 10°C in a stepwise manner over 7 days. Next, they were gradually acclimated to target temperatures over a period of 7 additional days. During the experiments scyphistomae were fed *A. franciscana* nauplii to repletion once per week with the water being changed in each of the wells the following day. Uneaten food was removed and water was changed using a pipette, and refilled with 5µm-filtered seawater of appropriate salinity and temperature.

3.2.4 *Recording data*

Each week the scyphistomae were examined under a dissecting stereomicroscope for the formation of new progeny scyphistomae, to check for strobilation, and to record any mortality. Progeny scyphistomae were removed from the wells as soon as they had separated from parent scyphistomae in order to eliminate the effects of crowding

on asexual reproduction. If at the end of the eight week experiment a scyphistoma was observed to still be undergoing the process of strobilation, incubations were continued until the last ephyrae was released from the strobila. This enabled an accurate count for the number of ephyra released by that strobila. At the ends of the incubations scyphistomae were removed from their experimental wells with fine tipped forceps, and the number of podocysts was counted.

3.2.5 *Statistics*

Response data were first explored using Cleveland dot plots to identify potential outliers, and then verified using leverage plots and Cook's distances. Scatter plots were produced to visualize the relationships between response variables and explanatory variables. Pair plots with Pearson correlation coefficients were used to assess for collinearity amongst the explanatory variables temperature and salinity. Response variables in the experiments were the number of progeny scyphistomae and podocysts produced, whether or not mortality or strobilation had occurred, the time until strobilation began, duration of strobilation events, and the numbers of ephyrae produced per individual in each treatment group. Since the response variables were either counts (e.g. number of podocysts produced), or were binomial in nature (e.g. strobilated or did not) generalized linear models (GLMs) were used to model the effects of temperature, salinity and their interaction on the response variables [1]:

$$(g)\mu = \beta_1 + \beta_2 X_1 + \beta_3 X_2 + \beta_4 X_1 * X_2 + \varepsilon \quad [1]$$

where $\mu$ is the mean value of the response variable, g denotes a link function (Table 2), $\beta_1$ is the intercept, $\beta_{2\text{-}4}$ are slope parameters, $X_1$ is temperature, $X_2$ is salinity, and $\varepsilon$ is the error distribution (i.e. Poisson or binomial). Temperature and salinity were coded as discrete factors rather than continuous variables since temperature and salinity treatments were in a limited number of distinct groups. Best fitting models were based on Akaike Information Criteria, followed by analysis of deviance likelihood ratio tests. Since there is no $R^2$ value computed in GLMs, an approximation may be achieved using explained deviance (Zuur et al., 2013) given by formula [2]:

$$\text{(null deviance – residual deviance)/null deviance x 100} \quad [2]$$

Model validation was applied to verify underlying assumptions which included checking and correcting for overdispersion if detected (Ver-Hoef and Boveng 2007, Zuur et al. 2013). In order to verify homogeneity of variance, residuals versus fitted values were plotted, and to check whether the residuals had normal distributions Q-Q plots were examined. All calculations were conducted using R version 2.15.1 (R Development Core Team 2012).

3.2.6 *Visualising modelled asexual reproductive output*

In order to generate figures illustrating the predicted asexual reproductive output of scyphistomae under different temperature scenarios best fitting models of results were first selected. Predictions were then made using the best fitting models such that 30 predicted probability values occurred within each 1°C temperature bin. The means of the predicted values of the respective probabilities within each temperature bin were

then matched with the months at which those mean temperatures are reported to occur (http://www.cefas.defra.gov.uk), and respective figures generated.

### 3.3 Results

#### 3.3.1 *Cyanea capillata*

A summary of the best fitting GLMs for the effects of temperature, salinity and their interaction on asexual reproductive output and survivorship of *C. capillata* scyphistomae are given in Table 2. Summaries of descriptive statistics and analysis of deviance results for all British species studied here may be found in appendices I and II respectively.

Table 2. *Cyanea capillata*. Summary of best fitting generalized linear models for the results of an experiment testing the effects of temperature and salinity on asexual reproductive output, strobilation and mortality of scyphistomae. The full model was: Response Variable ~ Temperature + Salinity + Temperature x Salinity + ε.

| Response variable | Significant predictor variables | Family | Link | Explained deviance (%) |
|---|---|---|---|---|
| Surviving scyphistomae | ~ Temperature | Binomial | Logit | 44.8 |
| Podocysts produced | ~ Temperature | Poisson | Log | 43.1 |
| Strobilating scyphistomae | ~ Temperature | Binomial | Logit | 49.2 |
| Onset of strobilation | ~ Temperature | Poisson | Log | 27.7 |
| Strobilation duration | ~ Temperature + Salinity | Poisson | Log | 35.6 |
| Ephyrae produced | ~ Temperature + Salinity | Poisson | Log | 53.5 |

##### 3.3.1.1 *Surviving scyphistomae*

As temperatures increased, survivorship of scyphistomae decreased (Fig. 3A). Survivorship of scyphistomae was significantly linked with temperature, but not with salinity or their interaction. Nearly all scyphistomae survived at 4°C, which was the lowest temperature tested. Conversely, all scyphistomae maintained at 23°C had perished within 3 weeks.

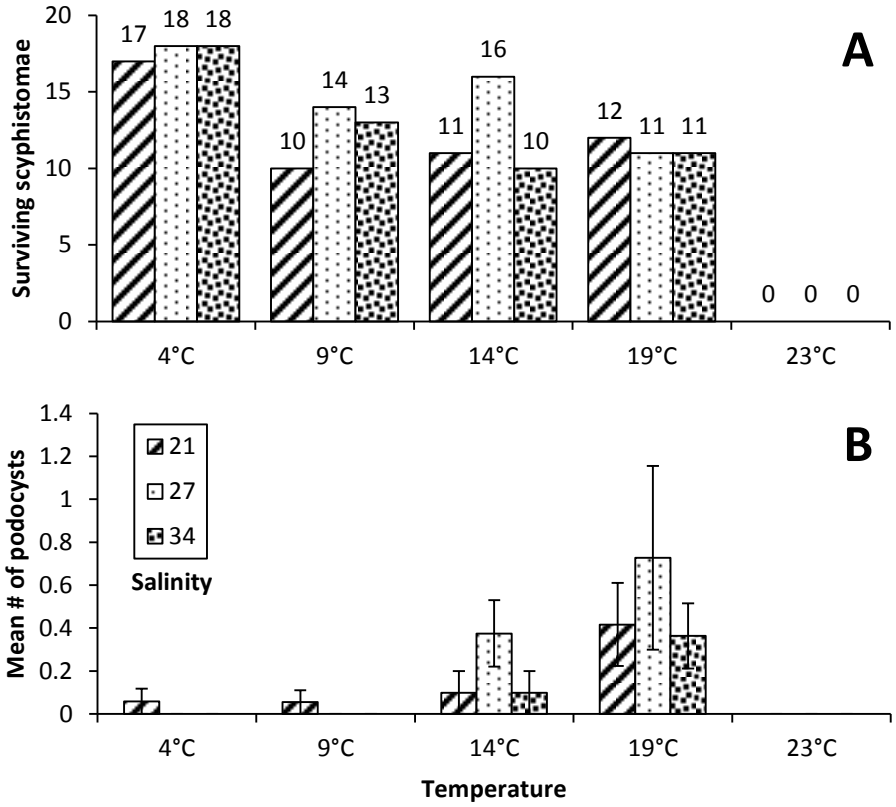


Figure 3. *Cyanea capillata*. (A) Total number of surviving scyphistomae out of 18 at the start of the experiment. (B) Mean number of podocysts produced per scyphistoma; n = 18, error bars = SE.

3.3.1.2 *Progeny scyphistomae*

Asexual reproductive output of *C. capillata* scyphistomae was limited to the production of podocysts, and ephyrae through the process of strobilation. No progeny scyphistomae were produced during the eight week experiment in any of the temperature and salinity combinations.

3.3.1.3 *Podocysts*

The mean number of podocysts produced by scyphistomae was significantly linked with temperature, but not with salinity, or their interaction. The greatest mean number of podocysts per scyphistoma, 0.73, was produced by scyphistomae maintained at 19°C and a salinity of 27 (Fig. 3B). Very few podocysts were produced in any of the 4 or 9°C treatments, and none were produced at 23°C since all of those scyphistomae died.

3.3.1.4 *Strobilating scyphistomae*

Scyphistomae strobilated between 4 – 19°C, with far more strobilating at 4 and 9°C than at 14 and 19°C (Fig. 4A). The numbers of strobilating scyphistomae maintained at 4 and 9°C ranged from 12 to 17. At 14 and 19°C, the numbers of strobilating scyphistomae ranged from 0 to 3. None of the scyphistomae maintained at 23°C strobilated before perishing. Generalised linear regression showed a significant relationship with the number of scyphistomae that strobilated and temperature, but not

with salinity, or their interaction. The predicted probability of *C. capillata* scyphistomae strobilating during an 8 week period at temperatures ranging from 4 – 23°C based on pooling the data from all the salinity treatments is shown in Fig. 4B.

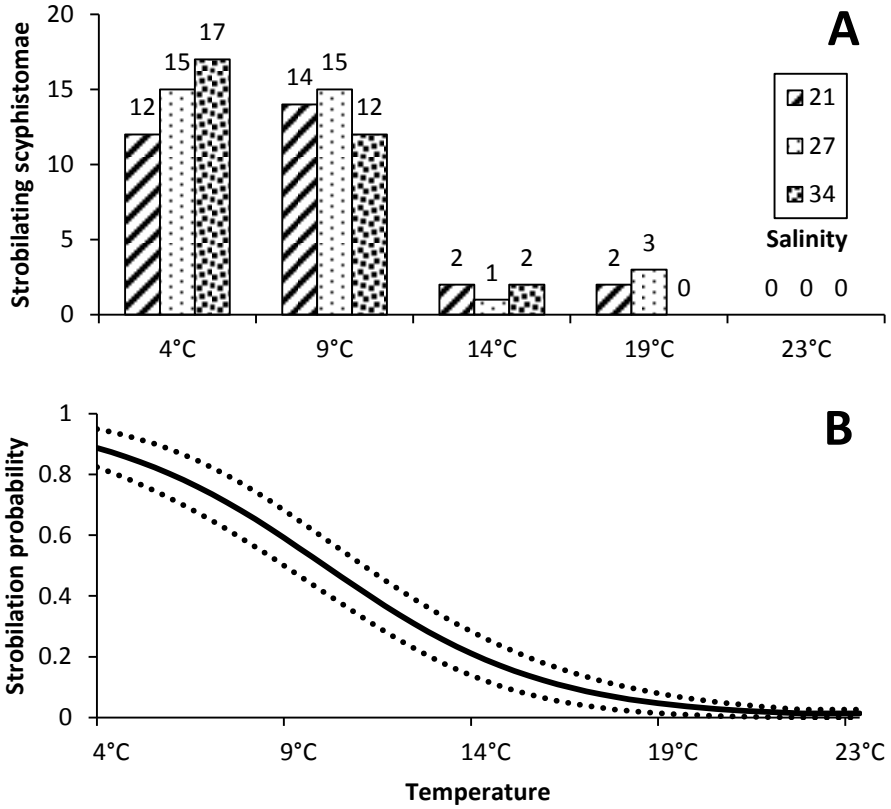


Figure 4. *Cyanea capillata*. (A) Total number of scyphistomae that strobilated during the experiment; n = 18 per treatment. (B) GLM predicted probability (solid line) of strobilating within 8 weeks when maintained at given temperatures; with 95% confidence intervals (dotted lines).

3.3.1.5 *Onset of strobilation*

Scyphistomae of *C. capillata* maintained in warmer temperatures strobilated sooner than scyphistomae in cooler temperatures. There was a significant relationship with the number of weeks until the process of strobilation began and temperature, but not with salinity or their interaction. Of the scyphistomae that strobilated, the mean number of weeks to initiate the process after the start of the experiment ranged from 1 to 3.2 weeks (Fig. 5A). The greatest mean number of weeks until the onset of strobilation, 3.2, was observed at 4°C, and the least mean number of weeks, 1.0, was observed in multiple treatment groups.

3.3.1.6 *Strobilation duration*

The mean number of weeks to generate and release all ephyrae in a strobilation event, or strobilation duration, varied significantly with both temperature and salinity, but not their interaction. Decreasing temperature and salinity increased strobilation durations (Fig. 5B). The greatest mean number of weeks to complete the process of

strobilation, 4.1, was observed at 4°C salinity 21, and the least mean number of weeks, 1.0, was observed in multiple warmer treatment groups (Fig. 5B).

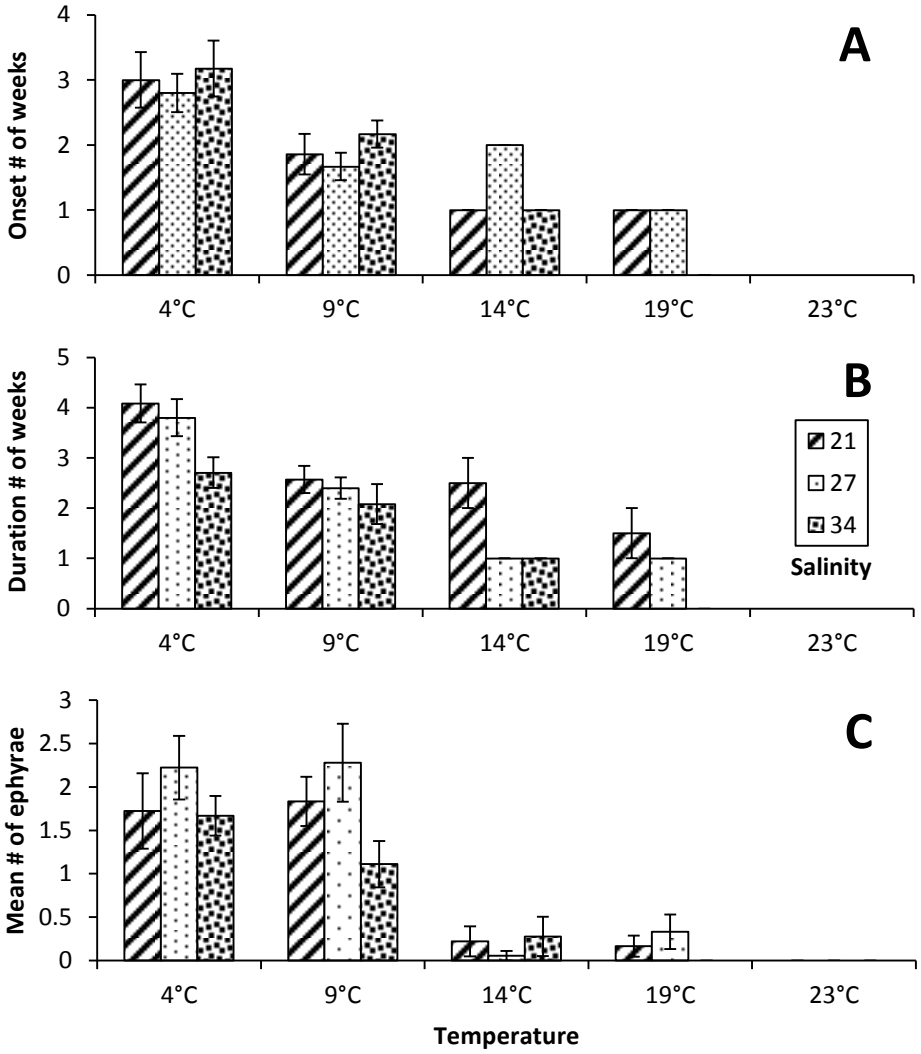


Figure 5. *Cyanea capillata*. (A) Mean number of weeks until the onset of strobilation. (B) Mean strobilation durations. (C) Mean number of ephyrae produced per scyphistoma in each treatment group; n = 18, error bars = SE.

3.3.1.7 *Ephyrae produced*

As temperature increased the mean number of ephyrae produced in treatment groups decreased (Fig. 5C). Temperature and salinity, but not their interaction, significantly affected the mean number of ephyrae produced in each treatment group. Scyphistomae maintained at 4 and 9°C produced more ephyrae than those maintained at 14 and 19°C (Fig. 5C). The greatest mean number of ephyrae produced per scyphistoma, 2.3, was produced at 9°C and salinity 27. No ephyrae were produced by scyphistomae maintained at 23°C before perishing.

### 3.3.2 *Cyanea lamarckii*

A summary of the best fitting GLMs for the effects of temperature and salinity on asexual reproductive output of *C. lamarckii* scyphistomae are shown in Table 3.

Table 3. *Cyanea lamarckii*. Summary of best fitting generalized linear models for an experiment testing the effects of temperature and salinity on asexual reproductive output, strobilation and mortality of scyphistomae. The full model was Response Variable ~ Temperature + Salinity + Temperature x Salinity + ε.

| Response variable | Significant predictor variables | Family | Link | Explained deviance (%) |
|---|---|---|---|---|
| Surviving scyphistomae | None | Binomial | Logit | NA |
| Progeny scyphistomae produced | None | Poisson | Log | NA |
| Podocysts produced | ~ Temperature | Poisson | Log | 31.0 |
| Strobilating scyphistomae | ~ Temperature | Binomial | Logit | 23.0 |
| Onset of strobilation | ~ Temperature + Salinity | Poisson | Log | 53.0 |
| Strobilation duration | ~ Temperature | Poisson | Log | 48.0 |
| Ephyrae produced | ~ Temperature + Salinity + Temperature x Salinity | Poisson | Log | 29.0 |

3.3.2.1 *Surviving scyphistomae*

The number of scyphistomae that survived for the duration of the experiment was high in all treatment groups ranging, from 16 to 18 individuals from a starting population of 18 (Fig. 6A). No mortality occurred in any of the 4°C treatment groups. A small amount of mortality did occur in each of the 9, 14 and 19°C treatment groups, but there were no significant relationships between survivorship and temperature, salinity or their interaction.

3.3.2.2 *Progeny scyphistomae*

Progeny scyphistomae were produced in all temperature and salinity treatments, but they were not produced in great abundance (Fig. 6B). The highest mean number of progeny scyphistomae, 0.83 progeny per scyphistoma, was produced at 4°C and a salinity of 34. The lowest mean numbers of progeny produced, 0.28, were observed in the 14°C salinity 34, and 19°C salinity 27 groups. There were no significant relationships with the number of progeny scyphistomae produced and temperature, salinity, or the temperature salinity interaction.

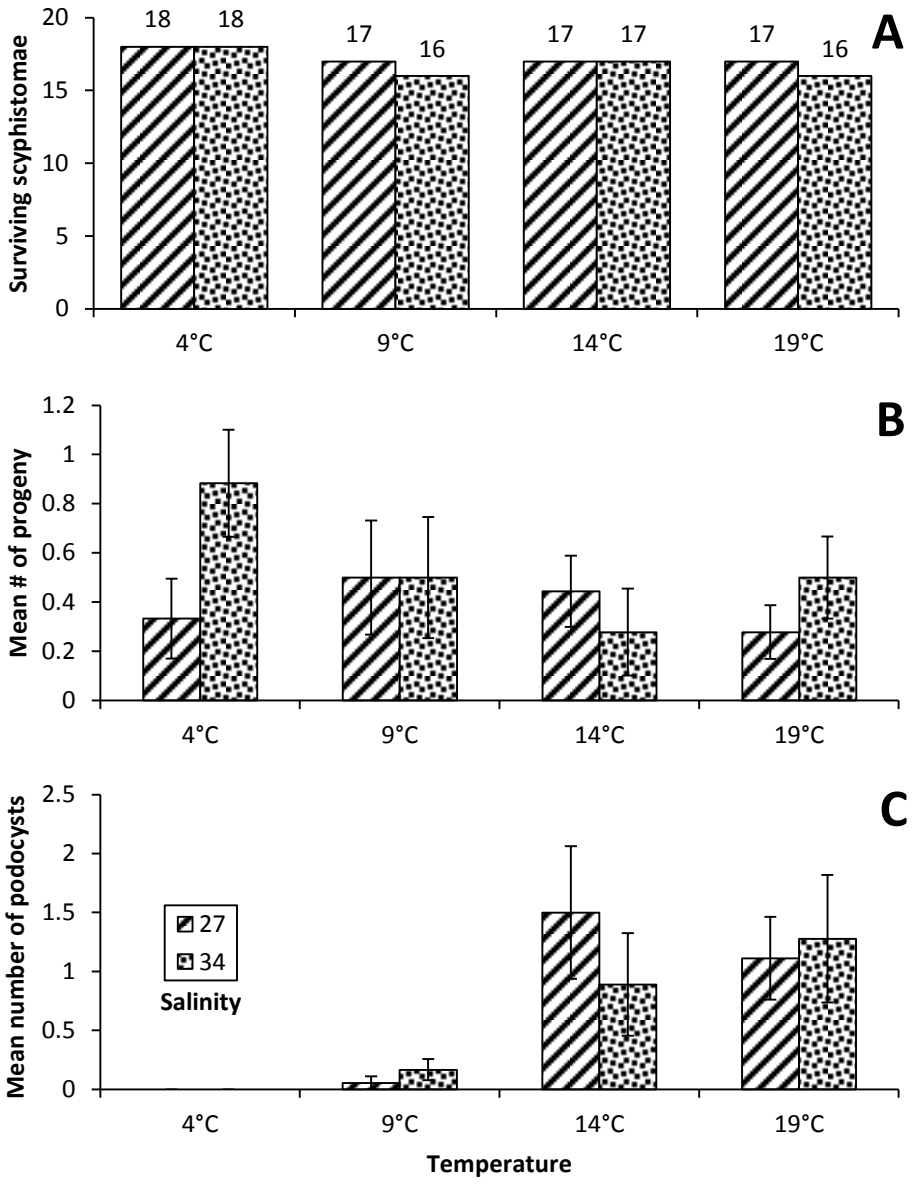


Figure 6. *Cyanea lamarckii*. (A) Total numbers of scyphistomae out of 18 that survived for the duration of the experiment. (B) Mean number of progeny scyphistomae produced per scyphistoma. (C) Mean number of podocysts produced per scyphistomae in 8 different combinations of temperature and salinity; n = 18, error bars = SE.

3.3.2.3 *Podocysts*

The mean number of podocysts produced per scyphistoma was significantly and positively linked temperature, but not with salinity or their interaction. The highest mean number of podocysts produced, 1.5 podocysts per scyphistoma, was observed at 14°C salinity 27 (Fig. 6C). No podocysts were produced at 4°C in either of the salinity treatments.

3.3.2.4 *Strobilating scyphistomae*

The number of scyphistomae that strobilated during the experiment was significantly and negatively linked with temperature, but not with salinity, or the temperature

salinity interaction. Strobilation occurred at 4, 9 and 14°C, with the greatest number at 4°C. No strobilation occurred in the 19°C treatment group (Fig. 7A). The predicted probability of *C. lamarckii* scyphistomae strobilating during an 8 week period when maintained at temperatures ranging from 4 – 23°C is shown in shown in Fig. 7B.

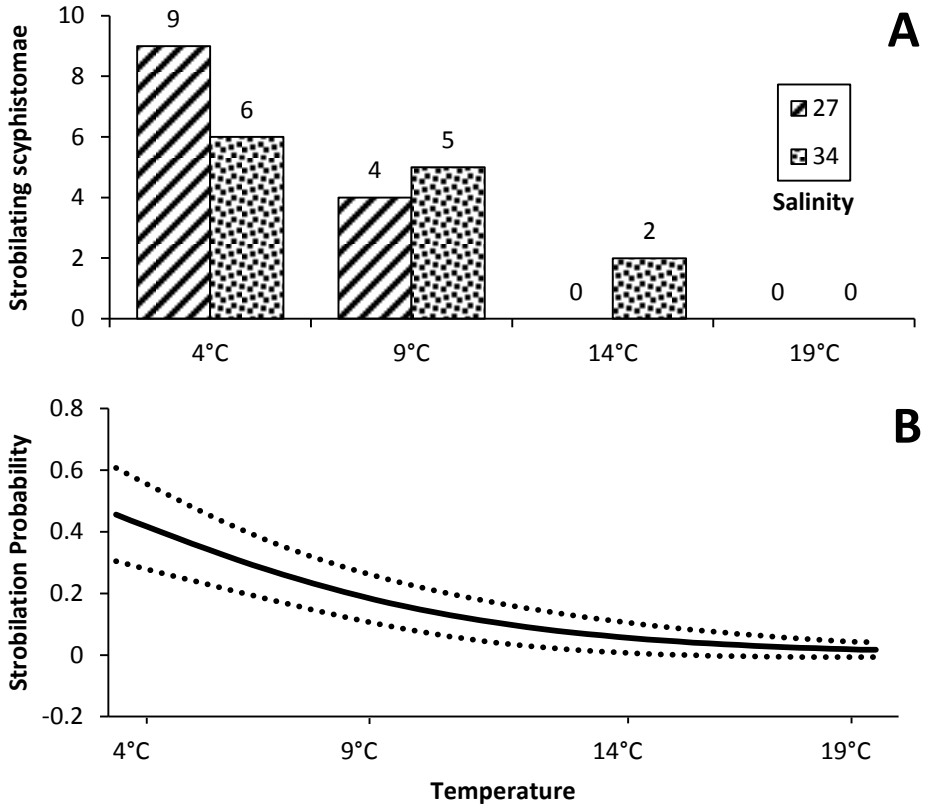


Figure 7. *Cyanea lamarckii*. (A) Total number of scyphistomae that strobilated during the experiment. (B) GLM predicted probability (solid line) of strobilating within 8 weeks when maintained at given temperatures; with 95% confidence intervals (dotted lines).

3.3.2.5 *Onset of strobilation*

As temperature and salinity decreased, the mean number of weeks until the onset of strobilation increased (Fig. 8A). The mean onset period was significantly linked with temperature, and salinity, but not their interaction. Of the treatment groups in which strobilation occurred the greatest mean onset period, 7.1 weeks per scyphistoma, was observed at 4°C and salinity of 27. The least, 2.0 weeks per scyphistoma, was observed at 14°C salinity 34.

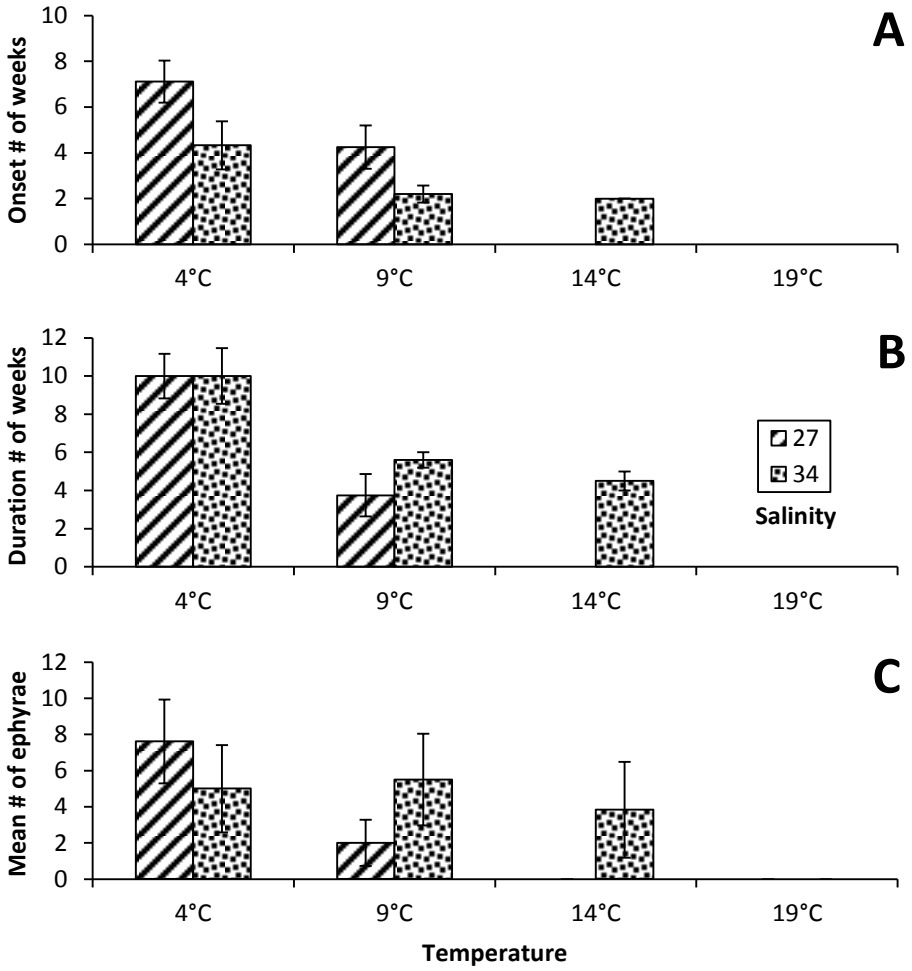


Figure 8. *Cyanea lamarckii*. (A) Mean number of weeks before onset of strobilation. (B) Mean number of weeks to complete the process of strobilation. (C) Mean number of ephyrae produced in treatment groups; n = 18, error bars = SE.

3.3.2.6 *Strobilation duration*

As temperature increased, the mean strobilation duration decreased (Fig. 8B). The mean strobilation duration was significantly linked with temperature, but not with salinity, or the temperature salinity interaction. The greatest mean strobilation durations, 10.0 weeks strobilating per scyphistoma, were observed at 4°C salinities 27 and 34. The shortest mean strobilation duration, 3.75 weeks strobilating per scyphistoma, was observed at 9°C salinity 27.

3.3.2.7 *Ephyrae produced*

The number of ephyrae produced in treatment groups was significantly linked with temperature, salinity, and the temperature salinity interaction. As temperature increased, the mean number of ephyrae produced decreased (Fig. 8C). Low temperature and salinity (4°C and salinity 27) had the effect of increasing the number of ephyrae produced, but as temperature increased from 4 to 9°C the effect of low salinity was reversed. The greatest mean number, 7.6 ephyrae per scyphistoma, was

produced at 4°C salinity 27. No ephyrae were produced at 14°C salinity 27, or in either 19°C group.

### 3.3.3 *Chrysaora hysoscella*

A summary of the best fitting GLMs describing the relationships between temperature and salinity on asexual reproductive output of scyphistomae of *Ch. hysoscella* during the experiment is given in Table 4.

Table 4. *Chrysaora hysoscella*. Summary of best fitting generalized linear models for the results of an experiment testing the effects of temperature and salinity on asexual reproductive output, strobilation and mortality of scyphistomae. The full model was Response Variable ~ Temperature + Salinity + Temperature x Salinity + ε.

| Response variable | Significant predictor variables | Family | Link | Explained deviance (%) |
|---|---|---|---|---|
| Surviving scyphistomae | ~ Temperature | Binomial | Logit | 42.0 |
| Podocysts produced | ~ Temperature + Salinity + Temperature x Salinity | Poisson | Log | 60.2 |
| Strobilating scyphistomae | ~ Temperature | Binomial | Logit | 18.8 |
| Onset of strobilation | None | Poisson | Log | NA |
| Strobilation duration | ~ Temperature | Poisson | Log | 50.9 |
| Ephyrae produced | ~ Temperature + Salinity + Temperature x Salinity | Poisson | Log | 23.1 |

#### 3.3.3.1 *Surviving scyphistomae*

Temperature, but not salinity, or their interaction significantly affected the number of *Ch. hysoscella* scyphistomae that survived for the duration of the experiment. No mortality occurred in any treatment groups maintained from 9 – 23°C (Fig. 9A). However, all scyphistomae maintained at 4°C, in both salinity treatments died by the end of the 7$^{th}$ week of the experiment.

#### 3.3.3.2 *Progeny scyphistomae*

No progeny scyphistomae were produced during the experiment. Asexual reproductive output of scyphistomae was limited to the production of ephyra larvae and benthic podocysts.

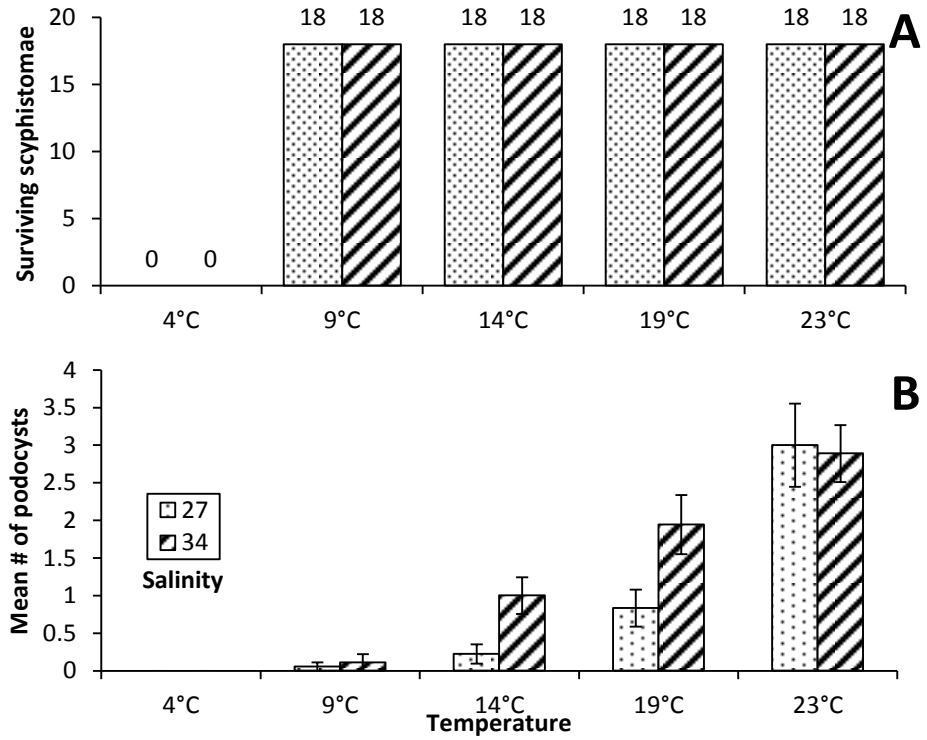


Figure 9. *Chrysaora hysoscella*. (A). Total number of scyphistomae that survived for the duration of the 8 week experiment. (B) Mean number of podocysts produced by scyphistomae in each treatment group; n = 18, error bars = SE.

3.3.3.3 *Podocysts*

Podocysts were produced in all temperature and salinity combinations except for at 4°C. As temperature and salinity increased so did the production of podocysts (Fig. 9B). Podocyst production was significantly linked with temperature, salinity, and their interaction. The greatest mean number of podocysts, 3.0 per scyphistoma, was produced at 23°C and a salinity of 27.

3.3.3.4 *Strobilating scyphistomae*

Strobilation occurred in all temperatures and salinities tested with the exception of 4°C where no scyphistomae strobilated before expiring. The majority of strobilation occurred between 9 and 19°C with fewer scyphistomae strobilating at 23°C (Fig. 10A). There was a significant relationship between strobilating scyphistomae and temperature, but not with salinity, or their interaction. The predicted probability of *Ch. hysoscella* scyphistomae strobilating during an 8 week period when maintained at temperatures ranging from 9 – 23°C is shown in Fig. 10B.

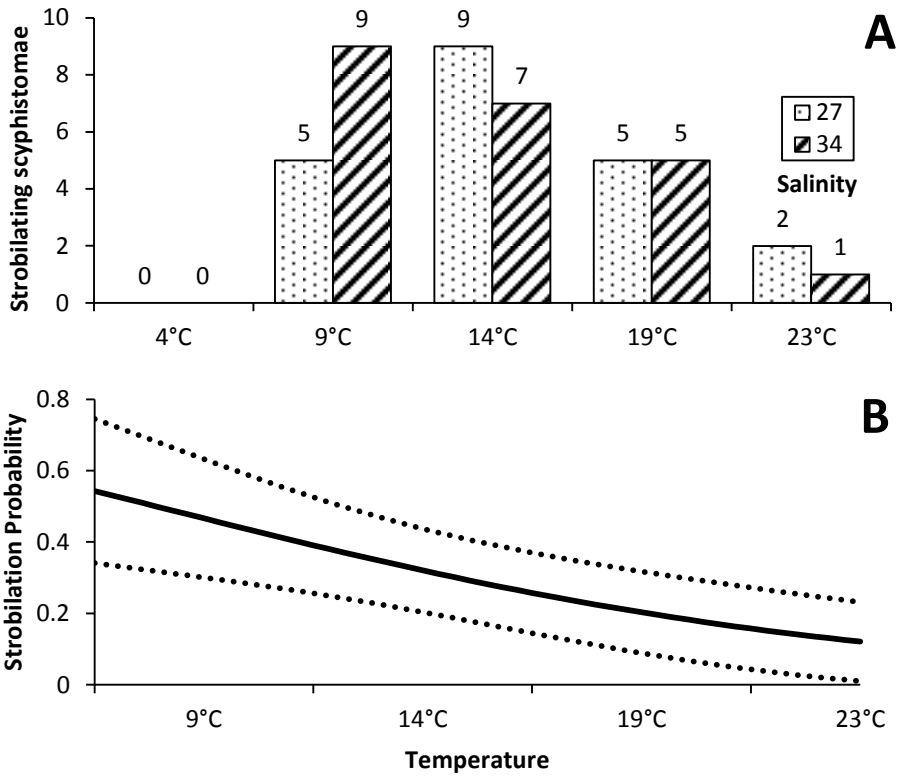


Figure 10. *Chrysaora hysoscella*. (A) Total numbers of scyphistomae that strobilated during the experiment. (B) Predicted probability of strobilating (solid lines) with 95% confidence intervals (dotted lines) during the 8 week experiment when 4°C treatment groups are excluded since all scyphistomae at 4°C perished.

### 3.3.3.5 *Onset of strobilation*

The mean number of weeks before the onset of strobilation was not significantly affected by temperature, salinity, or their interaction, and no clear trends were readily apparent (Fig. 11A). The greatest mean onset was, 4.2 weeks per scyphistoma, and occurred at 4°C salinity 27, and 19°C salinity 27. Of the scyphistomae that strobilated, the least mean onset, 2.0 weeks per scyphistoma, occurred at 23°C salinity 34.

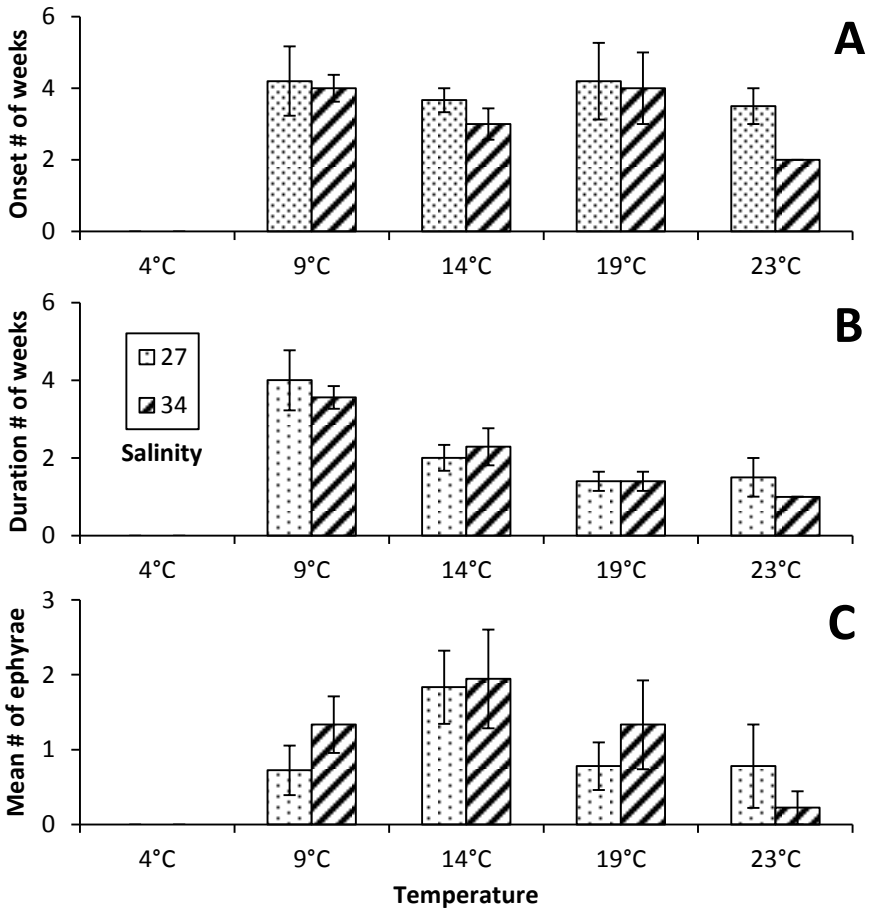


Figure 11. *Chyrsaora hysoscella*. (A) Mean number of weeks until the onset of strobilation. (B) Mean strobilation duration. (C) Mean number of ephyrae produced per scyphistoma in treatment groups; n = 18, error bars = SE.

3.3.3.6 *Strobilation duration*

As temperature increased strobilation durations decreased, and salinity had no discernable effect (Fig. 11B). The mean strobilation duration was significantly affected by temperature, but not by salinity, or their interaction. The greatest mean strobilation duration, 4.0 weeks per scyphistoma, occurred in the 9°C salinity 27 treatment. Of the scyphistomae that strobilated the shortest mean strobilation durations, 1.0 weeks per scyphistoma, occurred at 23°C salinity 34.

3.3.3.7 *Ephyrae produced*

The number of ephyrae produced was significantly linked with temperature, but not salinity. However the interaction between temperature and salinity was significant therefore salinity was retained in the model. The number of ephyrae produced was relatively equivalent at temperatures ranging from 9 – 19°C, and the amount decreased at 23°C (Fig. 11C). The greatest mean number, 1.9 ephyrae per scyphistoma, was produced in the 9°C salinity 34 treatment. Of those that strobilated, the least mean number, 0.2 ephyrae per scyphistoma, were produced by scyphistomae maintained at 23°C salinity 34.

### 3.3.4 *Aurelia aurita* (Southampton)

A summary of the best fitting GLMs for the effects of temperature and salinity on asexual reproductive output of *A. aurita* (Southampton) scyphistomae are shown in Table 5.

Table 5. *Aurelia aurita* (Southampton population). Summary of best fitting generalized linear models for the results of an experiment testing the effects of temperature and salinity on asexual reproductive output, strobilation, and mortality of scyphistomae. The full model was Response Variable ~ Temperature + Salinity + Temperature x Salinity + ε.

| Response variable | Significant predictor variables | Family | Link | Explained deviance (%) |
|---|---|---|---|---|
| Surviving scyphistomae | None | Binomial | Logit | NA |
| Progeny scyphistomae produced | ~ Temperature + Salinity + Temperature x Salinity | Poisson | Log | 47.9 |
| Podocysts produced | ~ Temperature | Poisson | Log | 34.1 |
| Strobilating scyphistomae after 8 weeks | ~ Temperature + Salinity | Binomial | Logit | 56.4 |
| Strobilating scyphistomae after 16 weeks | ~ Temperature + Salinity | Binomial | Logit | 74.0 |
| Onset of strobilation | ~ Temperature + Salinity | Poisson | Log | 59.7 |
| Strobilation duration | ~ Temperature | Poisson | Log | 57.9 |
| Ephyrae produced after 8 weeks | ~ Temperature + Salinity | Poisson | Log | 54.8 |
| Ephyrae produced after 16 weeks | ~ Temperature + Salinity + Temperature x Salinity | Poisson | Log | 90.1 |

#### 3.3.4.1 *Surviving scyphistomae*

There were no significant relationships between the number of scyphistomae that survived for the duration of the experiment and temperature, salinity, or the temperature salinity interaction. Survivorship was high in all temperature and salinity treatment groups and no trends were discernable (Fig. 12A).

#### 3.3.4.2 *Progeny scyphistomae*

Scyphistomae in all treatment groups produced progeny scyphistomae during the experiment. The mean number of progeny scyphistomae increased as temperature increased and salinity decreased (Fig. 12B). The effect was not apparent at 4°C, but began to manifest at 9°C, and was further magnified in warmer temperatures. There

were significant relationships between the number of progeny scyphistomae produced and temperature, salinity, and the temperature salinity interaction. The highest mean number of progeny scyphistomae, 8.6 per scyphistoma, were produced at 23°C salinity 21, whilst the lowest mean number, 0.8 progeny per scyphistoma, were produced at 4°C salinity 21.

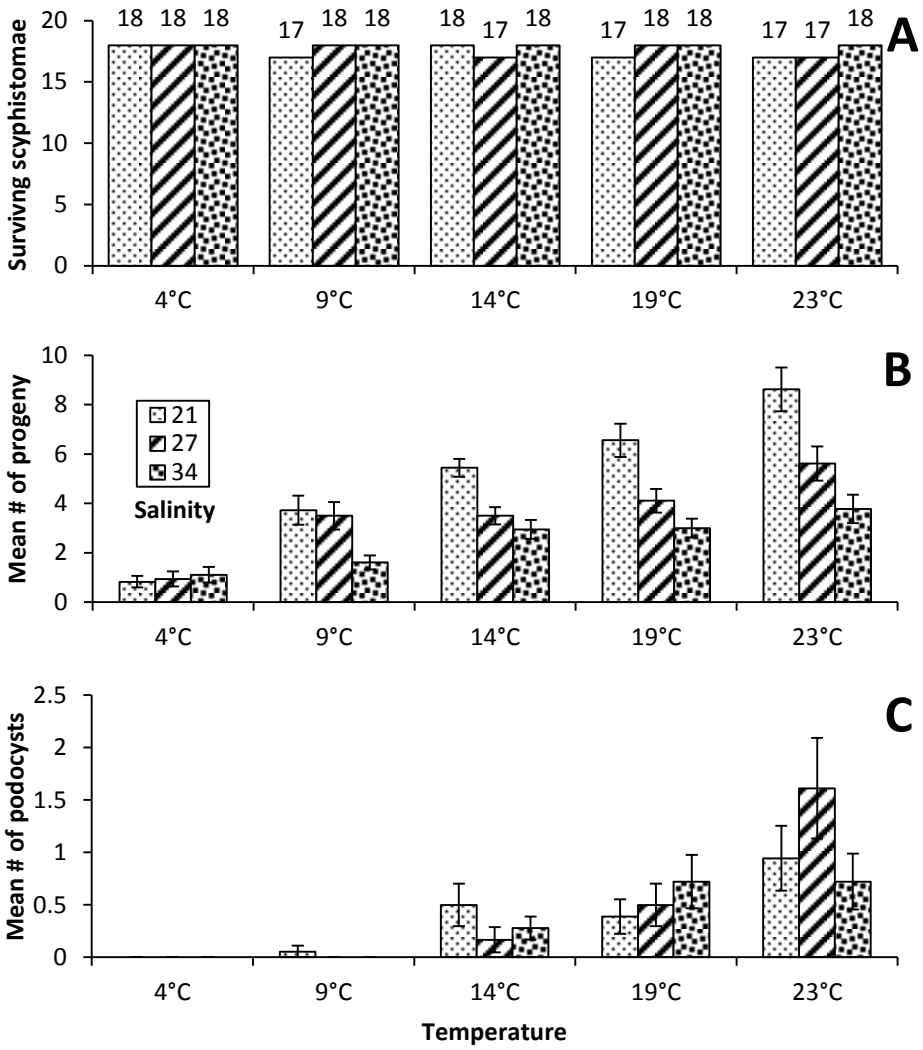


Figure 12. *Aurelia aurita* (Southampton). (A) Total number of surviving scyphistomae, out of 18 at the start of the experiment. (B) Mean number of progeny scyphistomae produced per parent scyphistoma. (C) Mean number of podocysts produced per scyphistoma.

### 3.3.4.3 *Podocysts*

Not all scyphistomae produced podocysts during the experiment. No podocysts were produced in any of the three salinity treatments at 4°C, and very few were produced at 9°C. However, podocysts were produced at 14, 19 and 23°C in all three salinities tested. The highest mean number of podocysts, 1.6 podocysts per scyphistoma, was produced in the 23°C salinity 27 treatment. As temperature increased so did the production of podocysts (Fig. 12C). There was a significant relationship between the number of podocysts produced per scyphistoma and temperature, but not with salinity, or the temperature salinity interaction

3.3.4.4 *Strobilating scyphistomae*

After 8 weeks, increasing numbers of scyphistomae strobilated as temperature decreased and salinity increased (Fig. 13A). There were significant relationships between the number of scyphistomae that had begun to strobilate within 8 weeks and temperature, and salinity, but not with the temperature salinity interaction. Not all scyphistomae that began to strobilate during the experiment had completed the process, as indicated by having released all ephyrae, by the end of 8 weeks. Therefore husbandry protocols were continued until the final ephyra was released for each strobilating scyphistoma. During this period additional scyphistomae in the 4°C treatment groups began to strobilate. Those scyphistomae were also allowed to continue to strobilate until their final ephyrae were released in order to obtain complete onset and duration data. Scyphistomae strobilated at 4 and 9°C, but did not strobilate in any of the other temperature and salinity combinations. Scyphistomae at 9°C in all three salinity treatments had begun to strobilate within the initial 8 week period, but none strobilated thereafter. The predicted probability of scyphistomae strobilating during an 8 week period when maintained at temperatures ranging from 4 – 23°C, and salinities of 21, 27 and 34 are shown in Figs. 13B – 13D.

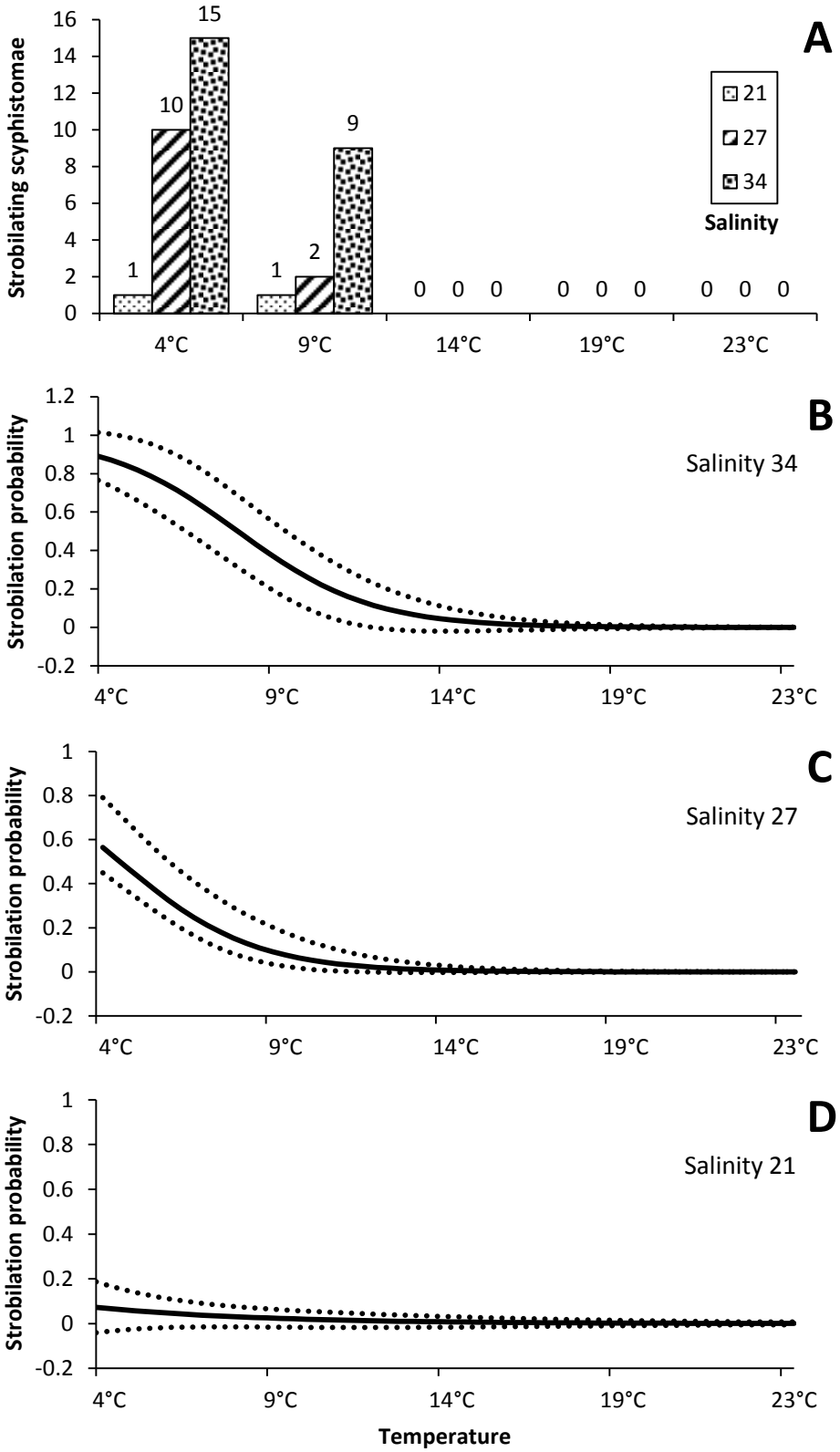


Figure 13. *Aurelia aurita* (Southampton). Summary of strobilation after 8 weeks. (A) Total number of scyphistomae that had begun the process of strobilation after 8 weeks. (B, C, D) GLM predicted strobilation probabilities with 95% confidence intervals that scyphistomae would have strobilated after 8 weeks at salinities 34, 27 and 21 respectively.

As temperature decreased, the total number of scyphistomae that strobilated within 16 weeks increased (Fig. 14A). There were significant relationships between the number of scyphistomae that had begun to strobilate within 16 weeks and temperature, and salinity, but not with their interaction. Scyphistomae did not strobilate more than once during the 16 week period, nor did they show any visible signs (i.e. neck elongation, segmentation etc.) that they were preparing to strobilate again. The predicted probability of *A. aurita* (Southampton) scyphistomae strobilating during a 16 week period when maintained at temperatures ranging from 4 – 23°C, and salinities of 21, 27 and 34 are shown in Figs. 14B – 14D.

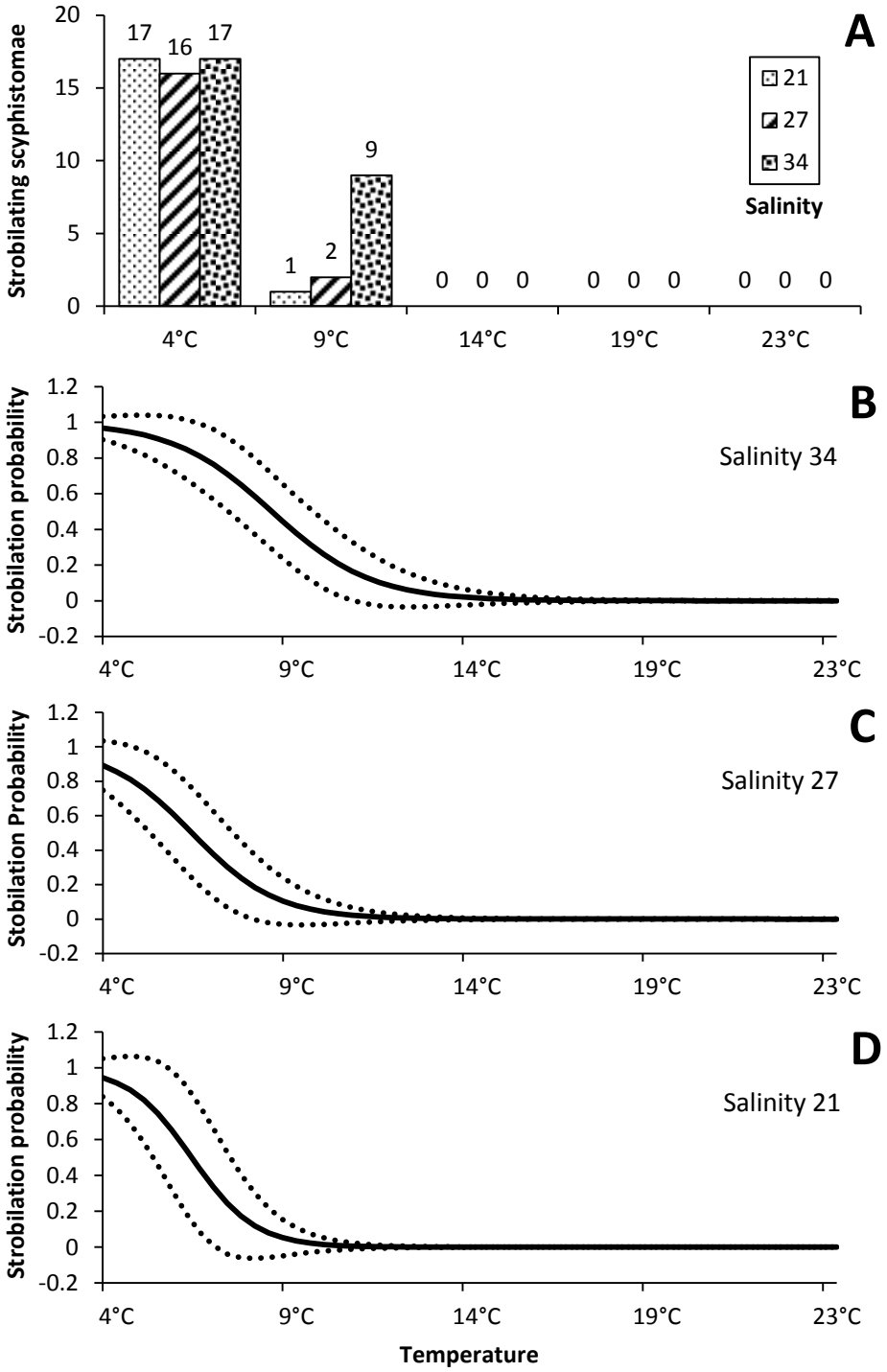


Figure 14. *Aurelia aurita* (Southampton). Summary of strobilation after 16 weeks: (A) Total number of scyphistomae that had begun the process of strobilation after 16 weeks. (B, C, D) GLM predicted strobilation (solid lines) probabilities with 95% confidence intervals (dotted lines) after 8 weeks at salinities 34, 27 and 21 respectively.

### 3.3.4.5 *Onset of strobilation*

As temperature and salinity decreased the onset of strobilation period increased (Fig. 15A). The onset period varied significantly with temperature and salinity, but not with the temperature salinity interaction. Of the scyphistomae that strobilated, the highest mean number of weeks until the onset, 10.9 weeks per scyphistoma, was

observed at 4°C salinity 21.  The lowest mean number of weeks until the onset of strobilation, 2.9 weeks per scyphistoma, occurred at 9°C salinity 34.

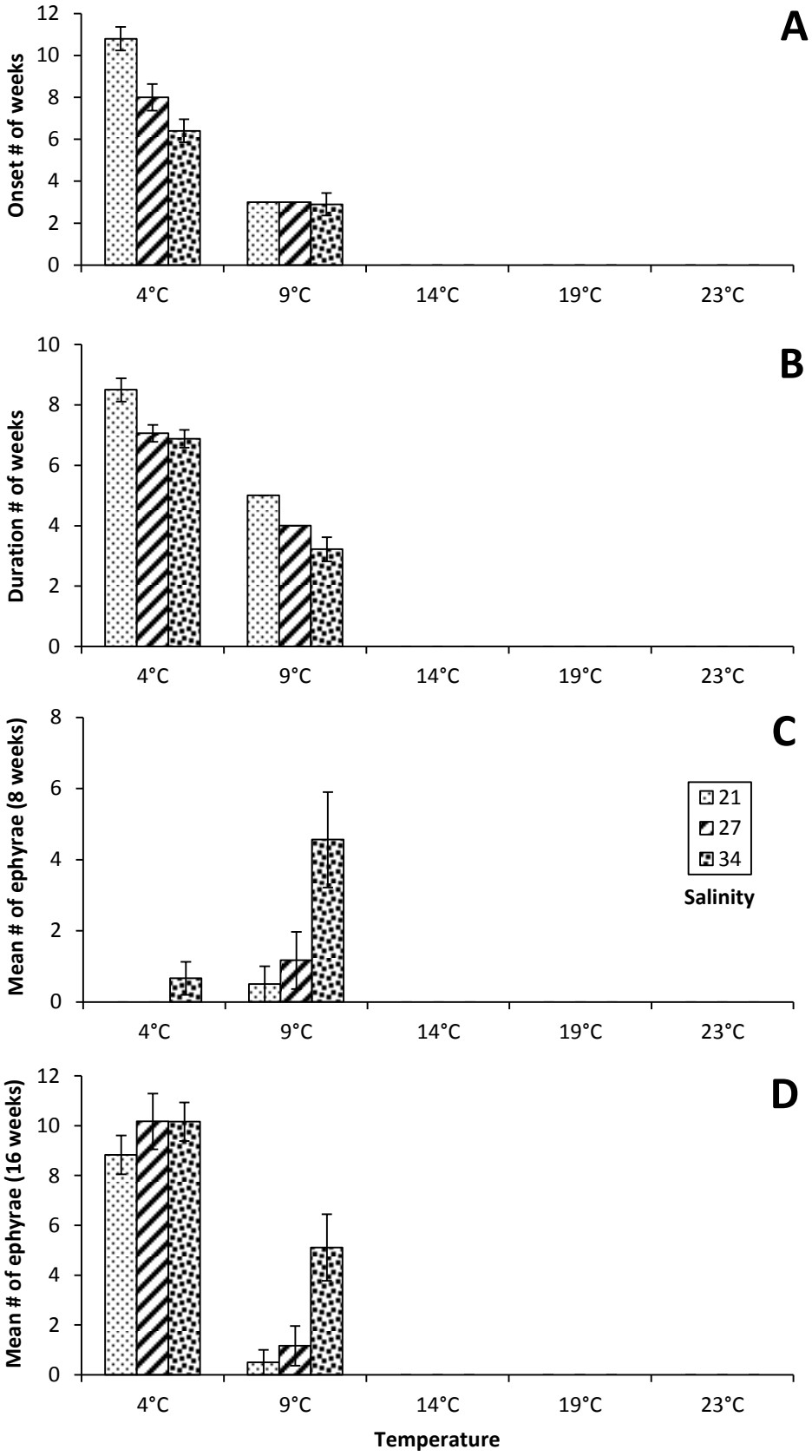


Figure 15. *Aurelia aurita* (Southampton). (A) Mean number of weeks until onset of strobilation. (B) Mean number of weeks to complete the process of strobilation. (C) Mean number of ephyrae produced per scyphistoma at the end of 8 weeks. (D) Mean number of ephyrae produced per scyphistoma at the end of 16 weeks; n = 18, error bars = SE.

3.3.4.6 *Strobilation duration*

The mean number of weeks to complete the process of strobilation increased as temperature, and to some degree salinity, decreased (Fig. 15B). There was a significant relationship between the mean strobilation duration and temperature, but not with salinity, or the temperature salinity interaction. The highest mean number of weeks to complete the process of strobilation, 8.6 weeks per scyphistoma, was observed at 4°C salinity 21, and the lowest mean strobilation duration 3.3 weeks scyphistoma$^{-1}$, was observed at 9°C salinity 34.

3.3.4.7 *Ephyrae produced*

The mean number of ephyrae produced per scyphistoma in treatment groups after 8 weeks varied significantly with temperature and salinity, but not with the temperature salinity interaction. After 8 weeks more ephyrae were produced as temperature and salinity increased (Fig. 15C). The highest mean number of ephyrae produced per scyphistoma, 5.2, was observed in the 9°C salinity 34 treatment. However, not all scyphistomae had released all developing ephyrae by the end of 8 weeks since the onset of strobilation and strobilation durations were longer in 4°C treatments.

After 16 total weeks the mean number of ephyrae produced in treatment groups increased as temperature decreased and salinity increased (Fig. 15D). There were significant relationships between the mean number of ephyrae produced per scyphistoma after 16 weeks and temperature, salinity, and the temperature salinity interaction. No ephyrae were produced in any temperature or salinity combinations occurring at ≥ 14°C. The greatest mean number of ephyrae produced after 16 weeks, 10.1 ephyrae per scyphistoma, were maintained at 4°C and salinities 27 and 34.

**3.3.5 *Aurelia aurita*, (Orkney)**

A summary of the best fitting generalised linear models for each response variable is given in Table 6.

3.3.5.1 *Surviving scyphistomae*

Survivorship was high in all of the temperature and salinity combinations tested (Fig. 16A) with only three total scyphistomae perishing by the end of the experiment. There were no significant relationships between mortality and temperature, salinity or the temperature salinity interaction.

Table 6. *Aurelia aurita* (Orkney). Summary of best fitting generalized linear models for the results of an 8 week experiment testing the effects of temperature and salinity on asexual reproductive output, strobilation and mortality of scyphistomae. The full model was Response Variable ~ Temperature + Salinity + Temperature x Salinity + ε.

| Response variable | Significant predictor variables | Family | Link | Explained deviance (%) |
|---|---|---|---|---|
| Surviving scyphistomae | None | Binomial | Logit | NA |
| Progeny scyphistomae produced | ~ Temperature + Salinity + Temperature x Salinity | Poisson | Log | 12.0 |
| Podocysts produced | ~ Temperature + Salinity + Temperature x Salinity | Poisson | Log | 24.0 |
| Strobilating scyphistomae | ~ Temperature + Salinity | Binomial | Logit | 80.0 |
| Onset of strobilation | None | Poisson | Log | NA |
| Strobilation duration | None | Poisson | Log | NA |
| Ephyrae produced | ~ Temperature + Salinity | Poisson | Log | 86.0 |

3.3.5.2 *Progeny scyphistomae*

Scyphistomae of *A. aurita* (Orkney) produced relatively few progeny scyphistomae. There were significant relationships between the number of progeny scyphistomae produced and temperature, but not with salinity. The interaction was however significant, therefore salinity was retained in the model. The highest mean number of progeny scyphistomae, 0.8 progeny per scyphistoma, was produced at 9°C salinity 21, and no progeny were produced at 4°C salinity 21. Fewer progeny were produced by scyphistomae maintained at 4 and 23°C with similar numbers being produced at 9, 14 and 19°C (Fig. 16B). A salinity trend was not visibly detectable.

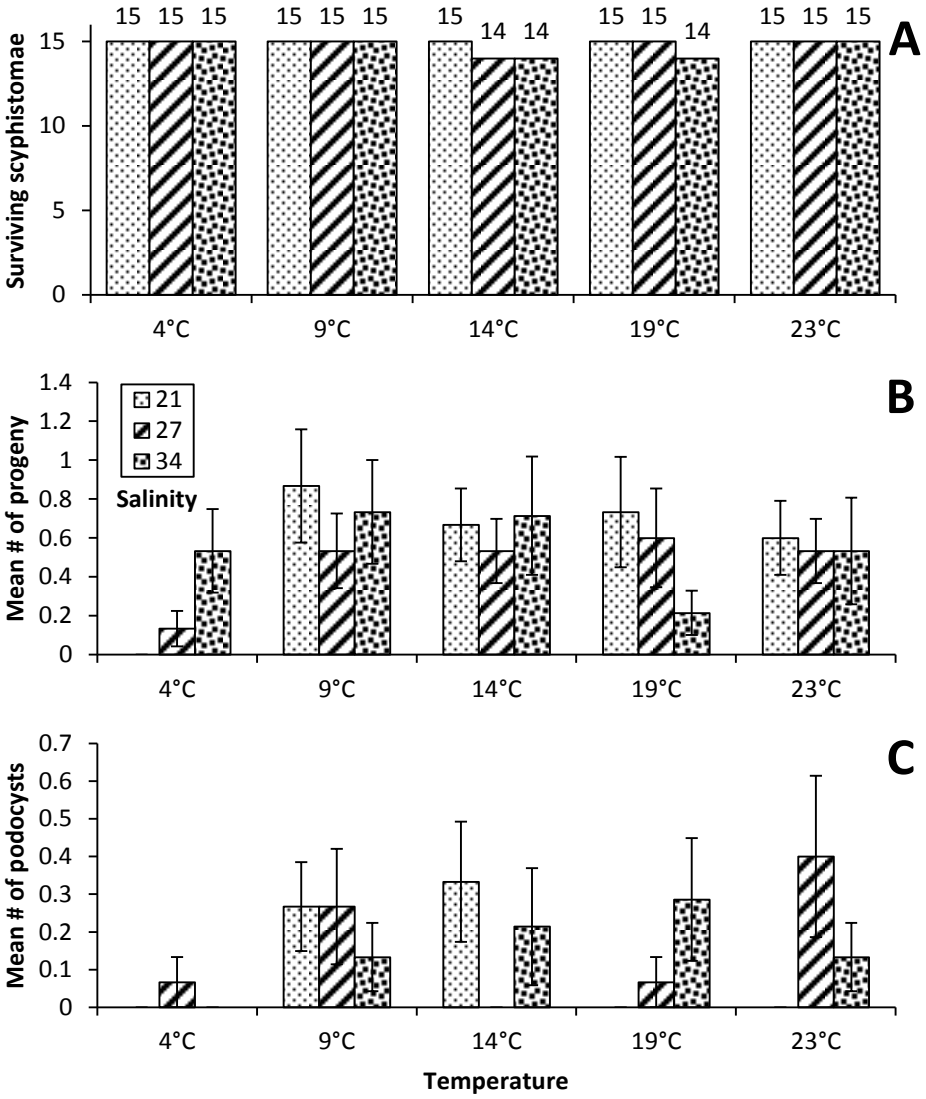


Figure 16. *Aurelia aurita* (Orkney). (A) Total number of surviving scyphistomae (of 15). (B) Mean number of progeny scyphistomae budded per parent scyphistoma. (C) Mean number of podocysts produced per scyphistoma; n = 15; error bars = SE.

3.3.5.3 *Podocysts*

As temperature increased the number of podocysts increased (Fig. 16C). There were no clear effects of salinity trends. There were significant relationships with the mean number of podocysts produced per scyphistoma and temperature, but not with salinity. The interaction term was however significant, and therefore salinity was retained in the model. Few podocysts were produced by scyphistomae in any of the treatment combinations during the experiment. The highest mean number, 0.4 podocysts per scyphistoma, was produced at 23°C salinity 27. No podocysts were produced at 4°C, salinity 27 or 34.

3.3.5.4 *Strobilating scyphistomae*

Scyphistomae maintained in the 4°C treatment groups were the only ones to strobilate during the study (Fig. 17A). There were significant relationships between the number

of scyphistomae that strobilated and temperature, and salinity, but not with the temperature salinity interaction. Strobilating scyphistomae were allowed to complete the process of strobilation, with husbandry protocols maintained, even when the total strobilation duration went beyond the initially planned 8 week experiment. Scyphistomae were observed for 16 weeks to determine whether scyphistomae would strobilate more than once. No scyphistomae strobilated more than once and no scyphistomae other than those in the 4°C treatments strobilated within the 16 weeks. The highest number of scyphistomae to strobilate at 4°C were maintained at salinity 21 (14/15) followed by those maintained at salinity 27 (13/15). The least numbers of scyphistomae to strobilate (9/15) were maintained salinity 34.

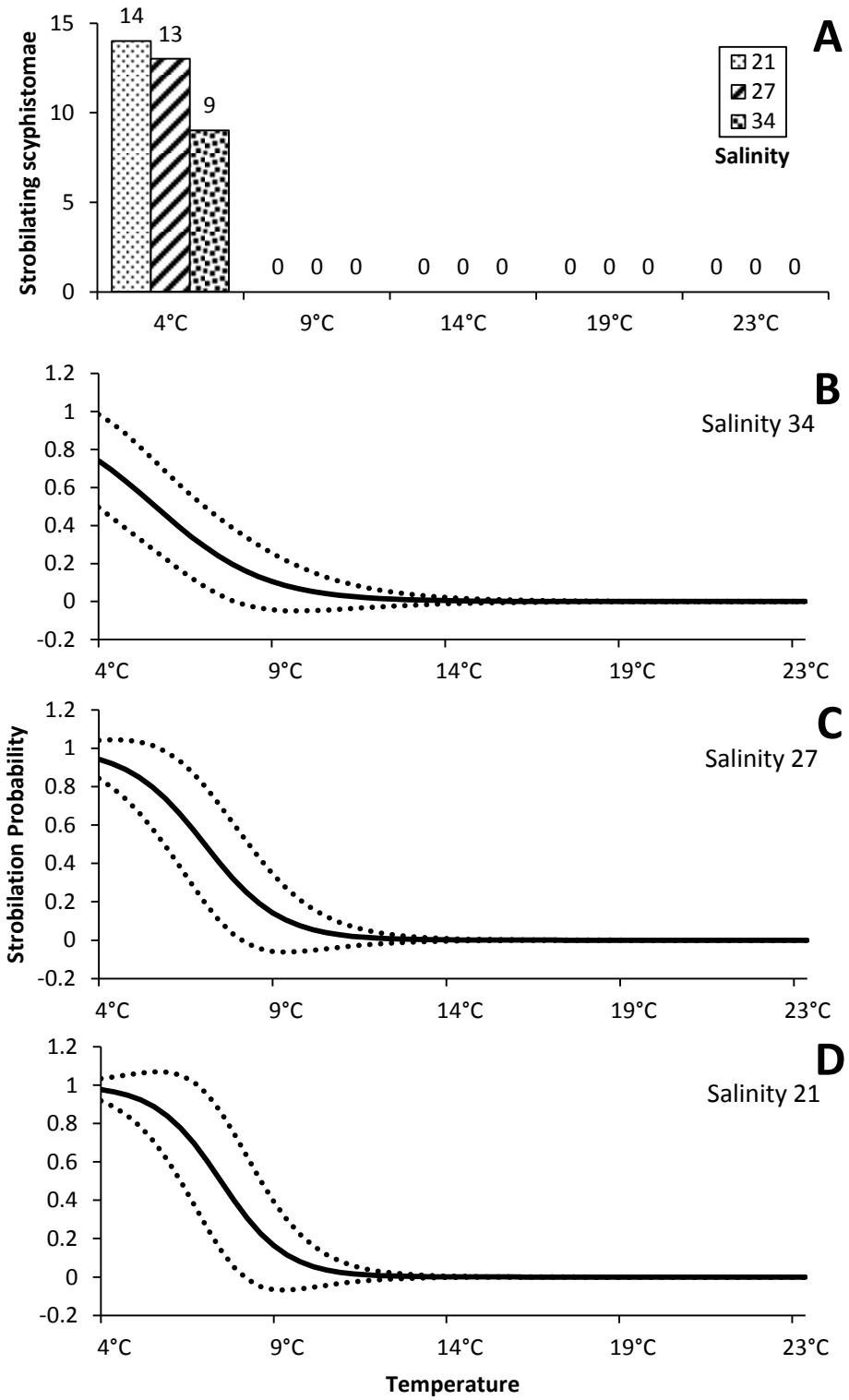


Figure 17. *Aurelia aurita* Orkney. (A) Total number of scyphistomae that strobilated during the study. (B, C, D) GLM predicted strobilation probabilities (solid lines) with 95% confidence intervals (dotted lines) after 8 weeks at salinities 34, 27 and 21 respectively.

3.3.5.5 *Onset of strobilation*

The mean number of weeks until the onset of strobilation ranged from 6.1 – 7.6 at 4°C (Fig. 18A), but there were no significant relationships between the onset of strobilation and temperature, salinity or the temperature salinity interaction.

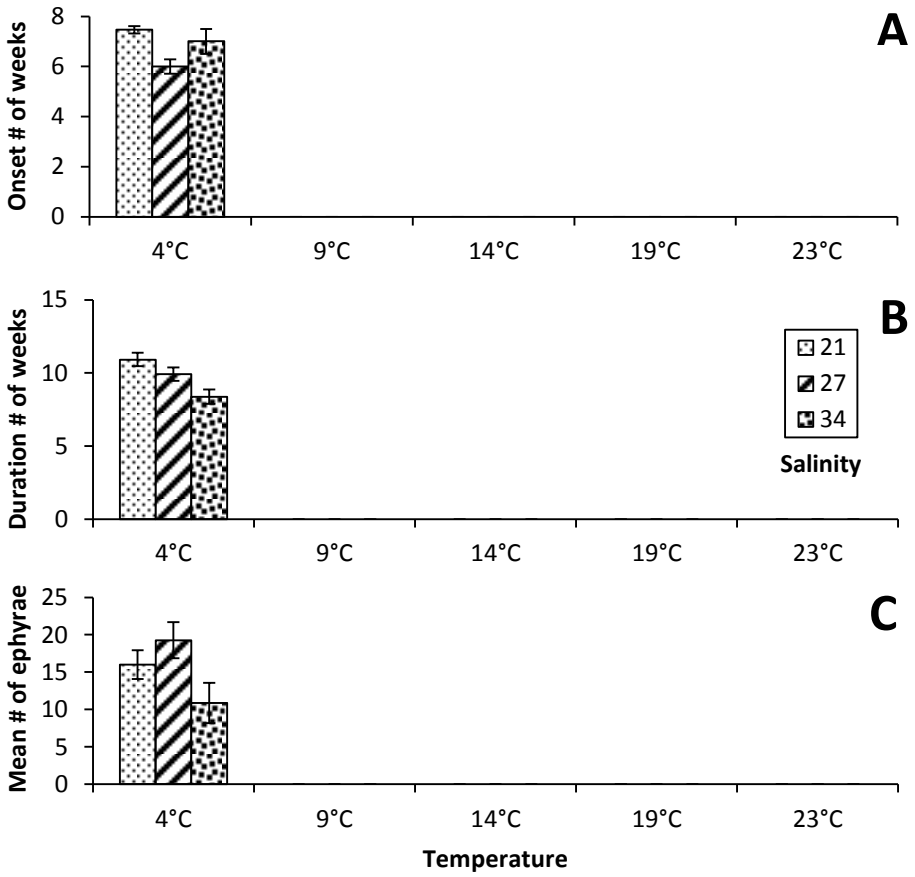


Figure 18. *Aurelia aurita* (Orkney). (A) Mean number of weeks until the onset of strobilation. (B) Mean strobilation duration. (C) Mean number of ephyrae produced scyphistoma$^{-1}$ in the treatment groups; n = 15, error bars = SE.

3.3.5.6 *Strobilation duration*

The mean strobilation duration ranged from 8.4 – 10.9 weeks at 4°C (Fig. 18B), but there were no significant relationships between strobilation duration and temperature, salinity or their interaction.

3.3.5.7 *Ephyrae produced*

Since none of the scyphistomae maintained in temperatures higher than 4°C strobilated, no ephyrae were produced in those treatment groups (Figure 18C). Temperature, salinity, and their interaction significantly affected the number of ephyrae produced per scyphistoma in treatment groups. The highest mean number of ephyrae, 20.3 ephyrae per scyphistoma, were produced at 4°C salinity 27, and the lowest mean number of ephyrae, 11.9 ephyrae per scyphistoma, were produced at salinity 34.

### 3.3.6 Modelling asexual reproductive output of scyphistomae in present and predicted temperature scenarios

3.3.6.1 *The potential effect of future elevated SST on podocyst production*

The effect of increasing SSTs over time may be that British scyphistomae generate more podocysts over longer periods (Fig. 19). The effect of increasing SSTs on podocyst production may not be as strongly expressed for *A. aurita* (Orkney), or *C. capillata* since the number of podocysts produced for those species was not as greatly affected by temperature as for the other species examined. At current temperatures, podocysts are generally produced more slowly than progeny scyphistomae, but in the future their production rates may increase.

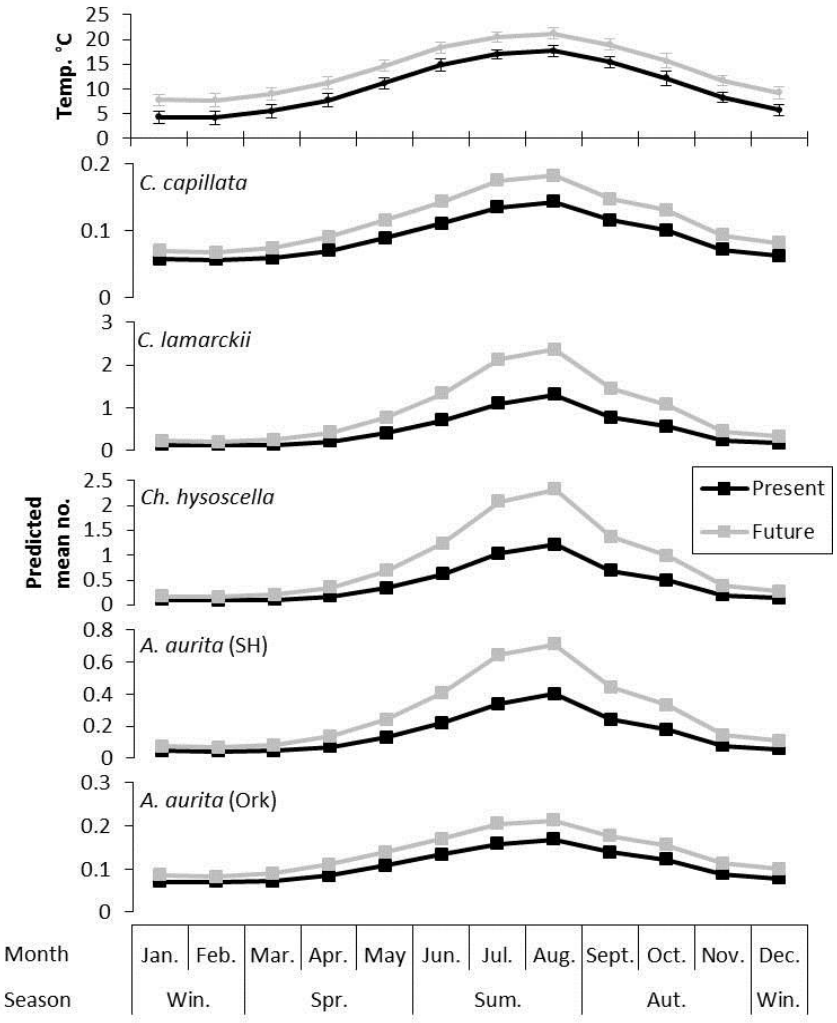


Figure 19. Hypothetical model of the mean number of podocysts predicted to be produced by British scyphistomae in response to current and predicted seasonal sea surface temperatures in the 2080s (Hughes et al. 2010). Predictions were derived from present results made at salinity 34, error bars for temperature= SE.

3.3.6.2 *The potential effect of future elevated SST on progeny scyphistoma production*
Temperature, salinity, and the temperature salinity interaction were significantly linked with progeny scyphistomae production for both populations of *A. aurita* studied here. The mean numbers of progeny scyphistomae predicted to be produced by parent scyphistomae of *A. aurita* from Orkney populations are likely to be less affected by projected future temperatures than *A. aurita* from Southampton (Fig. 20), and if North Sea temperatures continue to increase, production of scyphistomae may be slightly enhanced in southern populations, but slightly depressed in more northern populations. Neither temperature, nor salinity, or the temperature salinity interaction was significantly linked with progeny scyphistomae production in *C. lamarckii*.

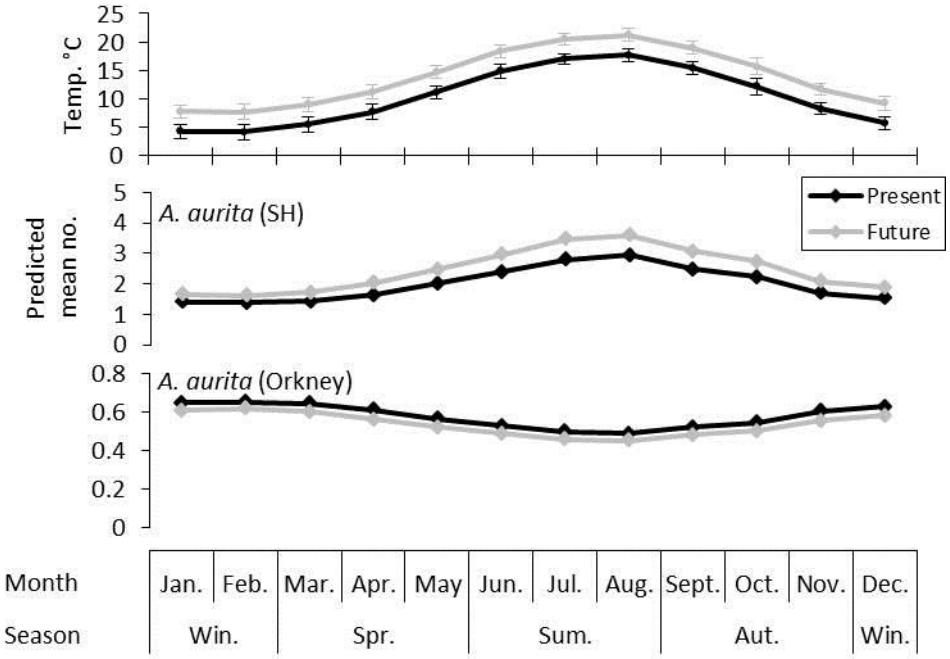


Figure 20. Hypothetical model of the mean number of progeny scyphistomae predicted to be produced by British scyphistomae in response to current and future North Sea temperatures predicted to occur in the 2080s (Hughes et al. 2010). Progeny scyphistoma GLM predictions are based on present experimental results made at salinity 34, error bars for temperature = SE.

3.3.6.3 *The potential effect of future elevated SST on strobilation*
Generalised linear models based on present results predicted less strobilation, with shorter durations, to occur annually in elevated temperatures for all British species except for *Ch. hysoscella* (Fig. 21). Scyphistomae of *Ch. hysoscella* strobilated in a wide range of temperatures and the GLM did not fit the data well, with only 18.8% of the deviance explained. Since the predicted probability of strobilation in elevated temperatures was lower for both British *Aurelia* and *Cyanea* species fewer medusae may be observed in the North Sea during summers in the future due to fewer ephyrae being generated during warmer winters.

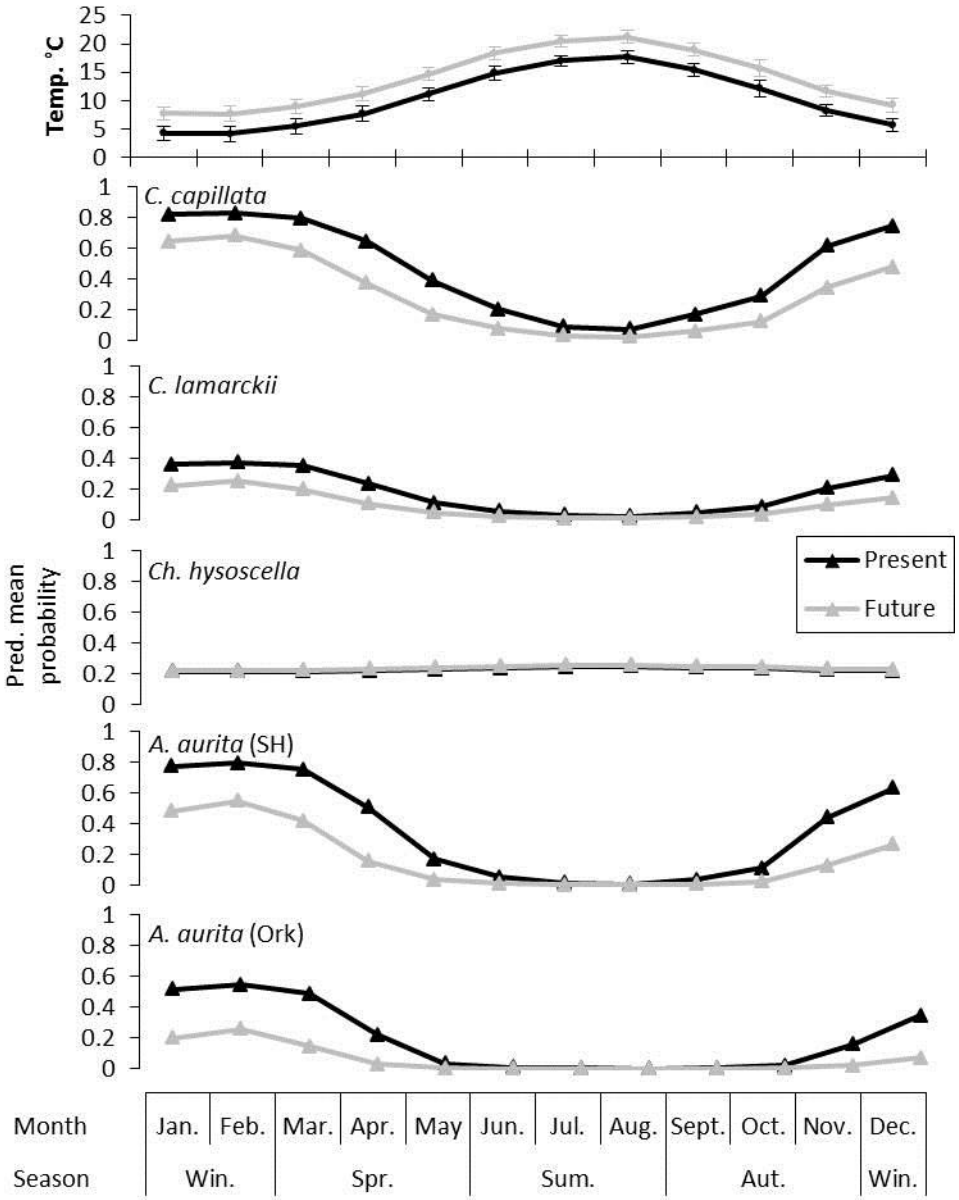


Figure 21. Hypothetical model of the predicted mean probability that British scyphistomae strobilate in response to current and future predicted seasonal temperatures predicted to occur by the 2080s (Hughes et al. 2010). GLM predictions were derived from present experimental results made at salinity 34, error bars for temperature = SE.

### 3.3.6.4 *The potential effect of high and low NAO scenarios on the production of ephyrae*

When the NAO is in a positive phase warmer sea temperatures during winter may decrease the number of *A. aurita* and *C. lamarckii* scyphistomae that strobilate with the effect being fewer ephyrae are added to the system (Fig. 22). Conversely, when the NAO is in a negative phase cooler sea temperatures during winter may increase the number of scyphistomae that strobilate, resulting in more ephyrae being added to the system.

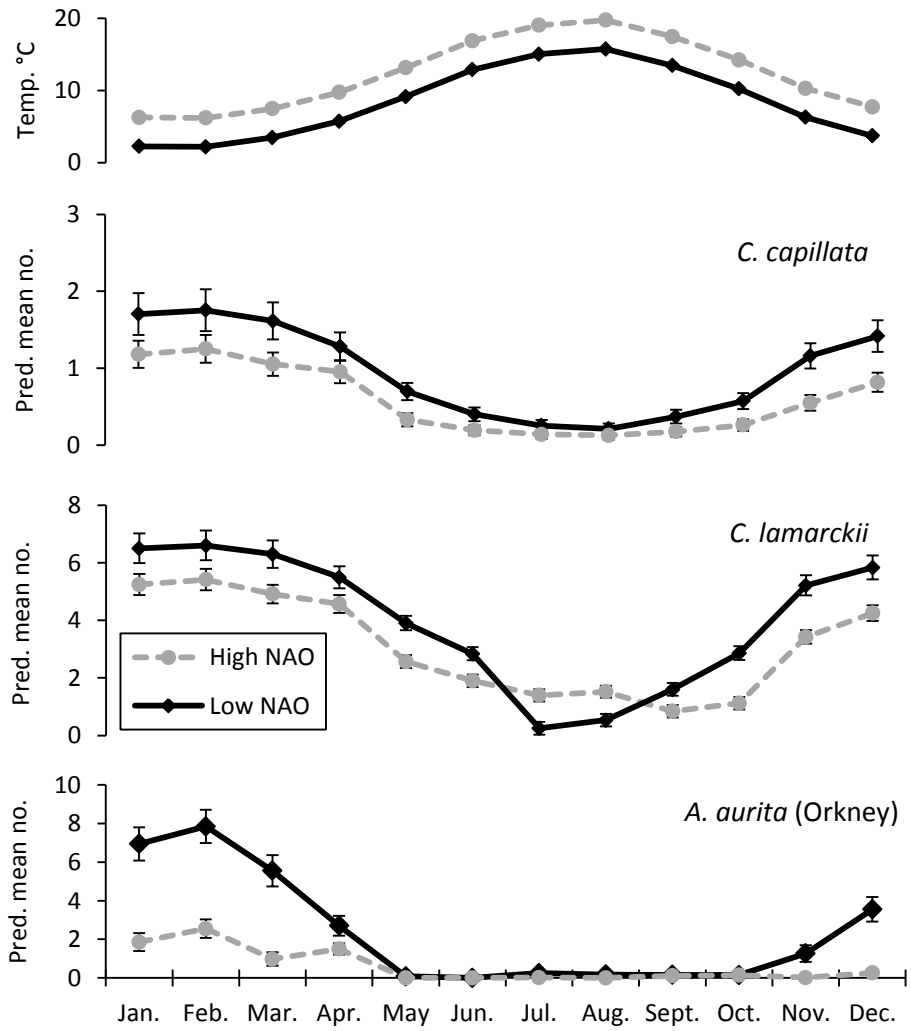


Figure 22. Hypothetical model of the mean number of ephyrae produced per colony member of *C. capillata*, *C. lamarckii* and *A. aurita* (Orkney) at salinity 34 under high and low NOA sea surface temperature conditions. GLM predictions were derived from present experimental results made at salinity 34, error bars = SE.

## 3.4 Discussion

Jellyfish scyphistomae are an important life history stage to study in order to better understand patterns of medusa abundance since it is the scyphistoma stage that undergoes the process of strobilation and thereby produces juvenile medusae. In this study, both temperature and salinity significantly affected asexual reproductive activities of scyphistomae, including medusae production.

### 3.4.1 *Survivorship*

Survivorship of scyphistomae was high for all species studied across a wide range of temperatures and salinities which is in agreement with other studies (Lucas et al. 2012, and references therein). Neither temperature, nor salinity was significant in predicting survivorship of *C. lamarckii* scyphistomae, or for either population of *A. aurita*. Temperature was however significant in determining survivorship of *C. capillata* and *Ch. hysoscella* scyphistomae with decreased survivorship in warm water

for *C. capillata*, but the opposite for *Ch. hysoscella*. Decreasing survivorship with increasing temperature has been observed in Taiwanese *A. aurita* where each 1°C increase in temperature decreased the survival period by 4.7 days (Liu et al. 2009). Scyphistomae of *C. quinquecirrha* experienced mortality when the temperature was raised from 34 to 36°C (Cargo and Schultz 1967). Natural populations of *Cotylorhiza tuberculata* scyphistomae in the western Mediterranean Sea (Prieto et al. 2010), and *Cassiopea xamachana* in the Caribbean Sea (Fitt and Costley 1998) experience mortality in cold temperatures.

Many of the coastal bloom-forming jellyfish species are euryhaline, and are most often observed in coastal and estuarine environments (Lucas et al. 2012). British scyphistomae are probably adapted for survival in highly variable environments with annual fluctuations in seasonal salinity. Salinity in the ranges tested here for scyphistomae did not inhibit settlement of *C. capillata*, *C. lamarckii*, *Ch. hysoscella* or *A. aurita* planulae from Keil Bight, Germany (Holst and Jarms 2010), and salinity was not a significant factor in determining scyphistoma survivorship in this study. Once colonies of British scyphistomae are established, salinity ranging from 21 – 34 would not be a limiting factor in maintaining geographic ranges of jellyfish based upon scyphistomae mortality.

3.4.1.1 *The potential effect of future elevated SST on scyphistoma mortality*
Temperature played the most important role in determining survivorship of scyphistomae, but only extreme temperatures (> 19°C for *C. capillata*, and < 9°C for *Ch. hysoscella*) resulted in significant mortality. Medusae of *C. capillata* are described to have a more northern boreal distribution whereas *Ch. hysoscella* occupy a more southern distribution in British waters (Russell 1970, Doyle et al. 2007, Holst 2012). Sea surface temperatures in the southern North Sea have risen at a rate of between 0.6 and 0.8°C per decade since the 1980s (Hughes et al. 2010). If southern North Sea temperatures continue to increase at the present rate poor scyphistoma survivorship in warm temperatures at the southern extents of biogeographic ranges may contribute to a gradual northward range shift for *C. capillata*. On the other hand, enhanced scyphistoma survivorship in warmer temperatures at the northern extents of the biogeographic range may lead to a gradual northward range expansion for *Ch. hysoscella*.

3.4.2 *Podocysts*
Podocysts were produced by scyphistomae of all species and populations during the study. The mean number of podocysts produced by scyphistomae of *C. capillata*, *C. lamarckii* and *A. aurita* (Southampton) significantly increased with temperature, but not salinity. Increasing temperature also accelerated podocyst production rates in *A. aurita* s.1., *C. nozakii* and *Ch. pacifica* from the Inland Sea of Japan (Thein et al. 2012b, 2013), and *A. aurita* s.1. scyphistomae from Honjo District, Shimane Prefecture, Japan (Han and Uye 2010). Similarly, transfer from low to high temperature was favourable for formation of podocysts by scyphistomae of *C.*

*capillata* from the Niantic River estuary, Connecticut, USA (Brewer and Feingold 1991) but in my experiments few podocysts were produced by any British species at 4 or 9°C. In the Gullmar Fjord, Western Sweden *A. aurita* formed podocysts in the winter whilst conversely, *C. capillata* formed them during summer and autumn (Grondahl 1988a).

The influence of salinity variation on production of podocysts was minimal over the range tested. The mean number of podocysts produced by scyphistomae of *A. aurita* (Orkney) and *Ch. hysoscella* were significantly influenced by temperature, salinity and the temperature salinity interaction, but no clear trend for the effect of salinity was obviously discernable for *A. aurita* (Orkney). The mean number of podocysts produced increased with increasing salinity for *Ch. hysoscella* at 14 and 19°C, but at 23°C the effect was masked. These results are similar to those for *A. aurita* s.1., *C. nozakii*, or *Ch. pacifica* scyphistomae from the Inland Sea of Japan where salinities ranging from 15 – 32 did not significantly influence podocyst production rates (Thein et al. 2012b, 2013).

The contribution of podocysts to the expansion of benthic colonies has received relatively little attention (Kawahara et al. 2012). Studies measuring the effects of variables on asexual reproductive modes and output of scyphistomae sometimes do not report results for the production of podocysts, even though studied species produce them e.g., (Purcell et al. 1999, 2012, Liu et al. 2009). Benthic asexual reproductive output by scyphistomae of British *C. capillata* and *Ch. hysoscella* in this study was limited to the production of podocysts and in natural populations, may be the major mode of benthic colony expansion for those two species. Podocysts are also important because they play a role in colony preservation. Nudibranchs, shrimp and gastropods prey upon scyphistomae whilst ignoring podocysts (Cargo and Schultz 1967, Grondahl 1988a, Arai 1997, 2009, Thein et al. 2012b). When large numbers of scyphistomae are consumed by such predators surviving podocysts may enable colonies to persist and regenerate.

Podocyst production increased with increasing temperature for all British species. In natural populations, podocyst production is probably maximal during the summer to early autumn. This is in agreement with findings for other *Cyanea* (Grondahl 1988a, Brewer and Feingold 1991, Thein et al. 2013) and *Chrysaora* spp. (Cargo and Schultz 1967, Cargo and Rabenold 1980, Thein et al. 2013). Excystment of podocysts was not measured in the present study, but if podocyst excystment patterns for British scyphistomae are similar to other species (Cargo and Schultz 1967, Cargo and Rabenold 1980, Grondahl 1988a, Brewer and Feingold 1991, Thein et al. 2013) then podocysts probably excyst when sea temperatures drop during autumn. In that way, emergent scyphistomae may be able to develop in time to strobilate during winter, thereby contributing to the following spring medusa bloom.

### 3.4.3 *Progeny scyphistomae*

Asexually budded progeny scyphistomae were produced by parent scyphistomae of *C. lamarckii* and *A. aurita* (both populations), but not by those of *C. capillata* or *Ch. hysoscella*. Neither temperature nor salinity was significant in determining the numbers of progeny scyphistomae produced by parent scyphistomae of *C. lamarckii*. Progeny scyphistomae of *C. lamarckii* were produced at a slow and steady rate in all treatment combinations therefore in natural populations they are probably produced slowly and continually year round. Progeny scyphistoma production in *A. aurita* (both populations) was significantly affected by temperature, salinity and their interaction, but the responses of the two populations differed. *A. aurita* from Southampton increased the production of progeny scyphistomae with increasing temperature and decreasing salinity. This finding is similar to those for a population of *A. aurita* from Tasmania where the number of progeny scyphistomae produced increased with temperature, but was unaffected by salinities 25 – 35 (Willcox et al. 2007). Scyphistomae of *A. aurita* from the Northwest Mediterranean Sea also increased progeny scyphistomae production with increasing temperature (Purcell et al. 2012). *A. aurita* scyphistomae from Orkney did not, however, exhibit any clear patterns in terms of progeny scyphistoma production. At 4°C fewer progeny scyphistomae were produced compared to higher temperatures, and production decreased with decreasing salinity, which is opposite to the trend observed for Southampton *A. aurita*. Orkney progeny scyphistomae were produced slowly in treatments above 9°C with a slight trend towards fewer progeny scyphistomae being produced with increasing temperature. Decreasing progeny scyphistoma production at high temperatures was also observed in *A. aurita* from Taiwan (Liu et al. 2009), and *A. labiata* from Hood Canal, Washington, USA (Purcell 2007). These apparently conflicting results probably reflect differences in thermal tolerances, and *in situ* water conditions experienced by different populations. Experiments from a much wider variety of locations are needed to elucidate whether there are underlying patterns of local thermal adaption in this species.

Based on results presented here, natural populations of *C. lamarckii* and *A. aurita* (Orkney) probably produce low numbers of progeny scyphistomae at a steady rate year round. Progeny scyphistomae are also probably produced year round by natural populations of *A. aurita* (Southampton), with the difference being that there is more seasonal variation with fewer being produced during winter, and more during summer and early autumn.

### 3.4.4 *Strobilation*

Scyphistomae of all British species studied here underwent the process of strobilation under experimental conditions. Differences existed in the ranges of temperatures, and in some cases salinities, at which strobilation occurred amongst British species. Temperature alone was significantly linked with strobilation for scyphistomae of *C. capillata, C. lamarckii* and *Ch. hysoscella,* with the general trend being that for *C. capillata* and *C. lamarckii* that as temperatures increased, the predicted probability of

strobilation decreased (Figs. 4, 7). In the Gullmar Fjord, Sweden *C. capillata* strobilated during the coldest months of the year (Grondahl 1988a). The same was observed with *C. capillata* from the Niantic River estuary, Connecticut (Brewer and Feingold 1991). Scyphistomae of *Ch. hysoscella* strobilated in a wide range of temperatures, from 9 – 19°C, and if 4°C treatment groups are excluded from consideration since 100% mortality occurred, the trend for strobilation in *Ch. hysoscella* scyphistomae was similar to the trend described for *Cyanea* species presented above. As temperature increased the probability of strobilation decreased. Strobilation of *A. aurita* scyphistomae was significantly affected by temperature and salinity with the effect being that as temperature increased the predicted probability of strobilation decreased (Figs. 13, 14, 17). There were however, differences in the range of temperatures at which strobilation occurred. Scyphistomae of *A. aurita* (Orkney) only strobilated at 4°C, whereas *A. aurita* (Southampton) scyphistomae strobilated at 4 and 9°C. Fewer *A. aurita* scyphistomae (Orkney) strobilated in low salinities whereas more *A. aurita* scyphistomae (Southampton) strobilated at high salinity. In England *A. aurita* ephyrae are have been observed in the sea from the end of January through the middle of March (Lucas and Williams 1994, Lucas 2001) alluding to the potential importance of low temperatures during winter for strobilation of British *A. aurita*.

3.4.5 *Onset of strobilation*

Increasing temperature decreased the amount of time to visibly initiate the process of strobilation in *C. capillata*, *C. lamarckii* and *A. aurita* (Southampton). Decreasing salinity increased the onset of strobilation period for *C. lamarckii* and *A. aurita* (Southampton). Neither temperature nor salinity affected the onset of strobilation period for *Ch. hysoscella*. Each 5°C reduction in temperature delayed the onset of strobilation in scyphistomae of *C. quinquecirrha* by about 1 week (Purcell et al. 1999) and cool temperatures delayed the appearance of their medusae in Chesapeake Bay (Cargo and King 1990). Warm temperatures decreased the onset of strobilation temperatures in *A. aurita*, *Rhizostoma pulmo* and *Cotylorhiza tuberculata* from the northwest Mediterranean Sea (Purcell et al. 2012), *A. labiata* from Washington (Purcell 2007), and *Ch. quinquecirrha* from the Chesapeake Bay (Purcell et al. 1999). This trend led Purcell et al. (2012) to conclude that medusae might appear earlier seasonally, and that scyphistomae may be able to strobilate more than once annually. In the present study no scyphistomae strobilated more than once, or began to show visible signs that the process of strobilation was about to begin again although the experiments were of relatively short duration.

Delaying strobilation in cooler temperatures and lower salinities may enable ephyrae to be released during periods more advantageous for growth and survival. If ephyrae were released early due to rapid strobilation in warmer temperatures they would be required to survive for extended periods until environmental conditions were suitable. In the Gullmar Fjord, Sweden and in Kiel Bight, Germany ephyrae are released in autumn, afterwards they descend, and overwinter on the bottom in a state resembling

diapause (Moller 1980, Hernroth and Grondahl 1985a). This may also be a possibility for British species, which would enable them to potentially avoid problems associated with trophic mismatch. Ephyrae of *A. aurita* (both populations) are able to survive for periods of up to 8 weeks without food (Chapter 4). Signals that cue overwintering ephyrae to ascend are presently unknown and should be the subject of future study, but good starting candidate variables to explore include changes in light, temperature, salinity, currents, and the benthic arrival of marine snow.

### 3.4.6 *Minimum strobilation temperature thresholds*

It has been suggested that there is a minimum temperature threshold needing to be met in order for scyphistomae of British species to strobilate (Russell 1970, and references therein). The results presented here support this hypothesis. Numerous workers have sought to uncover the internal mechanisms responsible for strobilation in scyphistomae (Arai 1997, Lucas et al. 2012), and recent work has shown that the precursor hormone controlling strobilation in *A. aurita* (Keil, Germany) is encoded in response to seasonal temperature change (Fuchs et al. 2014). Thus temperature is critical in determining whether or not strobilation will take place, and therefore whether medusae will be generated.

The findings here support the hypothesis that most species of British scyphistomae must experience low sea temperatures for appropriate durations in order for the majority of colony members to strobilate. The precise minimum temperatures required are species and population specific. Strobilation of British scyphistomae is enhanced by long winters with colder than average sea temperatures and low rainfall, following which more medusae should be expected during summer. During shorter, warmer and wetter than average winters, strobilation is reduced, and therefore fewer medusae are expected the following summers.

### 3.4.7 *Strobilation duration*

Where significant, increasing temperature decreased strobilation durations. These findings are in accordance with those for temperate (Purcell et al. 1999, Purcell 2007, Holst 2012) and tropical (Suguira 1965, Lotan and Fine 1994) species. In order to determine whether natural populations of British scyphistomae are able to strobilate more than once during an annual cycle, and therefore generate more medusae annually, it is important to know the amount of time required for scyphistomae to initiate the process of strobilation (onset), the strobilation duration, and the amount of time required for scyphistomae to recover and be ready to strobilate again. These three variables taken together might be considered as a strobilation requirement timeline (SRT). The recovery periods for British scyphistomae were not the focus of this study, so those periods must be surmised and probably have durations of at least four weeks in well fed individuals (personal observation). Therefore in order to determine whether for example, *A. aurita* (Southampton) scyphistomae might be able to strobilate more than once during an annual season one must first determine the SRT

which, at 4°C salinity 34, would be about 17 weeks (data from Appendix I, Table A4.), e.g.:

Onset (6 weeks) + Duration (7 weeks) + Estimated recovery (4 weeks) = 17 weeks.

The next step is to determine the "strobilation window," or length of time annual sea surface temperatures fall below critical minimum temperature thresholds in scyphistomae habitats, which for Southampton sea water is roughly 16 weeks (http://www.cefas.defra.gov.uk/). Since the SRT for *A. aurita* (Southampton) was 17 weeks those populations probably do not strobilate more than once during an annual season, which agrees with the presence of observed natural populations of ephyrae in Southampton (Lucas and Williams 1994). Similarly, *A. aurita* (Orkney) scyphistomae probably do not strobilate more than once in an annual season (SRT = 19.4 weeks at 4°C, salinity 34; data from Table A5). It is important to take into consideration that as seasons advance, so do temperatures. Therefore, it would be prudent in future modelling attempts utilising this concept to include changing variables with time.

3.4.7.1 *When the strobilation window closes*

Once initiated, the process of strobilation can be inhibited by changes in temperature (Chen and Ding 1983, Widmer 2008a, You et al. 2008, Holst 2012). Affected ephyrae continue to develop and are released as normal, but no further ephyrae are produced (Widmer 2008a). In the North Sea, SSTs are annually variable. As SST increase following cool periods, minimum strobilation temperature thresholds for British scyphistomae cease to be met thus closing strobilation windows and ending the process for the season. Asexual reproduction then shifts to the production of podocysts and progeny scyphistomae.

3.4.7.2 *On strobilation durations and multiple annual strobilations*

Scyphistomae of *Ch. hysoscella*, and both *Cyanea* species strobilated within a wide range of temperatures meaning that in natural populations strobilation potentially occurs throughout much of the year. However, the majority of strobilation takes place during winter (this study). In the Irish Sea, beach stranded *C. capillata* and *Ch. hysoscella* medusae varied widely in size leading Houghton et al. (2007) to suggest a protracted strobilation period for these species. The results presented here agree with Houghton et al. (2007) and further suggest the combination of SRTs and strobilation windows as mechanisms to describe how differently sized medusae might strand together. Within strobilation windows, multiple-strobilating scyphistomae in different stages of the SRT would release ephyrae asynchronously. Assuming similar growth rates of medusae, one result would be differently sized medusae in the sea at the same time.

Protracted strobilation periods are beneficial for *Ch. hysoscella* because this species is a sequential protandric hermaphrodite (Russell 1970). In British populations *Ch.*

*hysoscella* medusae smaller than 10 cm in diameter are exclusively male (Wright 1861). Larger medusae gradually transition, having both male and female elements, leading to specimens greater than 25 cm in diameter being exclusively female (Russell 1970). Whether or not the potential for self-fertilization in this species exists is presently unknown (A. Morandini, personal communication). If it does not exist then sexual reproduction for this species might not be possible if differently sized *Ch. hysoscella* medusae were not present in the water at the same time.

3.4.8 *Ephyrae produced*

For all species and populations tested, as temperature increased the mean number of ephyrae produced per scyphistoma decreased. This in accordance with findings for *A. aurita* from the northwest Mediterranean Sea (Purcell et al. 2012), and *A. aurita* from Taiwan (Liu et al. 2009). However, the trend for British species was opposite that observed for northeast Pacific moon jellyfish, *A. labiata* (Purcell 2007). In the case of *Ch. hysoscella* the mean number of ephyrae produced was similar across a broad range of temperatures (9 – 19°C) beyond which strobilation and ephyrae production decreased. The same trend was observed in *Rhopilema nomadica* from the eastern Mediterranean Sea (Lotan and Fine 1994). In both *Cyanea* species and *Aurelia* populations the maximal number of ephyrae were produced at salinity 27, and decreased in other levels. The exception was *Ch. hysoscella* for which ephyrae production increased with increasing salinity. That more ephyrae were produced at salinity 27 than salinity 34 may provide clues as to locations of natural populations of *Ch. hysoscella* scyphistomae. Bays and estuaries, or proximity to the surface may be more important in terms of maximal ephyrae production for all British species tested except *Ch. hysoscella*.

The greatest numbers of ephyrae in this study were produced by treatment groups with the most strobilating scyphistomae, which likely occurs in natural colonies. Both the ability to strobilate, and diet, influence the number of ephyrae produced, and ultimately the magnitudes of bloom sizes. In this study, the effect of diet on ephyrae production was not investigated, but all scyphistomae were fed to repletion once per week which was sufficient for growth and maintenance. Diet determines the number of ephyrae produced per strobilating scyphistoma, with well-fed ones producing more ephyrae than poorly fed ones (Spangenberg 1967, Purcell et al. 1999, Ishii and Watanabe 2003, Wiesenthal 2012). Temperature determines the number of scyphistomae in the colony that strobilate (this study), and thus affects the overall number of ephyrae put into the system. If minimum low temperatures are met for strobilation, thus opening the "strobilation window," but food is limiting, the magnitudes of jellyfish blooms produced by affected colonies will be minimal. If however, the strobilation window is open and scyphistomae are well-fed, blooms with larger magnitudes should be expected from those colonies. Such an effect is likely to be observed in eutrophic coastal areas (Richardson et al. 2009, Robinson and Graham 2013), or in areas where competing zooplankton predators (i.e. commercially important fishes) have been depleted (Richardson et al. 2009).

3.4.9 *The effects of temperature and salinity on* A. aurita *scyphistomae from Orkney, Scotland and Southampton, England*

Specimens from both UK populations of *Aurelia* were supplied to S. Piraino and G. Aglieri at the Universitia del Salento, Leece, Italy for COI (cytochrome c oxidase subunit I) DNA barcoding who reported that the UK *Aurelia* studied here were not genetically distinct from each other, at least on the basis of this particular marker (Piraino and Aglieri, personal communication). Despite this scyphistomae from the two British *A. aurita* populations responded differently to identical incubator experiments. Orkney scyphistomae produced fewer podocysts and progeny scyphistomae than Southampton scyphistomae. Furthermore, Orkney scyphistomae strobilated at a lower temperature than scyphistomae from Southampton, and Orkney scyphistomae produced more ephyrae when they strobilated. Southampton scyphistomae strobilated quickly at 9°C, but required more time for the full potential of being maintained at 5°C to be realised. Were the experiment to have been terminated without allowing scyphistomae in the Southampton group to finish the strobilation process, as indicated by releasing the last of their ephyrae, one might inaccurately have concluded that increased temperature could lead to increased ephyra production in Southampton *A. aurita*. Allowing the scyphistomae to complete the process of strobilation once initiated demonstrated that spending more time below strobilation threshold temperatures actually increased the number of ephyrae produced.

The differences in responses to similar environmental conditions in laboratory experiments between the two populations may be explained by differences in the characteristics of the habitats and water quality parameters for which these populations are adapted. Seasonally, the temperature and salinity in the North Sea is variable, with salinity being highest in the late winter (Turrell et al. 1992). Salinity in the southern North Sea is affected greatly by precipitation whereas in the northern North Sea salinity is more affected by oceanic inflow (Lynam et al. 2005b). The Scapa Flow Orkney *A. aurita* scyphistomae utilised here normally experience annual SSTs ranging from *ca.* 4 – 14°C (http://www.divesitedirectory.co.uk/uk_scotland_scapa.html) with salinities near 35 year round (Turrell et al. 1996). Southampton *A. aurita* experience annual SSTs ranging from *ca.* 7 – 19°C (http://www.cefas.defra.gov.uk/ ), with salinities ranging from 25 to 33 (Lucas and Williams 1994). British scyphistomae populations are likely to respond differently to climate variability depending upon the biogeographic regions they are adapted for.

3.4.10 *Hypothetical model for seasonal colony maintenance of British scyphistomae*

Plasticity in asexual reproductive modes of scyphistomae play important roles in the long term maintenance of jellyfish populations (Arai 2009, Lucas et al. 2012). In the present study, the trend for all species was that as temperature increased the number of podocysts, and progeny scyphistomae when produced, increased. The effects of

salinity on those variables, was species and population specific. British progeny scyphistomae and podocysts are probably generated throughout much of the year to varying degrees depending upon temperature, with the majority being produced during summer and late autumn (Fig. 23). In Gullmar Fjord, Sweden the majority of podocyst production for *A. aurita* took place during winter, but in *C. capillata* and *C. lamarckii* podocysts were produced during summer (Grondahl 1988a) which is more in line with findings for British congeners. The majority of strobilation in British species probably takes place during winter, which is in agreement with deductions based upon presence of ephyrae in the sea (Verwey 1942, Russell 1970, Hernroth and Grondahl 1985b, Lucas and Williams 1994). During years when strobilation window durations are short (i.e. short warm-winter years) fewer ephyrae are produced by British scyphistomae, and scyphistomae instead maximise benthic asexual reproduction, thus contributing to long term colony maintenance. During years with long strobilation window durations (i.e. long cold-winter years) benthic reproduction is slowed, but ephyrae production is increased. Dispersal is thus enhanced which contributes toward distant scyphistoma colony maintenance, and increased genetic diversity.

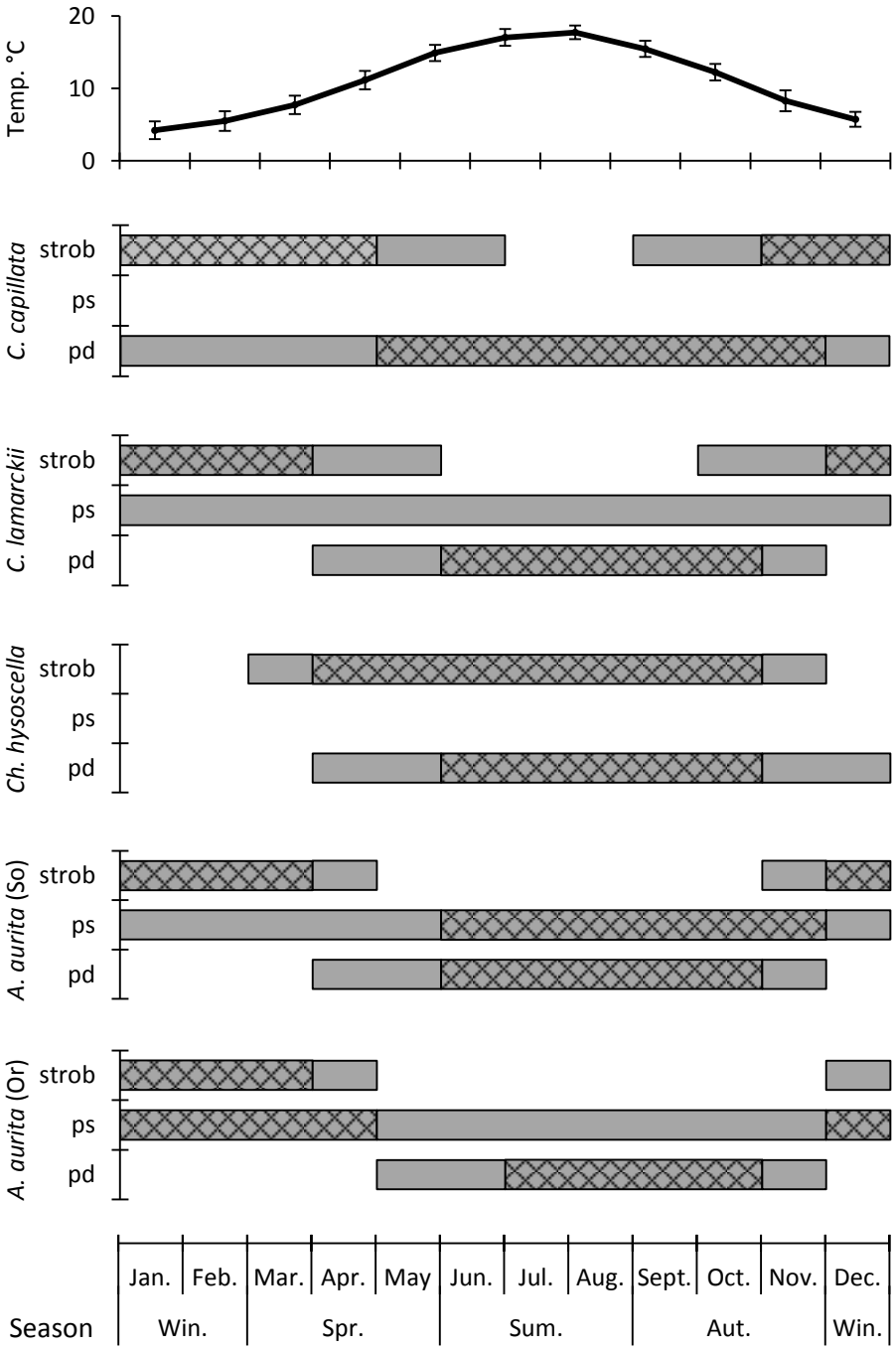


Figure 23. Hypothetical model for benthic colony maintenance of British scyphistomae based upon asexual reproductive modes and output at different temperatures. Shaded bars indicate timings of seasonal production with the crosshatched areas showing timings of maximal output. Strob = strobilation, ps = progeny scyphistomae, pd = podocysts. Monthly average sea surface temperatures reported at Cromor, Norfolk England, located at 52° 56'N, 1° 18'E covering the period 1971 – 2000; bars = SD; data from http://www.cefas.defra.gov.uk.

### 3.4.11 *Mechanisms linking NAO to observed medusae abundance*

Jellyfish blooms in the North Sea most often occur from May – September (Russell, 1970) the timing of which corresponds with warmer sea temperatures and increased food availability which facilitate growth and subsequent reproductive success for medusae. Medusae abundance of *A. aurita* and *C. lamarckii* in the southern North

Sea has been shown to be negatively correlated with the NAO, thus when the NAO is positive blooms are less likely. No significant correlation of blooms with the NAO was shown for *C. capillata* (Lynam et al. 2004, 2005b, 2010). When the NAO is in a positive phase, southern North Sea temperatures are generally warmer throughout the year with episodic decreased salinity near the coasts due to increased river run-off resulting from increased storm activity (Drinkwater et al., 2003). Conversely, when the NAO is in a negative phase the water is colder and salinity near the coasts remains higher. Depending on location, SST in the southern North Sea generally ranges between 3.5°C during winter to 18°C in summer. Winter SST can vary by up to 4°C depending upon whether the NAO is in a high or low phase (Hughes and Lavin 2004). For example, the Cefas monitoring station at Cromer, Norfolk England, located at 52° 56'N, 1° 18' recorded January SSTs during the NAO low phase periods in 1977 and 1979 of 3.0°C and 2.7°C respectively. When the NAO was in high phases during 1973 and 1975 the mean temperatures during January were 7°C and 6.2°C respectively (www.cefas.defra.gov.uk).

The combination of strobilation requirement timelines (SRTs) and minimum temperature thresholds needing to be met in order for strobilation to occur (i.e., open strobilation windows) explain in part the medusa abundance patterns linked with NAO in the North Sea reported by Lynam et al. (2004, 2005). Since decreased salinities resulted in increased SRTs, the combination of short strobilation windows and increased SRTs in high NAO scenarios would further decrease the number of ephyrae produced during high NAO years. Conversely, during low NAO years strobilation windows are open for longer and SRTs are shorter due to increased salinity, resulting in more ephyrae being generated (Fig. 22). Medusae of *C. capillata* may be able to overwinter (Hay et al. 1990a) thus potentially masking the effects of NAO on their abundance, and since scyphistomae of *C. capillata* strobilated in a wider range of temperatures than *C. lamarckii* or *A. aurita* (Orkney) changes in SST brought on by NAO phase shifts may not be as strongly expressed by *C. capillata*.

In summary, the asexual reproductive modes of the scyphistomae studied here were significantly affected by temperature and salinity, with temperature being the more important driver of the two factors. Scyphistomae responded to increased temperatures by decreasing or ceasing strobilation altogether, and by increasing rates of benthic asexual reproduction. Scyphistomae strobilated in response to cool temperatures, and the results presented here support the hypothesis of a minimum temperature threshold needing to be met for sufficient durations in order for strobilation to occur. Generalised linear models based on present results predicted a decreased probability of strobilation in response to warmer temperatures which would have the effect of generating fewer ephyrae. Scyphistomae from two different populations of *A. aurita* responded differently to identical environmental conditions during laboratory experiments. Scyphistomae from Orkney, Scotland, the northern population were larger, produced more ephyrae and strobilated in lower temperatures than did the *A. aurita* from Southampton, England, the southern population which

points to the importance of considering the ways in which different populations of the same species may respond to similar environmental conditions in future modelling efforts.

# Chapter 4

**The effects of temperature, salinity and starvation on growth and survivorship of British scyphozoan ephyra larva**

## 4.1 Introduction

The majority of scyphomedusae have both planula and ephyra larval stages in their life histories. Planula larvae are released by pelagic medusae and eventually settle, then develop into benthic scyphistomae. Ephyrae are generated by benthic scyphistomae through the process of strobilation, and after being released go on to develop into pelagic medusae. The ephyra stage is perhaps the least studied and therefore least understood life history stage of scyphomedusae (Arai, 1997; Bamstedt et al., 1999). Natural selection operates on all jellyfish life history stages, therefore understanding how factors affect survivorship and growth of ephyrae ultimately contributes to a better understanding of mechanisms regulating medusa abundance. Climate variability may have significant effects on survivorship and growth of ephyrae, affecting the numbers that eventually go on to become medusae. How temperature, salinity, and starvation affect growth and survivorship of ephyrae will be the subjects of this chapter.

Most existing studies regarding ephyrae investigated the effects of different factors on growth. Both temperature and salinity have been shown to have significant effects on growth. For example, in a 10 day experiment ephyrae of *Aurelia aurita* from the Gullmar Fjord, Sweden had an average daily growth rate of 31.3% $d^{-1}$ calculated from the difference between initial and ending ash free dry weight at 18°C, the highest temperature tested (Bamstedt et al. 1999). In a separate experiment the average daily growth rate of *A. aurita* ephyrae was determined to be 30.6% at salinity 35, 18°C. Although the effect of salinity on ephyral growth was statistically significant, it was not as pronounced as was the effect of temperature (Bamstedt et al. 1999). Ephyrae of *Aurelia labiata* from the northeast Pacific Ocean had an average daily growth rate of 28.9% $d^{-1}$ at 21°C (Widmer, 2005) which is similar to the maximum daily growth rate reported for *A. aurita* by Bamstedt et al. (1999) from Sweden. Different species of ephyrae inhabiting different latitudes share the trait of possessing the potential for remarkably high growth rates under optimal conditions.

Diet also significantly affects ephyral growth. For example, newly released ephyrae of *Cyanea capillata* from Norwegian waters showed poor growth when fed a mixture of copepod zooplankton and *Artemia* nauplii, even though such food was suitable for ephyral growth of *A. aurita* (Bamstedt et al., 1997). Norwegian *C. capillata* ephyrae did however grow well when the lobate ctenophore *Bolinopsis infundibulum* was offered as prey leading the authors to conclude that *C. capillata* may be dependent upon gelatinous zooplankton for development (Bamstedt et al. 1997). Ephyrae of *Chrysaora quinquecirrah* from the Chesapeake Bay showed growth rates of about 30% $d^{-1}$ when fed rotifers, *Brachionus plicatilus*, and that growth rate increased to nearly 70% $d^{-1}$ when fed larvae of the ctenophore *Mnemiopsis leidyi* (Olesen et al., 1996). The previous two studies allude to the potential importance of some scyphomedusae in regulating the abundance of other gelatinous zooplankton through predation.

The timing of ephyral release in northern regions may be seasonally restricted (Bamstedt et al. 1999). Depending on species and geographic location, northern populations of ephyrae may be produced in the autumn (Hernroth and Grondahl 1985b), winter (Lucas & Williams, 1994; Moller, 1980) or spring (Bamstedt et al., 1994). In British waters ephyrae are generally released in cold water during winter and early spring (Lucas, 1996; Russell, 1970). Natural populations of scyphistomae are often found in water less than 30m deep (Hernroth & Grondahl, 1985; Olesen et al., 1996; Purcell et al., 2009; personal observation), a region potentially influenced by changes in temperature and salinity, meaning that ephyrae may be likely to experience similar conditions. In Chapter 3 I demonstrated that strobilation and numbers of ephyrae produced by the scyphistomae of several common British species are significantly influenced by temperature and salinity. With the exception of the study on growth of *A. aurita* ephyrae from the Gullmar Fjord, Sweden (Bamstedt et al. 1999) there are currently no reports regarding how temperature and salinity affect growth of newly released northern *A. aurita*, *C. capillata*, *C. lamarckii* or *Chrysaora hysoscella* ephyra larvae.

Populations of *A. aurita* ephyrae in the coastal waters of Sweden and in Kiel Bight, Germany are reported to be released in autumn where after they descend to deeper waters and overwinter in a state similar to diapause (Moller 1980, Hernroth and Grondahl 1985b, Arai 1997). This sequence of events seems paradoxical since the ephyrae are generated and released during a period when food availability is low. One might expect that the timing of larval release would be synchronized with spring phytoplankton and subsequent zooplankton blooms since food would be plentiful at that time. However, the ability to overwinter near the bottom may enable ephyrae to delay their ascent to surface waters until conditions are favourable for growth. Factors that cue the migration of ephyrae from deep waters to surface waters are unknown, but potentially include changes in temperature, the arrival of "marine snow" signalling surface food availability, and changes in day length. Whether or not British populations of *A. aurita* possess the capability to overwinter in a state similar to diapause is unknown.

Newly released ephyrae were maintained in laboratory incubation experiments in order to better understand mechanisms regulating medusa abundance. Two separate hypotheses were investigated. The first was that temperature and salinity significantly affected growth and survivorship of newly released ephyrae during short term laboratory experiments. Secondly, the effects of starvation in longer term experiments were examined with the clear goal of determining whether ephyrae of *A. aurita* could survive for extended periods to investigate the potential for overwintering in ephyrae.

### 4.2 Methods

Two types of experiments were conducted during this study. First, ephyrae of four different species of British scyphomedusae were incubated for seven day periods in order to test the effects of different combinations of temperature and salinity on ephyral growth. In order to test the effects of starvation on survivorship, newly released ephyrae from northern (Lat. 58°54'00.00") and southern (Lat. 50°51'50.10") populations of British *A. aurita* were maintained without food for a period of 8 weeks

at 7°C, the temperature at which strobilation occurred, and their conditions at the ends of the experiments recorded.

Ephyrae used in the study were produced by stock cultures of strobilating scyphistomae maintained at 7°C at the Scottish Oceans Institute. Methods for initiating the stock cultures of scyphistomae are described in Chapter 3. Ephyrae that had been released by their parent strobilae within 48 hours were used to begin all experiments. The mean diameters of 50 newly released ephyrae randomly selected from their stock cultures are given in table 1.

Table 1. Mean diameters (mm) of newly released ephyrae larvae of four species of British scyphomedusae, n = 50.

| Species | Mean diameter (mm) | Std. Dev. | Std. Error |
|---|---|---|---|
| *C. capillata* | 4.1 | 0.7 | 0.1 |
| *C. lamarckii* | 4.3 | 0.6 | 0.1 |
| *Ch. hysoscella* | 3.2 | 0.4 | 0.1 |
| *A. aurita* Southampton population | 4.0 | 0.7 | 0.1 |
| *A. aurita* Orkney population | 3.2 | 0.5 | 0.1 |

4.2.1 *Effects of temperature and salinity on growth of ephyrae*

Ephyrae of *A. aurita* (Southampton population), *C. capillata*, *C. lamarckii* and *Ch. hysoscella* were gently collected from their stock cultures using a wide-mouthed pipette and transferred individually into each well of 6-well polycarbonate culture plates (Thermo Scientific, Walthom, MA) filled with 12 ml of 5µm-filtered North Sea water at salinity 34. Only ephyrae with 8 ephyral arms and without gross dissymmetry were used. During the acclimation period ephyrae were not fed. Ephyrae were first gradually acclimated in a stepwise manner to target salinities (34, 27, 21) at 9°C ±1°C over three days, and then to target temperatures (4, 9, 14, 19 and 23°C) ±1°C, over four additional days. There were no apparent deleterious effects to this relatively rapid acclimation scheme as was found for *A. aurita* ephyrae originating from Corpus Christi, Texas (Dillon 1977). These temperatures and salinities were chosen because they are within the range to be potentially encountered by natural populations during the year (Baxter et al. 2011), with the addition of a 23°C treatment meant to represent the extreme sea temperature predicted to possibly occur in the North Sea 100 years from today (Hughes et al. 2010). North Sea water at salinity 34 was mixed with distilled water in order to compose sea water of salinities 21 and 27. Salinity was measured with a hand held refractometer (Bellingham and Stanley, Kent UK)

Experiments were carried out in darkened temperature controlled incubators (Lucky Reptile Herp Nursery II incubator, Waldkirch, Germany; Fig. 1, Chapter 2), and temperature was measured daily in each incubator throughout the acclimation and experimental periods with temperature data loggers (Lascar EL-USB-1, Wiltshire, UK). A total of 18 ephyrae per treatment were used for all species tested. Ephyrae were measured at the start and end of each experiment, on days 1 and 7 respectively. In order to measure ephyrae they were first gently transferred from their individual wells using a wide mouthed pipette into a shallow concavity slide. After being allowed to relax for one minute they were measured from lappet tip to lappet tip to the nearest 0.1mm using a calibrated measuring ocular mounted on an Olympus SZ40 dissecting microscope (Hamburg, Germany). Water was changed each day with 5µm-

filtered North Sea water of appropriate temperatures and salinities. Ephyrae were fed *Artemia salina* nauplii to excess each day such that food was not a limiting factor.

Ephyrae growth rates (% $d^{-1}$) were calculated using the following equation after Bamstedt et al. (1997) where $D_1$ and $D_2$ are mean ephyrae diameters measured from lappet tip to lappet tip on days one and seven respectively and at two consecutive times $t_1$ and $t_2$ (days) respectively.

$$\% \text{ growth day}^{-1} = \ln[(D_2/D_1)^3]/(t_2 - t_1) \times 100$$

This equation takes into account the gradual development from ephyra to medusa (Bamstedt et al. 1997), and does not require the destruction ephyrae as do methods utilizing ash free dry weights.

4.2.2 *The effects of starvation on survivorship of* Aurelia aurita *ephyrae*
Ephyrae that had been released within 48 hours by strobilating stock cultures maintained at 7°C of *A. aurita* (Southampton population) and *A. aurita* (Orkney population) were utilized during the starvation experiments. Fifty-four ephyrae from each population were collected and placed individually into each well of 6-well polycarbonate culture plates filled with 12 ml of 5µm-filtered North Sea water at salinity 34. Culture plates were maintained at 7°C ±1°C inside darkened incubators for a period of eight weeks, and ephyrae were not fed during this period. Each week the water inside the replicate wells was changed with new 5µm-filtered North Sea water and ephyrae were checked for mortality and general health condition. At the end of the experiments individual ephyrae were measured and growth rates calculated using the equation presented above with the exception that growth rate was expressed as % growth $week^{-1}$ rather than % growth $day^{-1}$.

4.2.3 *Statistics*
Data were analysed using the statistical software IBM SPSS version 21. Two-way ANOVAs were used to determine whether the effects of temperature, salinity, or their interaction on growth of ephyrae of *A. aurita, C. capillata* and *Ch. hysoscella* were significant. A one-way ANOVA was used to determine the significance of temperature on growth of *C. lamarckii* ephyrae since only salinity 34 was tested. Tukey's HSD post hoc tests were conducted following significant ANOVA results. Prior to conducting the ANOVAs data were first tested for normality and homoscedasticity with Shapiro-Wilk and Levene's tests respectively. For *C. lamarckii* only $H_{o1}$ was tested, but for *A. aurita, C. capillata* and *Ch. hysoscella* the following three null hypotheses were tested:

$H_{o1}$: Growth of ephyrae was independent of temperature.
$H_{o2}$: Growth of ephyrae was independent of salinity.
$H_{o3}$: There was no interaction between the main effects factors temperature and salinity.

A two sample t-test was used to determine whether growth rates of starved ephyrae from the northern and southern populations of *A. aurita* were significantly different. Again, prior to conducting the two sample t-test data were first tested for normality and homoscedasticity with Shapiro-Wilk and Levene's tests respectively. The following null hypothesis was tested:

$H_{o4}$: There is no difference in mean decrease in growth rate between *A. aurita* (Southampton population) and *A. aurita* (Orkney population).

**4.3 Results**

4.3.1 *The effects of temperature and salinity on growth of* Cyanea capillata *ephyrae*

The general effect of temperature and salinity on growth of *C. capillata* ephyrae was that at the end of the seven day experiment ephyrae were largest in the two coldest temperatures tested, 4 and 9°C, and final sizes decreased as temperature increased (Figure 1). The main effect of temperature on growth of ephyrae was significant, $F_{(4,255)} = 78.64$, $p < 0.001$, as was the main effect of salinity, $F_{(2,255)} = 13.57$, $p < 0.001$, and their interaction, $F_{(8, 255)} = 3.28$, $p < 0.01$. Post-hoc Tukey's HSD tests showed that ephyrae in the 4 and 9°C treatments were significantly larger at the end of the experiment than the warmest temperatures tested (Table 2), therefore they also had the highest growth rates (Table 3).

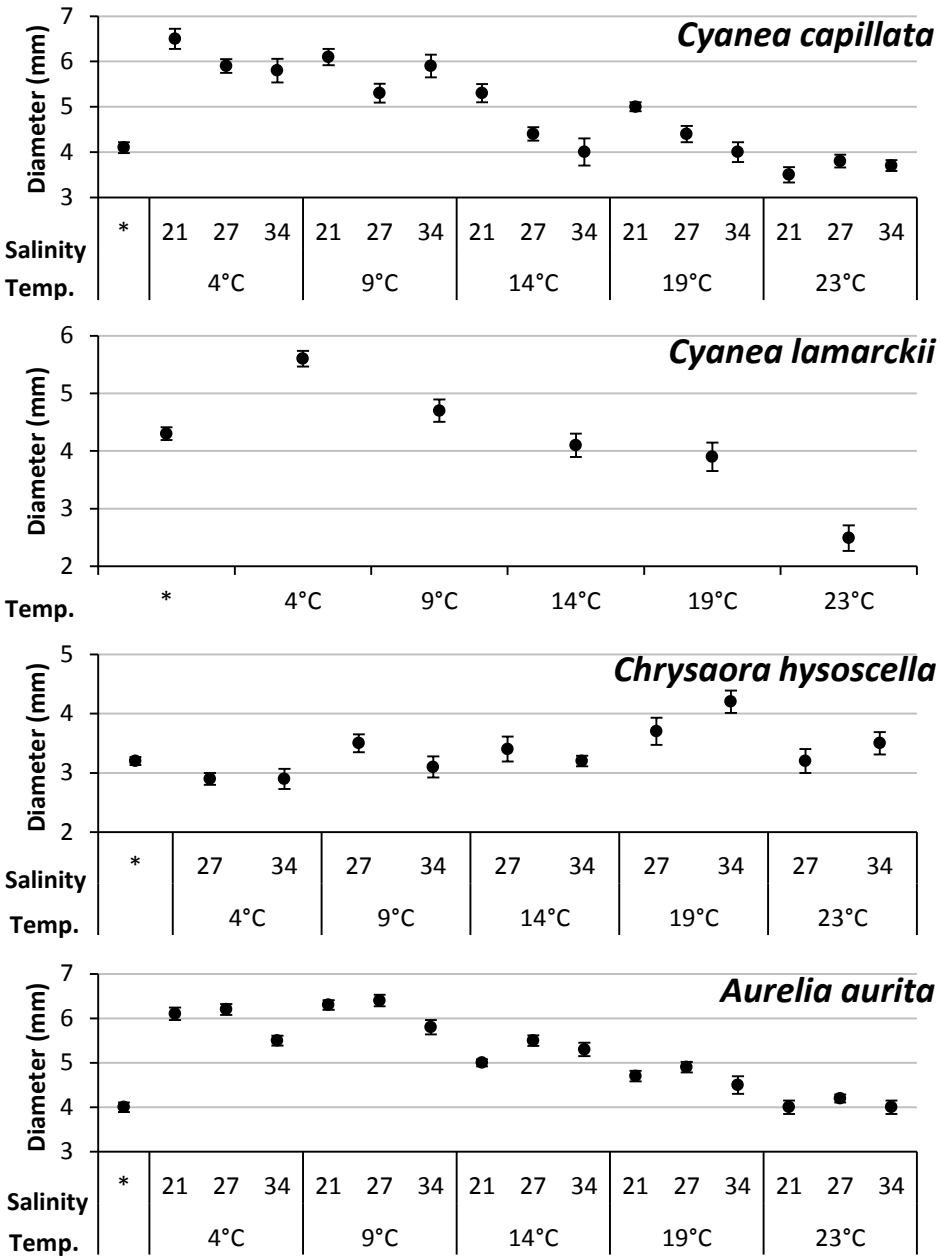


Figure 1. Starting (*) and final diameters of ephyrae in a seven day experiment testing the effects of temperature and salinity on growth; error bars = S.E.; n = 18 per treatment; * = starting diameters of newly released ephyrae from strobilating scyphistomae maintained at 7°C, n = 50.

Table 2. Descriptive statistics and post hoc test results for experiments testing the effects of temperature and salinity on growth of ephyra larvae of four species of British scyphozoa. Means that share a letter for each species were shown not to be statistically significant with Tukey's HSD tests.

| | | 4°C | | 9°C | | 14°C | | 19°C | | 23°C | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Species | Salinity | Mean | SD | Mean | SD | Mean | SD | Mean | SD | Mean | SD |
| *Cyanea capillata* | 21 | 6.5 A | 0.94 | 6.1 A,B | 0.75 | 5.3 B,C,D | 0.86 | 5.0 C,D | 0.39 | 3.5 F | 0.71 |
| | 27 | 5.9 A,B,C | 0.65 | 5.3 B,C,D | 0.91 | 4.4 D,E | 0.64 | 4.4 D,E | 0.77 | 3.8 E,F | 0.61 |
| | 34 | 5.8 A,B,C | 1.09 | 5.9 A,B,C | 1.06 | 4.0 E,F | 1.22 | 4.0 E,F | 0.97 | 3.7 E,F | 0.49 |
| *Cyanea lamarckii* | 34 | 5.6 A | 0.58 | 4.7 B | 0.83 | 4.1 B,C | 0.81 | 3.9 C | 0.93 | 2.5 D | 0.66 |
| *Chrysaora hysoscella* | 27 | 2.9 B | 0.43 | 3.4 B | 0.63 | 3.4 B | 0.91 | 3.7 A,B | 0.96 | 3.2 B | 0.83 |
| | 34 | 2.9 B | 0.74 | 3.1 B | 0.75 | 3.2 B | 0.38 | 4.2 A | 0.81 | 3.5 B | 0.82 |
| *Aurelia aurita* | 21 | 6.1 A,B | 0.59 | 6.3 A | 0.48 | 5.0 D,E,F | 0.36 | 4.7 E,F,G | 0.52 | 4.0 G | 0.63 |
| | 27 | 6.2 A | 0.51 | 6.4 A | 0.57 | 5.5 B,C,D | 0.52 | 4.9 D,E,F | 0.52 | 4.2 G,H | 0.38 |
| | 34 | 5.5 B,C,D | 0.47 | 5.8 A,B,C | 0.66 | 5.3 C,D,E | 0.64 | 4.5 F,G,H | 0.84 | 4.0 H | 0.62 |

Ephyrae at 4 and 9°C showed positive growth rates in all three salinities tested, whereas at 14 and 19°C positive growth was only achieved at salinities 27 and 21. At 23°C growth rates were negative in all three salinities tested. Ephyrae in these treatments were beginning to disintegrate and in generally poor condition.

Table 3. Growth rates (% $d^{-1}$) of *Cyanea capillata* ephyrae maintained in 15 different combinations of temperature and salinity in a 7 day experiment, n = 18 per treatment.

| Temperature °C | Salinity | Growth rate % $d^{-1}$ | 95% Confidence interval Lower | Upper |
|---|---|---|---|---|
| 4 | 21 | 22.79 | 19.36 | 26.01 |
| | 27 | 17.95 | 15.39 | 20.38 |
| | 34 | 17.10 | 12.50 | 21.31 |
| 9 | 21 | 19.62 | 16.64 | 22.43 |
| | 27 | 12.59 | 8.55 | 16.33 |
| | 34 | 17.95 | 13.61 | 21.94 |
| 14 | 21 | 12.59 | 8.75 | 16.16 |
| | 27 | 3.28 | -0.17 | 6.52 |
| | 34 | -1.47 | -9.42 | 5.37 |
| 19 | 21 | 9.67 | 7.67 | 11.60 |
| | 27 | 3.28 | -0.89 | 7.14 |
| | 34 | -1.47 | -7.18 | 3.64 |
| 23 | 21 | -8.15 | -13.15 | -3.61 |
| | 27 | -4.04 | -7.79 | -0.55 |
| | 34 | -5.37 | -8.65 | -2.29 |

4.3.2 *The effects of temperature on growth of* Cyanea lamarckii *ephyrae*

Temperature had a similar effect on final ephyra diameters for *C. lamarckii* as for *C. capillata*, which is to say that greater growth was achieved by *C. lamarckii* ephyrae in the coldest temperatures tested with a decreasing growth trend as temperature increased (Figure 1). The effect of temperature on growth of *C. lamarckii* was significant, $F_{(4,74)} = 26.62$, $p < 0.001$, and post hoc tests showed that ephyrae maintained at 4°C were significantly larger at the end of the experiment than in all other treatments (Table 2). Ephyrae maintained at 4 and 9°C were the only ones to show positive growth during the experiment (Table 4) and they appeared to be in good condition, actively swimming around their replicate wells.

Table 4. Growth rates (% $d^{-1}$) of *Cyanea lamarckii* ephyrae maintained at 5 different temperatures at salinity 34 in a 7 day experiment, n = 18 per treatment.

| Temperature °C | Growth rate % $d^{-1}$ | 95% Confidence interval Lower | Upper |
|---|---|---|---|
| 4 | 13.84 | 11.38 | 16.19 |
| 9 | 5.16 | 0.88 | 9.09 |
| 14 | -1.07 | -6.15 | 3.53 |
| 19 | -4.44 | -11.18 | 1.49 |
| 23 | -26.69 | -36.29 | -18.64 |

Even though ephyrae maintained at 14 and 19°C showed negative growth rates they appeared to be in good condition, albeit smaller than when initially released from their strobilae. Ephyrae maintained at 23°C were in poor condition and appeared to be moribund at the end of the experiment.

4.3.3 *The effects of temperature and salinity on growth of* Chrysaora hysoscella *ephyrae*

Ephyrae of *Ch. hysoscella* were smaller at the end of the experiment in the coldest temperatures tested and larger as temperature increased (Figure 1). The main effect of temperature on growth of ephyrae was significant, $F_{(4,170)} = 9.49$, $p < 0.001$. However, the main effect of salinity was not significant, $F_{(1,170)} = 0.27$, $p > 0.05$, and neither was the interaction between temperature and salinity, $F_{(4,170)} = 2.02$, $p > 0.05$. Post hoc Tukey's HSD tests showed that ephyrae maintained at 19°C salinity 34 were significantly larger than all other ephyrae at the end of the study (Table 2). Ephyrae of *Ch. hysoscella* had lower maximal growth rates than the other species tested. Positive growth rates were only achieved in the 4 warmest temperatures tested, 9, 14, 19 and 23°C with the highest growth rate, 14.11% $day^{-1}$ occurring at 19°C and salinity 34 (Table 5).

Table 5. Growth rates (% $d^{-1}$) of *Chrysaora hysoscella* ephyrae maintained at 10 different combinations of temperature and salinity in a 7 day experiment, n = 18 per treatment.

| | | | 95% Confidence interval | |
|---|---|---|---|---|
| Temperature °C | Salinity | Growth rate % $d^{-1}$ | Lower | Upper |
| 4 | 27 | -5.29 | -8.85 | -1.97 |
| 4 | 34 | -5.00 | -11.25 | 0.55 |
| 9 | 27 | 3.84 | -0.56 | 7.89 |
| 9 | 34 | -1.39 | -7.32 | 3.91 |
| 14 | 27 | 3.04 | -3.49 | 8.82 |
| 14 | 34 | 0.51 | -2.30 | 3.17 |
| 19 | 27 | 6.88 | 0.43 | 12.59 |
| 19 | 34 | 14.11 | 9.52 | 18.31 |
| 23 | 27 | 0.52 | -5.75 | 6.10 |
| 23 | 34 | 3.68 | -2.15 | 8.91 |

At the end of the experiment ephyrae maintained at 19 and 23°C were in excellent condition and actively swimming about. Those maintained at 14°C were less active, but still in generally good condition. Ephyrae maintained at 4 and 9°C were not actively swimming, and sat on the bottoms of their replicate wells weakly pulsing.

4.3.4 *The effects of temperature and salinity on growth of* Aurelia aurita *ephyrae (Southampton population)*

The general trend for the effects of temperature and salinity on growth of *A. aurita* ephyrae was similar to that of *C. capillata* and *C. lamarckii*, which is to say that greatest growth was achieved in the lowest temperatures tested and growth decreased as temperature increased (Figure 1). The main effect of temperature on growth of *A. aurita* ephyrae was significant, $F_{(4,255)} = 124.86$, $p < 0.001$, as was the main effect of salinity, $F_{(2,255)} = 12.75$, $p < 0.001$. There was not a significant interaction between temperature and salinity, $F_{(8, 255)} = 1.78$, $p > 0.05$. Post hoc Tukey's HSD tests showed that ephyrae at the end of the experiment were significantly larger in the 4, 9 and 14°C treatments than in the 23°C treatments for all three salinities tested (Table 2). Positive growth rates were achieved for ephyrae maintained from 4 – 19°C at all three salinities, and negative growth rates were only observed for specimens

maintained at 23°C in all salinities. Specimens in the 4 and 9°C treatments had the highest growth rates overall ranging from 11.11 to 18.5 % growth day$^{-1}$(Table 6).

Table 6. Growth rates (% d$^{-1}$) of Southampton *Aurelia aurita* ephyrae maintained at 15 different combinations of temperature and salinity in a 7 day experiment, n = 18 per treatment.

| Temperature °C | Salinity | Growth rate % d$^{-1}$ | 95% Confidence interval Lower | Upper |
|---|---|---|---|---|
| 4 | 21 | 15.94 | 13.80 | 18.31 |
| 4 | 27 | 16.59 | 14.98 | 18.78 |
| 4 | 34 | 11.11 | 8.93 | 12.85 |
| 9 | 21 | 17.48 | 15.97 | 19.40 |
| 9 | 27 | 18.50 | 16.47 | 20.45 |
| 9 | 34 | 13.49 | 10.80 | 16.21 |
| 14 | 21 | 5.66 | 4.57 | 7.71 |
| 14 | 27 | 10.65 | 8.74 | 13.02 |
| 14 | 34 | 8.60 | 6.22 | 11.77 |
| 19 | 21 | 3.28 | 0.50 | 5.51 |
| 19 | 27 | 5.05 | 2.69 | 7.49 |
| 19 | 34 | 0.67 | -3.66 | 5.07 |
| 23 | 21 | -4.86 | -8.81 | -1.44 |
| 23 | 27 | -2.31 | -4.69 | -0.49 |
| 23 | 34 | -5.24 | -8.81 | -1.44 |

Ephyrae maintained at 23°C in all salinities tested were in poor condition at the end of the experiment. Those specimens were observed on the bottoms of their replicate wells, weakly pulsing. Some of them had everted their ephyral arms (Figure 2) which is a symptom that they were moribund (Kikkawa et al., 2010; Widmer, 2005). All other *A. aurita* ephyrae in all other treatments were in good condition and actively pulsing.

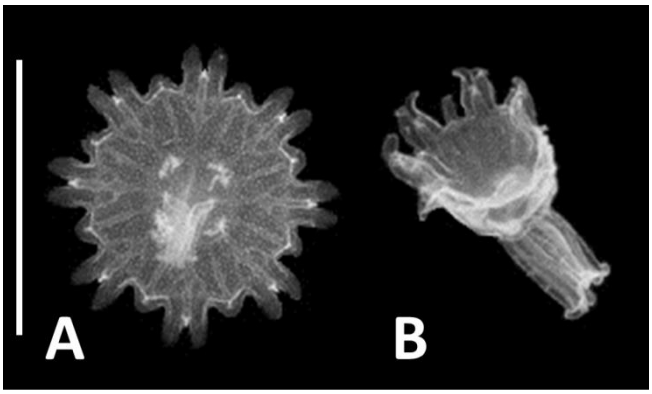


Figure 2. Ephyrae of *Aurelia labiata* maintained at different temperatures for 14 days (after Widmer, 2005). (A) Healthy meta-ephyra in good condition maintained at 17°C. (B) Unhealthy, everted and moribund meta-ephyra maintained at 24°C. Scale bar = 10mm.

4.3.5 *The effects of starvation on survivorship of* Aurelia aurita *ephyrae*

Ephyrae of *A. aurita* from Orkney and Southampton populations became gradually smaller as time progressed. However, there was a significant difference in the decrease in growth rate between *A. aurita* ephyrae from Southampton (M = -62.4% w$^{-}$

$^{1}$, SD = 14.7) and those from Orkney (M = -14.13% $w^{-1}$, SD = 8.02), $t_{(61)} = 19.39$, $p < 0.001$. There was no mortality for ephyrae of *A. aurita* from the Orkney population at the end of the eight week experiment whereas 11 of the ephyrae from Southampton died. Further, ephyrae from the Orkney population were in good condition at the end of the experiment actively pulsing several times per minute. However, ephyrae from the Southampton population were in generally poor condition. Some had tattered lappets, others had everted their ephyral arms (Figure 2), and none were actively pulsing or swimming.

**4.4 Discussion**

The ephyra life history stage is one of the least studied, perhaps because they are cryptic in nature, or perhaps because they spend so little time as ephyrae due to their very high growth rates. However, factors affecting their growth and development are important because they may ultimately affect species fitness.

Temperature had statistically significant effects on ephyral growth for all species tested. Salinity had significant effects on growth for both *C. capillata* and *A. aurita*, but did not have significant effects of final sizes of *Ch. hysoscella* ephyrae. More *A. aurita* ephyrae from the starved Orkney population survived until the end of the 8 week experiment than starved ephyrae from the Southampton population, and the Southampton population had a significantly greater decrease in size than did ephyrae from the Orkney population. Ephyrae from the Southampton population were in generally poor condition at the end of the experiment, whereas those from the Orkney population were not.

4.4.1 *The effects of temperature and salinity on growth of ephyrae*

In a similar study testing the effects of temperature (6, 9.5, 12, 15, 18°C) and salinity on growth of newly released *A. aurita* ephyrae from Gullmar Fjord, Sweden the optimal temperature for growth was determined to be 18°C at the end of a 10 day experiment (Bamstedt et al. 1999); various salinities (30.5, 26, 22, 17.5) were then tested at 18°C. A drawback to the Bamstedt et al. (1999) experimental design was that it did not allow for the detection of an interaction. In the present study, the interaction effect between the factors temperature and salinity was not statistically significant for *A. aurita* or *Ch. hysoscella*. However, the interaction was statistically significant for *C. capillata* meaning the order of the magnitude of the effect of temperature on final ephyra diameters depended in part on salinity. Ephyrae of *A. aurita* had significantly higher growth in the lowest temperatures and salinities tested. *A. aurita* had the highest growth rates in the two lowest salinities which is in line with their being euryhaline species and having scyphistomae that are often observed in estuaries (Lucas & Williams, 1994). Ephyrae of *C. capillata* also had high growth rates at low temperatures and salinities. While the locations for scyphistomae of *C. capillata* in the North Sea are presently unknown, I have observed their scyphistomae at depths of 5 – 10m deep in waters near Fiskebackskil, Sweden which would likely experience changes in temperature and salinity due to seasonal fluctuations.

Around the British Isles ephyrae of *Aurelia* and *Cyanea* may be found in plankton tows as early as January through to early April (Russell 1970). Ephyra larvae in this study showed positive growth rates at or near temperatures their parent scyphistomae strobilated. Scyphistomae of *A. aurita* (Southampton population), *C. lamarckii* and *C. capillata* strobilated at 4 and 9°C in all salinities tested (Chapter 3). Accordingly,

ephyrae of those three species showed the highest growth rates at those temperatures and salinities. Scyphistomae of *Ch. hysoscella* had a wide range of strobilation temperatures (9, 14, 19 and 23°C), but salinity was not a significant factor (Chapter 3). Accordingly, ephyrae of *Ch. hysoscella* showed positive growth from 9 – 23°C, with the influences of the same salinities tested not being significant.

4.4.2 *Growth rate comparisons amongst different species of ephyrae*

The optimal temperatures and salinities for growth of jellyfish ephyrae from different locations around the world change, but growth rates during the first seven days of development are remarkably high for some species. The highest growth rates in this study were from ephyrae of *C. capillata* and ranged from 12.59 to 22.79% $d^{-1}$ at 9°C and a salinity of 27, and 4°C and a salinity of 21 respectively. During the first seven days of development ephyrae of *P. camstchatica* showed optimal growth rates of 13.66% $d^{-1}$ at 17°C (Table 7) which is similar the growth rate range reported here for British *C. capillata*. Ephyrae of *Ch. hysoscella* had generally lower growth rates than did other species of British ephyrae, with the maximum growth rate being 14.11% $d^{-1}$ at 19°C, salinity 34. Ephyrae of *Chyrsaora fuscescens* from the northeast Pacific Ocean had a maximum growth rate of 12.08% $d^{-1}$ at 17°C, salinity 34 (Table 7), which is again similar to the maximum growth rate reported here for *Ch. hysoscella*. The highest growth rate for newly released ephyrae of British *A. aurita* was 18.5% $d^{-1}$ at 9°C, salinity 27 which was lower than maximum growth rates observed for other species of *Aurelia*. Ephyrae of *A. aurita* from the Gullmar, Fjord, Sweden had an initial average daily growth rate of 70% $d^{-1}$, salinity 34 which decreased to around 10% $d^{-1}$ by the end of their 10 day experiment (Bamstedt et al. 1999). In a 14 day experiment ephyrae of *A. labiata* from the northeast Pacific Ocean had an average daily growth rate of 43.29% $d^{-1}$ at 21°C, salinity 34 during the first seven days of development which decreased to 16.55% $d^{-1}$ during days 7 – 14 (Widmer, 2005). Initial growth rates of ephyrae are relatively high which may enable them to grow rapidly in response to optimal environmental conditions.

Table 7. Growth rates of newly released scyphomedusa ephyra larvae from the northeast Pacific Ocean at the end of seven day experiments (C. Widmer unpublished results).

| | | | | | 95% Conf. Interval | |
|---|---|---|---|---|---|---|
| Species | n | Temperatures tested (°C) | Optimal temperature (°C) | Growth rate % $d^{-1}$ at optimal temperature | Mean Lower | Mean Upper |
| *Phacellophora camstchatica* | 150 | 5, 10, 15, 17, 20 | 17 | 13.66 | 12.64 | 14.69 |
| *Chrysaora fuscescens* | 30 | 3, 9, 14, 17, 21.5 | 17 | 12.08 | 8.75 | 15.41 |
| *Aurelia labiata** | 45 | 8, 10, 12, 15, 17, 21, 22.5, 24.5, 26 | 21 | 43.29 | 40.45 | 46.13 |

*The growth rate for *A. labiata* was presented in (Widmer, 2005) however, the confidence interval data was not.

4.4.3 *Possible effects of projected temperature trends on growth of ephyrae*

The North Sea is characterized by large seasonal fluctuations in temperature, from 4°C in winter to about 18°C in summer, depending on location (Baxter et al. 2011). During the period from 1960 through 1990 annual mean sea surface temperatures (SST) in the southern North Sea increased at a rate of about 0.6°C per decade, but a clear trend in salinity was not identified (Hughes et al. 2010). If SSTs continue to rise

in the North Sea conditions may be enhanced for growth of newly released *Ch. hysoscella* ephyrae provided other conditions for growth are suitable, for example being able to find appropriate food in a changing sea. Medusae of *Ch. hysoscella* are reportedly uncommon in the northern North Sea (Russell 1970) however, they may be observed more frequently in the future if they are able to take advantage of warming waters and expand their range northward. Newly released ephyrae of *A. aurita* may not be noticeably affected in the near future by a gradually increasing SST trend. However, increasing SSTs may be deleterious for newly released ephyrae of *C. capillata* and *C. lamarckii*, ultimately resulting in their biogeographic ranges shifting gradually northward towards cooler waters.

Both *C. capillata* and *C. lamarckii* are medusivores (Hansson, 1997; Russell, 1970) and may help to mitigate bloom magnitudes of *A. aurita* which are sometimes deleterious to human enterprise. The potential disappearance of *Cyanea* species in the southern extents of their ranges could thus be favourable for medusae of *A. aurita*. However, medusae of *Ch. hysoscella* also prey upon *A. aurita* medusae (Russell 1970) and in the absence of the two *Cyanea* species *Ch. hysoscella* with gradually shifting northward ranges may be able to fulfil that role. Ultimately, the effects of increasing SST may be most important for strobilation of scyphistomae (Chapter 3). If scyphistomae fail to strobilate in the future due to increasing SSTs ephyrae will not be produced, an effect is most likely to be felt by members of the populations at the edges of biogeographic ranges.

### 4.4.4 *A possible shortcoming of methods*

A potential shortcoming to the methods used here during the temperature and salinity experiments was that *Artemia* nauplii were utilised as food for ephyrae which may have led to lower growth rates than otherwise possibly observed if natural zooplankton had been provided as food. Studies examining the effects of diet on newly released ephyrae (Bamstedt et al., 1997; Bamstedt et al., 2001; Olesen et al., 1996) generally conclude that natural zooplankton yield higher ephyral growth rates than do *Artemia* nauplii. Further, medusae of *C. capillata* may be dependent on gelatinous prey for development. However, *Artemia* nauplii were sufficient for yielding positive growth during the first 10 days of *C. capillata* ephyra development (Bamstedt et al. 1997), and *Artemia* nauplii are also sufficient for providing enough energy for initial growth for a host of other species of newly released scyphozoan ephyra larvae (Widmer, 2008). The composition of wild-caught zooplankton is inherently variable and I wanted to eliminate as many external sources of variability as possible. That way I could better focus on the effects of temperature and salinity on growth. Therefore the use of *Artemia* nauplii as food in this study was appropriate.

### 4.4.5 *On the potential for overwintering ephyrae*

In the Skagerrak, west of Sweden and in the Kiel Bight, Germany *A. aurita* medusa growth takes place in three phases. First, newly released ephyrae overwinter on the bottom with little or no growth, during spring growth of ephyrae is exponential, and in summer full medusa size is reached (Hansson, 1997; Hernroth & Grondahl, 1985; Moller, 1980). Of the animals studied here, ephyrae from the northern, Orkney population of *A. aurita* may be better adapted for overwintering than ephyrae from the southern, Southampton population. All of the ephyrae from the Orkney population were in good condition at the end of the eight week starvation experiment, albeit smaller than when initially released. In addition to shrinking at a significantly greater

rate, ephyrae from the Southampton population had 11 mortalities and were in generally poor condition at the end of the experiment. Overwintering may not be as important for Southampton populations of *A. aurita* because scyphistomae strobilate in a wider range of temperatures, 4 – 9°C (Chapter 3), than Orkney populations. Natural populations of Southampton *A. aurita* strobilate from the end of January (*ca.* 5°C SST) to the middle of March (*ca.* 10°C SST) thus Southampton *A. aurita* ephyrae are released when zooplankton are becoming more available (Lucas, 2001). In laboratory experiments, Orkney *A. aurita* scyphistomae strobilated at 4°C, but not 9°C (Chapter 3). Natural populations of northern North Sea *A. aurita* ephyrae are released during winter (Russell 1970) so may be required to wait longer for the arrival of zooplankton prey than Southampton ephyrae.

During the overwintering period ephyrae may be sustained by utilizing dissolved organic material (DOM) and microzooplankton. Ephyrae of *A. labiata* and *Chrysaora colorata* from the northeast Pacific Ocean are able to uptake and utilize DOM (Skikne et al., 2009) which may enable them to survive without, or at low levels of particulate food for extended periods. Scyphistomae of *A. aurita* from Corpus Christy, Texas have also been shown to uptake and utilize DOM (Shick 1973) as have other members of the phylum Cnidaria (Stephens and Schinske 1961). Ephyrae of *A. aurita* in the present study became gradually smaller over time however, periods of de-growth for scyphomedusae are not necessarily deleterious. Ephyrae of *A. labiata* from the northeast Pacific Ocean gradually became smaller when maintained at 8°C but positive growth resumed when ephyrae were afterward maintained in warmer temperatures (Widmer, 2005). Mature medusae of *A. aurita* from Tomales Bay, California also possess the ability to de-grow and grow again when conditions are favourable (Hamner and Jenssen 1974). The ability to overwinter near the bottom would enable *A. aurita* ephyrae to delay their emergence until conditions are optimal for growth. However, the factors cueing ephyrae to ascend to surface waters are presently unknown and should be the subject of future study.

# Chapter 5

**General discussion**

## 5.1 Introduction

Jellyfish play important roles in healthy ecosystems ranging from the sunlit surface waters to the deep sea floor (Arai 2005, Lebrato et al. 2013, Doyle et al. 2014), but large blooms can also cause harm to human industries. The idea that the intensity and frequency of jellyfish blooms are on the rise in response to global climate change has been frequently stated, a view that has been exacerbated by the media (Condon et al. 2012). However, the lack of reliable long term data sets make robust hypothesis testing regarding this issue a challenge (Lucas et al. 2014). Medusa abundance has been linked with climate variability (Goy et al. 1989, Lynam et al. 2004, 2005b, 2010, Lucas et al. 2014) and appears to fluctuate over decadal time scales (Condon et al. 2013). However, the underlying mechanisms responsible for driving patterns of medusa abundance are often unclear. The responses of different life history stages of British jellyfish when exposed to changed environmental conditions were largely unknown prior to this study. Here, I set out to conduct laboratory experiments to test how planulae, scyphistomae, and ephyrae stages of British jellyfish respond to changes in two important variables, temperature and salinity. The ultimate aim was to move from correlative associations linking medusa abundance and climate variability to better understanding of the underlying mechanisms driving medusa abundance.

The information presented in this thesis contributes to a better understanding of scyphozoan ecology in British waters, and to global scyphozoan ecology on the whole. For the first time, life history stages and species studied here have been demonstrated to respond differently to changes in temperature and salinity. Specifically, scyphistomae produced juvenile medusae in response to cool temperatures, and asexual reproduction of scyphistomae, and therefore benthic colony expansion activity was maximal in warmer temperatures. Models based on experimental results presented here predicted less strobilation, and therefore decreased medusa abundances, in the face of gradually increasing sea temperatures. Ultimately this may have the effect of potentially gradually shifting ranges for some species of medusae with potential follow on ecological effects from those changes. Different populations of *A. aurita* scyphistomae were shown to respond differently to identical conditions during incubator experiments. This has meaningful implications as different populations of medusae generating scyphistomae must be factored in to future efforts to model impacts of climate variability on medusa abundance in UK waters, and quite probably the rest of the world.

## 5.2 General findings

### 5.2.1 *Planulae*

Planula larvae of common British scyphomedusae were able to settle and successfully metamorphose into fully functional scyphistomae within the range of SSTs normally experienced annually in waters surrounding the British Isles, which is about 4 – 19°C depending on location (http://www.cefas.defra.gov.uk/ ). However, temperature had the effect of influencing the rates of planula settlement and development, with those two processes occurring more rapidly in warmer temperatures than in cooler ones, in

agreement findings for *Cotylorhiza tuberculata*, *Nemopilema nomurai* and *A. aurita* (Prieto et al. 2010, Kawahara et al. 2012, Webster and Lucas 2012). Significant mortality of planulae only occurred at temperature extremes. Increasing SSTs as predicted by climate change models for the coming century may have the effect of decreasing larval planktic durations and therefore dispersal distances. However, the results presented in this thesis suggest that increasing SSTs are not likely to greatly affect the ability of planulae to settle and metamorphose into viable scyphistomae.

5.2.2 *Scyphistomae*

Minimum temperatures needed to be met and maintained for sufficient durations in order for strobilation to occur for all species tested, agreeing with the minimum critical temperature threshold hypotheses of earlier workers (Russell 1970 and references therein). The precise minimum critical temperature thresholds for strobilation were species and population specific. In particular, *A. aurita* from Southampton strobilated at 4 and 9°C, and *A. aurita* (Orkney) strobilated at 4°C. *C. capillata* strobilated at temperatures ranging from 4 to 19°C, and *C. lamarckii* scyphistomae strobilated between 4 and 14°C. However the majority of strobilation for both *Cyanea* species took place at 4 and 9°C. *Ch. hysoscella* scyphistomae strobilated between 9 and 23°C. As temperature increased, the probability of strobilation decreased concomitant with a decrease in the number of ephyrae produced per colony member. Asexual reproductive output of scyphistomae in the study was more often affected by temperature than by salinity, or their interaction. As temperature increased, the asexual reproduction of podocysts and budded progeny scyphistomae (where species appropriate) also increased. Significant mortality occurred at the highest and lowest temperature extremes, 23 and 5°C, for *C. capillata* and *Ch. hysoscella* respectively, which occupy northernmost and southernmost biogeographic ranges correspondingly (Russell 1970, Barz and Hirche 2007).

5.2.3 *Ephyrae*

Ephyrae maintained in temperatures at or near the experimental temperatures parent scyphistomae strobilated had the highest maximal growth rates over the seven day experiment. Those maintained far beyond strobilation temperatures became moribund. Where tested, the effect of salinity on the growth of newly released ephyrae varied with species, but was statistically significant, although with small effects. Species often observed in near-shore coastal, and estuarine habitats had higher growth rates at reduced salinities (27 and 21) compared with 34. Different populations of newly released *A. aurita* ephyrae were able to survive for periods of up to 8 weeks in the absence of large particulate food supporting the idea that ephyrae potentially have the ability to overwinter, as was suggested by earlier workers (e.g., Moller 1980, Hernroth and Grondahl 1985). Overwintering ephyrae may be able to sense favourable conditions and ascend en masse. They may thus be able to avoid problems associated with phenological shifts and trophic mismatches with prey production that may occur in response to climate change (Edwards and Richardson 2004).

## 5.3 Theoretical implications

5.3.1 *Seasonally*

Populations of British jellyfish grow by a combination of sexual and asexual reproductive modes during an annual seasonal cycle. If minimum critical temperature thresholds are met during winter and spring, scyphistomae undergo the process of

strobilation and produce ephyrae. Asexual reproduction of benthic podocysts and progeny scyphistomae is minimal during this period. As SSTs increase, strobilation decreases and asexual reproduction of podocysts and progeny scyphistomae increases. Benthic asexual reproductive output is probably maximal during summer, and in this way benthic colonies are maintained and expanded *in situ*. Ephyrae normally grow into sexually mature medusae by the end of late summer (Russell 1970, Lucas 2001). Developing medusae may be transported away from parent colonies through a combination of directed swimming behaviour (Hamner et al. 1994), and passive drift in currents (Graham et al. 2001). In the North Sea, drifting female medusae disperse free-swimming planula larvae from July through late September, where after most medusae senesce (Russell 1970, Barz and Hirche 2007).

5.3.2 *Mechanisms linking medusa abundance and the NAO*

One of the goals of this study was to move from correlative associations linking environmental variables with medusa abundance in the North Sea to describing underlying mechanisms contributing to medusa abundance. As described above, the scyphistomae studied here had to experience minimum low temperatures for appropriate durations in order for the process of stobilation to begin. If these thresholds were not met, strobilation did not occur. When the NAOI is in a positive phase sea temperatures in the southern North Sea are generally warmer year round, and when the NAO is in a negative phase SSTs are lower (Drinkwater et al. 2003). A conceptual model (Fig. 5.1) for the ways in which the NAO may be linked to medusa abundance of *A. aurita* and *C. lamarckii* in the North Sea was proposed by Lynam et al. (2004). The laboratory results presented here support the conceptual model in several key areas. During years with a negative NAOI, minimum strobilation temperature thresholds are more likely to be met and in response, large numbers of scyphistomae strobilate releasing more ephyrae than in years fewer scyphistomae strobilate (Fig. 5.1B a, b). Low temperature and reduced salinities were also advantageous for growth and development of newly released ephyrae which also agrees with conditions associated with strong ephyral development proposed in the hypothetical model (Fig. 5.1B c). Although note that the proposed mechanism linking the NAO to ephyra development invoked effects on prey production, rather than a direct effect of temperature and salinity change on the ephyrae.

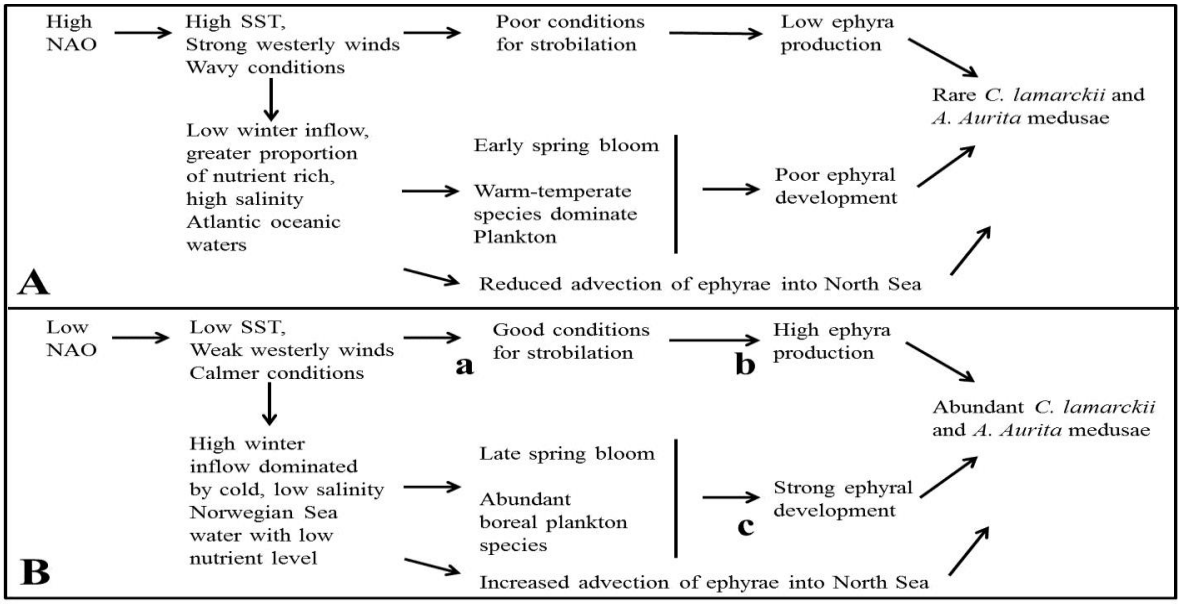


Figure 5.1. Conceptual model of possible associations between the NAO and medusa abundance of *Aurelia aurita* and *Cyanea lamarckii* in the southern North Sea. Figure after Lynam et al. 2004. A. How medusa abundance in the North Sea may be influenced by a positive NAOI, and B. by a negative NAOI, a, b and c are points at which the results presented in this thesis agree with the conceptual model.

### 5.3.3 **Medusa abundances in response to a variable climate**

#### 5.3.3.1 *A more gelatinous future for the North Sea?*

One of the issues confounding interpretation of jellyfish abundance trends over time is that in some studies the term jellyfish may be taken to mean all gelatinous zooplankton, or gelata (Haddock 2004), which may or may not include members of the Phlya Cnidaria, Ctenophora, and Urochordata etc. (Brotz et al. 2012, Condon et al. 2013, Lucas et al. 2014). Members of those phyla have very different life cycles and life history strategies. Changes in environmental variables are likely to affect each group in different ways. Simply collecting all gelatinous zooplankton into a catch-all group called jellyfish, and then making future predictions about their abundance in the face of changing climate ignores differences in the ecology of both functional groups and species. Furthermore, studies reporting that jellyfish numbers are predicted to increase in the future often do not differentiate between problematic species and those that are not (e.g., Attrill et al. 2007). These publications have often been misinterpreted by the media leading to unwarranted alarm. For this reason I was very clear from the outset to define the word jellyfish in this thesis to mean the medusa stages of members of the Phylum Cnidaria.

Another issue when attempting to assess jellyfish abundance trends is the paucity of long term monitoring data sets. Jellyfish populations appear to fluctuate on cycles of about 20 years (Condon et al. 2013), and studies analysing shorter time series may offer misleading conclusions. After analysing patterns of medusa abundance based upon Continuous Plankton Recorder (CPR) data from 1958 onwards, Attrill et al. (2007) predicted an increase in jellyfish abundance in the North Sea over the next 100 years. Unfortunately, the CPR records only nematocysts and gelatinous tissue as evidence of the presence of cnidarians and so does not provide species specific information. However, recent advances in molecular discrimination have in fact suggested that much of the gelatinous PCR tissue is from the oceanic species, *Pelagia noctiluca* (Licandro et al. 2010), the life history of which does not include

scyphistomae. Based upon a system of fuzzy logic which assigned credibility scores to various sources Brotz et al. (2012) concluded with a low level of confidence that "jellyfish" abundance in the North Sea had increased since the 1950s. However, Condon et al. (2013) found no such trend for increasing jellyfish abundance in the North Sea since the mid-1980s. The lack of global long term jellyfish abundance monitoring schemes and standardized research methodologies are issues needing to be addressed in order to better assess long term global medusa trends.

5.3.3.2 *Quantitative-based speculation on the future of jellyfish in the North Sea*
The experimental results presented in this thesis suggest that increasing sea temperatures are likely to affect the abundances and ranges of scyphomedusae species inhabiting near shore waters surrounding the British Isles mainly by affecting whether or not minimum temperatures are met that enable scyphistomae to strobilate, and through survival of scyphistomae. Mean global SSTs have been increasing at a rate of about 0.13°C each decade since 1979 (Solomon et al. 2007), and an increasing SST trend has also been reported for the North Sea, with the southern North Sea projected to be up to 3.5°C warmer than it presently is in the 2080s (Hughes et al. 2010). Based on predictions made from GLMs in this study, each 1°C in temperature beyond 19°C during late summer would result in a 4.9% increase in the probability of mortality occurring within 8 weeks for *C. capillata* scyphistomae. Increasing minimum SST from 4°C to 5°C would result in a 1% predicted decrease in mortality for scyphistomae of *Ch. hysoscella*, but when the temperature is raised from 5 to 6°C there is a further 47% predicted decrease in mortality. The temperatures and salinities tested here did not significantly affect mortality of *A. aurita* (both populations), or *C. lamarckii*. It should be noted that 23°C was not tested for *C. lamarckii*, however given its southern distribution (Russell 1970) projected SST scenarios are not expected to cause significant mortality of *C. lamarckii* scyphistomae. The predicted probabilities of mortality occurring within an 8 week period when maintained within the range of temperatures tested for *C. capillata* and *Ch. hysoscella* are given in Appendix III.

Gradually increasing SSTs would affect the probability of stobilation of the species studied here in similar ways. *A. aurita* from Orkney strobilated at 4°C whilst *A. aurita* from Southampton strobilated at 4 and 9°C. For each 1°C increase, beyond 4°C for *A. aurita* (Orkney) and 9°C for *A. aurita* (Southampton), the predicted probability of strobilation decreased by 14.8 and 10.3% respectively. The predicted probability that scyphistomae of *C. lamarckii* would strobilate beyond 9°C decreased by 3.4% with a 1°C increase in temperature, and the predicted probability that scyphistomae of *C. capillata* would strobilate decreased by 13.2% with a 1°C increase beyond 9°C. Gradually increasing temperature would probably not have great effects on the probability of strobilation for scyphistomae of *Ch. hysoscella*, with only a 2.3% decrease in the predicted probability of strobilation for each 1°C increase above 19°C. Gradually increasing SSTs over the next century are likely to affect each species differently, with range changing implications for some. The predicted probabilities of strobilation occurring when maintained within the range of temperatures tested for all species tested here are given in Appendix IV, with a special note to those who would use these data for management purposes. In Chapter 3 I demonstrated that different populations of *A. aurita* responded differently when maintained in identical laboratory conditions. The same may also be the case for the other species examined therefore

care should be taken to avoid making broad stroke generalizations about all populations of the same species based on the predictions presented here.

5.3.3.3 *Range changing*

Abiotic factors are clear determinants of range limits (Sexton et al. 2009), and recent climatic warming has caused poleward shifts in the geographical distributions for a large number of species (Parmesan 2006). When rates of environmental change are slow, species track their environment across space, unless they encounter barriers, otherwise they go extinct (Pease et al. 1989). In the North Sea abundances, population structures and biogeographic ranges of benthic and planktonic species have already been observed in response to recent environmental change (Hiscock et al. 2004, Hawkins et al. 2009, Wiltshire et al. 2009), and it is possible that ranges may also be presently in the process of shifting for some species of British jellyfish.

If jellyfish ranges gradually shift larger, but less frequent, blooms of jellyfish may occur at the southern extents of biogeographic ranges for a period of decades before gradually disappearing. Concurrently, different species of jellyfish will begin to move northward and colonize new areas. Each scenario can contribute to the perception that jellyfish populations are increasing for those in short term studies. In the waters surrounding the British Isles jellyfish populations naturally fluctuate around a baseline, and here I have shown mechanisms for how medusa abundance is affected mainly by temperature. Sea temperature in the North Atlantic in turn is influenced by the NAOI oscillations overlying the underlying trend for increasing temperature. (Drinkwater et al. 2003, Lynam et al. 2004, 2005b, 2010). If the SST baseline gradually increases over time minimum temperature thresholds for strobilation may be met less often. Therefore medusa blooms may occur less frequently. During inter-bloom periods benthic asexual reproduction continues, and colonies increase the numbers of scyphistomae in *in situ*. When minimum critical temperature thresholds for strobilation are occasionally met, larger than expected blooms will be produced by colonies that have cryptically expanded since the last noticeable bloom event. The sudden appearance of medusae after such an absence may contribute to the idea that blooms are increasing in magnitude. In the long run, if the minimum winter temperatures gradually increase over time colonies will cease to be renewed, as fewer strobilation events occur, leading to less dispersal to and from affected colonies.

If the ranges of jellyfishes in the North Sea begin to shift in response to increasing SST the positive ecosystem services provided by medusae may begin to shift as well. Medusae of *C. capillata* are zooplankton predators that also prey upon a wide variety of other gelatinous zooplankton, including medusae of *A. aurita* (Hansson 1997a). As such *C. capillata* medusae may help to regulate *A. aurita* abundance (Bamstedt et al. 1997). Native *C. capillata* may also be important in controlling non-native species in the North Sea such as the ctenophore *Mnemiopsis leidyi* (Hosia and Titelman 2011) which is itself a voracious predator that can dramatically reduce amounts of zooplankton and ichthyoplankton (Purcell and Arai 2001). If the range of *C. capillata* retreats northward their positive ecosystem services in the North Sea may be lessened. However, those roles may be filled instead by medusae of *Ch. hysoscella* and *C. lamarckii* since they too prey upon gelatinous zooplankton (Russell 1970). Whether or not *Ch. hysoscella* and *C. lamarckii* are as effective at regulating gelatinous zooplankton abundance as *C. capillata* warrants future study.

5.3.3.4 *Can jellyfish scyphistomae adapt at a rate commensurate with climate change?*

Species ranges naturally expand and contract over time which may be due in part to gradual niche evolution, or spatial tracking of environmental conditions suitable for population maintenance (Pease et al. 1989, Brown et al. 1996, Pfenninger et al. 2007). Jellyfish are well adapted for range shifting given their resilient life histories and effective dispersal mechanisms. Whether British scyphistomae populations *in situ* can adapt new minimum strobilation temperature thresholds at a rate commensurate with predicted SST baseline increases, or if ranges will more simply shift northward or perhaps expand, is unknown at present, and should also be the subject of future study.

**5.4 Recommendations for marine resource managers**

Jellyfish medusae compete for food with commercially important fishes and may have direct detrimental impacts on fish early survival through predation (Lynam et al. 2005a, 2011). Jellyfish have also been implicated as being problematic when they interact with aquaculture cages in European seas (Nickell et al. 2010). The source of at least some of the medusa in the northern North Sea may actually be along the west coast of Scotland since currents associated with oceanic inflows affect medusa abundance (Lynam et al. 2010) in the northern North Sea (Fig. 5.2A). The undersides of human made floating surfaces make for ideal scyphistoma habitat (Purcell et al. 2007, Lo et al. 2008) since planula larvae show a preference for settling on the horizontal undersides of floating surfaces (Holst and Jarms 2007). During summer 2013 a single salmon farming base station barge located near Craobh Haven, Scotland was photographed by SCUBA divers. Nearly 2/3rds of the underside of the floating feed storage barge was completely covered (A. Kintner pers. comm.) by scyphistomae of *A. aurita* (Fig. 5.2B). Using data on ephyra production rates of *A. aurita* scyphistomae obtained from this study, I estimated that the salmon barge at that site had the potential to contribute roughly 4.6 – 8.8 hundred million ephyrae annually to the surrounding sea. When the combined number of salmon barges, oyster farms, marine renewable structures, marinas, and other floating human made objects probably being used as scyphistoma habitat are considered (Fig. 5.2C), the number of medusae contributed to British seas may substantially outnumber the amount produced from natural habitats.

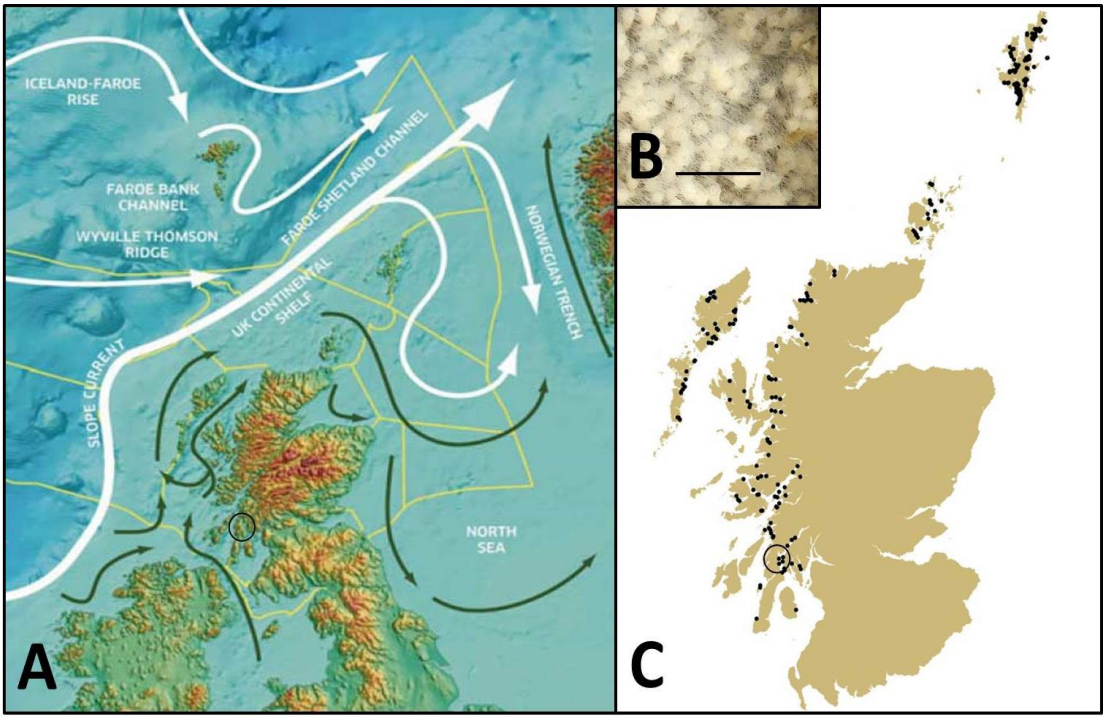


Figure 5.2. A. Shelf sea currents surrounding Scotland, white arrows represent Atlantic circulation and green arrows represent coastal circulation around Scotland; this figure was modified from (Baxter et al. 2011); B. Scyphistomae of *Aurelia aurita* living on the underside of the salmon barge at Craobh haven, Scotland; scale bar = 1 cm. C. Active fish farming sites in Scotland in 2008, figure taken from (Nickell et al. 2010); The black circles indicate the approximate position of the Craobh haven salmon farm barge.

Management decisions regarding jellyfish surrounding the British Isles should take the dispersal patterns into consideration, as well as the management of artificial scyphistoma habitats. Ephyrae produced on the West Coast of Scotland, and in the Orkney and Shetland Isles, are likely to be advected by currents into the northern North Sea (Fig. 5.2A). Although there is no salmon aquaculture on the north-east coast, other human activities have been affected. In June 2011 the Torness nuclear power station was forced into a partial shut-down in response to clogging of the cooling intake pipes by a bloom of *A. aurita*. Whether the jellyfish originated locally or from farther afield is unknown. One strategy for decreasing the number of medusae could be to decrease the number of scyphistomae living on the bottoms of human made structures. Removing aquaculture rafts, and thereby scyphistomae habitat, was effective in reducing problematic blooms of *A. aurita* medusae in Tapong Bay Taiwan (Lo et al. 2008), and active annual removal of scyphistomae under artificial structures may be effective for the waters surrounding British Isles as well. However, this would require a large annual effort and re-colonisation might be rapid. Human made structures should be cleaned in October or November after planula-bearing female medusae have disappeared from surface waters. Strategic barge cleaning would also decrease problems associated with hydrozoan jellyfish that have similar life histories as the scyphozoan jellyfish studied here. Strategic barge cleaning is of course a costly undertaking, but one that should be initiated at the national level.

### 5.5 Additional work

One of the challenges in finding practical applicability with studies linking environmental variables with medusa abundance is the fact that the locations of parent scyphistomae are often unknown, leaving the origins of drifting medusae a mystery.

It has been possible to identify genetically distinct populations of *Rhizostoma octopus* (Lee et al. 2013), and matching medusae with the scyphistomae colonies that produced them would be a significant step in developing practical predictive models for medusa bloom timings and magnitudes. However, where dispersal distances are large this might not be practical. In more enclosed waters however it might be possible to locate the origin of localised retained blooms. Metabolomics may also be useful in this endeavour, as may also tools used in the genetic identification of diet. Knowing responses of *in situ* scyphistomae colonies to environmental variables is also crucial information for modellers, and when that information is combined with particle drift models it may be possible to simulate the paths medusae travel whilst they develop from ephyrae into mature medusae. Until then, the work described herein describes mechanisms that explain why after a long cold winter people should expect and prepare for a jelly-filled summer. Conversely, following a short warm winter people should expect fewer medusae.

### 5.6 Parting words

Jellies were present before fish evolved, and they have outlived the disappearance of the dinosaurs (Condon et al. 2012). They have deceptively simple body plans, yet complex and plastic life histories that enable them take advantage of, and respond rapidly to, environmental variability. Cnidarian medusae are likely to continue to do well in a changing world and may be benefiting from some human activities such as urbanization of the coastal margin. It would behove humankind to continue to study, and develop strategies for coexistence with such successful organisms when sharing the marine environment.

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# Appendix I

Descriptive statistics of results for laboratory experiments testing the effects of temperature and salinity of asexual reproductive output of British scyphistomae.

Table A1. *Cyanea capillata*: descriptive statistics for results of an 8 week experiment testing the effects of 15 different combinations of temperature and salinity on asexual reproductive output of *C. capillata* scyphistomae.

| Salinity | Temperature °C | | | | |
|---|---|---|---|---|---|
| | 4 | 9 | 14 | 19 | 23 |
| Total surviving scyphistomae | | | | | |
| 21 | 17 | 10 | 11 | 12 | 0 |
| 27 | 18 | 14 | 16 | 11 | 0 |
| 34 | 18 | 13 | 10 | 11 | 0 |
| Mean no. of podocysts produced scyphistoma$^{-1}$ (SE) | | | | | |
| 21 | 0.06 (0.06) | 0.06 (0.06) | 0.10 (0.1) | 0.42 (0.19) | 0 |
| 27 | 0 | 0 | 0.30 (0.2) | 0.73 (0.43) | 0 |
| 34 | 0 | 0 | 0.10 (0.1) | 0.35 (0.15) | 0 |
| Total strobilating scyphistomae | | | | | |
| 21 | 12 | 14 | 2 | 2 | 0 |
| 27 | 15 | 15 | 1 | 3 | 0 |
| 34 | 17 | 12 | 2 | 0 | 0 |
| Mean number of weeks before strobilation initiated | | | | | |
| 21 | 3.0 (0.43) | 1.9 (0.31) | 1.0 (0.0) | 1.0 (0.0) | NA |
| 27 | 2.8 (0.29) | 1.7 (0.21) | 2.0 (0.0) | 1.0 (0.0) | NA |
| 34 | 3.2 (0.43) | 2.2 (0.21) | 1.0 (0.0) | NA | NA |
| Mean strobilation duration in weeks (SE) | | | | | |
| 21 | 4.1 (0.38) | 2.6 (0.27) | 2.5 (0.5) | 1.5 (0.5) | NA |
| 27 | 3.8 (0.37) | 2.4 (0.21) | 1.0 (NA) | 1.0 (0.0) | NA |
| 34 | 2.7 (0.31) | 2.1 (0.39) | 1.0 (0.0) | NA | NA |
| Mean number of ephyrae scyphistoma$^{-1}$ (SE) | | | | | |
| 21 | 1.7 (0.43) | 1.8 (0.28) | 0.2 (0.17) | 0.2 (0.12) | 0 |
| 27 | 2.2 (0.37) | 2.3 (0.45) | 0.1 (0.06) | 0.3 (0.19) | 0 |
| 34 | 1.7 (0.23) | 1.1 (0.27) | 0.3 (0.23) | 0.0 (0.0) | 0 |
| Total number of ephyrae produced treatment group$^{-1}$ | | | | | |
| 21 | 31 | 33 | 4 | 3 | 0 |
| 27 | 40 | 41 | 5 | 6 | 0 |
| 34 | 30 | 20 | 1 | 0 | 0 |

*The format of this table is modelled after Purcell 2007.

Table A2. *Cyanea lamarckii*: descriptive statistics for results of an 8 week experiment testing the effects of 15 different combinations of temperature and salinity on asexual reproductive output of *C. lamarckii* scyphistomae.

| Salinity | Temperature °C | | | |
|---|---|---|---|---|
| | 4 | 9 | 14 | 19 |
| Total surviving scyphistomae | | | | |
| 27 | 18 | 17 | 17 | 17 |
| 34 | 18 | 16 | 17 | 16 |
| Mean no. of progeny scyphistomae produced parent scyphistoma$^{-1}$ (SE) | | | | |
| 27 | 0.33 (0.16) | 0.5 (0.23) | 0.44 (0.15) | 0.28 (0.11) |
| 34 | 0.83 (0.22) | 0.5 (0.25) | 0.28 (0.18) | 0.50 (0.18) |
| Mean no. of podocysts produced scyphistoma$^{-1}$ (SE) | | | | |
| 27 | 0 | 0.06 (0.06) | 1.50 (0.56) | 1.11 (0.35) |
| 34 | 0 | 0.17 (0.09) | 0.89 (0.44) | 1.28 (0.54) |
| Total strobilating scyphistomae | | | | |
| 27 | 9 | 4 | 0 | 0 |
| 34 | 6 | 5 | 2 | 0 |
| Mean number of weeks before strobilation initiated | | | | |
| 27 | 7.11 (0.92) | 4.25 (0.95) | NA | NA |
| 34 | 4.33 (1.05) | 2.2 (0.38) | 2.0 (0.0) | NA |
| Mean strobilation duration in weeks (SE) | | | | |
| 27 | 10.0 (1.17) | 3.75 (1.11) | NA | NA |
| 34 | 10.0 (1.46) | 5.60 (0.4) | 4.50 (0.5) | NA |
| Mean number of ephyrae scyphistoma$^{-1}$ (SE) | | | | |
| 27 | 7.6 (2.31) | 2.0 (1.28) | 0 | 0 |
| 34 | 5.0 (2.24) | 5.5 (2.54) | 3.83 (2.65) | 0 |
| Total number of ephyrae produced treatment group$^{-1}$ | | | | |
| 27 | 137 | 36 | 0 | 0 |
| 34 | 99 | 99 | 69 | 0 |

Table A3. *Chrysaora hysoscella*: descriptive statistics for results of an 8 week experiment testing the effects of 15 different combinations of temperature and salinity on asexual reproductive output of *C. lamarckii* scyphistomae.

| Salinity | Temperature °C | | | | |
|---|---|---|---|---|---|
| | 4 | 9 | 14 | 19 | 23 |
| Total surviving scyphistomae | | | | | |
| 27 | 0 | 18 | 18 | 18 | 18 |
| 34 | 0 | 18 | 18 | 18 | 18 |
| Mean no. of podocysts produced scyphistoma$^{-1}$ (SE) | | | | | |
| 27 | 0 | 0.06 (0.06) | 0.22 (0.13) | 0.83 (0.25) | 3.0 (0.55) |
| 34 | 0 | 0.11 (0.11) | 1.0 (0.24) | 1.94 (0.39) | 2.9 (0.38) |
| Total strobilating scyphistomae | | | | | |
| 27 | 0 | 5 | 9 | 5 | 2 |
| 34 | 0 | 9 | 7 | 5 | 1 |
| Mean number of weeks before strobilation initiated | | | | | |
| 27 | NA | 4.2 (0.97) | 3.6 (0.33) | 4.2 (1.07) | 3.5 (0.5) |
| 34 | NA | 4.0 (0.37) | 3.0 (0.44) | 4.0 (1.0) | 2.0 (NA) |
| Mean strobilation duration in weeks (SE) | | | | | |
| 27 | NA | 4.0 (0.78) | 2.0 (0.33) | 1.4 (0.25) | 1.5 (0.5) |
| 34 | NA | 3.5 (0.29) | 2.2 (0.47) | 1.4 (0.25) | 1.0 (NA) |
| Mean number of ephyrae scyphistoma$^{-1}$ (SE) | | | | | |
| 27 | 0 | 0.72 (0.33) | 1.83 (0.49) | 0.78 (0.32) | 0.79 (0.56) |
| 34 | 0 | 1.33 (0.38) | 1.94 (0.66) | 1.33 (0.59) | 0.22 (0.22) |
| Total number of ephyrae produced treatment group$^{-1}$ | | | | | |
| 27 | 0 | 13 | 33 | 14 | 14 |
| 34 | 0 | 24 | 35 | 24 | 4 |

Table A4. *Aurelia aurita* (Southampton): descriptive statistics for results of an 8 week experiment testing the effects of 15 different combinations of temperature and salinity on asexual reproductive output.

| Salinity | Temperature °C | | | | |
|---|---|---|---|---|---|
| | 4 | 9 | 14 | 19 | 23 |
| Total surviving scyphistomae | | | | | |
| 21 | 18 | 17 | 18 | 17 | 17 |
| 27 | 18 | 18 | 17 | 18 | 17 |
| 34 | 18 | 18 | 18 | 18 | 18 |
| Mean no. of progeny produced scyphistoma$^{-1}$ (SE) | | | | | |
| 21 | 0.8 (0.23) | 3.7 (0.58) | 5.4 (0.36) | 6.5 (0.67) | 8.6 (0.88) |
| 27 | 0.9 (0.30) | 3.5 (0.55) | 3.5 (0.34) | 4.1 (0.47) | 5.6 (0.69) |
| 34 | 1.1 (0.32) | 1.6 (0.28) | 2.9 (0.38) | 3.0 (0.37) | 3.7 (0.58) |
| Mean no. of podocysts produced scyphistoma$^{-1}$ (SE) | | | | | |
| 21 | 0.0 | 0.1 (0.06) | 0.5 (0.2) | 0.4 (0.16) | 0.9 (0.31) |
| 27 | 0.0 | 0.0 | 0.2 (0.12) | 0.5 (0.2) | 1.6 (0.48) |
| 34 | 0.0 | 0.0 | 0.3 (0.11) | 0.7 (0.25) | 0.7 (0.27) |
| Total strobilating scyphistomae after 8 weeks | | | | | |
| 21 | 1 | 1 | 0 | 0 | 0 |
| 27 | 10 | 2 | 0 | 0 | 0 |
| 34 | 15 | 9 | 0 | 0 | 0 |
| Total strobilating scyphistomae after 16 weeks | | | | | |
| 21 | 17 | 1 | 0 | 0 | 0 |
| 27 | 16 | 2 | 0 | 0 | 0 |
| 34 | 17 | 9 | 0 | 0 | 0 |
| Mean number of weeks before strobilation initiated | | | | | |
| 21 | 10.8 (0.56) | 3.0 (NA) | NA | NA | NA |
| 27 | 8.0 (0.63) | 3.0 (0.0) | NA | NA | NA |
| 34 | 6.4 (0.549) | 3.1 (0.53) | NA | NA | NA |
| Mean strobilation duration in weeks (SE) | | | | | |
| 21 | 8.5 (0.38) | 5.0 (NA) | NA | NA | NA |
| 27 | 7.1 (0.28) | 4.0 (0.0) | NA | NA | NA |
| 34 | 6.8 (0.29) | 3.2 (0.4) | NA | NA | NA |
| Mean number of ephyrae scyphistoma$^{-1}$ (SE) after 8 weeks | | | | | |
| 21 | 0.0 | 0.5 (0.5) | 0.0 | 0.0 | 0.0 |
| 27 | 0.0 | 1.167 (0.80) | 0.0 | 0.0 | 0.0 |
| 34 | 0.67 (0.46) | 4.56 (1.34) | 0.0 | 0.0 | 0.0 |
| Mean number of ephyrae scyphistoma$^{-1}$ (SE) after 16 weeks | | | | | |
| 21 | 8.8 (0.7) | 0.5 (0.5) | 0.0 | 0.0 | 0.0 |
| 27 | 10.1 (1.1) | 1.1 (0.8) | 0.0 | 0.0 | 0.0 |
| 34 | 10.1 (0.7) | 5.1 (1.3) | 0.0 | 0.0 | 0.0 |
| Total number of ephyrae produced treatment group$^{-1}$ | | | | | |
| 21 | 170 | 9 | 0 | 0 | 0 |
| 27 | 196 | 37 | 0 | 0 | 0 |
| 34 | 195 | 104 | 0 | 0 | 0 |

Table A5. *Aurelia aurita* (Orkney): descriptive statistics for results of an 8 week experiment testing the effects of 15 different combinations of temperature and salinity on asexual reproductive output.

| Salinity | Temperature °C | | | | |
|---|---|---|---|---|---|
| | 4 | 9 | 14 | 19 | 23 |
| Total surviving scyphistomae | | | | | |
| 21 | 15 | 15 | 15 | 15 | 15 |
| 27 | 15 | 15 | 14 | 15 | 15 |
| 34 | 15 | 15 | 14 | 14 | 15 |
| Mean no. of progeny scyphistoma produced scyphistoma$^{-1}$ (SE) | | | | | |
| 21 | 0 (0.0) | 0.8 (0.29) | 0.6 (0.18) | 0.7 (0.28) | 0.6 (0.19) |
| 27 | 0.1 (0.09) | 0.5 (0.19) | 0.5 (0.16) | 0.6 (0.25) | 0.5 (0.16) |
| 34 | 0.5 (0.22) | 0.7 (0.26) | 0.7 (0.30) | 0.2 (0.11) | 0.5 (0.27) |
| Mean no. of podocysts produced scyphistoma$^{-1}$ (SE) | | | | | |
| 21 | 0.0 | 0.27 (0.12) | 0.33 (0.16) | 0.0 | 0.0 |
| 27 | 0.07 (0.07) | 0.27 (0.15) | 0.0 | 0.07 (0.07) | 0.4 (0.21) |
| 34 | 0.0 | 0.13 (0.09) | 0.21 (0.16) | 0.29 (0.16) | 0.13 (0.09) |
| Total strobilating scyphistomae | | | | | |
| 21 | 14 | 0 | 0 | 0 | 0 |
| 27 | 13 | 0 | 0 | 0 | 0 |
| 34 | 9 | 0 | 0 | 0 | 0 |
| Mean number of weeks before strobilation initiated | | | | | |
| 21 | 7.5 (0.14) | NA | NA | NA | NA |
| 27 | 6.0 (0.3) | NA | NA | NA | NA |
| 34 | 7.0 (0.5) | NA | NA | NA | NA |
| Mean strobilation duration in weeks (SE) | | | | | |
| 21 | 10.9 (0.46) | NA | NA | NA | NA |
| 27 | 9.9 (0.45) | NA | NA | NA | NA |
| 34 | 8.4 (0.49) | NA | NA | NA | NA |
| Mean number of ephyrae scyphistoma$^{-1}$ (SE) | | | | | |
| 21 | 16.0 (1.9) | 0 | 0 | 0 | 0 |
| 27 | 19.27 (2.4) | 0 | 0 | 0 | 0 |
| 34 | 10.87 (2.6) | 0 | 0 | 0 | 0 |
| Total number of ephyrae produced treatment group$^{-1}$ | | | | | |
| 21 | 240 | 0 | 0 | 0 | 0 |
| 27 | 289 | 0 | 0 | 0 | 0 |
| 34 | 163 | 0 | 0 | 0 | 0 |

# Appendix II

Analysis of deviance tables of results for laboratory incubator experiments testing the effects of temperature and salinity of asexual reproductive output of British scyphistomae.

Table A6. *Cyanea capillata*: Analysis of deviance summaries for response variables used in model selection.

| | Df | Deviance | Residual Df | Residual Deviance | Pr (>Chi) |
|---|---|---|---|---|---|
| Surviving scyphistomae | | | | | |
| NULL | | | 269 | 357 | |
| Temperature | 4 | 159.9 | 265 | 197 | $p < 0.001$ |
| Salinity | 2 | 2.6 | 263 | 195 | $p = 0.28$ |
| Temperature x Salinity | 8 | 14.1 | 255 | 180 | $p = 0.08$ |
| Podocysts scyphistoma$^{-1}$ | | | | | |
| NULL | | | 218 | 136.3 | |
| Temperature | 4 | 49.9 | 214 | 86.3 | $p < 0.001$ |
| Salinity | 2 | 3.4 | 212 | 82.9 | $p = 0.18$ |
| Temperature x Salinity | 8 | 5.3 | 204 | 77.6 | $p = 0.72$ |
| Strobilating scyphistomae | | | | | |
| NULL | | | 269 | 350 | |
| Temperature | 4 | 172.2 | 265 | 178 | $p < 0.001$ |
| Salinity | 2 | 1.0 | 263 | 177 | $p = 0.62$ |
| Temperature x Salinity | 8 | 10.3 | 255 | 167 | $p = 0.24$ |
| Onset of strobilation | | | | | |
| NULL | | | 94 | 71.4 | |
| Temperature | 3 | 19.79 | 91 | 51.6 | $p < 0.001$ |
| Salinity | 2 | 0.88 | 89 | 50.7 | $p = 0.645$ |
| Temperature x Salinity | 6 | 0.97 | 84 | 49.8 | $p = 0.965$ |
| Strobilation duration | | | | | |
| NULL | | | 94 | 67.0 | |
| Temperature | 3 | 18.02 | 91 | 49.0 | $p < 0.001$ |
| Salinity | 2 | 5.83 | 89 | 43.2 | $p = 0.054$ |
| Temperature x Salinity | 5 | 1.52 | 84 | 41.7 | $p = 0.911$ |
| Ephyrae produced | | | | | |
| NULL | | | 269 | 509 | |
| Temperature | 4 | 264.2 | 265 | 244 | $p < 0.001$ |
| Salinity | 2 | 7.7 | 263 | 237 | $p = 0.021$ |
| Temperature x Salinity | 8 | 13.0 | 255 | 224 | $p = 0.112$ |

Table A7. *Cyanea lamarckii*: Analysis of deviance summaries for response variables used in model selection.

| | Df | Deviance | Residual Df | Residual Deviance | Pr (>Chi) |
|---|---|---|---|---|---|
| Surviving scyphistomae | | | | | |
| NULL | | | 143 | 61.8 | |
| Temperature | 3 | 5.04 | 140 | 56.8 | p = 0.17 |
| Salinity | 1 | 0.55 | 139 | 56.2 | p = 0.46 |
| Temperature x Salinity | 3 | 0.19 | 136 | 56.0 | p = 0.98 |
| Progeny scyphistomae scyphistoma$^{-1}$ | | | | | |
| NULL | | | 143 | 165 | |
| Temperature | 3 | 2.46 | 140 | 163 | p = 0.48 |
| Salinity | 1 | 1.52 | 139 | 161 | p = 0.22 |
| Temperature x Salinity | 3 | 4.32 | 136 | 157 | p = 0.23 |
| Podocysts scyphistoma$^{-1}$ | | | | | |
| NULL | | | 143 | 312 | |
| Temperature | 3 | 97.6 | 140 | 214 | p < 0.001 |
| Salinity | 1 | 0.4 | 139 | 214 | p = 0.53 |
| Temperature x Salinity | 3 | 3.7 | 136 | 210 | p = 0.30 |
| Strobilating scyphistomae | | | | | |
| NULL | | | 143 | 136 | |
| Temperature | 3 | 31.17 | 140 | 105 | p < 0.001 |
| Salinity | 1 | 0.0 | 139 | 105 | p = 1.0 |
| Temperature x Salinity | 3 | 4.07 | 136 | 101 | p = 0.25 |
| Onset of strobilation | | | | | |
| NULL | | | 25 | 42.0 | |
| Temperature | 2 | 14.42 | 23 | 27.6 | p < 0.001 |
| Salinity | 1 | 7.68 | 22 | 19.9 | p = 0.005 |
| Temperature x Salinity | 1 | 0.13 | 21 | 119.8 | p = 0.717 |
| Strobilation duration | | | | | |
| NULL | | | 25 | 50.2 | |
| Temperature | 2 | 24.08 | 23 | 26.2 | p < 0.001 |
| Salinity | 1 | 0.36 | 22 | 25.8 | p = 0.55 |
| Temperature x Salinity | 1 | 1.26 | 21 | 24.5 | p = 0.26 |
| Ephyrae produced | | | | | |
| NULL | | | 143 | 1697 | |
| Temperature | 3 | 351 | 140 | 1345 | p < 0.001 |
| Salinity | 1 | 20 | 139 | 1325 | p < 0.001 |
| Temperature x Salinity | 3 | 112 | 136 | 1213 | p < 0.001 |

Table A8. *Chrysaora hysoscella*: Analysis of deviance summaries for response variables used in model selection.

| | Df | Deviance | Residual Df | Residual Deviance | Pr (>Chi) |
|---|---|---|---|---|---|
| Surviving scyphistomae | | | | | |
| NULL | | | 179 | 180 | |
| Temperature | 4 | 180 | 175 | 0 | $p < 0.001$ |
| Salinity | 1 | 0 | 174 | 0 | $p = 1.0$ |
| Temperature x Salinity | 4 | 0 | 170 | 0 | $p = 1.0$ |
| Podocysts scyphistoma$^{-1}$ | | | | | |
| NULL | | | 179 | 401 | |
| Temperature | 4 | 223.2 | 175 | 178 | $p < 0.001$ |
| Salinity | 1 | 6.1 | 174 | 172 | $p = 0.014$ |
| Temperature x Salinity | 4 | 12.2 | 170 | 159 | $p = 0.016$ |
| Strobilating scyphistomae | | | | | |
| NULL | | | 179 | 198 | |
| Temperature | 4 | 37.2 | 175 | 161 | $p < 0.001$ |
| Salinity | 1 | 0.0 | 174 | 161 | $p = 0.85$ |
| Temperature x Salinity | 4 | 2.7 | 170 | 158 | $p = 0.61$ |
| Onset of strobilation | | | | | |
| NULL | | | 42 | 23.6 | |
| Temperature | 3 | 1.796 | 39 | 21.8 | $p = 0.62$ |
| Salinity | 1 | 0.588 | 38 | 21.2 | $p = 0.44$ |
| Temperature x Salinity | 3 | 0.528 | 35 | 20.6 | $p = 0.91$ |
| Strobilation duration | | | | | |
| NULL | | | 42 | 31.8 | |
| Temperature | 3 | 15.74 | 39 | 16.1 | $p = 0.001$ |
| Salinity | 1 | 0.02 | 38 | 16.0 | $p = 0.898$ |
| Temperature x Salinity | 3 | 0.43 | 35 | 15.6 | $p = 0.933$ |
| Ephyrae produced | | | | | |
| NULL | | | 179 | 500 | |
| Temperature | 4 | 103.6 | 175 | 396 | $p < 0.001$ |
| Salinity | 1 | 1.1 | 174 | 395 | $p = 0.55$ |
| Temperature x Salinity | 4 | 10.9 | 170 | 384 | $p = 0.45$ |

Table A9. *Aurelia aurita* (Southampton): Analysis of deviance summaries for response variables used in model selection.

| | Df | Deviance | Residual Df | Residual Deviance | Pr (>Chi) |
|---|---|---|---|---|---|
| Surviving scyphistomae | | | | | |
| NULL | | | 269 | 49.8 | |
| Temperature | 4 | 2.81 | 265 | 47.0 | p = 0.59 |
| Salinity | 2 | 4.33 | 263 | 42.7 | p = 0.11 |
| Temperature x Salinity | 8 | 4.04 | 255 | 38.6 | p = 0.85 |
| Progeny scyphistomae scyphistoma$^{-1}$ | | | | | |
| NULL | | | 269 | 700.52 | |
| Temperature | 4 | 240.347 | 265 | 460.17 | p < 0.001 |
| Salinity | 2 | 79.861 | 263 | 380.31 | p < 0.001 |
| Temperature x Salinity | 8 | 15.323 | 255 | 364.99 | p = 0.053 |
| Podocysts scyphistoma$^{-1}$ | | | | | |
| NULL | | | 269 | 366.68 | |
| Temperature | 4 | 125.334 | 265 | 241.35 | p < 0.001 |
| Salinity | 2 | 1.469 | 263 | 239.88 | p = 0.479 |
| Temperature x Salinity | 8 | 12.693 | 255 | 227.19 | p = 0.122 |
| Strobilating scyphistomae 8 weeks | | | | | |
| NULL | | | 269 | 219.405 | |
| Temperature | 4 | 87.411 | 265 | 131.994 | p < 0.001 |
| Salinity | 2 | 36.329 | 263 | 95.665 | p < 0.001 |
| Temperature x Salinity | 8 | 1.755 | 255 | 93.91 | p = 0.98 |
| Strobilating scyphistomae 16 weeks | | | | | |
| NULL | | | 269 | 290.967 | |
| Temperature | 4 | 205.241 | 265 | 85.726 | p < 0.001 |
| Salinity | 2 | 10.143 | 263 | 75.583 | p = 0.006 |
| Temperature x Salinity | 8 | 2.341 | 255 | 73.242 | p = 0.968 |
| Onset of strobilation | | | | | |
| NULL | | | 61 | 109.075 | |
| Temperature | 1 | 45.803 | 60 | 63.272 | p < 0.001 |
| Salinity | 2 | 19.32 | 58 | 43.952 | p < 0.001 |
| Temperature x Salinity | 2 | 1.105 | 56 | 42.847 | p = 0.575 |
| Strobilation duration | | | | | |
| NULL | | | 61 | 46.366 | |
| Temperature | 1 | 26.845 | 60 | 19.52 | p < 0.001 |
| Salinity | 2 | 4.18 | 58 | 15.33 | p = 0.12 |
| Temperature x Salinity | 2 | 0.33 | 56 | 15.008 | p = 0.84 |
| Ephyrae produced 8 weeks | | | | | |
| NULL | | | 269 | 764.24 | |
| Temperature | 4 | 320.29 | 265 | 443.95 | p < 0.001 |
| Salinity | 2 | 98.59 | 263 | 345.36 | p < 0.001 |
| Temperature x Salinity | 8 | 7.05 | 255 | 338.31 | p = 0.53 |
| Ephyrae produced 16 weeks | | | | | |
| NULL | | | 269 | 1785.21 | |
| Temperature | 4 | 1584.52 | 265 | 200.68 | p < 0.001 |
| Salinity | 2 | 2.07 | 263 | 198.62 | p = 0.35 |
| Temperature x Salinity | 8 | 21.59 | 255 | 177.03 | p = 0.005 |

Table A10. *Aurelia aurita* (Orkney): Analysis of deviance summaries for response variables used in model selection.

| | Df | Deviance | Residual Df | Residual Deviance | Pr (>Chi) |
|---|---|---|---|---|---|
| Surviving scyphistomae | | | | | |
| NULL | | | 224 | 31.9 | |
| Temperature | 4 | 5.91 | 220 | 26.0 | p = 0.21 |
| Salinity | 2 | 2.85 | 218 | 23.1 | p = 0.24 |
| Temperature x Salinity | 8 | 1.06 | 210 | 22.0 | p = 1.0 |
| Progeny scyphistomae scyphistoma$^{-1}$ | | | | | |
| NULL | | | 222 | 263 | |
| Temperature | 4 | 13.8 | 218 | 249 | p = 0.008 |
| Salinity | 2 | 0.9 | 216 | 248 | p = 0.638 |
| Temperature x Salinity | 8 | 17.4 | 208 | 231 | p = 0.027 |
| Podocysts scyphistoma$^{-1}$ | | | | | |
| NULL | | | 221 | 142 | |
| Temperature | 4 | 9.98 | 217 | 132 | p = 0.041 |
| Salinity | 2 | 0.51 | 215 | 131 | p = 0.773 |
| Temperature x Salinity | 8 | 24.13 | 207 | 107 | p = 0.002 |
| Strobilating scyphistomae | | | | | |
| NULL | | | 224 | 197.9 | |
| Temperature | 4 | 152.8 | 220 | 45.0 | p = < 0.001 |
| Salinity | 2 | 5.7 | 218 | 39.3 | p = 0.05 |
| Temperature x Salinity | 8 | 0.0 | 210 | 39.3 | p = 1.0 |
| Onset of strobilation | | | | | |
| NULL | | | 33 | 7.03 | |
| Salinity | 2 | 2.13 | 31 | 4.9 | p = 0.34 |
| Strobilation duration | | | | | |
| NULL | | | 33 | 11.54 | |
| Salinity | 2 | 3.31 | 31 | 8.23 | p = 0.19 |
| Ephyrae produced | | | | | |
| NULL | | | 224 | 2628 | |
| Temperature | 4 | 2227 | 220 | 400 | p < 0.001 |
| Salinity | 2 | 36 | 218 | 364 | p < 0.001 |
| Temperature x salinity | 8 | 0 | 210 | 364 | p = 1.0 |

# Appendix III

The GLM predicted probabilities of scyphistomae surviving for the duration of an eight week laboratory incubator experiment when exposed to different temperature conditions.

Table A11. *Cyanea capillata*. GLM predicted probabilities of scyphistoma survival when maintained for 8 weeks at given temperatures. Predictions were made at salinity 34 based upon results presented in Chapter 3.

| Temperature °C | Mean survival probability | Std. Dev. | Std. Error |
|---|---|---|---|
| 4 | 0.939 | 0.004 | 0.001 |
| 5 | 0.923 | 0.005 | 0.001 |
| 6 | 0.904 | 0.006 | 0.002 |
| 7 | 0.882 | 0.007 | 0.002 |
| 8 | 0.855 | 0.009 | 0.003 |
| 9 | 0.823 | 0.010 | 0.003 |
| 10 | 0.786 | 0.012 | 0.004 |
| 11 | 0.744 | 0.014 | 0.004 |
| 12 | 0.696 | 0.015 | 0.005 |
| 13 | 0.643 | 0.016 | 0.005 |
| 14 | 0.587 | 0.017 | 0.006 |
| 15 | 0.529 | 0.018 | 0.006 |
| 16 | 0.469 | 0.018 | 0.006 |
| 17 | 0.411 | 0.017 | 0.005 |
| 18 | 0.355 | 0.016 | 0.005 |
| 19 | 0.303 | 0.015 | 0.005 |
| 20 | 0.254 | 0.014 | 0.004 |
| 21 | 0.212 | 0.012 | 0.004 |
| 22 | 0.175 | 0.010 | 0.003 |
| 23 | 0.145 | 0.008 | 0.003 |

Table A12. *Chyrsaora hysoscella*. GLM predicted probabilities of scyphistoma survival when maintained for 8 weeks at given temperatures. Predictions were made at salinity 34 based upon results presented in Chapter 3.

| Temperature °C | Mean survival probability | Std. Dev. | Std. Error |
|---|---|---|---|
| 4 | 0.00 | 0.000 | 0.000 |
| 5 | 0.01 | 0.002 | 0.001 |
| 6 | 0.481 | 0.393 | 0.113 |
| 7 | 0.999 | 0.003 | 0.001 |
| 8 | 1.0 | 0.000 | 0.000 |
| 9 | 1.0 | 0.000 | 0.000 |
| 10 | 1.0 | 0.000 | 0.000 |
| 11 | 1.0 | 0.000 | 0.000 |
| 12 | 1.0 | 0.000 | 0.000 |
| 13 | 1.0 | 0.000 | 0.000 |
| 14 | 1.0 | 0.000 | 0.000 |
| 15 | 1.0 | 0.000 | 0.000 |
| 16 | 1.0 | 0.000 | 0.000 |
| 17 | 1.0 | 0.000 | 0.000 |
| 18 | 1.0 | 0.000 | 0.000 |
| 19 | 1.0 | 0.000 | 0.000 |
| 20 | 1.0 | 0.000 | 0.000 |
| 21 | 1.0 | 0.000 | 0.000 |
| 22 | 1.0 | 0.000 | 0.000 |
| 23 | 1.0 | 0.000 | 0.000 |

# Appendix IV

The GLM predicted probabilities of scyphistomae strobilating during an eight week laboratory incubator experiment when exposed to different temperature conditions.

Table A13. *Aurelia aurita* (Orkney). GLM predicted strobilation probabilities when maintained for 8 weeks at given temperatures. Predictions were made at salinity 34 based upon results presented in Chapter 3.

| Temperature °C | Mean strobilation probability | Std. Dev. | Std. Error |
|---|---|---|---|
| 4 | 0.680 | 0.041 | 0.013 |
| 5 | 0.532 | 0.047 | 0.015 |
| 6 | 0.377 | 0.044 | 0.014 |
| 7 | 0.244 | 0.035 | 0.011 |
| 8 | 0.146 | 0.039 | 0.007 |
| 9 | 0.083 | 0.014 | 0.004 |
| 10 | 0.046 | 0.008 | 0.002 |
| 11 | 0.025 | 0.004 | 0.001 |
| 12 | 0.013 | 0.002 | 0.000 |
| 13 | 0.007 | 0.001 | 0.000 |
| 14 | 0.003 | 0.000 | 0.000 |
| 15 | 0.002 | 0.000 | 0.000 |
| 16 | 0.001 | 0.000 | 0.000 |
| 17 | 0.000 | 0.000 | 0.000 |
| 18 | 0.000 | 0.000 | 0.000 |
| 19 | 0.000 | 0.000 | 0.000 |
| 20 | 0.000 | 0.000 | 0.000 |
| 21 | 0.000 | 0.000 | 0.000 |
| 22 | 0.000 | 0.000 | 0.000 |
| 23 | 0.000 | 0.000 | 0.000 |

Table A14. *Aurelia aurita* (Southampton). GLM predicted strobilation probabilities when maintained for 8 weeks at given temperatures. Predictions were made at salinity 34 based upon results presented in Chapter 3.

| Temperature °C | Mean strobilation probability | Std. Dev. | Std. Error |
|---|---|---|---|
| 4 | 0.865 | 0.018 | 0.005 |
| 5 | 0.794 | 0.025 | 0.007 |
| 6 | 0.698 | 0.032 | 0.010 |
| 7 | 0.582 | 0.037 | 0.011 |
| 8 | 0.456 | 0.038 | 0.012 |
| 9 | 0.335 | 0.034 | 0.010 |
| 10 | 0.232 | 0.027 | 0.008 |
| 11 | 0.154 | 0.020 | 0.006 |
| 12 | 0.098 | 0.013 | 0.004 |
| 13 | 0.061 | 0.008 | 0.002 |
| 14 | 0.037 | 0.005 | 0.001 |
| 15 | 0.023 | 0.003 | 0.001 |
| 16 | 0.014 | 0.002 | 0.000 |
| 17 | 0.008 | 0.001 | 0.000 |
| 18 | 0.005 | 0.000 | 0.000 |
| 19 | 0.003 | 0.000 | 0.000 |
| 20 | 0.001 | 0.000 | 0.000 |
| 21 | 0.001 | 0.000 | 0.000 |
| 22 | 0.000 | 0.000 | 0.000 |
| 23 | 0.000 | 0.000 | 0.000 |

Table A15. *Cyanea lamarckii*. GLM predicted strobilation probabilities when maintained for 8 weeks at given temperatures. Predictions were made at salinity 34 based upon results presented in Chapter 3.

| Temperature °C | Mean strobilation probability | Std. Dev. | Std. Error |
|---|---|---|---|
| 4 | 0.427 | 0.019 | 0.006 |
| 5 | 0.365 | 0.018 | 0.005 |
| 6 | 0.308 | 0.016 | 0.005 |
| 7 | 0.256 | 0.014 | 0.004 |
| 8 | 0.209 | 0.012 | 0.004 |
| 9 | 0.170 | 0.011 | 0.003 |
| 10 | 0.136 | 0.009 | 0.002 |
| 11 | 0.109 | 0.007 | 0.002 |
| 12 | 0.086 | 0.006 | 0.001 |
| 13 | 0.068 | 0.004 | 0.001 |
| 14 | 0.053 | 0.003 | 0.001 |
| 15 | 0.041 | 0.003 | 0.000 |
| 16 | 0.032 | 0.002 | 0.000 |
| 17 | 0.025 | 0.001 | 0.000 |
| 18 | 0.019 | 0.001 | 0.000 |
| 19 | 0.015 | 0.001 | 0.000 |

Table A15. *Cyanea capillata*. GLM predicted strobilation probabilities when maintained for 8 weeks at given temperatures. Predictions were made at salinity 34 based upon results presented in Chapter 3.

| Temperature °C | Mean strobilation probability | Std. Dev. | Std. Error |
|---|---|---|---|
| 4 | 0.952 | 0.007 | 0.002 |
| 5 | 0.921 | 0.011 | 0.003 |
| 6 | 0.873 | 0.018 | 0.005 |
| 7 | 0.801 | 0.025 | 0.008 |
| 8 | 0.702 | 0.033 | 0.010 |
| 9 | 0.579 | 0.039 | 0.012 |
| 10 | 0.447 | 0.040 | 0.012 |
| 11 | 0.321 | 0.035 | 0.011 |
| 12 | 0.217 | 0.027 | 0.008 |
| 13 | 0.139 | 0.019 | 0.006 |
| 14 | 0.086 | 0.012 | 0.004 |
| 15 | 0.052 | 0.008 | 0.002 |
| 16 | 0.031 | 0.004 | 0.001 |
| 17 | 0.018 | 0.002 | 0.000 |
| 18 | 0.011 | 0.001 | 0.000 |
| 19 | 0.006 | 0.001 | 0.000 |
| 20 | 0.003 | 0.000 | 0.000 |
| 21 | 0.002 | 0.000 | 0.000 |
| 22 | 0.001 | 0.000 | 0.000 |
| 23 | 0.000 | 0.000 | 0.000 |

Table A16. *Chrysaora hysoscella*. GLM predicted strobilation probabilities when maintained for 8 weeks at given temperatures. Predictions were made at salinity 34 based upon results presented in Chapter 3. Note that this GLM did not include the 4°C treatment group since all members of that group perished without strobilating.

| Temperature °C | Mean strobilation probability | Std. Dev. | Std. Error |
|---|---|---|---|
| 9 | 0.525 | 0.011 | 0.003 |
| 10 | 0.487 | 0.011 | 0.003 |
| 11 | 0.448 | 0.011 | 0.003 |
| 12 | 0.410 | 0.011 | 0.003 |
| 13 | 0.373 | 0.010 | 0.003 |
| 14 | 0.338 | 0.010 | 0.003 |
| 15 | 0.304 | 0.009 | 0.003 |
| 16 | 0.272 | 0.009 | 0.002 |
| 17 | 0.242 | 0.008 | 0.002 |
| 18 | 0.215 | 0.007 | 0.002 |
| 19 | 0.190 | 0.007 | 0.002 |
| 20 | 0.167 | 0.006 | 0.002 |
| 21 | 0.147 | 0.005 | 0.001 |
| 22 | 0.128 | 0.005 | 0.001 |
| 23 | 0.113 | 0.004 | 0.001 |