Ecophysiology and Life Cycle Dynamics of North Sea Gelatinous Zooplankton

Dissertation

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Summary

Reports of gelatinous zooplankton blooms around the world are increasing. Gaining a cause-and-effect understanding of mechanisms behind jellyfish blooms is important to predict possible impacts on the structure and functioning of marine ecosystems. Life cycle dynamics of bloom forming gelatinous zooplankton such as cnidaria and ctenophora are complex, including benthic and pelagic stages. This impedes conclusions for taxa based on information obtained from only one life stage. Each life stage needs to be investigated in order to gain a full picture of the dynamics behind jellyfish blooms.

This thesis focuses on the impact of temperature on different life stages of scyphozoan jellyfish, as well as larvae of the ctenophore *Mnemiopsis leidyi*. In addition, possible habitats of the benthic life stage are simulated using data based on abundances of scyphomedusae collected in 2012 in the southern North Sea.

In ***Manuscript 1***, the ecophysiology of polyps was studied, measuring unfed (routine) respiration rate (R_R) of four scyphozoan species (*Aurelia aurita*, *Aurelia labiata*, *Aurelia limbata*, *Cyanea capillata*) acclimated to six temperatures between 7 and 20°C. With increasing test temperatures (e.g., 12 to 15°C for *C. capillata*, *A. labiata*, and *A. aurita*) R_R strongly increased (Q_{10} ~ 7 to 13). In some of the tested species the data suggested that sub-optimally warm temperatures were approached when R_R at 20°C was lower than at 15 or 18°C. In one species (*A. aurita*) R_R was measured under hypoxic conditions. Below 11, 22 and 24% O_2 saturation at 8.0, 15.5 and 19.0°C respectively, polyps of *A. aurita* were not able to perpetuate R_R. A literature review exhibited respiration rates of polyps, ephyrae and medusae of *A. aurita* at 15°C to be akin when considering differences in body size, irrespectively from differences in activity and habitat. The results of ***Manuscript 1*** on R_R together with previously published data suggest thermal windows to be narrower in individuals collected from higher latitudes.

In ***Manuscript 2***, temperature dependent feeding and growth of the larvae of the ctenophore *Mnemiopsis leidyi* from the North Sea was investigated. Tentaculate larvae (1.5 mm) were tested at temperatures between 6 and 30°C. Linear increase of carbon specific clearance and ingestion rates between 6 and 25°C, and rapid declines between

25 and 30°C were observed. With rising temperatures, both absolute- and carbon specific growth increased linearly (0.87 d^{-1} at 25°C). At low and high temperatures (6 and 30°C) extremely low or negative growth rates were observed, thus defining limits to population growth of *M. leidyi*.

In ***Manuscript 3***, settlement dynamics of two species of scyphozoan planula larvae from the North Sea were researched, examining broad temperature ranges in different experiments. Between 9 and 27°C more than 50% of the larvae of *C. capillata* settled within the first five days. Warmer waters (>18°C) were associated with faster settlement as well as increased settlement success of larvae. In a second experiment settlement was prevented, maintaining larvae in the water column at different temperatures (11.3, 13.4 and 19.4°C). After being removed from the water column, they remained competent to settle for 21, 21 and 14 days, respectively. A simulation of a hydrodynamic model in the North Sea suggested that larvae released in May could be transported up to 100 km, retaining the ability to settle. In a substrate choice experiment with planulae of *Chrysaora hysoscella* covering three temperatures (10, 15, 20°C) and two different light regimes (12/12 light/dark and total darkness), larvae settled in similar numbers onto wood, concrete and PET. Highest settlement was found at regimes with light at 20°C and lower settlement at 10 and 15°C in total darkness. The results of ***Manuscript 3*** propose that warming of the North Sea will not hinder settlement of planulae in the two resident species observed. Considering the ecophysiology of planula larvae, differences in species and/or populations may exist, which need to be investigated in order to understand underlying mechanisms promoting the establishment of benthic populations.

In ***Manuscript 4***, large scyphozoan medusae were collected from the southern North Sea in 2012 and 2013. Species composition, distribution and biomass of *Aurelia aurita*, *Cyanea lamarckii* and *Cyanea capillata* were analyzed and compared to the existing literature. The abundances found in the German Bight in these years were much lower than previously reported abundances from the North Sea, presumably due to the much larger net used in ***Manuscript 4***. Also, the water body sampled due to the large trawl may have provided a more realistic assessment of jellyfish abundances in the North Sea. For large-scale evaluations, comparable measures are needed when

collecting jellyfish. Accumulations of jellyfish were not influenced by abiotic factors, highlighting the influence of hydrodynamic conditions on the distribution of bloom forming species. A hydrodynamic drift model using the data from 2012 and previously published data approximated potential habitats for polyps and thus release areas of ephyrae.

The work of the present thesis demonstrates how different life stages of gelatinous zooplankton react differently to changing temperature regimes and consequently display different, presumably population-specific borders of thermal boundaries. As changing environmental conditions do not seem to impede the proliferation of these organisms, jellyfish are expected to benefit from warming marine systems and become even more dominant in the future.

CHAPTER 1

General Introduction

1 General Introduction

1.1 Jellyfish Blooms

Water temperatures in the oceans are rising (IPCC, 2014). Consequently, jellyfish and other organisms in the ocean food web and ecosystem are experiencing changing conditions. Recently, it has become more obvious that jellyfish, mostly scyphozoan medusae, can occur in large numbers, commonly referred to as “jellyfish blooms” (Condon et al., 2013, 2012; Lee et al., 2013; Mills, 2001; Purcell, 2012; Purcell et al., 2007).

Gelatinous zooplankton blooms are best described as large patches of medusae usually drifting within the upper meters of the ocean (Hamner and Dawson, 2009). Jellyfish blooms consist of scyphozoan medusae (Hamner and Dawson, 2009) but also other taxa within the cnidaria, as well as ctenophores and pelagic tunicates have been reported to bloom (Boero, 2013). Due to the limited number of time series data (e.g. Hay et al., 1990) and only sporadic reports of blooms (e.g. Brodeur et al., 2002), the debate, regarding whether jellyfish blooms are a phenomenon of natural oscillation (Condon et al., 2013, 2012), or repercussions of global warming and climate change continues (Dong et al., 2010; Duarte et al., 2012; Lee et al., 2013; Richardson et al., 2009). The frequent reporting of blooms in the scientific literature, in combination with accumulating news reports by the media may have biased perceptions towards climate-driven increases in jellyfish blooms (Condon et al., 2012; Mianzan et al., 2012) in lieu of the possibility that these are a natural phenomenon (Condon et al., 2013).

Warming marine systems have been associated with increased abundances of scyphozoan jellyfish (Han and Uye, 2010; Holst, 2012a; Lynam et al., 2004). Some examples from around the globe include East Asian marginal seas. In these areas mass occurrences of scyphozoan medusae have been reported regularly in the last century, but are now increasing in frequency (Uye, 2008). In- and offshore blooms of scyphomedusae in temperate Chinese seas were reported (Dong et al., 2010). In the Northern Benguela upwelling system, an increase in the abundance of scyphozoan jellyfish arose simultaneously with declining numbers of pelagic fish stocks (Flynn et al., 2012). Additionally, blooming species in the Mediterranean Sea did not only

include the scyphozoan jellyfish *Pelagia noctiluca* (Brotz and Pauly, 2012), but also the invasive ctenophore *Mnemiopsis leidyi* (Fuentes et al., 2010).

If blooms occur in coastal regions, local economies can be negatively impacted. For example, in 2007, when a bloom of *P. noctiluca* hit Northern Ireland's only Atlantic salmon farm, 250000 fish were killed (Baxter et al., 2010). More negative impacts are the clogging of fishing nets (Dong et al., 2010) and power plants and increased stinging of tourists, which in turn harms the tourism business (Purcell et al., 2007, Purcell, 2012). The profitability of fisheries is also highly susceptible to jellyfish blooms, as recently reported in the Adriatic Sea (Palmieri et al., 2014). Other regions of the Mediterranean Sea show declines in the spawning stock biomass of various fish stocks concomitant with increasing abundances of jellyfish (Brotz and Pauly, 2012). Feeding across the marine food web (Mills, 2001), jellyfish are affecting the abundance of fish eggs, fish larvae and zooplankton (Barz and Hirche, 2007; Hamner and Dawson, 2009; Lynam et al., 2005b; Schneider and Behrends, 1994) as well as competing with fish for food (Lynam et al., 2005b; Mills, 2001), which empowers them to significantly alter the food web. Exploitation of dense patches of prey in short periods of time (Titelman and Hansson, 2006) and the ability to not only act as bottom up, but also as top down predators (Lynam et al., 2004) possibly favors the proliferation and dispersion of scyphozoan medusae. As a result, a shift from a fish dominated to a jellyfish dominated trophic structure becomes more likely (Richardson et al., 2009).

In order to understand cause-and-effect mechanisms behind jellyfish blooms, several aspects need to be considered. Fundamental knowledge on the life cycle dynamics and taxonomical differences of jellyfish is needed. Standardized, field survey protocols need to be created in order to establish quantitative and comparable time series. This would allow general comparison of jellyfish abundance and distribution (Gibbons and Richardson, 2013). Finally, physiological responses to environmental changes need to be understood in order to fully grasp the magnitude of and mechanisms behind gelatinous zooplankton blooms.

1.2 Taxonomy and Lifecycle of Jellyfish

The term “jellyfish” refers to different taxonomic groups. For this reason it is of utmost importance to be acquainted with divers life cycles and distinguish between blooming taxa. The “coelenterata” is a polyphyletic group consisting of animals with a hollow body cavity, a single mouth opening and two cell layers (endo- and ectoderm) with extracellular matrix in between, commonly referred to as mesogloea, giving these animals their gelatinous properties. It comprises cnidaria and ctenophora, two distinct taxonomic groups that are often lumped together when talking about jellyfish blooms (Purcell, 2005). Both groups share features such as the gelatinous and often transparent habitus, but differ in characteristics, such as the presence of nematocysts and typically diecious reproduction in cnidaria in comparison to colloblasts and hermaphroditic propagation in ctenophores. Taxonomic relationships between ctenophores and cnidarians are not yet clarified. The current textbook opinion (Westheide and Rieger, 2006) places ctenophores next to bilateria, whereas cnidarians appear at a much more basal point in the tree of life (see Fig. 1.1A). In fact, recent research shows that cnidaria and bilateria are actually sister taxa, whereas ctenophora are seen as an outside group (see Fig. 1.1B, see Box 1.1 for further details on ctenophores).

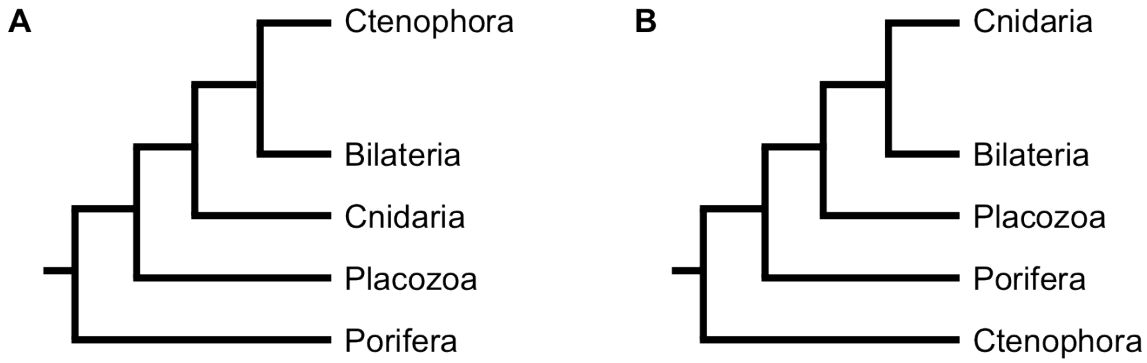

Figure 1.1: Taxonomic relationship of cnidaria and ctenophora according to (A) textbook (Westheide and Rieger, 2006) and (B) recently published research (Ryan et al., 2013).

Within the cnidaria, four recent groups (I-IV) can be found around the world. The most basal group of animals, the anthozoa (I), commonly referred to as corals and anemones lack an adult pelagic stage. The diverse hydrozoa (II) display different characteristics of sexual- and asexual reproduction in both, benthic and pelagic life

stages. Scyphozoa (III), the bloom forming taxon, is well known due to recurring interactions with the human interests (e.g. fishing). And finally cubozoa (IV), or box-jellyfish, are noted for being the most poisonous creatures on the planet. These four groups are connected through striking features. The possession of stinging cells (nematocysts or cnidocysts) is their name giving apomorphy. Additionally, free-swimming planula larvae as achievement of sexual reproduction from diecious medusae (hydrozoa, scyphozoa, cubozoa) or polyps (anthozoa), as well as asexual propagation unite cnidaria as a monophyletic group.

Box 1.1: Ctenophores in a nutshell

Ctenophores – or comb jellies – have a holopelagic lifecycle, lacking a sessile life stage. The possession of two retractable tentacles beset with sticky cells (colloblasts) to capture prey is a distinguishing feature between cnidarians and ctenophores. Swimming in oral pole direction by movement of ciliar propulsion reveals a different ontogenetic development as cnidarians, since the pelagic stage of cnidaria swims forth with the aboral pole. The fragile habitus of ctenophores can possibly result in misclassifying them as hydrozoa, but confusion with scyphozoan medusae is rather unlikely. In the last couple of decades, European waters have been invaded by a species within the ctenophores (Boersma et al., 2007; Faasse and Bayha, 2006; Hansson, 2006; Javidpour et al., 2006). The North American comb jelly *Mnemiopsis leidyi* (Purcell et al., 2001) was first observed in the North Sea in the early 2000 (Boersma et al., 2007; Hansson, 2006), initially being mistaken as the native *Bolinopsis infundibulum* (Faasse and Bayha, 2006; Oliveira, 2007). *Mnemiopsis leidyi* displays rapid population growth under favorable food conditions (Purcell et al., 2001) and shows devastating effects on higher and lower trophic levels (Shiganova et al., 2003), still reproducing when starved (Jaspers et al., 2015). It is considered to have a strong impact on ecosystems not only as an invasive, but also as a bloom forming species (Purcell, 2005; Purcell et al., 2007).

Most scyphozoan jellyfish follow a metagenetic life cycle (Fig. 1.2), first described by Agassiz in 1862 (Agassiz, 1862). Pelagic medusae release sexually produced free-swimming planula larvae (hatched from eggs) in batches (Holst and Jarms, 2007), which settle after having found a suitable substrate. They subsequently metamorphose into sessile scyphistomae (or polyps). Reaching maturity, polyps reproduce through various asexual ways such as budding, production of stolons, longitudinal fission (e.g. Adler and Jarms, 2009), planuloids and propagules (Vagelli,

2007), which facilitate population growth of polyps. Another asexual process called strobilation recruits the pelagic phase: through transversal fission (Arai, 1997) polyps produce numerous free-swimming ephyrae, which mature into adult medusae, thus closing the life cycle. Recently, a multi-modal, rather than a metagenetic life cycle is being discussed (Ceh et al., 2015). The authors argue that medusae most likely are able to overwinter. Furthermore, sexual- and asexual propagation are not necessarily temporal and / or spatial to be separated and the rather rigid metagenetic life cycle is not an imperative, since ephyrae and consequently medusae can derive from planula larvae, which is the case in the holoplanktonic scyphozoan *Pelagia noctiluca* (Canepa et al., 2014; Ceh et al., 2015).

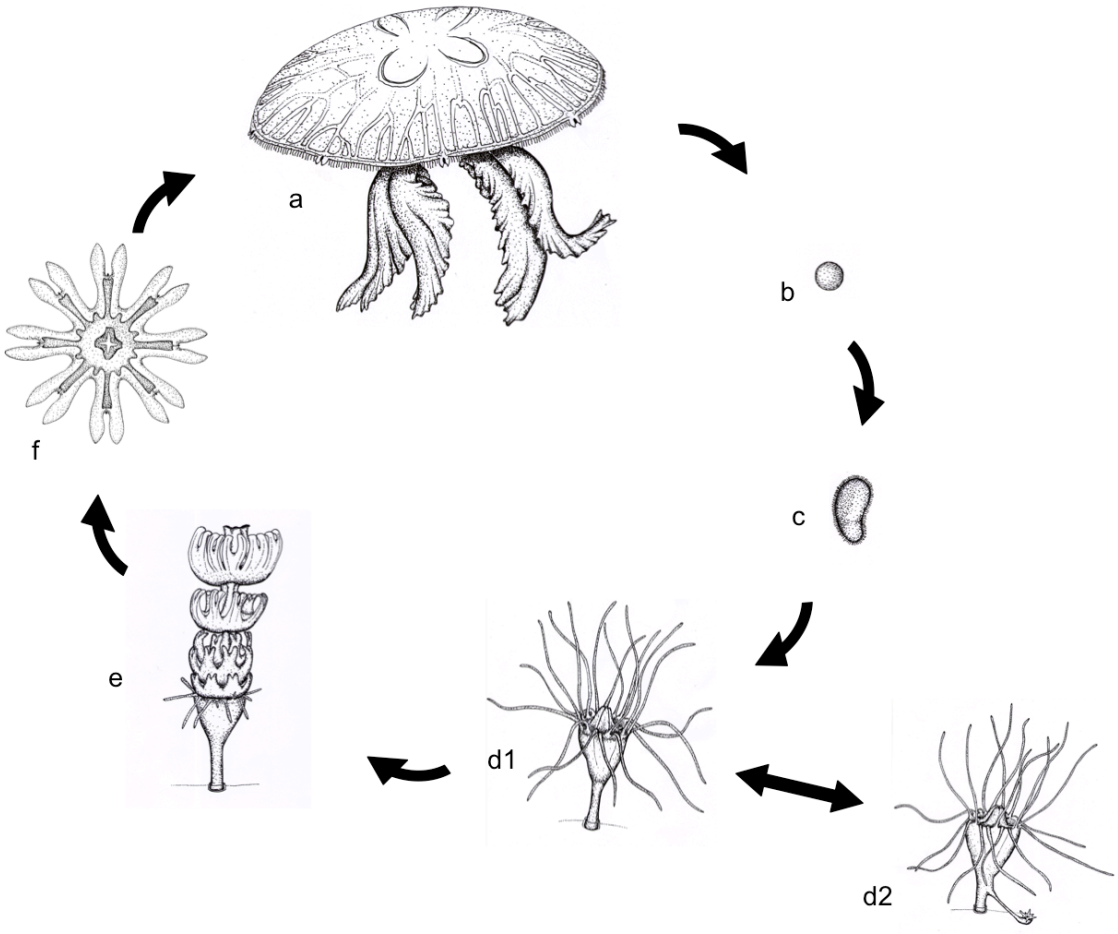

Figure 1.2: Metagenetic lifecycle of scyphozoa, instancing *Aurelia aurita*, adapted from Arratia et al. (2015): Pelagic medusae (a) produce fertilized eggs (b), which develop into free swimming planula larvae (c), metamorphosing into polyps (d1), which undergo asexual propagation by e.g. budding (d2) or strobilation (e), a process releasing pelagic ephyrae (f) which mature into medusae (a).

1.3 Jellyfish Sampling

Comparable information about the occurrence and magnitude of jellyfish blooms is scarce. Bloom events are being reported all over the world, but a plethora of sampling techniques (see Table 1.1) is applied, thus impeding quantitative and comparative evaluation. In addition, the existence of few time series (e.g. Brodeur et al., 2002; Hay et al., 1990) limits the options of modeling tools, which serve to address and identify causes of jellyfish blooms worldwide (Brotz et al., 2012; Condon et al., 2013).

The most commonly used gears to sample jellyfish are different types of nets such as surface-, pelagic- and bottom trawls (e.g. Brodeur et al., 2008; Dong et al., 2010; Hay et al., 1990), bongo nets (Barz and Hirche, 2007), and other kinds of plankton nets (e.g. Shoji et al., 2010). Bongo nets are considered to be unsuitable for quantitative sampling of jellyfish (Licandro et al., 2015), still, data collected with this net contribute to the growing information on jellyfish abundance (Barz and Hirche, 2007). Mesh sizes of horizontally towed nets including plankton nets and pelagic fish trawls are between 0.3-100 mm (see Table 1.1) to ensure capture of not only large individuals, but also smaller animals (Raskoff et al., 2003). Only one study used mesh sizes as large as 162 cm at the throat, a surface trawl deployed in the Northern California current to sample large scyphozoan medusae (Suchman and Brodeur, 2005). Tow speed generally lies between 1 and 4 knots (see Table 1.1). In one study using a WP2 net, vertical towing speed was at ~0.1 knots (Frost et al., 2012), in order to minimize damage to captured individuals. The risk of damaging jellyfish collected by using pelagic fish trawls or other nets increases with mesh size and towing speed, together with the risk of only sampling large specimen (Purcell, 2009). At the same time, larger nets allow to sample larger bodies of water, possibly balancing patchy abundances of large scyphozoans with areas entirely devoid of scyphozoan jellyfish. Still, an often communicated concern is to underestimate jellyfish abundances when collecting field data (Barz and Hirche, 2007; Hay et al., 1990; Suchman and Brodeur, 2005). Unfortunately, for the longest time being, jellyfish have been a product of by-catch (Hay et al., 1990). This may contribute to the reasons why data on jellyfish abundance and distribution are of poor quality and lack rigor.

Table 1.1: Common gears used to sample jellyfish and sampling locations

Gear	Meshsize	Net opening	Tow speed	Ocean	Reference
Net					
Bongo Net	335 and 500 µm	0.6 m diam	0.5 ms^{-1}	North Sea, German Bight	Barz and Hirche, 2007
Bottom trawl	100-38 mm (mouth-codend)	17 m wide	3 knots	Bering Sea	Brodeur et al., 2002
Bottom trawl	100-38 mm (mouth-codend)		3 knots	Bering Sea	Brodeur et al., 2008
CalCOFi net	0.5 mm	1 m diam	3-4 knots	Baltic Ocean, Kiel Fjord	Möller, 1980a
CalCOFi net	0.5 mm	1 m diam	3-4 knots	North Sea and Baltic	Möller, 1980b
Conical net	1 mm	0.5 m diam		Coastal waters, Japan	Uye et al., 2003
Jellynet	800 µm	1 m diam	1-2 knots	North Atlantic Basin	Licandro et al., 2015
Kom-Fyke	10x10 mm		stationary	North Sea, Dutch Wadden Sea	Van Walraven et al., 2014
Midwater trawl	2x3 mm (body), 1 mm (codend)	5 m^2	3 knots	Bering Sea	Brodeur et al., 2002
MIK	1 mm	6 m^2	0.5 ms^{-1}	North Sea, German Bight	Barz and Hirche, 2007
MIK	5 mm	5 m^2	3 knots	Irish Sea	Bastian et al., 2014
MIK	5 mm	5 m^2		Irish Sea	Lynam et al., 2011
Multinet	335 µm	0.5 m^2	0.5 ms^{-1}	North Sea, German Bight	Barz and Hirche, 2007
Net	10 mm	1.5 m diam		East Asian marginal Seas	Uye, 2008
Nordic 264 rope trawl	162.6-8.9 cm (mouth-codend)	86-125 m^2	3-3.5 knots	Northern California Current	Suchman and Brodeur, 2005
Pelagic trawls	100-10 mm (mouth-codend)	14 m^2	2.5 knots	North Sea	Hay et al., 1990
Plankton net	210 and 300 µm	0.5 m diam		Horsea Lake, England	Lucas, 1996
Plankton net	0.33 mm	0.5 m diam		Seto Inland Sea	Shoji et al., 2009
Plankton net	0.33 mm	0.5 m diam		Hiroshima Bay	Shoji et al., 2010
Plankton net	2 mm	0.7 m^2		North Sea, Western Wadden Sea	Van Der Veer and Oorthuysen, 1985
Surface trawl	20-7 mm (mouth-codend)	0.75 m^2		Northern Yellow Sea of China	Dong et al., 2012
WP2 net	300 µm	0.6 m diam	0.1 knots	North Sea Dogger Bank	Frost et al., 2012
WP3 net	1 mm	1 m diam		North Sea, Belgian Wadden Sea	Vansteenbrugge et al., 2015
Continuous Plankton Recorder					
	270 µm mesh collects samples	1.61 cm^2 per sample approx. 3 m^3 filtered seawater	20 km h^{-1}	North Sea	Attrill et al., 2007
				Ireland, Atlantic Ocean	Baxter et al., 2010
				North Atlantic	Gibbons and Richardson, 2009
				NE Atlantic / Mediterranean	Licandro et al., 2010
				North Atlantic Basin	Licandro et al., 2015
Ocean surface - and shore based surveys					
Aerial survey (airplane)				Prince William Sound, Alaska	Purcell et al., 2000
				Irish Sea	Houghton et al., 2006
				Coastal waters, Japan	Uye et al., 2003
Visual survey (boat)				Irish Sea	Bastian et al., 2011
				Pacific, Chilenian Coast	Ceh et al., 2015
				Northern Benguela, off Namibia	Sparks et al., 2001
				East Asian marginal Seas	Uye, 2008
Visual survey (shore)				Ireland	Fleming et al., 2013
				Patuxent River, Maryland	Cargo and King, 1990
				Irish Sea, Celtic Sea	Houghton et al., 2007
Visual survey (shore and boat)				Irish Sea, Celtic Sea	Doyle et al., 2007
Stranding data				Irish Sea, Celtic Sea	Houghton et al., 2007

Citizen Science		
	UK coastal waters	Pikesley et al., 2014
	Mediterranean Sea	www.jellywatch.org
	German Baltic coastline	Baumann and Schernewski, 2012
	Pacific, Chilenian Coast	Ceh et al., 2015
Other gears		
Acoustic sampling	Northern Benguela, off Namibia	Lynam et al., 2006
	Walvis Bay, Namibia	Brierley et al., 2004
ROV	Limfjorden	Båmstedt et al., 2003
	Monterey Bay	Raskoff, 2001

Abbreviations: CalCOFi net = Ring trawl; MIK = Method Isaacs Kidd net; ROV = Remote Operated Vehicle; Diam: diamter

The continuous plankton recorder (CPR) is another gear in use to assess jellyfish abundance (Gibbons and Richardson, 2009; Licandro et al., 2010). The collection of jellyfish tissue and the nematocysts therein (Baxter et al., 2010) enables to obtain an idea of jellyfish abundance. Still, these abundances refer to all pelagic cnidarians, comprising not only bloom forming scyphozoan medusae, but, predominantly members of the hydrozoa (Gibbons and Richardson, 2009), which seldom have been reported to bloom (Lynam et al., 2006). Analysis of CPR data is particularly difficult, due to the fact that, when evaluating nematocysts, identification on species level is complex (Gibbons and Richardson, 2009). Collected CPR data thereby provide information on changes in mostly hydrozoan species, also because scyphozoan jellyfish (except early life stages) are too large to be sampled and collected (Haddock, 2008). Genetic research on tissue collected by the CPR offers further, yet unexploited prospects on using this gear for jellyfish sampling (Licandro et al., 2015, 2010).

Visual surveys from airplanes allow fast sampling of large areas. A bloom of *Aurelia aurita* in coastal Japanese waters was reported, using photographs taken from a Cessna and comparing those densities to results from net sampling (conical net, 1mm mesh size) taken at random stations in the middle of the bloom, thus confirming the aerial method to be feasible and reliable (Uye et al., 2003). Additional aerial surveys have been conducted in Prince William Sound, Alaska (Purcell et al., 2000) and the Irish Sea (Houghton et al., 2006). This method allows identifying large patches of scyphozoan medusae, unfortunately, if no additional samples are taken, misclassification on species level may limit the significance of the results when

researching species-specific mass occurrences. This drawback can also bias data collected by visual surveys from boats (Bastian et al., 2011) or the shore (Doyle et al., 2007).

Data collection in terms of counting medusae performed by fishermen (Ceh et al., 2015) and lifeguards (Baumann and Schernewski, 2012) bear a risk of unintended misclassification and wrong counts. Involvement of citizens visiting beaches (Baumann and Schernewski, 2012) and the development of several websites with requesting the public to contribute their sightings of medusae online (Pikesley et al., 2014, MED-JELLYRISK: http://jellyrisk.eu/en/sightings), broadens the spectrum of methods to gain further insight into dynamics of jellyfish blooms.

1.4 The Ecophysiology of Jellyfish

Mass occurrences of jellyfish have often been associated with changes in temperature (Purcell, 2012; Riascos et al., 2013). Temperatures in the world's oceans are rising on a global scale (IPCC, 2014), impacting various additional abiotic factors such as variability in salinity and low oxygen conditions, which may foster proliferation and life cycle dynamics of scyphozoan jellyfish (Brewer and Feingold, 1991; Holst, 2012a; Holst and Jarms, 2010; Ishii et al., 2008; Lucas, 2001; Lucas et al., 2012; Purcell, 2007). Thus, temperature seemingly is the most important factor when evaluating physiological traits (characteristics) in gelatinous zooplankton.

Most metabolic functions in aquatic poikilotherms are directly impacted by temperature. Survival is restricted to a certain temperature range, in which metabolism is operating. Within this thermal window, given food availability to be sufficient, routine maintenance costs are covered. Surplus oxygen availability, depending on temperature, allows metabolism to invest in growth, reproduction, migration and foraging. This extra energy deriving from oxygen supply covering more than just the basal metabolic rate is referred to as aerobic scope, and applies as an indicator for fitness (Pörtner and Peck, 2010). The aerobic scope of a species highly depends on their geographical range (Pörtner and Farrell, 2008; Pörtner and Knust, 2007). Simultaneously, the thermal window is as narrow as possible, in order to keep maintenance costs at a minimum (Pörtner and Farrell, 2008), which reflects trade-offs in performance related to stenothermal environments versus the ability to tolerate

wide seasonal changes in temperatures. Thermal windows provide information about upper and lower boundaries of temperature ranges, in which metabolism succeeds. Temperature dependent oxygen deficiency close to the boundaries of the aerobic scope may be critical for survival (Pörtner and Farrell, 2008; Pörtner and Knust, 2007). Cnidaria have been reported to be very tolerant to hypoxic conditions (Vaquer-Sunyer and Duarte, 2008). In order to find the upper and lower limits of thermal windows of survival and consequently the boundaries of physiological performance, more research considering environmental factors is needed. In nature, these factors are generally confounded. Thus, it is of absolute importance to isolate variables and identify possible impacts of environmental factors, such as temperature, on physiological traits of jellyfish to gain a cause-and-effect knowledge.

Considering life cycle dynamics of jellyfish is essential when attempting to understand the physiology of jellyfish blooms. When feeding conditions are good, warming temperatures can be associated with larger individuals and higher fecundity in scyphomedusae (Lucas and Lawes, 1998). The release of planula larvae depends on the timing and periodicity of the sexual reproduction of medusae, being controlled, amongst other features, by temperature (Lucas et al., 2012; Lucas and Lawes, 1998; Riascos et al., 2013). So far, few studies examined the effect of temperature on settlement and metamorphosis of planula larvae in scyphozoa considering different temperature ranges and geographic regimes (Fitt and Costley, 1998; Prieto et al., 2010; Riascos et al., 2013; Webster and Lucas, 2012). The timing and frequency of the asexual reproduction of the sessile life stage of scyphozoan jellyfish has been researched to a greater extent (Han and Uye, 2010; Holst, 2012a; Purcell et al., 2012), showing elevated rates with increasing temperatures (reviewed in Lucas et al., 2012). Respiration rates in polyps, however, have only been investigated once, researching the polyps of *Chrysaora hysoscella* and *Aurelia aurita* (Mangum et al., 1972). Apparently, metabolism in polyps is insensitive to elevated temperatures (Mangum et al., 1972), which corresponds to findings made in scyphozoan medusae, which showed to be unsusceptible to low oxygen conditions (Condon et al., 2001; Richardson et al., 2009; Thuesen et al., 2005). Additionally, there is a significant relationship between body mass and respiration rate in medusae, but not between temperature and respiration rate (Frandsen and Riisgård, 1997), indicating that feeding rates increase

with body mass and prey density, not temperature (Purcell et al., 2010). The growth and feeding rates of ephyrae and adult medusae have been previously examined at different temperatures. Apparently, maximum specific growth rates of *Aurelia* sp. increased exponentially between 4 and 21°C in ephyrae (22% d^{-1} to 40% d^{-1}) and medusae (8% d^{-1}; Møller and Riisgård, 2007a; Widmer, 2005). Ephyrae of *A. aurita* doubled their weight depending on temperature every 2-4 days, with high feeding rates and maximum specific growth rates of 20-45% d^{-1} at 18°C (Båmstedt et al., 1999). Also, weight-specific respiration rate was up to 4 times higher in well-fed and fast growing ephyrae (Møller and Riisgård, 2007b). Other bloom forming species such as *Mnemiopsis leidyi* showed respiration rates to be dependent on both, weight and temperature (Kremer, 1977; Lilley et al., 2014; see Box 1.2).

Box 1.2: Selected ecophysiological traits of *Mnemiopsis leidyi*

Reproduction and survival of *Mnemiopsis* occurs across a wide range of temperatures and salinities (Baker and Reeve, 1974; GESAMP, 1997; Jaspers et al., 2011), although adult individuals most likely do not survive temperatures below 4 to 1°C (Oliveira, 2007; Shiganova et al., 2001). Nevertheless, survival at temperatures between -0.7 and 35°C has been reported (Miller, 1974). Breeding occurs between 19-23°C at darkness, provided that sufficient food is available (GESAMP, 1997). Within this temperature range, mass occurrences of *M. leidyi* have been reported (Faasse and Bayha, 2006). Reeve and Baker (1975) quantified growth of *Mnemiopsis*, considering different temperatures (21, 26, 30°C). Recently, researching adult *M. leidyi* revealed increasing feeding rates between temperatures of 13-27°C (Finenko et al., 2014) and exponential increases in growth rates with rising temperatures between 9 and 22°C (Robinson and Graham, 2014) in adult stages of this species.

These findings suggest rising temperatures in temperate regions will accelerate rates of growth, feeding and reproduction of pelagic stages of scyphozoa. Increased prevalence of hypoxia will also favor jellyfish, which are relatively insensitive to low oxygen conditions (Thuesen et al., 2005). The combination of warming and increased hypoxia in marine systems could markedly increase the trophodynamic impact of jellyfish. In order to estimate the future effects of jellyfish on marine food webs a mechanic understanding of temperature windows of individual species and even populations is essential.

1.5 Gelatinous Zooplankton in the North Sea

Shallow shelf regions such as the North Sea warm faster than deeper, offshore areas (Ådlandsvik, 2008; Ådlandsvik and Bentsen, 2007). Water temperatures within the North Sea have increased by a mean of 1.67°C since 1962 (Wiltshire et al., 2010). Being one of the most biological productive ecosystems in the world (Reid and Edwards, 2001), the North Sea is influenced by parameters such as a fluctuating North Atlantic oscillation index, and also by the influx from the North Atlantic (Ådlandsvik, 2008; Ådlandsvik and Bentsen, 2007; Skogen et al., 2011). As a result, two regime shifts have been described which led to strong modifications in the ecosystem (Alheit et al., 2005; Beaugrand, 2004; Beaugrand et al., 2002; Wiltshire and Manly, 2004). Resulting ecosystem changes were traced back to constantly rising temperatures (Beaugrand et al., 2008).

Hydrodynamic changes in the North Sea including warming and changes in wind-driven water currents and vertical mixing do not only shift the timing for spring phytoplankton bloom and the composition of zooplankton (Graham et al., 2001; Hay et al., 1990; Lynam et al., 2005a, 2004), they can have marked impacts on the development, survival and, hence population size of jellyfish (Purcell, 2005). Also, increasing temperatures promote incremental rates of sexual and asexual reproduction of jellyfish (Holst, 2012a; Lucas and Lawes, 1998). The physical boundaries of the North Sea seem to be aggregation sites (Graham et al., 2001; Hay et al., 1990; Lynam et al., 2005a, 2004), since jellyfish as part of the plankton community are not able to actively swim against currents. Their distribution seems to be forced by the effects of density driven currents and the presence of frontal zones. High abundances of scyphomedusae are expected in stratified waters, bordering estuaries (Doyle et al., 2007; Nielsen et al., 1997) and pycnoclines (Graham et al., 2001).

Six species within the cnidaria, *Aurelia aurita*, *Cyanea capillata*, *Cyanea lamarckii*, *Chrysaora hysoscella*, *Pelagia noctiluca* and *Rhizostoma octopus* are the main scyphozoans occurring in the North Sea (Hay et al., 1990). *Aurelia aurita* is common in the northwestern area of the North Sea (Möller, 1980b) and also aggregates around the eastern coast of Ireland and is found sporadically in the German Bight (Hay et al., 1990), but not in very large numbers (Barz and Hirche, 2007). It is well known to amass

inshore and in harbors (Russell, 1970). The mostly coastal *C. hysoscella* (Russell, 1970) was the dominant scyphozoan species in the late 1970s (Möller, 1980b), but was rarely abundant in the southern North Sea in the early 1970s (Hay et al., 1990) and the early 2000s (Barz and Hirche, 2007). *Cyanea capillata*, often referred to as northern boreal species (Russell, 1970), is found all over the North Sea, except in the central North Sea (Möller, 1980b). According to Hay et al. (1990) *C. capillata* occurs on the northwestern coast of Ireland and the southern North Sea, and the German Bight (Barz and Hirche, 2007). *Cyanea lamarckii* is referred to as southern boreal species (Russell, 1970), thus being strongly present in the German bight and the eastern North Sea (Barz and Hirche, 2007; Hay et al., 1990), but not in the central North Sea (Möller, 1980b). *Rhizostoma octopus* is seldom observed in the North Sea (Hay et al., 1990; Verwey, 1942) and is referred to as southern boreal species as well (Russell, 1970). The holoplanktonic species *P. noctiluca*, both coastal and oceanic (Hay et al., 1990), is scarce in the English Channel (Russell, 1970), but elsewhere abundances are increasing (Baxter et al., 2010). Ctenophores are also increasing in the North Sea, such as the common species *Pleurobrachia pileus* (Greve, 1971, 1970) and the invasive species *Mnemiopsis leidyi* (Boersma et al., 2007; Faasse and Bayha, 2006; Hansson, 2006; Javidpour et al., 2006).

Understanding metabolic responses of *M. leidyi* to a changing environment considering larval- and adult stages is essential in order to comprehend possible impacts on the food web and resulting blooms. Also, identifying the habitats of scyphozoan polyps and predicting potential outbursts of medusae would allow running drift models in order to forecast possible blooms in the future. This is a difficult task, since factors such as migration pattern, food availability and physiological response to temperature changes need more research.

1.6 Scope of the Thesis

In order to gain a better understanding of gelatinous zooplankton blooms and aggregations, life cycle dynamics and the impact of factors such as temperature need to be researched much more thoroughly. Although the metabolic response of jellyfish to changing environmental factors has been examined to some degree, there remain large gaps in knowledge, especially when considering all life stages. The goal of this

thesis is to address open questions concerning sessile- and larval stages such as which abiotic conditions are most favorable for growth and survival? Answering this and other open questions will help efforts to identify and understand the dynamics of blooms.

To date, respiration rates have been studied primarily in the pelagic stages of jellyfish. Only one study examined respiration rates of scyphozoan polyps (Mangum et al., 1972). Boundaries of thermal windows in polyps may influence respiration rates in polyps, hence routine respiration rates (R_R) in four different scyphozoan species from different geographical regions between 7-20°C were measured (*Manuscript 1*).

The effects of temperature on growth and food consumption have been investigated in larval and adult pelagic stages of gelatinous zooplankton. The fragile larvae of *M. leidyi* have been researched considering various aspects, but none of them concerned the impact of temperature on growth and food consumption. Optimal temperatures for growth and food consumption within thermal windows need to be detected, in order to assess possible consequences of rising temperatures on populations of *M. leidyi*. Food consumption and growth in newly hatched larvae of *M. leidyi* were studied, investigating changes between temperatures of 6-30°C (*Manuscript 2*).

The planula, the larval stage of scyphozoan jellyfish, has primarily gained attention concerning substrate choice or effects of salinity (Holst and Jarms, 2010, 2007), but also temperature and food regime (Webster and Lucas, 2012). Thermal windows, in which planula larvae are able to find suitable substrate, settle and metamorphose into polyps, affect settlement speed, settlement competency and substrate choice. Extensive laboratory experiments were conducted in order to research open questions considering the impacts of temperature on settling dynamics (*Manuscript 3*). A model provides valuable information on drift distances of planula larvae and thus possible polyp source locations (*Manuscript 3*).

Information on abundances and distribution of scyphozoan jellyfish in the North Sea are rare (Barz and Hirche, 2007; Van Walraven et al., 2014). Field data collected in 2012 and 2013 provide information on species composition, distribution and abundance, thus contributing to the growing body of information (*Manuscript 4*). A hydrodynamic model revealed potential areas of polyp populations, utilizing the data

collected in this and previously published studies (Hay et al., 1990). Different approaches to locate polyp populations, primarily liable for the release of large numbers of ephyrae, as well as including metabolic responses to temperature changes, illustrate the importance of incorporating all stages of the life cycle, in order to understand the full magnitude of jellyfish blooms.

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CHAPTER 2

Respiration rates of the polyps of four jellyfish species: Potential thermal triggers and limits

2 Respiration rates of the polyps of four jellyfish species: Potential thermal triggers and limits (*Manuscript 1*)

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Abstract

The bloom dynamics of metagenetic jellyfish are regulated, to a large degree, by the asexual reproduction of benthic polyps. The ecophysiology of polyps is poorly studied compared to pelagic (ephyrae and medusae) life stages. We measured unfed (routine) respiration rates (R_R) of the polyps of four scyphozoan species (*Cyanea capillata*, *Aurelia aurita*, *Aurelia labiata* and *Aurelia limbata*) acclimated to six temperatures between 7 and 20°C and one species (*A. aurita*) under hypoxic conditions. Strong increases (Q_{10} ~ 7 to 13) in R_R occurred after subtle warming across specific test temperatures (e.g., 12 to 15°C for *C. capillata, A. labiata,* and *A. aurita*). In some species, R_R at 20°C was lower than at 15 or 18°C suggesting that sub-optimally warm temperatures were approached. Polyps of *A. aurita* were unable to maintain R_R below 11, 22 and 24% O_2 saturation at 8.0, 15.5 and 19.0°C, respectively. Despite obvious differences in activity and habitat, rates of respiration in polyps, ephyrae and medusae of *A. aurita* at 15°C appear similar after taking into account differences in body size. A literature comparison of polyp respiration rates suggests a narrowing of thermal windows in individuals collected from higher latitudes. Common garden experiments are needed to thoroughly examine potential local adaptation.

Keywords: Aurelia, Cyanea, Metabolism, Oxygen consumption, Physiology, Scyphozoa

2.1 Introduction

Global water temperatures are expected to rise during the next decades which, along with increases in other anthropogenic pressures, are expected to increase blooms of pelagic scyphozoans in marine systems (e.g. Duarte et al., 2012; Purcell et al., 2007). Regardless of whether recent increases in the frequency of jellyfish blooms are due to climate change or natural oscillations in populations (Condon et al., 2013), warming waters have been correlated with increased abundance of scyphozoan jellyfish in some marine systems (Han and Uye, 2010; Holst, 2012; Lynam et al., 2004). Gaining a mechanistic (cause-and-effect) understanding of the factors that control bloom dynamics is important to project the ecological impacts such as altered food web dynamics as well as the consequences to various economic sectors such as fisheries and aquaculture (reviewed in Purcell et al., 2007). In the metagenetic life cycle of scyphozoans, benthic polyps play a critical role in population persistence. Polyps strobilate to produce ephyrae which mature into adult medusae which sexually reproduce to form planula larvae which settle and metamorphose into polyps thus closing the life cycle. Polyps are most often found in shallow (0 to 15 m) coastal areas but can occur to depths of 120 m (Hernroth and Gröhndahl, 1983; Miyake et al., 2002; Toyokawa, 2011). Polyps of some species display high tolerance to hypoxia, which increases their likelihood of persisting in benthic habitats and successfully outcompeting other fouling organisms such as mussels or barnacles (Condon et al., 2001; Ishii and Katsukoshi, 2010; Ishii et al., 2008; Miller and Graham, 2012). Temperature and prey availability interact to affect the reproduction and growth of polyps (Di Camillo et al., 2010; Lucas et al., 2012) with the former acting as a trigger for asexual reproduction such as budding and/or strobilation (Holst, 2012; Liu et al., 2009) and the en/excystment of polyps (Brewer and Feingold, 1991). Surprisingly, to the best of our knowledge only one previous study (Mangum et al., 1972) has examined the effect of temperature on respiration rates of scyphozoan polyps.

The present study measured the unfed (routine) respiration rate (R_R) of polyps of four scyphozoan species (*Cyanea capillata, Aurelia aurita, Aurelia limbata* and *Aurelia labiata*) acclimated to six temperatures between 7 and 20°C. Polyps of the five groups (two populations of *A. aurita*) originated from either oceanic or coastal waters displaying different annual ranges in water temperature (Fig. 2.1) which could provide

interesting contrasts in thermal windows of R_R. The effect of oxygen concentration on R_R of *A. aurita* polyps was also examined. Since changes in R_R have important consequences for the energy available for growth and reproduction, these measurements could shed light on how thermal windows (and oxygen concentrations) constrain the distribution and productivity of polyp populations in nature.

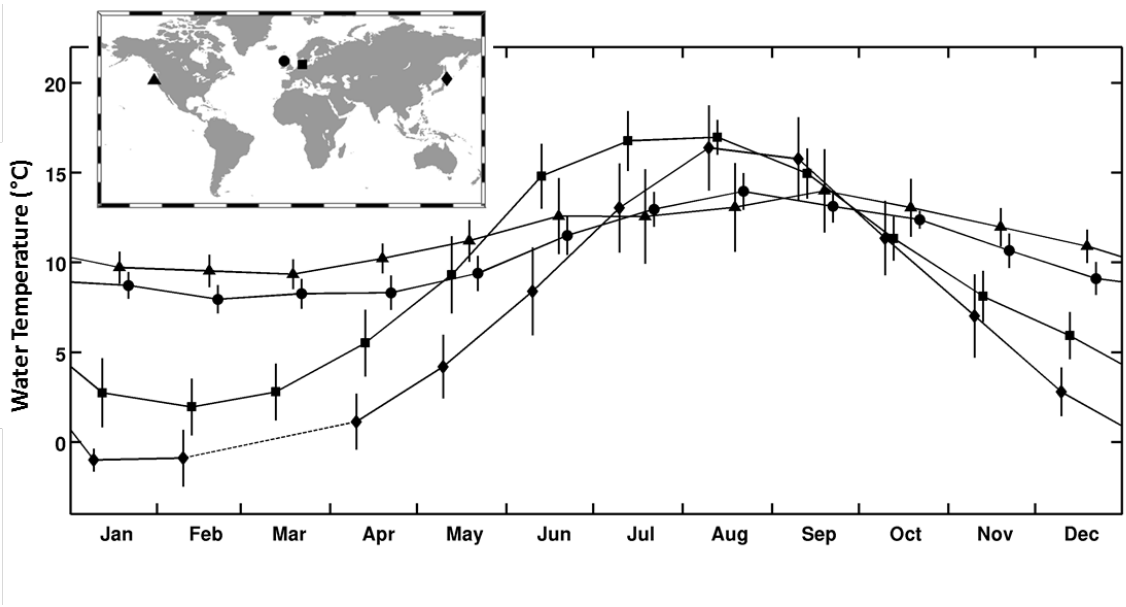

Figure 2.1: Mean (±SD) monthly water temperatures at each of the four areas where scyphozoan polyps were collected for this study. The region of field collection is shown on the insert map. Temperatures were compiled from the World Ocean Atlas (WOA) database. Data points were slightly shifted along the x-axis for visual clarity.

2.2 Material and Method

2.2.1 Origin and Maintenance of the Polyps

Polyps of *A. aurita* and *C. capillata* were collected from Kiel Bight (southwest Baltic Sea, 54.4°N, 10.2°E) and polyps of *A. aurita* were also obtained from the Hebrides, west coast of Scotland (North Atlantic, 57.6°N, 7.0°W). Two other *Aurelia* species originated from Pacific waters: polyps of *A. labiata* were from Coos Bay, Oregon (northeast Pacific 43.4°N, 142.2°W) and *A. limbata* was collected from northern Japan (Sea of Okhotsk, 44.2°N, 144.3°E) (Fig. 1.1). Polyps were maintained in laboratory cultures for >5 years at 15°C using 0.7 µm filtered seawater at a salinity of 32. Polyps were maintained without aeration in darkness (except a brief period each week when polyps were fed and the water changed). For several months prior to testing, polyps were fed late-stage copepodites (C5–C6) of a calanoid copepod (*Acartia tonsa*). Prior

to the experiment, polyps were slowly acclimated (2.5°C week^{-1}) to one of six test temperatures and maintained at that temperature for at least 2 weeks prior to measurements. Polyps had not received food for 2 or 3 days prior to respiration measurements.

Table 2.1: Summary information for trials measuring the respiration rate (R_R) of the polyps of five groups of scyphozoans: *Aurelia aurita* collected in the Baltic Sea (Aa1) and northeast Atlantic (Aa2), *A. labiata* (Ala), *A. limbata* (Ali) and *Cyanea capillata* (Cc).

Trial	T	Species	Polyps	Polyp Dry Weight (µg)	
ID	(°C)	(ID)	(n)	minimum	maximum
1	15	Aa1,Cc,Ala	2, 2, 2	117	263
2	15	Aa1,Cc,Ala	2, 2, 2	190	303
3	18	Aa1, Cc	2, 2	219	464
4	18	Aa1, Cc	2, 2	263	397
5	20	Aa1,Cc,Ala	2, 2, 2	186	413
6	20	Aa1,Cc,Ala	2, 2, 2	119	366
7	12	Aa1,Cc,Ala	2, 2, 2	132	346
8	12	Aa1,Cc,Ala	2, 2, 2	123	257
9	10	Aa1,Cc,Ala	2, 2, 2	78	240
10	10	Aa1,Cc,Ala	2, 2, 2	55	176
11	10	Aa2	4	177	370
12	12	Aa2	4	279	490
13	15	Aa2	4	204	377
14	18	Aa2	4	249	405
15	20	Aa2	4	137	172
16	7	Aa1,Cc,Ala	2, 2, 2	66	260
17	7	Aa1,Cc,Ala	2,2,1	56	276
18	7	Aa2	4	217	346
19	10	Ali	4	83	212
20	7	Ali	4	21	59
21	15	Ali	4	81	140
22	12	Ali	4	83	95
23	18	Ali	4	82	119
24	20	Ali	4	82	156

2.2.2 Respiration Measurements

The R_R of individual polyps was measured at six temperatures: 7, 10, 12, 15, 18 and 20°C (except *A. labiata* not measured at 18°C) using a Unisense A/S Micro-respiration System (Århus, DK, OX-10 sensor) equipped with 750-µl chambers submerged within a temperature controlled (±0.2°C) water bath. Oxygen diffusion between the chambers and the water bath, tested prior to the start of each experiment, was negligible. The

water within each chamber was well mixed by a small stir magnet (120 rpm) separated from the polyp by a mesh screen. The chambers were large enough to easily accommodate the largest polyps (diameter and height of the chamber were roughly twice the width and height of those polyps) but small enough to ensure that the respiration of polyps was easily registered. Seawater was filtered (0.7 μm) and autoclaved to avoid bacterial contamination. All components of the system were cleaned with ethanol prior to each trial. A total of 24 trials was conducted (Table 2.1) with, most often, six chambers with one polyp and two control (blank) chambers with only seawater and a small volume of transfer water from polyp cultures.

Trials were conducted over a 3-month period during which two or three scyphozoan groups/species were run in the same trial (except *A. limbata*) and test temperatures were always run in a random order. During each trial, each polyp had a short (7-min) acclimation period to the chamber prior to the first measurement period. Over the course of several hours, the oxygen concentration in each chamber was repeatedly measured four to seven times (a measurement lasted 7 to 10 min with only the middle 3 min used for analyses to avoid noise). In each temperature trial, oxygen within the chambers was never <55% saturation (pilot tests suggested that R_R was constant until O_2 was <30% saturation - see below). Differences between the two blank chambers were always <10% and the mean rate of oxygen consumption in these two chambers was always <50% of that of chambers with polyps and was often much less (<30% in the majority of trials). Directly after each trial, polyps were dipped into distilled water to wash away salt and frozen at −80°C. Samples were subsequently freeze-dried (Christ LCG) for >16 h, and dry weight (*DW*) was measured (Sartorius, 4503 MP6 microbalance, ± 0.1 μg).

In a second series of trials, the R_R of polyps of *A. aurita* collected from the southern North Sea (Helgoland, 54.18°N, 7.88°E) was measured at acclimation temperatures of 8.0 (n = 2 polyps), 15.5 (n = 4) and 19.0°C (n = 4). During these trials, polyps were allowed to consume all of the oxygen within the chambers. These runs provided estimates of the point at which R_R was no longer independent of O_2 saturation (the P_C, where oxygen regulators become oxygen conformers). The same technique was used

by Rutherford and Thuesen (2005) to examine the P_C in 12 jellyfish (scyphozoan and hydrozoan) species.

2.2.3 Calculations and Statistics

The rate of oxygen consumption was calculated from the slope of the linear decrease in O_2 concentration versus time (predictive regressions). Within each trial, the mean slope of the two control chambers was subtracted from that of each polyp chamber to obtain estimates of R_R (ng O_2 polyp^{-1} h^{-1}). Significant differences in polyp *DW* and R_R within groups among temperatures were tested using ANOVAs followed by a Tukey-HSD post-hoc test. Data were log-transformed to meet assumptions of normality and homogeneity of variances. In the trials examining O_2 saturation, slopes of linear regressions between adjacent measurements of O_2 concentration were calculated (yielding estimates of R_R) and a two-segment (broken stick) regression was fit to R_R vs % O_2 saturation. All statistical tests were conducted using R software (R Core Team, 2012).

2.3 Results

Significant differences existed in the *DW* of polyps among the different test temperatures in the four groups: (ANOVAs: *A. aurita* Baltic Sea (df=5, 18) (F=6.3) ($p < 0.01$), *A. aurita* northeast Atlantic (df=5, 17) (F=5.8) ($p < 0.01$), *A. labiata* (df=4, 14) (F= 16.3) ($p < 0.001$), *C. capillata* (df = 5, 18) (F = 4.5) ($p < 0.01$)). Therefore, R_R was standardized to a common *DW* within each group using the equation:

$$log(R_{Rcorr}) = log(R_{Rp}) - (log(DW_p) - log(DW_i)) * 0.75 \quad (1)$$

where DW_p and R_{Rp} are the dry weight (µg) and observed R_R (ng O_2 h^{-1}) of a polyp in group *i*, and DW_i is the mean dry weight of all polyps within group *i*. The value 0.75 was the mean slope (b = 0.754) of significant ($p < 0.05$), inter-specific regressions of polyp R_R versus *DW* ($R_R = aDW^b$) at five temperatures (7°C, b = 0.676, R^2 = 0.77; 10°C, b = 0.574, R^2 = 0.75; 12°C, b = 0.808, R^2 = 0.77; 18°C, b = 0.829, R^2 = 0.70; 20°C, b= 0.759 R^2= 0.74). Using Eq. (1), the R_R of polyps of *A. aurita* Baltic, *A. aurita* NE Atl, *C. capillata*, *A. labiata*, and *A. limbata* was standardized to a DW_i of 300, 525, 400, 150, and 150 µg, respectively.

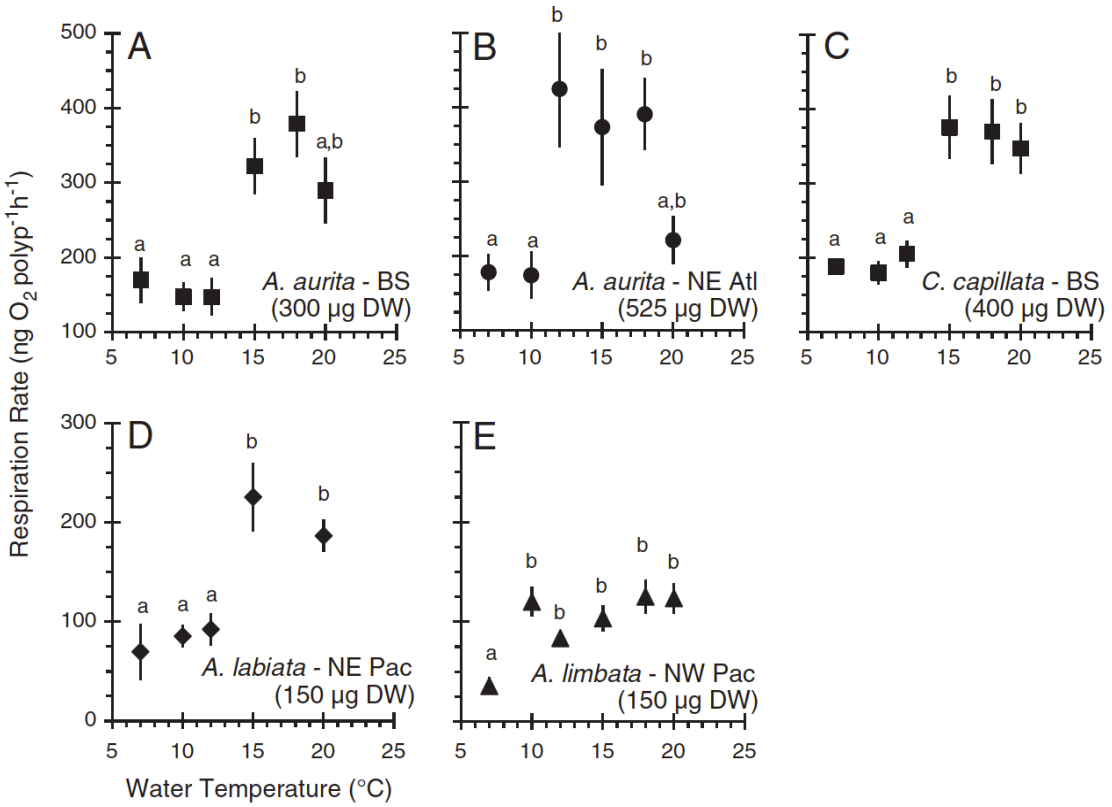

Figure 2.2: Mean (±SE) respiration rate (ng O_2 h^{-1}) of individual polyps (n = 3 to 4) acclimated to different water temperatures. Five groups were tested (Panels A-E, symbols refer to collection locations in Figure 2.1). For each group, respiration rates were standardized to a common polyp dry weight (*DW)*. Within each panel, rates not sharing a common letter were significantly different at the p > 0.05 level. (ANOVA and Tukey HSD), Panel A: F(5, 18) = 9.793, p < 0.001; Panel B: F(5, 17) = 6.248, p < 0.01; Panel C: F(5, 18) = 12.61, p < 0.0001; Panel D: F(4, 14) = 18.27, p < 0.0001. Panel E: F(5, 16) = 10.49, p < 0.001.

2.3.1 Polyp Respiration versus Temperature

At the six temperatures, R_R was between 150 and 450 ng O_2 $polyp^{-1}$ h^{-1} in *A. aurita* collected from the Baltic Sea (300-µg *DW*) and the northeast Atlantic (525 µg *DW*) as well as *C. capillata* (400 µg *DW*) (Fig. 2.2A–C). In the somewhat smaller (150 µg DW) polyps of *A. labiata* and *A. limbata*, R_R was generally <200 ng O_2 $polyp^{-1}$ h^{-1}, (Fig. 2.2D–E). In general, R_R was lower at colder temperatures and increased at warmer temperatures but an exponential increase with increasing temperature was not observed. Moreover, each group displayed relatively large changes in R_R across relatively small changes in temperature as described below. Between 12 and 15°C, polyps of *A. aurita* and *C. capillata* collected from the Baltic Sea displayed significant increases in R_R represented by Q_{10} values of ~13 and 7.5, respectively (Fig. 2.2A and C). Polyps of *A. aurita* collected from the northeast Atlantic displayed a significant increase in R_R between 10 and 12°C, and a significant reduction in R_R at 20°C (Fig.

2.2B). In *A. labiata*, a greater than two-fold (significant) increase in R_R also occurred between 12 and 15°C (Fig. 2.2D). Finally, mean R_R of *A. limbata* polyps was significantly lower at 7°C but similar at all warmer temperatures.

2.3.2 Polyp Respiration versus Oxygen Saturation

The R_R of *A. aurita* polyps remained fairly constant until certain, critical O_2 saturations were reached and then R_R decreased monotonically with decreasing oxygen concentration. Based upon breakpoints in two-segment regressions, the mean (±SE) P_C at 8.0, 15.5 and 19.0°C was equal to 10.7 (±1.7), 24.3 (±1.3) and 22.1 (±5.7)% O_2 saturation, respectively. All segmented regressions were significant ($p < 0.001$) and described between 77 and 98% of the variability in polyp respiration rates (2, 4 and 4 polyps at 8.0, 15.5 and 19.0°C, mean (±SE) *DW* of 1108.5 (±155.2), 928.7 (±119.3), and 948.2 (±187.1) µg, respectively).

2.4 Discussion

Optimal and sub-optimal ranges in temperature and critical thermal limits exist in all poikilotherms (Pörtner and Farrell, 2008) and a lack of research on thermal windows in jellyfish limits our ability to project how warming might affect (or potentially limit) life cycle and bloom dynamics. Previous work on benthic polyps of scyphozoans indicates that temperature not only influences respiration rates (Mangum et al., 1972; this study) but also other aspects of growth physiology including the induction and rate of strobilation, the quantity of ephyrae produced (e.g. Di Camillo et al., 2010; Fuchs et al., 2014; Holst, 2012; Liu et al., 2009; Lucas et al., 2012; Purcell, 2007) as well as the rate of asexual reproduction (budding) and growth rate of polyp populations (Di Camillo et al., 2010; Ishii and Katsukoshi, 2010; Lucas et al., 2012; Purcell, 2007).

Polyp budding and strobilation occur at different times of the life cycle (Di Camillo et al., 2010) and these processes appear to be linked to different temperatures (Han and Uye, 2010; Liu et al., 2009). For example, Han and Uye (2010) reported prey level-dependent induction of strobilation (at a specific, cold temperature) and budding (at warm temperatures). Furthermore, the strobilation process is known to be controlled by both retinoic acid signaling and up-regulation of specific proteins in response to a “temperature sensitive timer” (Fuchs et al., 2014). The work of Han and Uye (2010)

suggests the presence of “summer” and “winter” metabolic strategies, a distinction that could explain the changes in R_R observed with increasing temperature in the present study. The distinct increase in R_R between 12 and 15°C in *A. aurita*, *A. labiata* and *C. capillata* could be due to shifts in metabolic/ growth strategy. In ephyrae, a similar threshold-like effect of temperature is evident in respiration rates measured by Møller and Riisgård (2007). In that study, respiration rates from 7 to 11.5°C were essentially unchanged but strongly, exponentially increased (Q_{10} ~ 4.0) from 11.5 to 22°C. It is important to note that, although we are confident in the measurements made here, only 3 or 4 polyps were measured at each temperature.

Thermal limits to growth and survival arise from oxygen- and capacity-limited thermal tolerance (Pörtner and Farrell, 2008). Critical thermal limits are normally associated with decreases in aerobic and increases in anaerobic metabolism. Although, the present study did not measure anaerobic metabolism, polyps of *A. aurita* collected from the northeast Atlantic had much lower R_R at 20°C compared to 15 and 18°C, and polyps of other groups/species displayed modest declines in R_R at temperatures ≥18 °C. These temperatures are warmer than any monthly mean temperature reported for the sites of collection (44 to 58°N) of these groups of polyps (Fig. 2.1). Besides the present study, to the best of our knowledge only one previous study (Mangum et al., 1972) has reported respiration rates of scyphozoan polyps. In that study, *A. aurita* polyps from Chesapeake Bay (37°N) acclimated to 12 and 20°C exhibited an exponential increase in respiration rates with warming to 32°C (Fig. 2.3, inset). After converting to common units, the rates measured here and those reported by Mangum et al. (1972) agree well from 12 to 18°C but rates at 20°C were much lower in higher latitude conspecifics measured here (Baltic Sea and NE Atlantic, 54 to 58°N). Furthermore, lower latitude conspecifics died at <12°C whereas higher latitudes polyps could be acclimated to (and grown at) 7°C. Common garden experiments with polyps from different latitudes are needed to test for potential adaptation to local thermal conditions. *A. aurita* is a particularly well-studied scyphozoan and respiration rates at 15°C have been measured in medusae (Frandsen and Riisgård, 1997; Ishii and Tanaka, 2006; Kinoshita et al., 1997; Larson, 1987; Uye and Shimauchi, 2005), ephyrae (Frandsen and Riisgård, 1997; Kinoshita et al., 1997; Møller and Riisgård, 2007) and polyps (Mangum et al., 1972; this study).

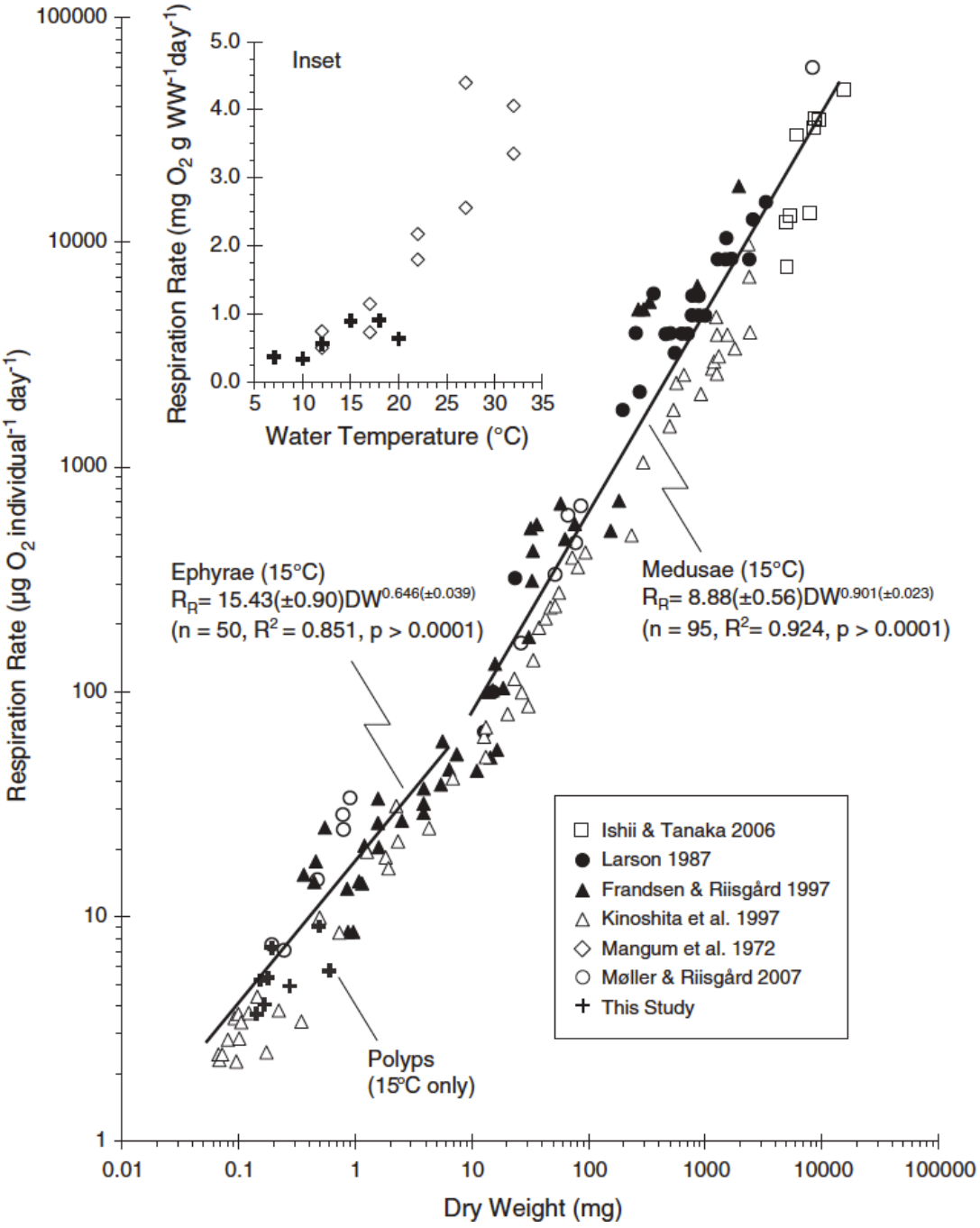

Figure 2.3: Respiration rate (µg O_2 individual^{-1} day^{-1}) versus dry weight (mg) of *Aurelia aurita* polyps, ephyrae and medusa at 15°C. A dry weight (*DW*) of 10 mg separates ephyrae from medusa. The two regression lines (mean ± SE parameter estimates provided) were fit to the pooled data of 3 and 5 studies on ephyrae and medusae, respectively. Insert: effect of water temperature on respiration rate (displayed in units of mg O_2 g wet weight (*WW*)$^{-1}$ day^{-1}) of polyps of *A. aurita* collected from the Chesapeake Bay (Mangum et al. 1972) and from the Baltic Sea and northeast Atlantic shelf (this study). Note, unlike Fig. 2.2, *DW* and R_R were measured values (not standardized) and data for both Baltic and NE Atl groups are shown). For conversion to units of *WW*, *DW* was assumed to be 5% *WW* (Uye and Shimauchi 2005).

Respiration rates of *A. aurita* polyps, ephyrae and medusae at 15°C appear to agree well after taking into account differences in body size (Fig. 2.3). Interestingly, respiration rates of ephyrae (Møller and Riisgård, 2007) appear to be similar to polyps (this study) at similar body masses (and temperatures) despite obvious differences in morphology and activity between these two life stages. Although our study was not designed to test for the effects of *DW* on respiration rate within each species/group, the slopes of inter-specific regressions of R_R versus *DW* (values of b in $R_R = a * DW^b$) were always <1.0 (mean 0.75). Arguments have been made that, with increasing body size, the metabolic rates of pelagic (active) and benthic (inactive) life stages of jellyfish should scale isometrically (b = 1) and allometrically (b ≠ 1), respectively. Intra-specific (*A. aurita*) regressions describing the pooled data collected at 15°C in 3 studies on ephyrae (<10 mg *DW*) and 5 studies on medusae (>10 mg *DW*) had mean (±SE) slopes of 0.646 (±0.039) and 0.904(±0.023), respectively (Fig. 2.3).

Although one should be cautious of pooling data collected in different studies (due to potential differences in methods), our findings support the idea that the slope is closer to isometric in medusae as suggested by Glazier (2006). Ideally, such an intra-specific (inter-stage) comparison would be made on the same population using similar methods.

Various metagenetic life stages of jellyfish (medusae, planula larvae, polyps) appear particularly tolerant to low concentrations of dissolved oxygen (Miller and Graham, 2012; Rutherford and Thuesen, 2005; Shoji et al., 2005) likely due to their high body water content and ability to store oxygen within the intragel layer (Thuesen et al., 2005). The settlement of planula larvae appeared to be enhanced (more rapid) under hypoxic conditions (Ishii et al., 2008; Miller and Graham, 2012). Polyps of *A. aurita* maintained at 22°C died within 7 days at 0.2 ml O_2 l^{-1} but grew well at 2.0 ml O_2 l^{-1} (Ishii et al., 2008) which are ~10% and ~40% oxygen saturation, respectively. These results are not unexpected given the marked reduction in R_R at <20% O_2 saturation observed at both 15.5 and 20°C in the present study. Lower oxygen thresholds (between 10 and 25% saturation = 0.5 and 1.6 mg O_2 l^{-1} at 22 to 24°C) were found for the survival and growth of polyps of another scyphozoan *Chrysaora quinquecirrha*

(DeSor)) collected from Chesapeake Bay, where seasonal hypoxia is a common feature (Condon et al., 2001).

In conclusion, we observed non-exponential increases in the respiration rates of polyps with increasing temperature, which may be related to temperature-dependent changes in life history/growth strategies and warm thermal limits of high-temperate populations. At the same temperature, respiration rates of pelagic ephyrae and medusae appear similar to those of benthic polyps in *A. aurita* after taking into account differences in body size. Polyps originating from lower and higher latitudes appear to have different thermal windows for growth and survival. Common garden experiments are needed to test for potential physiological adaptations of polyps to local temperature regimes and severity of hypoxia. A better understanding of the environmental triggers and physiological constraints of field populations of polyps is needed to advance our predictive capacity of jellyfish blooms using ecosystem models and other tools (Gibbons and Richardson, 2013).

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We would like to thank Dr. Gerhard Jarms and Stefan Bleck for providing the cultures of polyps used in this analysis. Valuable help with statistics and figures was obtained from Markus Kreus and Drs. Marta Moyano and Klaus Huebert. The research leading to these results has received partially funding from the European Community's Seventh Framework Program (FP7/2007-2013) under Grant Agreement No. 266445 for the project Vectors of Change in Oceans and Seas Marine Life, Impact on Economic Sectors (VECTORS). Funding was also received from the German Science Foundation (DFG, Physi^{2}CoGel, grant No. PE1157/3-1). The experiments performed comply with the current laws of Germany.

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CHAPTER 3

Effects of temperature on the feeding and growth of the larvae of the invasive ctenophore *Mnemiopsis leidyi*

3 Effects of temperature on the feeding and growth of the larvae of the invasive ctenophore *Mnemiopsis leidyi* (*Manuscript 2*)

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Abstract

Carbon-specific prey clearance and ingestion rates of 1.5-mm tentaculate larvae of the ctenophore *Mnemiopsis leidyi* increased linearly between 6 and 25°C but declined between 25 and 30°C. Both absolute (length) and carbon-specific growth rate increased linearly with increasing temperature. The latter was 0.87 d^{-1} at 25°C. Extremely low or negative growth rates observed at 6 and 30°C help define the thermal limits to population growth of this successful biological invader.

Keywords: Mnemiopsis leidyi, invasive species, tentaculate larvae, ecophysiology, North Sea

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3.1 Short Communication

In summer/fall 2006, *Mnemiopsis leidyi* was identified in the North and Baltic Seas (Faasse and Bayha, 2006; Javidpour et al., 2006) and its establishment represents one of the most potentially dramatic marine bioinvasions in northern European Seas in recent decades. The species has an "r" life history strategy and can increase rapidly in favorable conditions due to a combination of high rates of growth and reproduction (see Costello et al., 2012; Jaspers et al., 2015) that are fuelled by extremely high rates of feeding. Young larvae consume microplankton such as protists (Sullivan and Gifford, 2004, 2007) while larger larvae also consume mesozooplankton (Rapoza et al., 2005). The adults ingest a wide variety of taxa from microzooplankton to holo- and meroplankton, as well as the eggs and larvae of fish (see review by Purcell et al., 2001). The species occurs at high abundance in semi-enclosed coastal bays and estuaries in the southern North Sea, particularly during late spring and summer (Antajan et al., 2014) where warm temperatures likely support high rates of growth and feeding.

Information on the thermal windows supporting survival of *M. leidyi* has been mostly derived from presence/absence data from field surveys (e.g. Burrell and Van Engel, 1976; Fuentes et al., 2010). Although considerable laboratory work was conducted in the 1980s to understand and model the growth dynamics of this species (e.g. Kremer and Reeve, 1989), the vast majority of studies focused on the effects of body size/stage, prey quantity or prey type on rates of feeding and/or growth (Reeve et al., 1989; Purcell, 2009; Granhag et al., 2011). The effect of broad ranges in temperature on rates of feeding and growth has not been quantified in controlled laboratory experiments. Consequently, models constructed to depict feeding and growth have included assumptions on the effects of temperature on bioenergetics rates with little or no data to help constrain parameter estimates (see Salihoglu et al., 2011). The lack of measurements is surprising given the ecological importance of this species in its native and invaded habitats.

Adult *M. leidyi* were caught in February 2013 in the Gullmar Fjord (58°15'N, 11°24'E) and maintained in the laboratory (Sven Lovén Centre for Marine Sciences - Kristineberg, University of Gothenburg) in 50-L buckets with water salinity of 33 at 17°C. Adults were fed ad libitum on cultured copepods (*Acartia tonsa*). The adult

ctenophores were spawned overnight in darkness by raising the temperature and the cohort of larvae was fed *A. tonsa* nauplii. Laboratory trials were conducted on 1.5-mm larvae.

Newly hatched *A. tonsa* nauplii were used as prey. Nauplii had a mean prosoma length of 140 µm and an estimated mean carbon content of 0.04 µg C (Berggreen et al., 1988). Each trial had six, 1-L bottles with filtered (0.3 µm) seawater (salinity of 33). Three bottles had 3–7 ctenophores (depending on the temperature to ensure that the final prey concentration was not reduced more than 30% of the initial concentration) and three bottles were controls (only prey). Trials were conducted in darkness to avoid patchy prey distributions. Larvae were added in the morning and supplied with aliquots of a culture of known naupliar concentration. Larvae experienced an abrupt shift from the rearing (17°C) to the test temperature but were allowed to adjust to the trial conditions (temperature, prey, bottle, etc.) during a 24-h acclimatization period. After that acclimation period, ctenophores were gently removed from the bottle, their oral-aboral length (L_{OA}, *mm*) was measured (stereomicroscope, ±0.1 mm), and they were transferred to a new bottle with the same water temperature and initial prey concentration. Larvae were allowed to feed and grow for an additional 24 h and then were gently removed and their L_{OA} was measured. All larvae appeared to be in good condition at the completion of each trial. The remaining nauplii in each bottle were collected on an 80-µm filter and counted using a stereomicroscope. The initial prey concentration used for feeding calculations was set equal to the mean concentration of prey based on counts of copepod nauplii in the three control bottles at the end of the trial. These final counts of nauplii agreed well (mean coefficient of variation was 5.5%) and there was a <6% difference between the mean concentration estimated from initial aliquots supplied to controls and the number finally recovered/counted.

The first set of laboratory trials examined the growth rate of larvae at five (6°C) or seven (25°C) different prey concentrations. The second set of trials examined feeding and growth of larvae at eight temperatures (6, 8, 14, 17, 20, 25, 27 and 30°C). Carbon content (*C, µg*) was estimated from L_{OA} using a conversion published by Sullivan and Gifford (2004):

$$C = 0.0071 L_{OA}^{1.92} \qquad (\mu g)$$

The mean prey concentration (C_m), clearance rate (F) and ingestion rate (I) were calculated as:

$$C_m = e^{[ln(C0 \times Ct)/2]} \qquad (nauplii\ L^{-1}\ or\ \mu g\ C\ L^{-1})$$

$$F = (V/(t \times n)) \times ln(C_0/C_t) \qquad (mL\ d^{-1})$$

$$I = F \times C_m \qquad (nauplii\ d^{-1}\ or\ \mu g\ C\ d^{-1})$$

where C_0 and C_t are the prey concentration on Day 0 and Day t , respectively, n is the number of animals, and V is the volume of water in the bottle. The carbon-specific rates of clearance (F_W) and ingestion (I_W) were calculated as:

$$F_W = F/W \qquad (mL\ \mu g\ C^{-1}\ d^{-1})$$

$$I_W = I/W \qquad (\mu gC\ \mu gC^{-1}\ d^{-1})$$

where W = geometric mean carbon content (μg). F_W and I_W were calculated to eliminate any effect of the differences in size of the ctenophores during the incubation. Length growth (G) and carbon-specific growth rate (μ) were calculated as:

$$G = (L_{OAt} - L_{OAo})/t \qquad (mm\ d^{-1})$$

$$\mu = (ln(W_t/W_0))/t \qquad (d^{-1})$$

where subscripts *0* and *t* refer to Day *0* and Day *t*, respectively, and W = body carbon content. The gross growth efficiency (*GGE*) was calculated as:

$$GGE = 100 \times ((\mu \times W)/I) \qquad (\%)$$

Where I was expressed in $\mu g\ C\ d^{-1}$. Linear and non-linear regressions were used to estimate changes in clearance, ingestion and growth rates as functions of

temperature. All statistical analyses were conducted using the R freeware (URL http://www.R-project.org/).

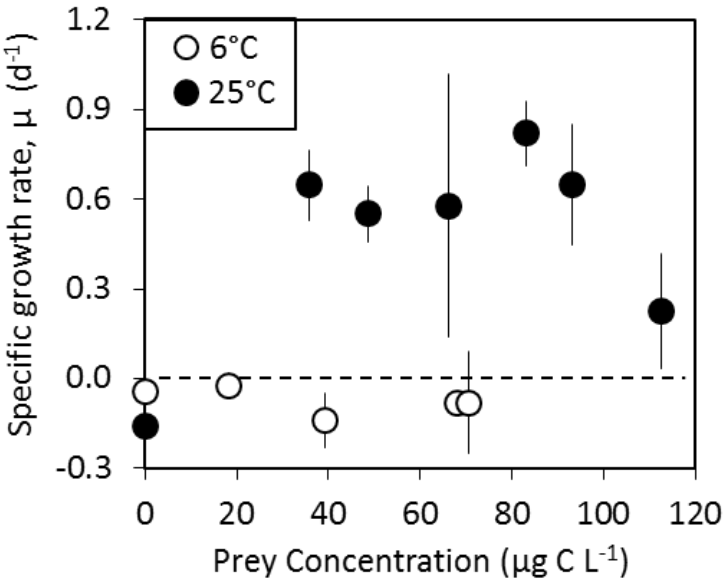

Figure 3.1: Mean (±SE, n= 3) Carbon-specific growth rate of the larvae of the ctenophore *Mnemiopsis leidyi* that were either unfed or fed different prey concentrations (geometric mean μg C L^{-1}) of nauplii of the copepod *Acartia tonsa*. Trials were conducted at 6°C (open symbols) and 25°C (filled symbols).

Our first set of trials indicated that the carbon-specific growth rate (μ) was negative at all prey concentrations at 6°C (Fig. 3.1). At 25°C, μ increased with prey concentration and reached a maximum (0.82 d^{-1}) at ~88 $\mu g\ C\ L^{-1}$ (Fig. 3.1) corresponding to an initial concentration of 2200 nauplii L^{-1}. That concentration was used in our second set of trials examining temperature effects. Clearance (F) and ingestion (I) rates increased exponentially with increasing temperature and reached maximum values at 25°C of 137.0 ± 28.0 $mL\ d^{-1}$ (Fig. 3.2A) and 314 ± 57 nauplii d^{-1} (Fig. 3.2B), respectively. At 30°C, F and I were relatively low. Although all larvae were the same initial size, growth occurred during the trials and the carbon-specific rates were calculated to take into account the differences in final size. Carbon-specific rates of clearance (F_W) and ingestion (I_W) increased linearly with increasing temperature (Fig. 3.2D and E); both reached maximum values at 25°C (15.6 ± 2.2 $mL\ \mu g\ C^{-1}\ d^{-1}$ and 1.44 ± 0.17 $\mu g\ C\ \mu g\ C^{-1}\ d^{-1}$, respectively) and declined between 25 and 30°C. At 30°C, the growth of larvae was variable and most often negative which explains the relatively large variability in carbon specific ingestion at that warm temperature. Between 6 and 27°C, rates of absolute growth ($G,\ mm\ d^{-1}$) and carbon-specific growth ($\mu\ d^{-1}$) increased linearly with

increasing temperature from 0.02 ± 0.04 to 0.80 ± 0.04 *mm* d^{-1} and from 0.1 ± 0.1 to 0.87 ± 0.04 d^{-1}, respectively. At 30°C, growth rate declined to very low levels.

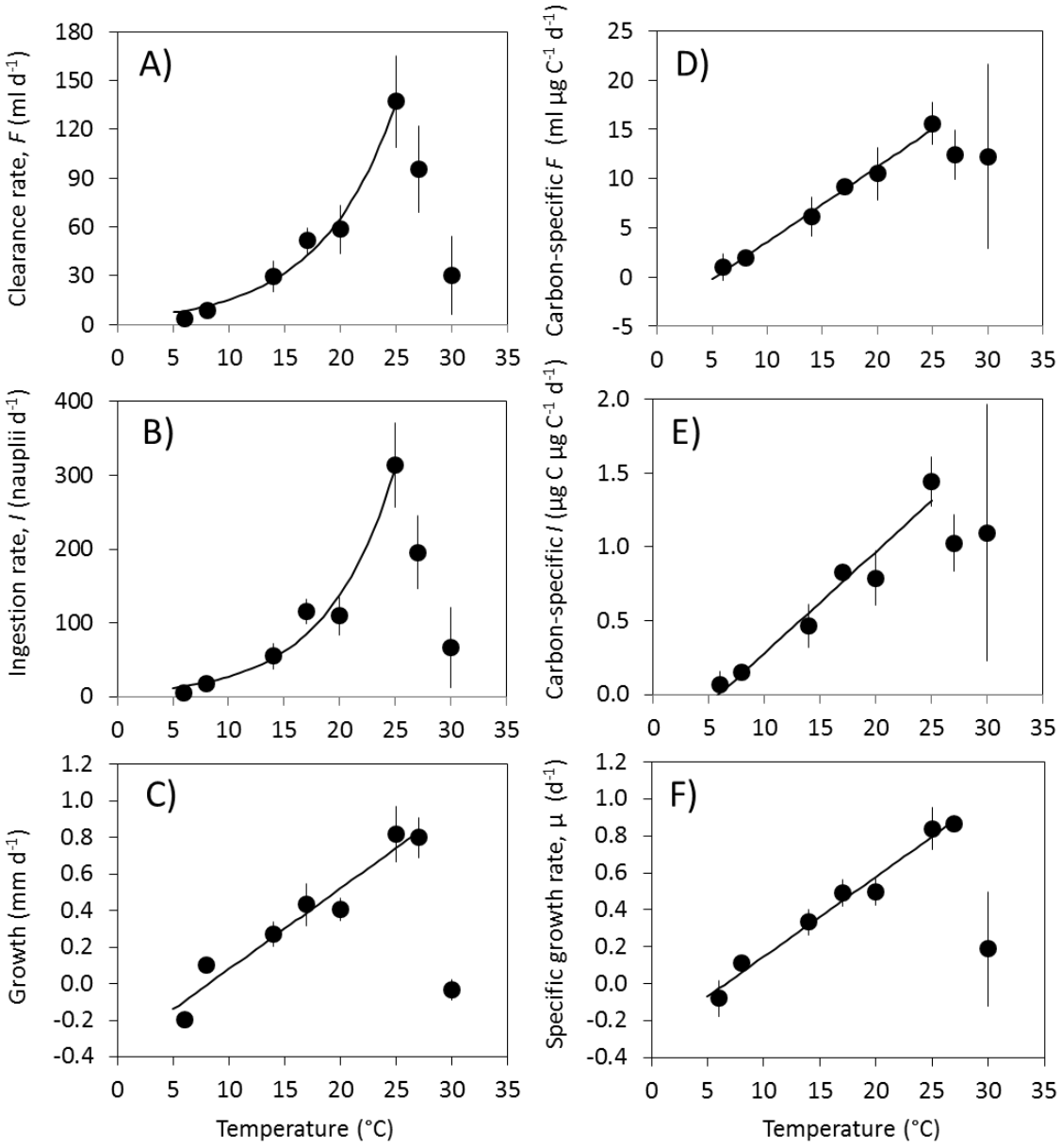

Figure 3.2: Mean (±SE, n = 3) clearance rate (F, FW: A and D), ingestion rate (I, IW: B and E) and growth rate (G, m: C and F) of larvae of the ctenophore Mnemiopsis leidyi at each of eight different temperatures. Both measured (A–C) and carbon-specific (D–F) values are provided. Regression equations (P, 0.001): A: F . 3.54 (+1.00) e(0.146(+0.012)T), R2 . 0.986; B: I . 5.40 (+2.57) e(0.161(0.020)T), R2 . 0.971; C: G . 0.044 (+0.005) T 2 0.361(+0.088), R2 . 0.943; D: FW . 0.762 (+0.036) T 2 4.03(+0.58), R2 . 0.991; E: IW . 0.069 (+0.008) T 2 0.407 (+0.130), R2 . 0.950; F: m . 0.043 (+0.003) T 2 0.287(+0.054), R2 . 0.977.

The rates of ingestion and clearance reported in the present study are similar to those reported by Sullivan and Gifford (Sullivan and Gifford, 2004) for larval *M. leidyi* feeding on an assemblage of microplankton at 18 to 22°C. Similarly, the maximum rate of

carbon-specific growth measured here (0.87 ± 0.04 d^{-1} at 27°C) was similar to that (0.83 d^{-1}) previously reported for newly hatched *M. leidyi* larvae (Stanlaw et al., 1981) and for small, 6-mm individuals (0.8 d^{-1}) at 26°C (Reeve et al., 1989).

Controlled laboratory experiments are needed to define the thermal windows supporting the survival, growth and feeding of organisms, not only to understand the ecology and potential impacts of biological invaders, but also to project climate change effects. To our knowledge, only Reeve and Baker (Reeve and Baker, 1975) quantified the growth in *M. leidyi* at different temperatures (21, 26 and 30°C). That study did not make concomitant measurements of prey concentration; thus, it is unclear whether the true magnitude of the effect of temperature was revealed. A second study examined in situ feeding dynamics of adults collected from the northwestern Black Sea at different times of the year corresponding to three ranges in temperatures (Finenko et al., 2014). That study calculated a Q_{10} of 4.5 for clearance rates of adults between 13 and 22°C. In the present study, carbon-specific clearance rates increased more modestly between 13 and 23°C (2.4-fold, see linear regression, Fig. 3.2D). Similar to the present study, Finenko et al. (Finenko et al., 2014) reported that *F* did not continue to increase from 27 to 30°C. Previous studies on the effect of temperature on rates of energy loss reported a Q_{10} value of 3.4 to 3.7 for respiration rate of *M. leidyi* from 10.4 to 24.5°C (Kremer, 1977; Purcell et al., 2001). A more recent study (Lilley et al., 2014) reported a lower effect of temperature (Q_{10} of 2.57) on respiration rates from 8.5 to 30.0°C and that respiration rates were much more variable >25°C. The latter observation and results of our study suggest that temperatures >25°C are tolerable but metabolically stressful for *Mnemiopsis leidyi.*

A recent modeling study on transitional and adult *M. leidyi* assumed that the effect of temperature on feeding was described by a Q_{10} of 1.7 (Salihoglu et al., 2011). The model in that study appeared to capture the growth dynamics and generation times of *M. leidyi* in the Black Sea. If the effect of temperature on feeding is actually stronger (e.g. about 2-fold stronger), offsetting errors in other energetic parameters such as energy loss (metabolism) may have occurred. Knowledge on growth efficiency would help constrain parameter estimates but it is difficult to interpret our, and previously reported, estimates of *GGE* because different studies used different prey types and

examined different sizes/stages of *M. leidyi*. In the present study, the mean (± SD) gross growth efficiency (estimated between 8 and 27°C, where *G* was positive) was 75(±15)% with values ranging between 60 and 91%. Reeve et al. (Reeve et al., 1989) estimated *GGE* to be 20 to 45% in adults. Working with newly hatched (0.5- to 5-mm) larvae fed a natural assemblage of microplankton including thecate dinoflagellates, diatoms and aloricate ciliates, Sullivan and Gifford (Sullivan and Gifford, 2007), reported *GGE* of 3%. The large difference between values of larval *GGE* reported here and by Sullivan and Gifford (Sullivan and Gifford, 2007) is likely due, at least in part, to differences in the type of prey consumed as well as the age/size of larvae. Additional estimates of *GGE* are needed to clarify potential changes with diet and/or ontogeny.

Our study suggests that temperatures colder than 7 or 8°C and warmer than 27°C pose limits to population growth (negative growth of 1.5-mm larvae). Model-derived weekly temperatures in the southern North Sea from 1996–2006, (HAMSOM; T. Pohlmann, University of Hamburg) suggest that *M. leidyi* larvae could survive but have very low rates of feeding and growth from mid- January to the end of April. Our temperature thresholds for growth match well with the observed seasonality in the Dutch coastal zone where spawning occurred in May, maximum abundance was observed in mid-June and August, and abundance declined in late October (P. van Avesaath, NIOZ, unpublished observations, 2010–2012). Our laboratory estimates provide a mechanistic, cause and- effect understanding for these seasonal patterns as well as global (latitudinal) patterns of abundance reviewed by Costello et al. (Costello et al., 2012, see their Fig. 3.1), and will prove useful to modeling efforts attempting to simulate the impacts of this ctenophore in native and invaded habitats.

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CHAPTER 4

Temperature-dependent settlement of planula larvae of two scyphozoan jellyfish from the North Sea

4 Temperature-dependent settlement of planula larvae of two scyphozoan jellyfish from the North Sea (*Manuscript 3*)

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Abstract

Exploring the settlement dynamics of the planula larvae is critical to understanding the establishment of polyp populations that can give rise to jellyfish blooms. We conducted experiments to examine the effects of temperature on settlement of planulae of the scyphozoans *Cyanea lamarckii* and *Chrysaora hysoscella*, two jellyfish commonly encountered within the North Sea. When provided immediate access to substrate, larvae of *C. lamarckii* were able to settle at each of 12 temperatures between 9 and 27°C. Most settlement occurred within the first five days and warmer temperatures were not only associated with decreased time to settlement but also increased settlement success. When not allowed access to substrate and maintained in the water column, planula larvae remained competent to settle for 21, 21 and 14 days at 11.3, 13.4 and 19.4°C, respectively. Hydrodynamic model simulations suggested that the planula larvae of *C. lamarckii* released in May could be transported up to 100 km and still remain competent to settle to benthic habitats. A substrate choice experiment indicated that larvae of *C. hysoscella* settled in similar numbers onto PET, wood and concrete. Settlement was highest at 20°C and a 12/12 light/dark regime and lower at 10°C and 15°C in total darkness. The results of all three experiments suggest that warming in the North Sea will not impede the settlement of planula larvae of resident *C. lamarckii* and *C. hysoscella* populations. Species- and/or population-specific differences may exist in the ecophysiology of planula larvae and additional experiments are needed to understand the mechanisms promoting the establishment of new benthic populations of polyps. That information, combined with process knowledge on the productivity of benthic polyps, will be needed to better understand and predict climate-dependent changes in the production of scyphozoans and other gelatinous plankton.

Keywords: Chrysaora hysoscella; Cyanea lamarckii; climate change; substrate choice; pelagic larval duration; light condition

4.1 Introduction

Bloom-forming scyphozoan jellyfish can alter the food web dynamics of marine systems and large blooms can lead to negative impacts on fisheries, tourism and other economic sectors (Duarte et al., 2012; Gibbons and Richardson, 2013; Purcell, 2012; Richardson et al., 2009). Although debate continues whether the frequency and magnitude of jellyfish blooms have increased in response to global climate change (Condon et al., 2013), increased temperature has been reported to have a positive effect on aspects of the reproduction of some species of jellyfish in some regions (Brewer and Feingold, 1991; Lucas et al., 2012). However, species-specific differences in ecophysiology of jellyfish life stages (e.g. Riascos et al., 2013; Gambill and Peck, 2014) and differences in local habitat characteristics will undoubtedly cause population-specific responses to climate driven warming.

Settlement dynamics of planulae are important to examine if we hope to understand how polyp populations become established in benthic habitats (Lucas et al., 2012). Planula larvae of semaeostomeaen jellyfish are released from maternal brood pouches in batches (Holst and Jarms, 2007). Many scyphozoan species in temperate waters release planula larvae in the late spring, summer or fall (Brewer, 1989; Cargo and Schultz, 1966; Gröndahl, 1988; Lucas, 2001). In moon jellyfish (*Aurelia aurita*), the energy allocation to the production of planulae by adult medusae has been linked to periods of low prey concentrations (Ishii and Båmstedt, 1998). In the southern North Sea (Island of Helgoland in the German Bight), scyphozoan planula larvae have been observed between May and August (Holst and Jarms, 2010, 2007). Once released into the water column, dispersal distances of planulae will be affected by changes in pelagic larval duration (PLD). Schneider and Weisse (1985) reported carbon-specific respiration rates of 9.8% d^{-1} for planula larvae of the moon jellyfish and suggested that individuals would have enough energy to survive and settle for a few days to a week at ~20°C. In contrast, at the same temperature (19 to 21°C), planula larvae of a warm-water coral (Octocorallia *Corallium rubrum*) in the Mediterranean Sea had a range in median PLDs between 25 to 33 days (500 to 660°days = °C x time (days)), and a range in maximum PLDs of 39 to 47 days (780 to 940°d) (Martínez-Quintana et al., 2014).

Scyphozoan planula larvae need appropriate types of substrate in order to settle and metamorphose into polyps, thus completing the metagenetic life cycle. The success of settlement and metamorphosis of planula larvae can be affected by different physical factors. Responses to changes in physical factors appear to depend on the specific species and/or population. For example, decreases in salinity significantly increased the PLD and decreased settlement success of the larvae of *A. aurita* (Conley and Uye, 2015) and *Cyanea capillata* (Holst and Jarms, 2010), whereas survival of planula larvae of the Mediterranean scyphozoan *Cotylorhiza tuberculata* appeared relatively insensitive to increased salinity (Prieto et al., 2010). Semaeostomeaen planulae and polyps from around the globe appear relatively tolerant to hypoxia (Brewer, 1976; Gambill and Peck, 2014; Ishii et al., 2008). Moreover, planula larvae can detect light and exhibit photonegative behavior when searching for appropriate substrate (Brewer, 1976; Cargo and Schultz, 1966; Svane and Dolmer, 1995) but have been reported to suffer increased mortality in total darkness (Brewer, 1976). Finally, planulae exhibit strong preference to settle on the shaded underside of substrates (e.g. Brewer, 1984; Cargo, 1979; Gröndahl, 1988) and specific substrates are preferred, chosen due to the presence of chemical cues and also likely texture (Brewer, 1976; Hoover and Purcell, 2009). Settlement can also occur on artificial substrates such as plastic (e.g. Holst and Jarms, 2007; Hoover and Purcell, 2009).

To the best knowledge, relatively few studies have examined the effects of temperature on settlement of scyphozoan planula larvae (e.g. Fitt and Costley, 1998; Prieto et al., 2010; Riascos et al., 2013; Webster and Lucas, 2012) which is surprising given the importance of temperature in controlling PLD (O'Connor et al., 2007). For example, Fitt and Costley (1998) reported that planulae of a tropical rhizostome displayed decreased settlement success at 15 and 20°C compared to 30°C. In contrast, Prieto et al. (2010) reported that settlement success was similar at 20 and 30°C. In the northeast Atlantic, settlement success of *A. aurita* declined with increasing temperature from 6 to 18°C (Webster and Lucas, 2012). In a review of the available literature on the settlement, metamorphosis and survival of planula larvae of four jellyfish species inhabiting various marine waters, Riascos et al. (2013) reported that changes with temperature were species- and often population- (latitude-) specific.

We examined the effect of temperature on the settlement dynamics of the scyphozoan planula larvae of *Cyanea lamarckii* and *Chrysaora hysoscella*. Three laboratory experiments were performed to quantify: i) the success of settlement across 12 temperatures, (ii) the time limits of competency for larvae to settle, and (iii) the choice of substrate as influenced by light and temperature. The data on PLD were utilized in a drift model simulation to explore potential drift distances of planula larvae while the data on substrate choice are important to collect given the active development of offshore wind farms (potentially increasing the availability of new benthic habitats for polyps) in the North Sea and elsewhere.

4.2 Materials and Methods

4.2.1 Animals

Five ripe female medusa of *Cyanea lamarckii* were gently collected off the coast of Helgoland, southern North Sea on June 15th 2011 and transported to laboratory facilities at the University of Hamburg within 7 hrs. In the laboratory, each medusa was transferred to a ~10-L aquarium where they were held at 15°C and a salinity of 33.0 (close to in situ conditions). Planula larvae were collected from each tank 11 hours later and pooled to examine the effects of temperature (Exp 1) and delayed substrate availability (Exp 2) on settlement success. To obtain a suspension with a known concentration of larvae, the water containing the larvae was carefully poured through sieves with different mesh sizes (1000, 200, 100 and 30 µm) at a salinity of 33.0 and 15°C. The same procedure was used on August 16th 2012 to collect the planula larvae from four ripe female medusae of *Chrysaora hysoscella*. The larvae of *C. hysoscella* were used in an experiment examining substrate choice during settlement (Exp 3).

Experiment 1: Magnitude and timing of settlement at different temperatures

The settlement of planula larvae of *C. lamarckii* was examined in five replicate 250-ml glass beakers at 12 temperatures between 9.4 and 26.8°C. Temperatures were created with two, linked thermal gradient tables, large blocks of aluminum with hot and cold water pumped through holes in either end (Thomas et al., 1963). Table 1 had the colder 6 temperatures and table 2 had the warmer 6 temperatures. To minimize variation in temperature (±0.5°C), the tables were used within a controlled-

temperature room (~15°C). A total of 4ml of a planula suspension of known concentration (501.5±74.2 planulae ml^{-1}, mean±sd) was added into each of 60, 250-ml beakers all at 15°C. The beakers were then randomly distributed across 12 temperatures (5 replicates each). After 48 h, daily counts of settled larvae were made for a total of 55 days (including the first 48 h). Each day, the water in each beaker was gently swirled and the unsettled planula larvae and water were gently poured into a new beaker. The water was not changed during the experiment. The number of larvae settled in the original beaker was counted from a digital image. At any temperature, beakers were removed from the experiment when no movement of planula larvae was observed; this indicated that all larvae had settled, developed into planulocysts, or died. Due to technical problems, salinity was - to some extent - not properly monitored. We only used data collected when salinities were between 33.0 to 35.0 (which encompassed the time period of 50% settlement in all replicates). A previous study suggested no effect of high salinity (to 53) on larval settlement of a rhizostome jellyfish *Cotylorhiza tuberculata* from the Mediterranean Sea (Prieto et al., 2010). But no previous study has examined the effect of salinity on planula larvae of *C. lamarckii* (used in this study). For the sake of completeness, we also included the results for 95% settlement, being aware that salinities >35 may have affected the survival of settlement of planula larvae.

4.2.2 Experiment 2: Delayed Settlement Proficiency

Planula larvae of *C. lamarckii* were maintained in three, 112-L, plastic round tanks with water currents created by aeration to prevent larvae from settling on the bottom or sides of the tank. A total of ~ 200,000 (400 ml, containing 501.5±74.2 planulae ml^{-1}, mean±sd) larvae was transferred to each tank. All tanks were initially 15°C and then allowed to adjust to either 11.4°C, 13.4°C or 19.6°C within the next 8 hours.

Every 24 h, planula larvae within 1-L of water were removed from each tank (gently sieved in order to not damage the larvae – 30µm) and transferred to 250-ml bowl containing water with the same temperature and salinity. This process was repeated three times (creating 3 replicate bowls per tank per day). As the experimental setup did not consider predation pressure or other factors that could affect mortality, we assumed a natural mortality rate of 1.05% d^{-1} (based on subsequent estimates of the

concentration of larvae in each tank). The settlement success of planulae (when planulae were settled and attached to the glass bottom of the bowl) was checked every day. When no movement of larvae was observed in a bowl a final count of settled larvae was made and encysted larvae were documented. Salinity was at 33.0. Note, no antibiotics were employed to retard the growth of biofilms on the bowls.

4.2.3 North Sea Hydrodynamic Model Simulations of Planula Larvae

Information on PLD obtained from Exp 1 and Exp 2 was used to perform drift simulations of planula larvae using the three-dimensional, baroclinic shallow-water circulation model HAMSOM (Backhaus, 1985) modified with respect to the transport equation for temperature and salinity and the formulation of vertical eddy viscosity. The current model version has been previously employed to simulate hydro- and thermodynamic processes in the North Sea taking into account all relevant driving mechanisms (Pohlmann, 2006). The model has a 20-km horizontal grid and 21 depth layers using a z-coordinate system. To better resolve the thermocline and other important features, surface waters from 10 to 50 m depth were resolved in 5-m depth layers and deeper depths (to max 160 m) were resolved in 10-m layers. The larvae were assumed to be passive drifters with a diffusive random walk, which was used with a horizontal diffusivity of 50 m^2 s^{-1}. Larvae were assumed to be released by medusae at 5 m in the southern North Sea. Larvae were released at all grid locations across the North Sea to explore maximum drift distances.

Lagrangian particle tracks were simulated based on HAMSOM output using mean values of transport velocities, eddy diffusion coefficients, temperature and salinity, all averaged over the time step of 1 hour for incorporating tidal effects. Vertical diffusion was included by applying a diffusive random walk algorithm using a Monte-Carlo method (Visser, 1997). To mimic daily fluctuations of the velocity, a constant horizontal diffusion coefficient (50 m^2 s^{-1}) was employed. For each particle and time step (60 s), temperature was linearly interpolated between the surrounding nodes. More details concerning the interpolation of velocities and a comparison scenario of modeled and observed ichthyoplankton were provided by Hufnagl et al. (2013). To calculate the time period planula larvae could drift, the temperature experienced by each larva on each day was summed until the cumulative temperature matched the

PLD (in degree-days, °C x time (in days)) found in Experiments 1 and 2. Each larva was removed as soon as the PLD was reached and its position was recorded. The distance travelled between the start and end point was then calculated.

4.2.4 Experiment 3: Settlement Substrate Choice

The larvae of *C. hysoscella* were provided concrete, polyethylene terephthalate (PET) and wood as potential substrates for settlement within the same 1600-ml glass (Pyrex) bowl. We observed the cumulative settlement of larvae within three replicate bowls maintained in either total darkness or at a 12:12 L:D light regime at three temperatures (10, 15 and 20°C; 3x2x3 = 18 bowls). Salinity was maintained at 33.0 at all times. Substrates (5x5 cm) were soaked in seawater prior to the experiment to make sure bacterial fouling would provide an optimal substrate for the larvae to settle (e.g. Holst and Jarms, 2007). The concrete substrate was a prototype of that used for offshore wind farms in the North Sea (supplied by Ed. Züblin Ag, Offshore Wind). Each glass bowl contained a 5-cm layer of thoroughly washed and autoclaved white sand. The three substrates were embedded (horizontally) at the surface of the sand. Approximately 1500 larvae (50 ml of suspension containing 1505.0±410.6 larvae, mean±sd) were gently transferred into each bowl. The bowls were loaded with planula larvae and randomly assigned to a different treatment. Replicate bowls were arranged in random directions in order to prohibit substrate choice due to direction (e.g., via magnetotaxis which may or may not occur in planula larvae). The number of larvae settled on each substrate in each bowl was counted every other day starting on day 3 of the experiment until no additional settlement was observed (day 12). The number of settled larvae versus time (cumulative settlement) was compared among the treatments.

4.2.5 Evaluation and Statistical Analyses

Data in Exp 1 did not meet assumptions for parametric analyses. A Kruskal-Wallis-Test (KWT) was performed to evaluate statistical differences in the time to 50% and 95% settlement among the 12 temperatures. Data in Exp 3 met all assumptions for parametric analyses. A multifactorial ANOVA was conducted using substrate type, light and temperature on settlement. Statistical analysis and graphs were conducted using R 3.1.2 (R Core Team, 2014).

4.3 Results

4.3.1 Experiment 1: Magnitude and Timing of Settlement at Different Temperatures in *Cyanea lamarckii*

Larvae of *C. lamarckii* were negatively buoyant and accumulated on the bottom of each glass beaker after passively sinking. Across all temperatures, 50% settlement was more or less accomplished within five days.

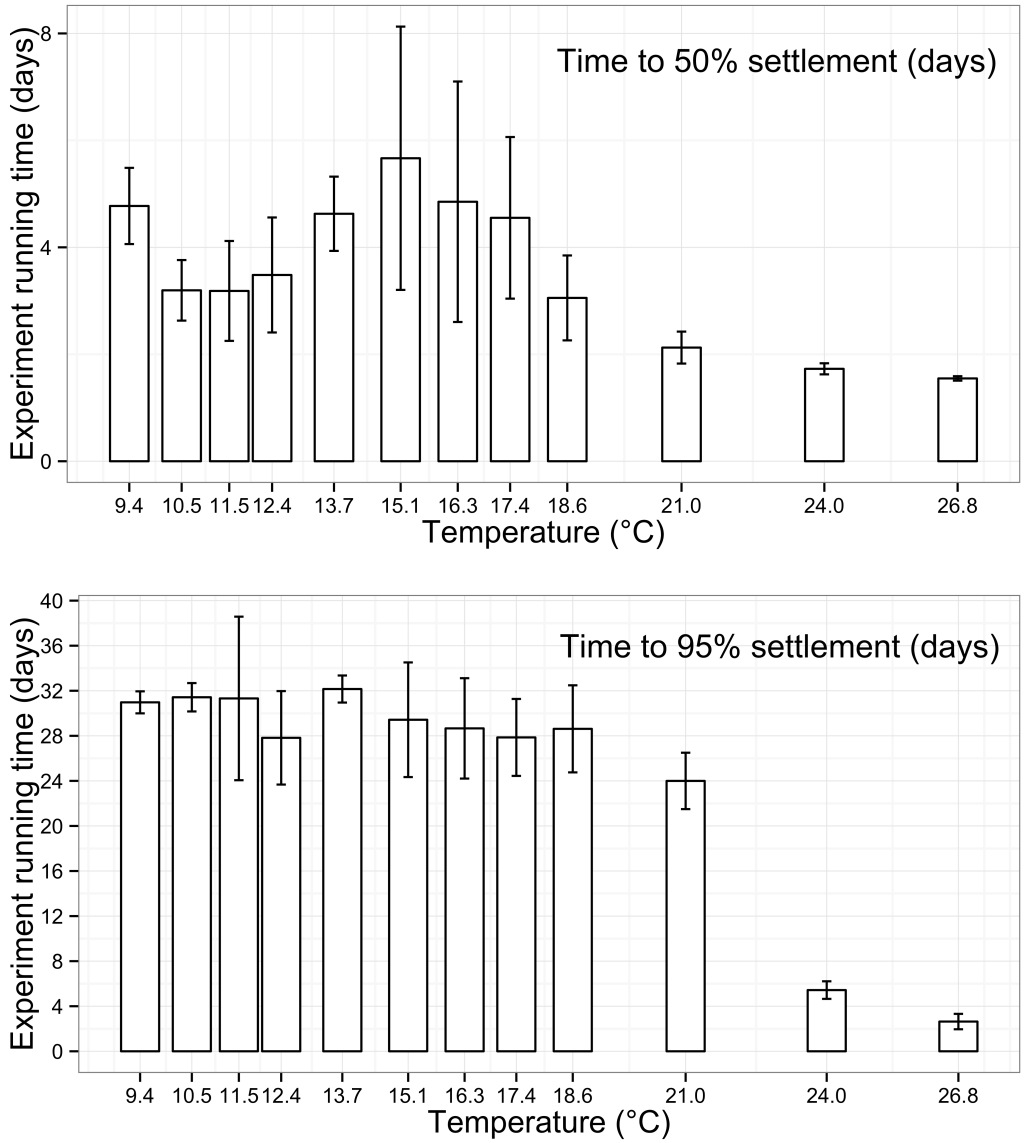

Figure 4.1: Time to 50% (upper panel) and 95% (lower panel) settlement of planula larvae of *Cyanea lamarckii* at each of the 12 temperatures between 9.4 and 26.8°C. Error bars indicate the standard deviation (n = 5 replicate per temperature).

The time to 50% settlement ranged from 3.2 to 5.7 days at temperatures between 9.4°C and 26.8°C, respectively, following a Gaussian distribution across all but the lowest temperature (see fig. 4.1A). Temperature significantly increased the rate of

settlement of planula larvae (KWT, X^2 = (11, N = 12) = 40.0425, $p < 0.0001$) and the time to 50% settlement at 26.8°C was significantly less than that at 9.4°C, 13.7°C, 15.1°C and 17.4°C.

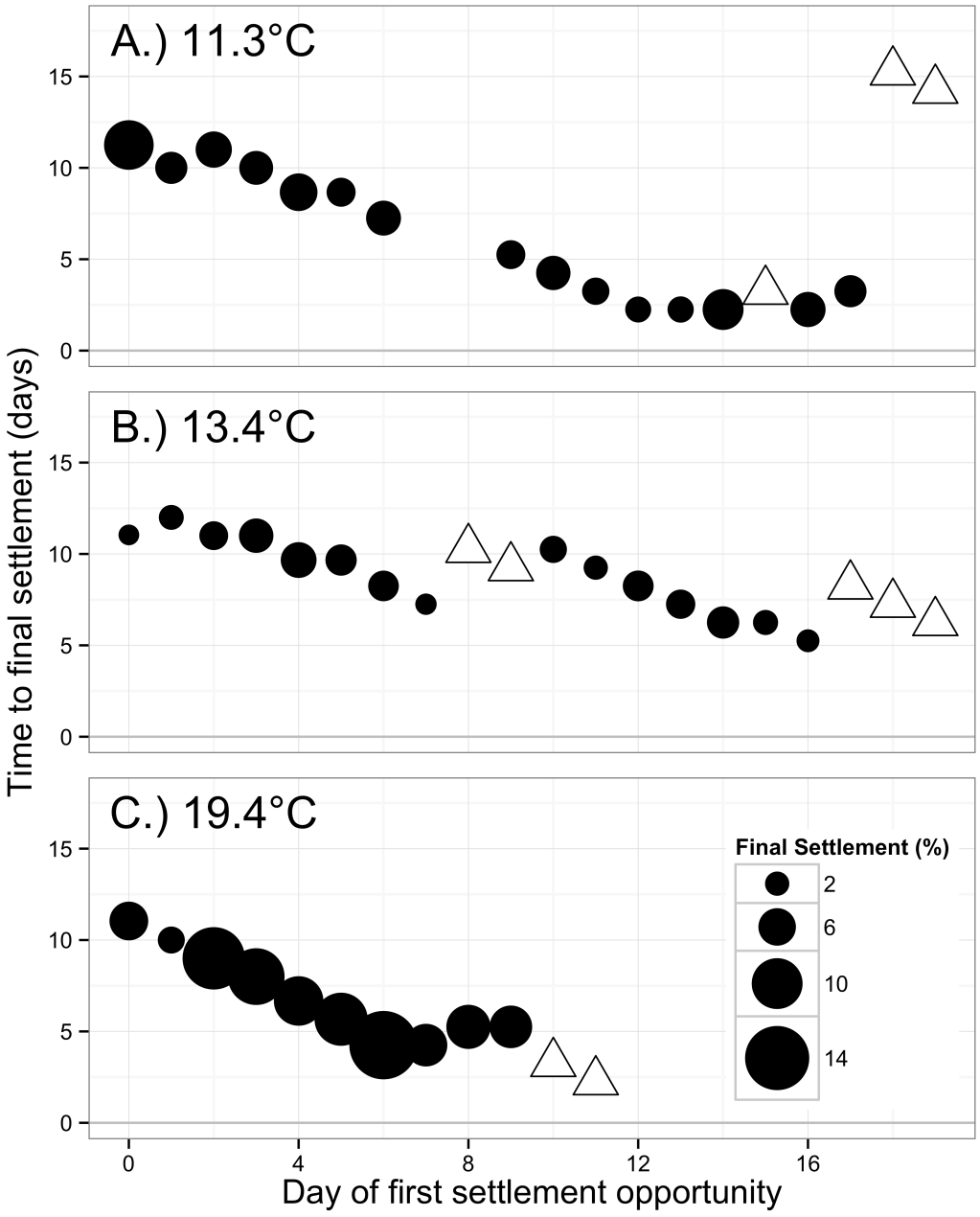

Figure 4.2: Time to settlement (days) and the magnitude of settlement (size of bubble) versus the time (days) that planula larvae of *Cyanea lamarckii* were maintained in the water column. Occurrences of planulocysts are marked with unfilled triangles. Panel A) 11.3°C, Panel B) 13.4°C), Panel C (19.4°C). For areas with no bubble or triangle no data were collected.

Planulae settled for a total period of 55 days and 95% settlement occurred from 25 to 33 days at temperatures ≤ 21°C. At higher temperatures, 95% settlement occurred

within 7 days. The time to 95% settlement was significantly less at 26.8°C compared to all other temperatures (KWT, X^2 = (11, N = 12) = 37.2741, $p < 0.001$) (fig. 4.1B).

4.3.2 Experiment 2: Delayed Settlement Proficiency in *Cyanea lamarckii*

At 11.3°C larvae were still competent to settle after being maintained in the water column for a maximum of 17 days, fig. 4.2A). Once transferred to beakers, larvae maintained in the water column for 1, 4, 8 and 12 days, completed settlement in 11, 9, 5 and 2 days, respectively. Mean settlement success was 5.0±2.0% (mean±sd) with maximum settlement of 10.4% (fig. 4.2A). At 13.4°C larvae were still competent to settle after being maintained in the water column for a maximum of 16 days, fig 4.2A). Once transferred to beakers, larvae maintained in the water column for 1, 5, 10 and 15 days, completed settlement in 11, 10, 10 and 6 days, respectively. Average settlement success was 3.0±1.7% with a maximum settlement success of 8.5% (fig. 4.2B). At a temperature of 19.4°C, larvae were still competent to settle after being maintained in the water column for a maximum of 9 days, fig 4.2C). Once transferred to beakers, larvae maintained in the water column for 1, 3, 6 and 9 days, completed settlement in 11, 9, 4 and 5 days, respectively. Mean settlement was at 9.3±3.9% and the maximum settlement success was 16.7% (fig. 4.2C). Planulocysts were formed and this consistently occurred at each temperature during the two or three days prior to the loss of settlement ability (e.g. days 18-19, 17-19, and 10-11 at 11.3, 13.4 and 19.4°C). The treatment was terminated, when planulocysts were formed over a course of three days or larvae disintegrated.

4.3.3 Hydrodynamic Simulations of Maximum Drift Distances of *Cyanea lamarckii* Planulae

Given a maximum time of 300°d for competent settlement, planulae produced in May and June (assumed peak reproductive times for *Cyanea lamarckii*) were expected to travel different, maximum distances depending on the release location in the North Sea (fig. 4.3). In May, larvae could potentially travel ~75 to 100 km in the southern North Sea but shorter distances were often simulated near the coasts (fig. 4.3A) where waters were warmer. In June, warmer water temperatures decreased maximum drift distances to between ~25 to 75 km (fig. 4.3B).

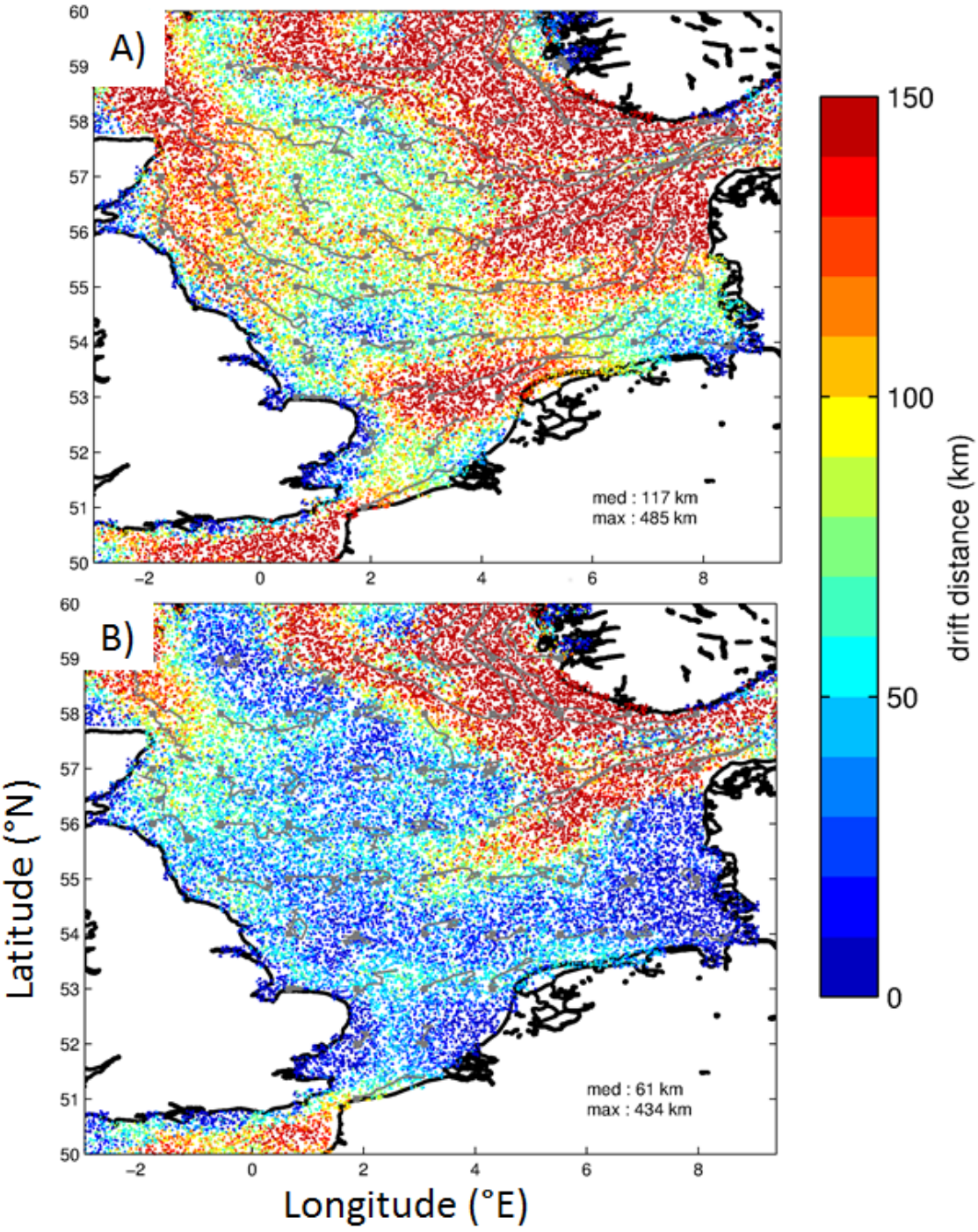

Figure 4.3: Map of the North Sea showing the results of a drift simulation of planula larvae of the jellyfish *Cyanea lamarckii* starting on the 15th May (A) and 15th June (B), 2000 using a three-dimensional, baroclinic shallow water circulation model HAMSOM (Backhaus, 1985). The grey lines indicate the drift direction while the colors denote drift distance based on a pelagic larval duration of 300 °d (see text).

4.3.4 Experiment 3: Settlement Substrate Choice in *Chrysaora hysoscella*

Across all treatments, settlement was fairly low. Highest settlement was found to be 59 individuals (wood, 20°C, light) of the initially introduced 1500 individuals; lowest settlement was found to be 22 individuals (concrete, 20°C, permanent darkness).

There was no significant difference in substrate preference. We discovered a significant effect of light condition on larval settlement as well as significant effects of temperature and light condition as interacting factors (*F(1,36) = 7.048, p < 0.05* and *F(2,36) = 4.957, p < 0.05*, respectively). Effects of light condition on larval settlement at both 15°C and 20°C were different from each other, with effects at 15°C being just significant *(t(5) = 3.07, p = 0.05* and *t(5) = 6.43, p < 0.01*, respectively). At 15°C and 20°C numbers of settled planulae were higher in the "light" compared to the "dark" treatment (see fig. 4.4).

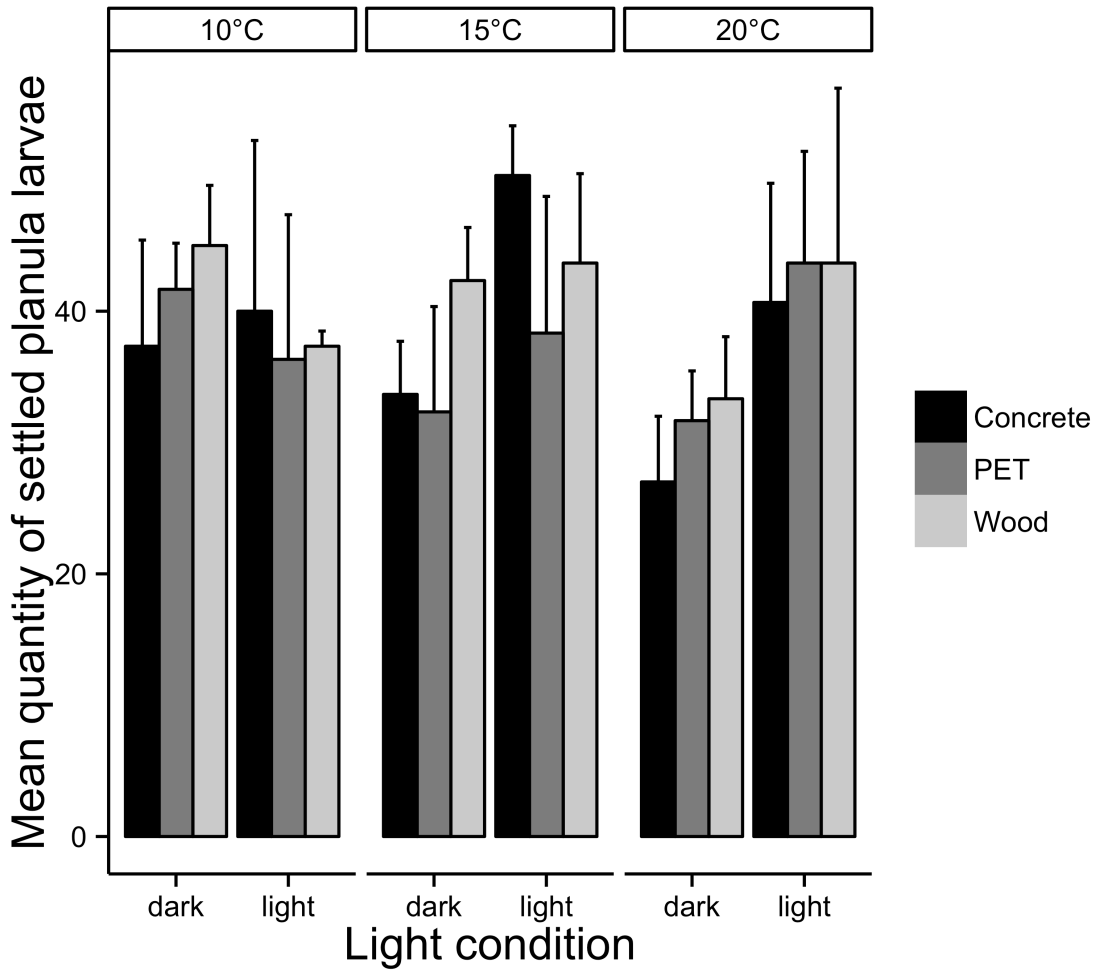

Figure 4.4: Mean (±SD, n = 3 replicates) total settlement of planula larvae of *Chrysaora hysoscella* incubated in constant darkness (dark) and using a 12/12 light/dark regime (light) at each of three temperatures (10, 15, 20°C) offering concrete, PET and wood.

4.4 Discussion

Dynamics of planula larvae play an important role in the metagenetic life cycle of scyphozoan jellyfish by directly contributing to the establishment of new populations of polyps, which potentially give rise to jellyfish blooms (e.g. Duarte et al., 2012). Our results suggest strong effects of warming temperatures on settlement of planula larvae of *Cyanea lamarckii* and *Chrysaora hysoscella*, two species of jellyfish, which commonly occur in the North Sea.

Previous work on planula larvae has reported a mixture of results depending on the species. For example, planulae of *A. aurita* displayed slower rates but a higher magnitude of settlement at 6°C compared to 18°C (Webster and Lucas, 2012). In the Mediterranean Sea, *Cotylorhiza tuberculata*, planulae settled more slowly but had the same magnitude of settlement at 20°C compared to 30°C (Prieto et al., 2010). In the tropical scyphozoan *Cassiopea xamachana*, settlement occurred within 72 hours between 15 and 30°C but settlement was significantly lower at relatively cold temperatures (Fitt and Costley, 1998). Finally and in contrast to the aforementioned studies, planulae of the Pacific species *Chrysaora plocamia* had low settlement success at warm temperatures experienced during El Niño events (22.3°C) compared to lower temperatures experienced on average (~14.0°C) or during La Niña (12.5°C; Riascos et al., 2013). Looking at temperature-dependent settlement (23-29°C) in the Anthozoan *Stylophora pistillata*, increasing temperatures decreases the time needed for settlement as well as settlement and metamorphosis of planula larvae (Putnam et al., 2008).

The results of our first experiment examining settlement at 12 different temperatures, suggested that relatively warm temperatures (19-27°C) decreased the time needed for settlement. Although *C. lamarckii* has been previously reported in the Mediterranean Sea (Delap, 1902), it more commonly occurs in temperate zones (Lendenfeld, 1887) and has been referred to as a "southern boreal" species restricted to European waters (Russell, 1970). Planula larvae do not feed, as they have no mouth or gastric cavity. To meet metabolic demands under stressful conditions such as low oxygen (Conley and Uye, 2015) or high temperatures (O'Connor et al., 2007; Schneider and Weisse, 1985) larvae need to rapidly find suitable substrate to settle, metamorphose and start

feeding (Ishii et al., 2008). In the present study, 95% settlement occurred between ~290 to ~530°d between the temperatures of 9.4 and 21°C but was markedly less (80 to 120°d) at the two warmest temperatures. In general, our estimates agree with previously published estimates of the time required for settlement in the planula larvae of other jellyfish. For example, Prieto et al. (2010) reported that planula larvae of *Cotylorhiza turberculata* required 30 days at 12°C (360°d) and 15 days at 30°C (450°d) while Webster and Lucas (2012) reported that planula larvae of *A. aurita* required 14 days at 6°C (84°d) and 5 days at 18°C (90°d). However, the fact that settlement was much more rapid at the two warmest temperatures (24 and 26.8°C) could suggest that those temperatures approach stressful conditions. Previous studies have documented large reductions in the time needed for settlement at warm temperatures such as work on *C. tuberculata* (30°C versus 15°C, Prieto et al., 2010) and *A. aurita* (18°C versus 6°C, Webster and Lucas, 2012). It is unclear, in which way these high temperatures may influence larval metamorphosis and survival of polyps but large reductions in PLD may (depending on water depth and other characteristics) make it less likely that planula larvae encounter appropriate settlement habitats before energy reserves are exhausted.

Due to the temperature dependence of metabolism, larval dispersal and PLD are strongly impacted by temperature (O'Connor et al., 2007). Our second experiment tested the limits of PLD which were approximately 250 to 300°d (temperature (°C) x time (days)) for *Cyanea lamarckii* (a maximum of 9 to 17 days plus an additional 4 to 6 days to settle, depending on the temperature). Our estimate is somewhat longer than that (108°d) reported for *C. lamarckii* at 18°C from the North Sea (Holst and Jarms, 2007). Previous work on *A. aurita* suggested a PLD between 111°d (15.8°C from Bergen, Norway, Ishii and Båmstedt, 1998) and 144°d (18°C, Connecticut, USA; Brewer, 1978). However, more recent work on *A. aurita* revealed that planulae were able to swim for up to 504°d in relatively warm (24°C) east Asian coastal waters (Conley and Uye, 2015). These various studies on *A. aurita* suggest population-specific differences in ecophysiology perhaps in response to differences in prevailing temperatures. Relatively shorter PLDs between 84 to 135°d have been reported for planula larvae of rhizostome scyphozoans (Calder, 1982; Lotan et al., 1992; Pitt, 2000), although a recently study reported a PLD of 450 to 600°d for *Cotylorhiza tuberculata* (Prieto et al.,

2010). It is important to make a distinction between survival, swimming and the ability to complete settlement. For example, Prieto et al. (2010) reported that larvae of *C. tuberculata* could survive 850°d (71 days at 12°C) but were not able to settle or metamorphose. These findings are in line with results at 11.3°C, where larvae given access to settlement substrate on days 18 and 19 survived two more weeks without settling to subsequently form planulocysts.

Our PLD results, when combined with drift modeling, suggested that larvae could be transported a median distance of 117 km (May) and 61 km (June), from their initial release location in the North Sea. Drift trajectories of "passive" plankton are known to be influenced by a variety of behaviors such as diel vertical migration and/or selective tidal stream transport (e.g. Hufnagl et al., 2013) and our simulations did not incorporate any behavior due to a lack of process knowledge. It is likely that drift distances would be reduced, particularly if larvae exhibit bottom-seeking behavior or if their specific gravity increased with time (Brewer, 1976; Martínez-Quintana et al., 2014). Future studies should research the response of planula larvae to potential behavioral cues (light, temperature) and include estimates with source (areas of known reproduction) and maps of suitable benthic habitats within drift models to more thoroughly explore the opportunities and constraints on the recruitment of planula larvae to benthic polyp populations.

Increasing the surface area of artificial substrates in the sea can potentially expand suitable habitats for scyphozoan polyps (Holst and Jarms, 2007). Plans to increase off-shore wind farms especially in the North Sea and the Baltic (Burkhard et al., 2011; Janßen et al., 2013), will provide new settlement surfaces for the polyps of scyphozoan jellyfish and other organisms. In experiment 3, planula larvae of *Chrysaora hysoscella* did not display enhanced settlement on plastic or wind farm concrete compared to a natural (wood) substrate. These results are surprising since previous studies have reported clear substrate preference for artificial over natural substrates (Holst and Jarms, 2007; Hoover and Purcell, 2009; Lotan et al., 1992; Pitt, 2000). Our results may be biased since larvae were not given the opportunity to settle on the underside of substrates, a preference which has been repeatedly demonstrated (e.g. Miyake et al., 2002; Willcox et al., 2008; Yoon et al., 2014). Settlement on the underside of

substrates not only reduces the potential for contamination by defecation (Holst and Jarms, 2007) but also facilitates detachment of ephyrae during strobilation (Brewer, 1976).

Despite the preference to settle in microhabitats, which appear relatively dark, the absence of light during the settlement process appears to have a negative effect on planula larvae. For example, Brewer (1976) described significantly higher mortality in darkness for planula larvae of *Cyanea capillata*. Mayorova et al. (2014) demonstrated that planula larvae of *A. aurita* have serotonin-like immunoreactive cells close to the apical organ at their anterior pole and suggested that serotonin is most likely involved in the initiation of settlement, since settlement was suppressed by serotonin-inhibitors (Mayorova et al., 2014). In vertebrates, it is well known serotonin production is easily inhibited by the lack of light (Gastel et al., 1998). It is possible that there is a similar reaction in scyphozoan larvae, which consequently leads to lower settlement rates at darkness due to the absence of serotonin. We speculate that these findings, in combination with increased metabolic costs at warmer temperatures (O'Connor et al., 2007; Schneider and Weisse, 1985), would explain the declining numbers of successfully settled larvae with increasing temperature in the darkness treatment as opposed to the general increase in settlement observed at increasing temperature in the 12:12 L:D light regime treatment.

4.4.1 Conclusion

We explored the effect of temperature on the settlement competency and rates of settlement in the planula larvae of two species of jellyfish occurring in the North Sea. Temperatures utilized in the present study (9 to 27°C) did not appear cold or warm enough to inhibit or deter settlement in *C. lamarckii* suggesting a wide thermal window for planula larvae of this species in the North Sea. Given 300°d PLD for this species, drift simulations suggested a potential for wide dispersion (in most cases 50 to 100 km from release locations) where settlement would be possible if appropriate substrate was available. Our results suggest that planulae released from *Chrysaora hysoscella* can utilize a broad range of substrates for settlement including the concrete used to construct offshore wind farms. Our results suggest that climate-driven increases in temperature will not be a factor limiting the settlement dynamics of the

planula larvae of these two species of jellyfish in the North Sea. More ecophysiological research is needed to gain a cause-and-effect understanding of how multiple, interacting factors (e.g. temperature, oxygen, pH, substrate availability) may affect the vital rates, behavior and settlement dynamics of planula larvae of scyphozoan jellyfish.

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CHAPTER 5

Abundance of large bloom forming semaeostomeaen jellyfish in the southern North Sea and potential habitats of scyphistomae

5 Abundance of large bloom forming semaeostomeaen jellyfish in the southern North Sea and potential habitats of scyphistomae (*Manuscript 4*)

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Abstract

During two cruises in May and June of 2012 and 2013 in the North Sea, scyphozoan medusae were collected using a pelagic young fish trawl. The data were utilized to identify patterns of species composition, distribution and biomass of three scyphozoan species (*Aurelia aurita, Cyanea lamarckii, C. capillata*). Abundances found in this study ($n \cdot 100\ m^{-3}$) are lower than previously reported abundance of scyphozoan jellyfish, possibly due to the much larger size of the net and the resulting flow through of water used here. Influence of abiotic factors on the accumulation and potential blooms of medusae was statistically excluded, confirming the well-known influence of hydrodynamic conditions on the distribution of bloom forming species. In order to identify possible habitats of polyps and consequently release areas of ephyrae, a hydrodynamic drift model using the catch data obtained from Hay et al. (1990) and from 2012 in this study was conducted. Spawning times and temperatures revealed by the model largely seem to be consistent with what is already known for scyphozoan polyps in the North Sea.

Keywords: Aurelia, Cyanea, polyps, drift model, sampling

5.1 Introduction

Recently, more research effort around the world has been aimed at understanding blooms of scyphozoan jellyfish (large patches of scyphozoan medusae typically drifting within the upper meters of the ocean (Hamner and Dawson, 2009)). Nevertheless, it is still unclear whether these mass occurrences are only "apparent blooms" (Graham et al., 2001) which result from natural oscillations in populations (Condon et al., 2013, 2012) rather than an increasing prevalence of jellyfish due to global warming and climate change (e.g. Dong et al., 2010; Duarte et al., 2012; Lee et al., 2013; Richardson et al., 2009). Independently of the cause, mass appearances of jellyfish bear consequences to the economy, as well as to the ecology of an ecosystem. As often reported, economic losses result from the interference of jellyfish with aquaculture, the fisheries industry, power plants and tourism (e.g. Baumann and Schernewski, 2012; Dong et al., 2010; Purcell, 2012). Feeding high in the marine food chain (Mills, 2001), jellyfish have a heavy impact on the abundance of fish eggs, fish larvae and zooplankton (Barz and Hirche, 2007; Hamner and Dawson, 2009; Lynam et al., 2005; Schneider and Behrends, 1994). Also, competing with fish for food (Lynam et al., 2005; Mills, 2001), empowers them to significantly affect the ecosystem. The fast depletion of patchy prey fields (Titelman and Hansson, 2006) and their accomplishment to not only act as bottom up-, but also as top down predators (Lynam et al., 2004) empowers scyphozoan medusae to be dangerous predators. Resulting from this, the ecosystem could shift and become dominated by jellyfish in the near future (Richardson et al., 2009).

Most scyphozoan jellyfish are r strategists, which have a metagenetic life cycle, with two alternating adult stages, the pelagic medusa and the sessile scyphistomae (or polyp), generally reproducing sexually and asexually, respectively. Ripe medusae produce free-swimming planula larvae through sexual reproduction. After finding a suitable substrate, planulae settle and metamorphose into polyps. With maturity, polyps reproduce through an asexual process commonly referred to as strobilation. As a result of strobilation, large numbers of free-swimming ephyrae are released which, depending on predation pressure and food availability (e.g. Pauly et al., 2009; Purcell, 2012), survive and mature into adult medusae. Consequences of global warming such as increasing temperatures, unstable salinities and low oxygen conditions may be

beneficial for the survival and reproduction of scyphozoan jellyfish (e. g. Gambill and Peck, 2014; Holst, 2012; Holst and Jarms, 2010; Ishii et al., 2008; Lucas, 2001; Purcell, 2007). Potential settling grounds for planula larvae increase by matters of offshore wind parks (Janßen et al., 2013) and anthropogenic litter (Holst and Jarms, 2007; Jambeck et al., 2015; Law et al., 2010), and in return, more medusae might occur.

Information on the abundance and distribution of the bloom-forming medusiod life stage in the North Sea is limited to five publications so far (Barz and Hirche, 2007; Hay et al., 1990; Möller, 1980; Vansteenbrugge et al., 2015; Van Walraven et al., 2014). On the basis of these publications it is not possible to make robust statements regarding whether or not scyphozoan jellyfish are increasing in the North Sea. Finding the habitats of the benthic polyp stage as the source of the pelagic bloom forming life stage (Holst, 2012a, 2012b) could contribute significantly to the question whether numbers of scyphozoan medusae are changing (or rising). But this information unfortunately is not available (Di Camillo et al., 2010; Lynam et al., 2010). Particle backtracking offers one technique to help locate source populations, but producing reliable estimates is difficult due to uncertainties regarding vertical migration patterns, growth rates and age of medusae. A first modeling approach to identify possible locations for polyps based on the location of scyphozoan medusae in the English Channel has been conducted (Dulière et al., 2014).

We provide an overview of scyphozoan medusae caught during cruises with RV Heincke in the German Bight in 2012 and 2013 together with possible release areas and conditions of ephyrae based on hydrodynamic drift models. Increasing the knowledge of vectors responsible for changes in jellyfish productivity will help us project how gelatinous species may alter the structure of pelagic communities in the North Sea and elsewhere (Hosia et al., 2010).

5.2 Materials and Method

5.2.1 Field Sampling of Scyphozoan Jellyfish

Jellyfish were collected during four cruises aboard the German research vessel Heincke (HE380, HE381, HE401 and HE402) in May and June 2012 and 2013. The samples were collected in the southern North Sea (see Fig. 5.1). Scyphozoan jellyfish were sampled at 49 stations, 29 in May and June 2012 and 20 in May and June 2013.

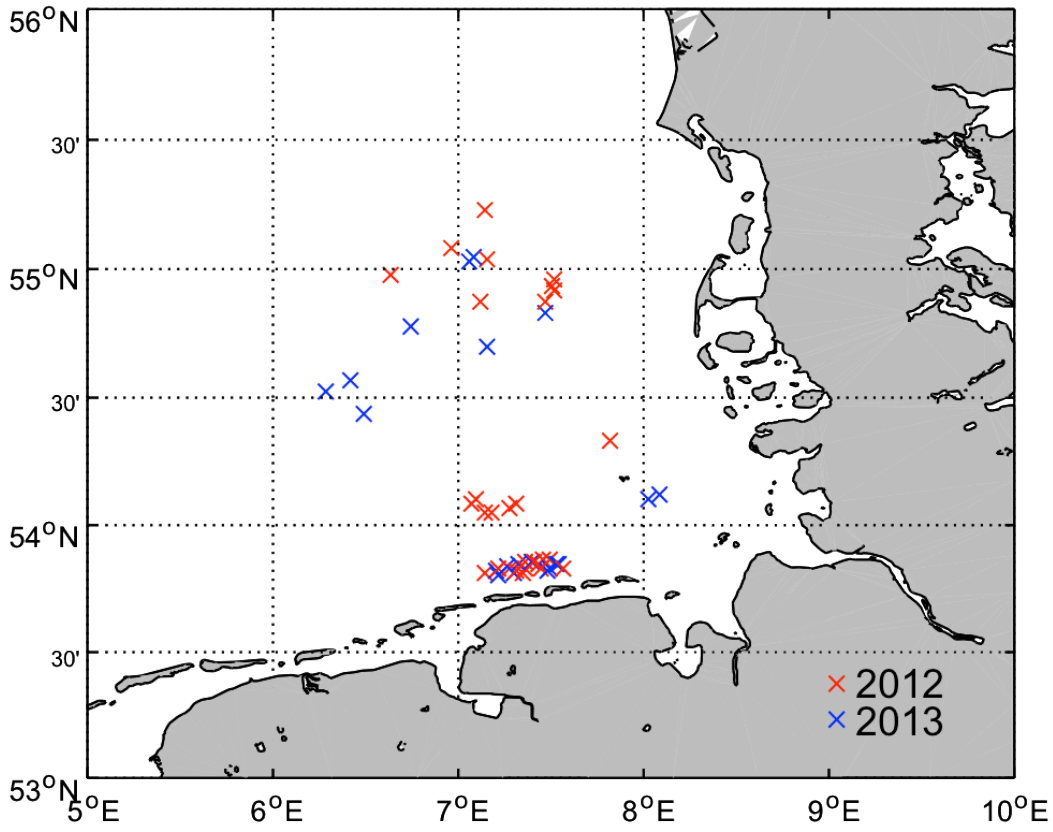

Figure 5.1: Sampling and CTD positions for years, 2012 and 2013.

Jellyfish were captured using a young fish trawl (YFT, 864 ma Millionaer Trawl i 200 m/m Nymplex, 14 mm Tæller, Nordsøtrawl Thyborøn), 40 m long with a 6-8 m x 10 m mouth opening, the vertical distance depending on speed and wind. The horizontal opening of the net was not measured. We assumed a linear relationship between speed and net opening, with a median opening of 10 m at 3.5 knots, as described for the 83/112 Eastern trawl used in AFSC's annual crab and groundfish survey of the EBS (Weinberg, 2003). The mesh size was 200 mm at the mouth, gradually decreasing to 6 mm towards the cod end. Travelling velocity was between 2.3 – 4.9 knots. Effective trawling time was 16 - 40 minutes.

Abiotic parameters were measured using a CTD profiler (SBE 911 plus; Watersampler: Hydro-Bios Freeflow (12 x 4 Liter)).

5.2.2 Identification of Jellyfish and Calculations

Scyphozoan jellyfish caught by the YFT were counted and taxonomically identified to species level. Species identification of individuals belonging to the taxon *Cyanea* was conducted according to Holst & Laakmann (2013), whereas species smaller than

40 mm were only identified as *C. lamarckii* if the blue color was obvious. All other individuals were identified as *C. capillata*. Also, diameters (D, mm) of all captured individuals were measured. The biomass (wet weight, WW, g) of each individual was calculated from its D using species-specific equations published by Hay et al. (1990) and references therein:

Aurelia aurita: $WW = 0.07*D^{2.8}$

Cyanea capillata: $WW = 0.078*D^{2.689}$

Cyanea lamarckii: $WW = 0.104*D^{2.560}$

The net opening (m^2) was multiplied with the distance covered (km) under consideration of the trawling time in order to calculate the water body run through the net during the tow. The catch data were standardized calculating caught individuals per 100 m^3 water and biomass per 100 m^3 water.

5.2.3 Drift Model

Potential release areas of ephyrae and strobilation periods of scyphistomae were identified using a Lagrangian drift approach assuming passive transport of the medusae with the ocean current. Rocky areas, which might serve as potential habitats for polyps, were used as start point of the simulation. The basic assumption for calculating advection and diffusion are described in Hufnagl et al. (2014a, 2014b, 2013). The underlying oceanographic model was the Hamburg Shelf Ocean Model (HAMSOM) with a 1/5° and 1/3° resolution in latitudinal and longitudinal direction and 31 vertical layers. The model covers the whole shelf area spanning from 15.1° W and 63.9° N to 14.25° E and 47.48° S. Velocity fields were updated every hour to include tidal currents. The position of each drifter was updated in steps of one minute. A horizontal diffusion of 10 $m^2 \cdot s^{-1}$ and vertical diffusion based on a diffusive random walk following Visser (1997) with vertical exchange coefficients obtained from the ocean circulation model, was included. Within the forward approach every week from calendar day 300, approximately 35,000 particles were started at random locations and water depth in all areas classified as “hard substrate” in the EMODnet dataset

(http://www.emodnet-seabedhabitats.eu/). To simplify the identification of the origin, natural hard substrate areas in and surrounding the North Sea were combined into 14 large areas as indicated in Fig. 5.2.

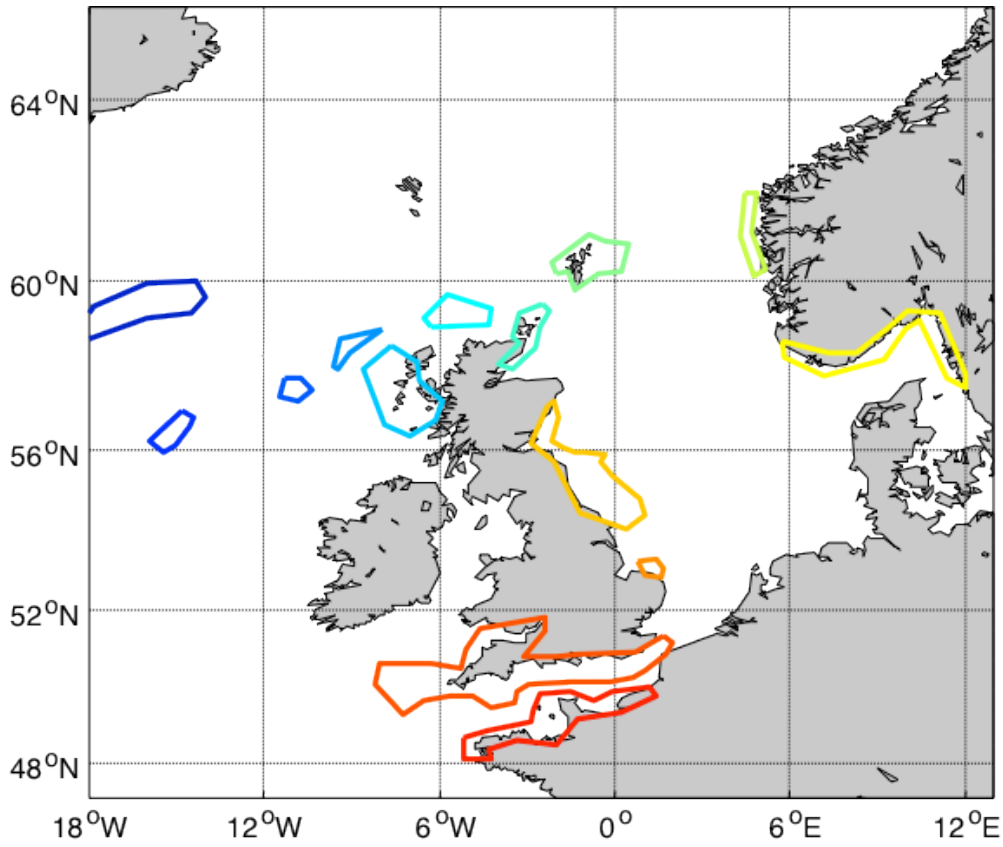

Figure 5.2: Areas with hard substrate as potential habitat of polyp populations and consequent release area of ephyrae.

As soon as a drifter reached the proximity of an observation point ± 0.1° after July 1st (about the time when Hay et al. (1990) started sampling in 1979, 1982 and 1983) the start date, start position, start area and start temperature was noted as suitable and used for calculating the relative start time and temperature index. This was determined by the sum of all "successful" particles from one start date (temperature) times the abundance of jellyfish observed at the "connected" end location divided by all particles that started at the same date (temperature). Furthermore, for each observation point, the relative potential contribution of each start area could be determined.

The distributional data used in this model were obtained from the ICES international 0-group Gadoid surveys in the North Sea (June and July 1971-1986, Hay et al., 1990).

Additionally we used the data we collected in 2012 and ran the model for *A. aurita*, *C. lamarckii* and *C. capillata*.

5.2.4 Evaluation and Statistical Analyses

The data collected in 2012 and 2013 were used to identify whether hydrographic features, catch conditions or location influenced the occurrence of the three observed species *A. aurita*, *Cyanea lamarckii* and *C. capillata*. CTD data collected before each tow were used to determine stratification, surface and bottom salinity, temperature, transmission, oxygen concentration and fluorescence. Furthermore tow length, water depth, latitude and longitude were included.

Statistical analysis were conducted using R 3.1.2 (R Core Team, 2014). First it was tested whether size, weight and concentration differences existed between species. The collected data did not meet assumptions for parametric analyses, thus a Kruskal-Wallis-Test (KWT) was performed. Post hoc we applied a multiple comparison test using the R package pgirmess (Giraudoux, 2015).

Furthermore a hierarchical cluster analyses, a principal component analysis (PCA) and an Anosim were performed to identify factors influencing mean jellyfish size, weight and concentration / abundance observed at each location and significance of clusters, using the R package vegan (Oksanen et al., 2015). Multivariate dispersion to identify solidity of clustering, as a basis for the Anosim application was determined based on Bray-Curtis distances, permutation and Tukey Honest Significant Differences.

Distribution of species and interpolation of hydrographic features were created using the software MATLAB and nearest neighbor interpolations by latitude, longitude and year.

5.3 Results

5.3.1 Overall Distribution and Abundance of Scyphozoan Jellyfish

In 2012, *C. lamarckii* was mostly abundant (n·100 m^{-3}) near the coast in the German Bight (Fig. 5.3). Moving up north, individuals per 100 m^3 decreased, until above 55° N longitude almost no *C. lamarckii* were found at all. *Cyanea capillata* was present at all station were jellyfish were caught. The moon jelly, *A. aurita,* was rarely found close to the shore, becoming more and more abundant further into the central North Sea. In

2013 the picture changed: *A. aurita* was present with higher numbers of individuals at all stations, besides stations north of 55.7° N latitude. *Cyanea lamarckii* however, was much less abundant 2013 than 2012. The amount of *C. capillata* caught in 2013 resembled the numbers from 2012 (see Fig. 5.3). For more information see also Tables 5.1 and 5.2.

In 2012 we caught 54 *A. aurita* as opposed to 750 in 2013. *Cyanea capillata* was more or less the same in both years with 950 individuals caught in 2012 and 649 individuals caught in 2013. *Cyanea lamarckii* was highly abundant in 2012 with 3946 individuals and about the same as the other two species with a total number of 554 individuals in 2013.

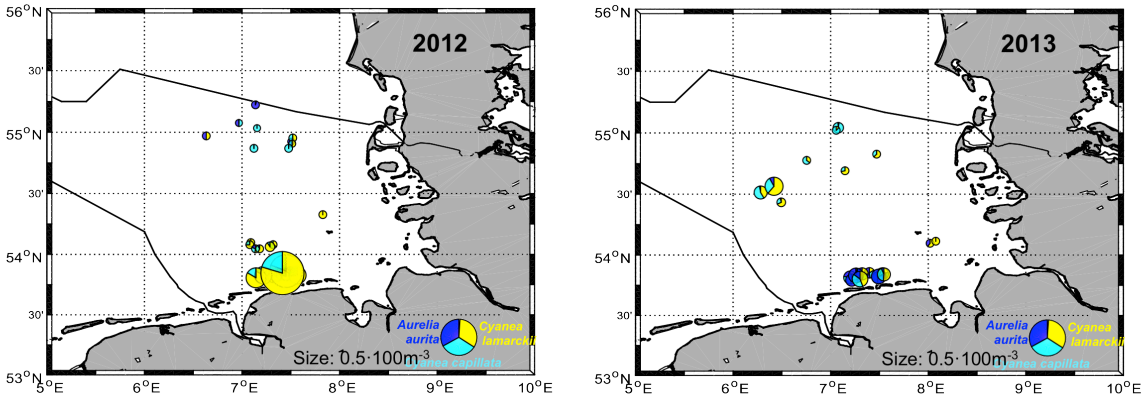

Figure 5.3: Stations in 2012 and 2013. Jellyfish caught per unit water (n·100 m^{-3}). Blue = *A. aurita*, yellow = *C. lamarckii*, turquoise = *C. capillata*.

Overall, significantly less *A. aurita* than *C. lamarckii* were caught (KWT, X^2 = (2, N = 3) = 11.3815, $p < 0.01$). Testing 2012 alone, the results are similar (KWT, X^2 = (2, N = 3) = 21.0707, $p < 0.001$), with significantly less numbers of *A. aurita* than both, *C. lamarckii* and *C. capillata*. In 2013 no significant differences between numbers of caught scyphozoans were detected (KWT, X^2 = (2, N = 3) = 1.4771, p = 0.4778, see Fig. 5.4A). All three species displayed significantly different diameters (KWT, X^2 = (2, N = 3) = 1260.46, $p< 0.001$), *A. aurita* being the largest and *C. capillata* being the smallest (see Fig 5.4B). In 2012, *C. lamarckii* was significantly larger than the other species (KWT, X^2 = (2, N = 3) = 187.2853, $p< 0.001$). For 2013, all three species were significantly different, with *A. aurita* being the largest (KWT, X^2 = (2, N = 3) = 877.1817, $p<0.001$).

Table 5.1: Species Abundance per m^3 and percentages for all stations 2012

2012			numbers per m³				percentage		
ID	**lat**	**long**	***Aurelia aurita***	***Cyanea capillata***	***Cyanea lamarckii***	**total n/m³**	***Aurelia aurita***	***Cyanea capillata***	***Cyanea lamarckii***
15_2	55.23	7.14	8.88E-02	4.04E-03	0.000E+00	9.28E-02	96	4	0
15_26	53.84	7.44	5.29E-03	1.27E-01	7.15E-01	8.47E-01	1	15	84
17_27	53.83	7.36	3.98E-03	5.17E-02	2.59E-01	3.14E-01	1	16	82
17_3	55.08	6.97	4.43E-03	4.43E-03	0.000E+00	8.86E-03	50	50	0
19_28	53.82	7.32	1.38E-02	4.59E-02	4.50E-01	5.09E-01	3	9	88
19_4	55.04	7.15	0.000E+00	5.12E-03	0.000E+00	5.12E-03	0	100	0
26_29	53.83	7.45	9.77E-03	4.89E-02	2.10E-01	2.69E-01	4	18	78
28_30	53.81	7.35	0.000E+00	3.46E-02	2.15E-01	2.50E-01	0	14	86
33_31	53.83	7.57	4.30E-03	4.99E-01	1.40E+00	1.90E+00	0	26	74
33_5	54.93	7.50	3.74E-03	0.000E+00	0.000E+00	3.74E-03	100	0	0
37_6	54.87	7.12	0.000E+00	1.76E-02	0.000E+00	1.76E-02	0	100	0
39_32	53.87	7.45	1.28E-02	8.88E-01	3.82E+00	4.72E+00	0	19	81
39_7	54.98	6.63	4.65E-03	0.000E+00	4.65E-03	9.31E-03	50	0	50
4_23	53.86	7.36	1.40E-02	9.77E-02	2.70E-01	3.82E-01	4	26	71
41_33	53.83	7.22	4.00E-03	3.00E-01	1.50E+00	1.81E+00	0	17	83
43_34	53.81	7.14	4.69E-03	3.90E-01	1.99E+00	2.38E+00	0	16	83
45_35	53.85	7.41	0.000E+00	1.36E+00	5.28E+00	6.64E+00	0	20	80
47_8	54.96	7.52	0.000E+00	9.18E-03	9.18E-03	1.84E-02	0	50	50
48_9	54.91	7.52	0.000E+00	8.45E-03	8.45E-03	1.69E-02	0	50	50
50_10	54.87	7.48	0.000E+00	4.34E-03	0.000E+00	4.34E-03	0	100	0
56_11	54.33	7.83	0.000E+00	0.000E+00	2.20E-02	2.20E-02	0	0	100
66_12	54.10	7.09	0.000E+00	0.000E+00	1.21E-02	1.21E-02	0	0	100
68_13	54.08	7.32	0.000E+00	8.72E-03	4.36E-03	1.31E-02	0	67	33
7_24	53.83	7.28	1.65E-02	1.05E-01	3.80E-01	5.01E-01	3	21	76
70_14	54.08	7.07	4.32E-03	4.75E-02	1.43E-01	1.94E-01	2	24	73
76_16	54.07	7.28	0.000E+00	3.51E-02	3.31E-01	3.66E-01	0	10	90
79_18	54.05	7.14	1.87E-02	2.81E-02	5.15E-02	9.84E-02	19	29	52
81_19	54.05	7.18	9.29E-03	3.72E-02	6.04E-02	1.07E-01	9	35	57
9_25	53.86	7.50	1.38E-02	5.99E-02	3.91E-01	4.65E-01	3	13	84

Pooling both years, 2012 and 2013, we did not find significant differences in biomass per unit water (100 m^3) between the different species (KWT, X^2 = (2, N = 3) = 4.35, p = 0.1). Looking at the years separated, in 2012, significant differences in biomass between species were detected (KWT, X^2 = (2, N = 3) = 16.6747, p < 0.001). *Cyanea lamarckii* had significantly more biomass than *A. aurita*. In 2013, differences in biomass per unit water where also significantly different from each other (KWT, X^2 = (2, N = 3) = 12.0765, p <0.01), this time with *A. aurita* having significantly more biomass than *C. lamarckii*.

Table 5.2: Species abundance per m^3 and percentages for all stations 2013

2013			**numbers per m³**				**percentage**		
ID	**lat**	**long**	***Aurelia aurita***	***Cyanea capillata***	***Cyanea lamarckii***	**total n/m³**	***Aurelia aurita***	***Cyanea capillata***	***Cyanea lamarckii***
1_1	54.10	8.02	1.87E-02	0.000E+00	2.80E-02	4.66E-02	40	0	60
17_6	55.05	7.08	5.11E-03	4.55E-01	1.02E-02	4.71E-01	1	97	2
2_2	54.12	8.08	0.000E+00	0.000E+00	5.17E-03	5.17E-03	0	0	100
21_7	55.03	7.06	0.000E+00	1.15E-01	1.71E-02	1.32E-01	0	87	13
24_9	54.83	7.47	0.000E+00	1.68E-02	2.81E-02	4.49E-02	0	37	63
31_10	54.78	6.75	0.000E+00	4.20E-02	2.29E-02	6.48E-02	0	65	35
33_11	54.70	7.15	0.000E+00	2.39E-02	5.97E-02	8.35E-02	0	29	71
4_24	54.44	6.49	6.27E-03	4.39E-02	1.07E-01	1.57E-01	4	28	68
45_13	53.86	7.40	2.61E-01	1.61E-01	8.07E-02	5.04E-01	52	32	16
47_14	53.82	7.20	1.88E-01	2.51E-01	3.95E-01	8.34E-01	23	30	47
51_15	53.85	7.53	4.33E-01	1.62E-01	1.58E-01	7.53E-01	58	22	21
53_16	53.80	7.22	4.14E-01	1.18E-01	1.69E-01	7.01E-01	59	17	24
58_17	53.82	7.48	2.43E-01	1.53E-01	8.96E-02	4.85E-01	50	32	18
59_18	53.83	7.49	8.66E-01	9.70E-02	6.72E-02	1.03E+00	84	9	7
6_25	54.52	6.28	2.39E-02	4.48E-01	3.34E-01	8.06E-01	3	56	41
7_26	54.57	6.42	1.24E-01	4.69E-01	9.38E-01	1.53E+00	8	31	61
79_20	53.85	7.32	2.46E-01	3.03E-01	1.88E-01	7.37E-01	33	41	26
80_21	53.84	7.26	9.85E-01	3.48E-02	9.95E-03	1.03E+00	96	3	1
83_22	53.81	7.30	1.60E-01	4.34E-01	4.71E-01	1.07E+00	15	41	44
84_23	53.85	7.54	4.58E-02	2.95E-01	3.61E-01	7.02E-01	7	42	51

5.3.2 Principle Component Analysis (PCA)

The hierarchical cluster analysis revealed that maximum, minimum and mean values of abiotic factors aggregate well (see supplementary, Fig. S5.8). Based on these findings, the PCA was conducted only with mean values of abiotic factors. The Anosim did not reveal any significant impact of environmental conditions on diameter or weight of scyphozoan jellyfish. The principal component analysis (PCA) investigated the influence of abiotic factors on species distribution and –composition (Fig. 5.5). Principal component 1 explained 35.0% of the proportion of variance. Principal component 2 explained 23.1% of the proportion of variance. This way, PC1 and PC2 explained a total of 58.1% of the total variance. We were able to identify six clusters. The first cluster mostly consists of *C. lamarckii* and *C. capillata*, with close proximity to the shore in high oxygen areas (probably well mixed areas) with high primary production. The more oxygenated the water became, the more *A. aurita* and the less *C. lamarckii* were found. The second group was associated with greater depths, lower mean

temperatures and higher latitudes, most likely more in the center of the North Sea, primarily consisting of *C. lamarckii* and *C. capillata*. Cluster three was associated with high salinities, where catches mainly consisted of *A. aurita*. There may be an additional influence of high latitudes and clear water. The fourth group was strongly associated with high transmission (clear water), potentially under the influence of high temperatures. Species composition mainly consisted of *C. lamarckii* and *C. capillata*. As temperature became more influential, more *A. aurita* occurred. Cluster five was associated with high longitude, (abundant in the coastal region of the German Bight), high transmission (clear water) and high temperatures, mostly consisting of *C. lamarckii* and *C. capillata*. The last cluster was dominated by *A. aurita*, more at intermediate temperatures, but also in the coastal region of the German Bight.

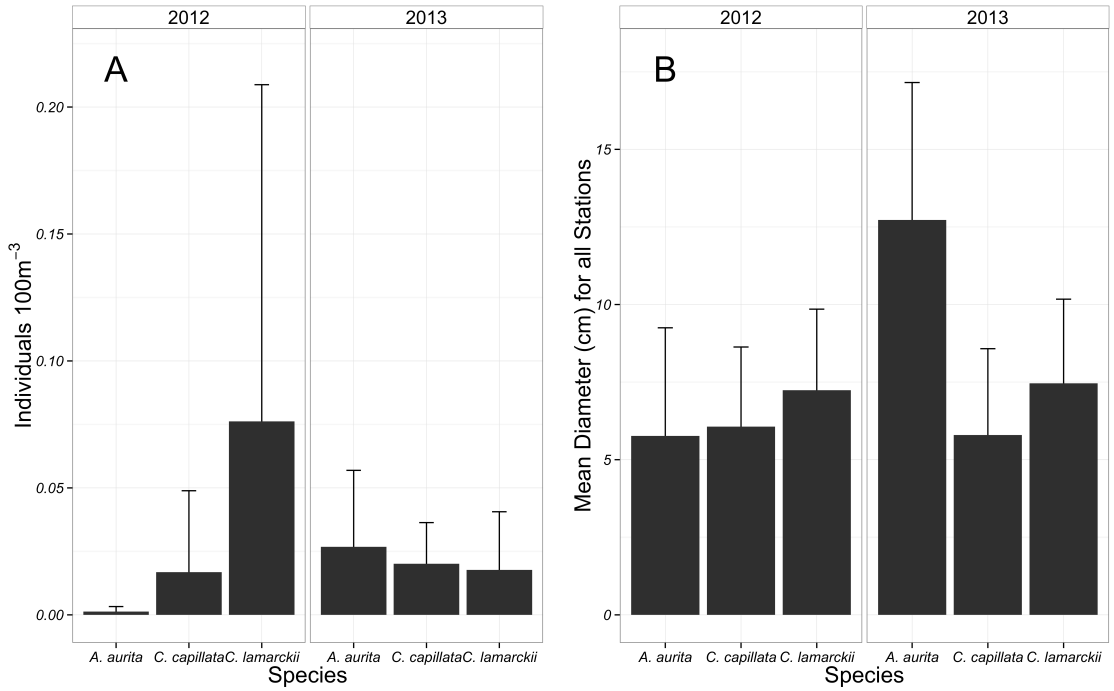

Figure 5.4: (A) Individuals vs. Species in 2012 and 2013 (n·100 m^{-3} ±SD) and (B) Diameter vs. Species in 2012 and 2013.

5.3.3 Abiotic factors

Close to the shore the water was more mixed in 2013 than in 2012, which lead to greater differences in salinity in 2013. The riverine fresh water influx in 2013 was greater than in 2012 vertically. The year 2012 was generally warmer than 2013. In 2012, the temperature in the upper 5 m never was below 12°C in the whole (jellyfish-)

sampling area. In 2013 temperatures along the coastline were at constant 13°C, but rapidly decreased to 8°C moving further away from the coastal area. In 2013 transmission was generally lower in coastal areas than in 2012, accordingly fluorescence was higher. In 2012 fluorescence was only high in areas with coastal fresh water influx.

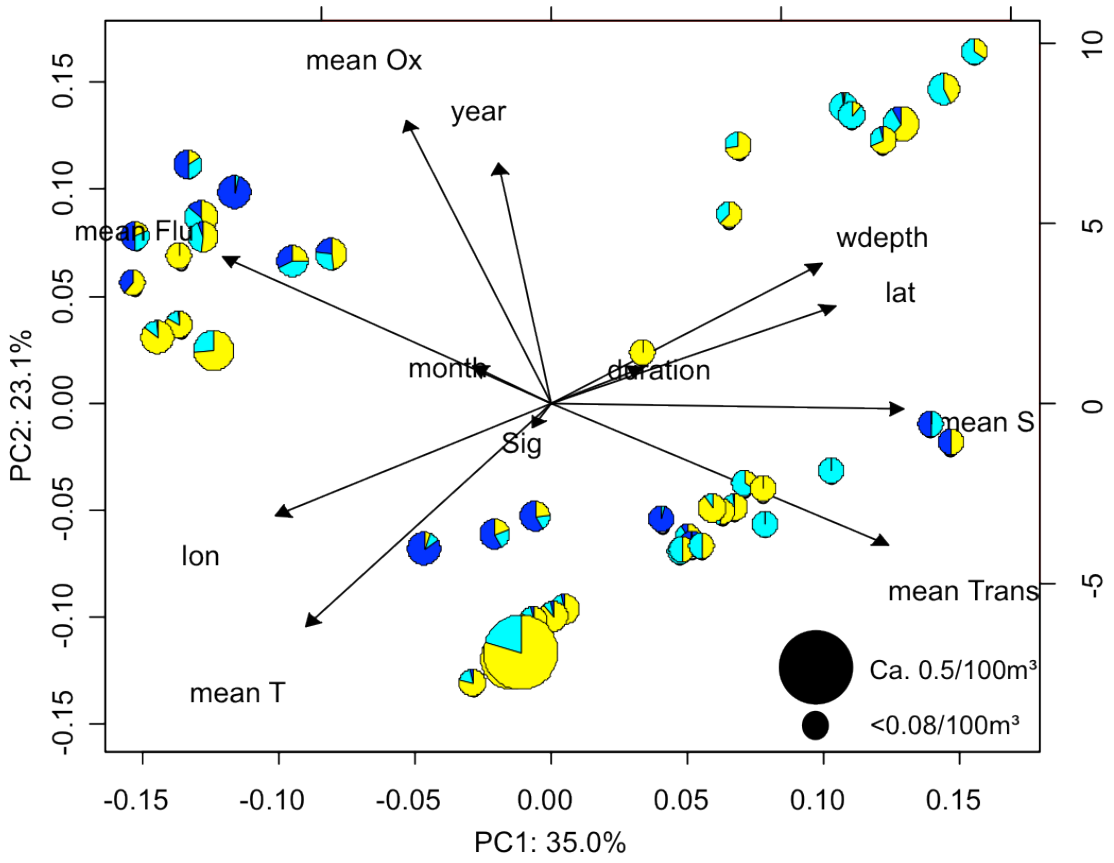

Figure 5.5: Principal component analysis (PCA): *Aurelia aurita* = blue, *Cyanea capillata* = green, *C. lamarckii* = yellow. Mean Flu = mean fluorescence, Sig = stratification, mean Ox = mean oxygen concentration, year = year, month = month, duration = towing duration, wdepth = water depth, lat = latitude, lon = longitude, mean S = mean salinity, mean Trans = mean transmission, mean T = mean temperature.

5.3.4 Model Output

Modeling the drift of jellyfish enabled us to refine (i) where captured species potentially originated from, (ii) what the potential best start temperature for release of ephyrae (and consequently the beginning of their drift) would have been and (iii) what time of the year could potentially be the right one for the release, whereas (ii) and (iii) are not necessarily to be separated from each other.

A large variety of possible strobilation dates and temperatures emerged from the drift model exercise. They were not consistent between or within years or species. As one common feature of the analysis a spatial pattern emerged; in the north eastern North Sea observed jellyfish most likely originated from rocky habitats surrounding the Orkney Islands. The eastern parts of the North Sea were mainly supplied from polyps that settled around Flamborough Head (eastern UK coast). Habitats surrounding the Shetland Islands mainly supplied northeastern parts of the North Sea (Fig. 5.6).

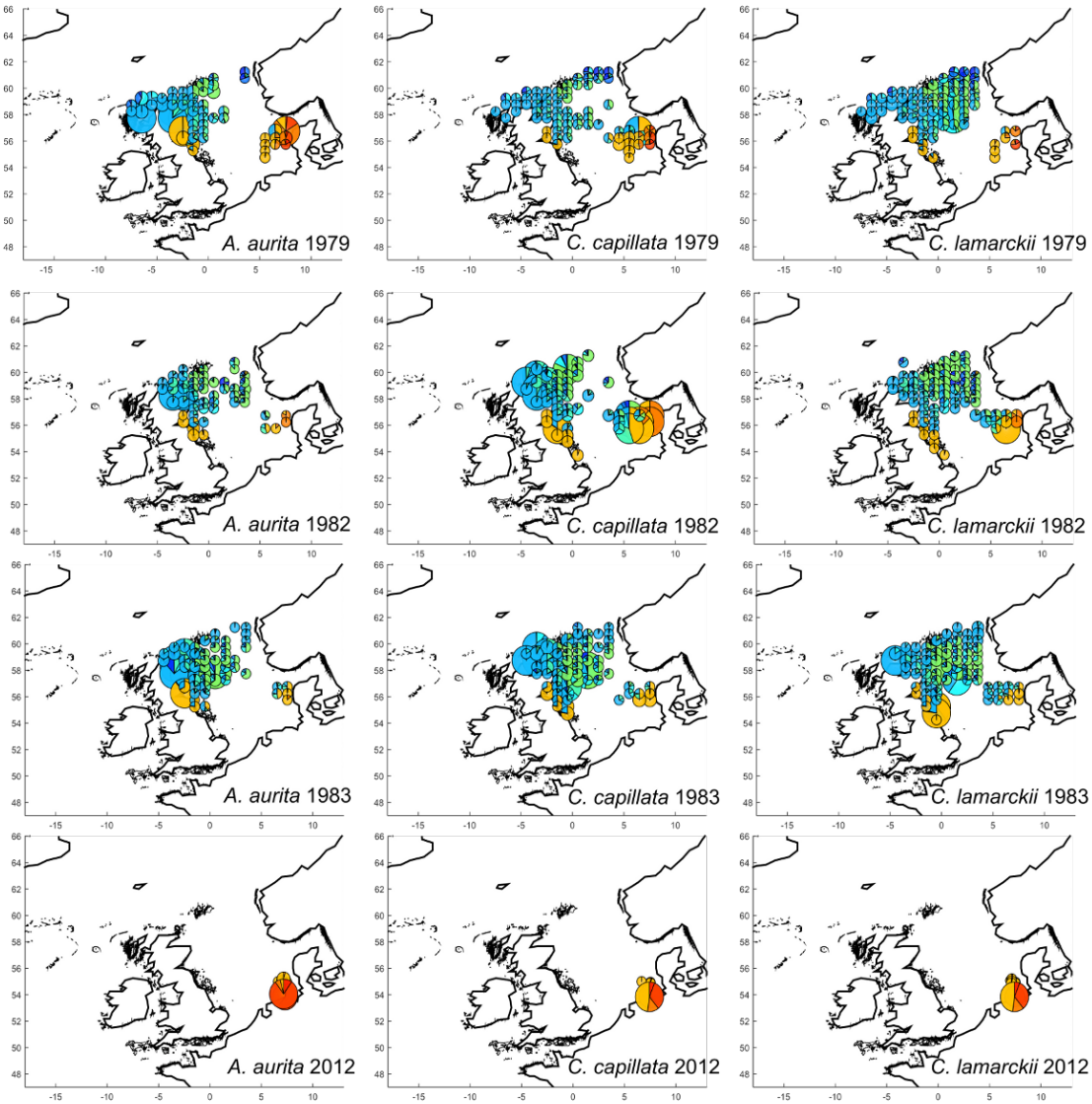

Figure 5.6: Model output from 1979, 1982, 1983 (Hay et al. 1990) and 2012 (this study). For possible habitats of benthic polyps see also Figure 5.2; colors reference possible release areas of ephyrae. For further information see supplementary material.

Most likely dates for strobilation and the release of ephyrae, based on the relative success index which included the number of particles started in a habitat, the number of drifters that made it to the observation point and the jellyfish concentration reported and measured at the observation point, indicated that in 1979 *A. aurita* and *C. capillata* mainly released ephyrae in November and December while the most likely start date for *C. lamarckii* was May to June and thus approximately 1 to 2 months before the sampling campaigns took place (Fig 5.7C). Average estimated strobilation temperatures started around 6°C but included values up to 15°C (Fig. 5.7A). Lower strobilation temperatures were mainly determined for the Orkney Shetland habitats whereas higher temperatures were mainly estimated for potential strobilation habitats located in the North Sea (Fig. 5.7B). While in 1979 the winter period emerged as the most likely strobilation time for *A. aurita*, it was less significant in 1983 and more shifted to the summer in 1982. For both *Cyanea* species no clear date emerged in 1982 and 1983 (5.7C and 5.7D).

In 2012 sampling locations were located in the German Bight and in this year, comparable to the earlier sampling campaigns, all three species most likely originated from the southeastern UK coast and the English Channel (Fig. 5.6). Only drifters that started in November and December made it into the German Bight (Fig. 5.7). This was due to a weak anticyclonic circulation in the North Sea starting in April.

5.4 Discussion

Information on the abundance and distribution of scyphozoan jellyfish in the North Sea is scarce. Two time series only covering parts of the North Sea have been conducted so far (Hay et al., 1990; Van Walraven et al., 2014). Apart from little knowledge of the pelagic life stage, the whereabouts of the sessile life stage, known as asexually reproducing polyp or scyphistoma in the North Sea are unknown. In this study, new data on the distribution, size and abundance of scyphozoan jellyfish were collected in the southern North Sea in 2012 and 2013. Some relation between location and physical properties of the environment could be identified, however these were not always significant indicating that either other factors play a more important role, the study area was too small or no strong environmental constraints limit jellyfish distribution in the North Sea.

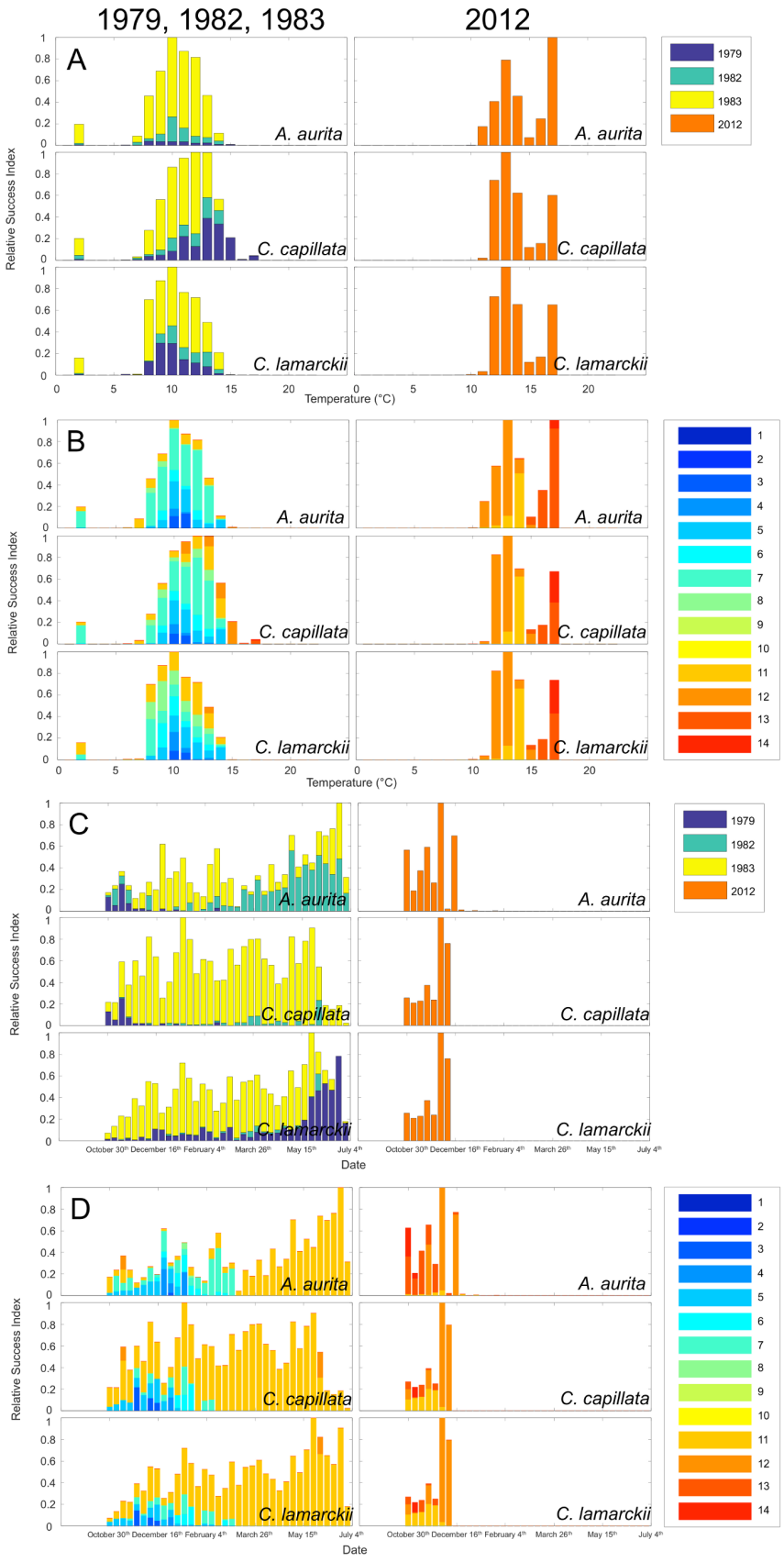

Figure 5.7: Model output with potential best start temperatures in different years, and potential best start temperatures for different areas. Potential best start date in different years, and potential best start time for different areas. For color code translation refer to Fig. 5.2. The relative success index is explained in the method section.

The latter was supported by the modeling exercise calculated to determine origins of large jellyfish and to identify hydrographical conditions during strobilation. Here as well no clear trend in potential drivers like e.g. time of the year, temperature or salinity inducing strobilation activity were identified. However, the drift studies indicated that transport with currents plays an important role and that large jellyfish mainly originate from rocky habitats of the western North Sea.

Samples were dominated by *A. aurita*, *C. lamarckii* and *C. capillata* although other scyphozoans regularly occur in the North Sea (Barz and Hirche, 2007; Holst et al., 2007). Sampling took place in May and June 2012 and 2013 respectively, a season, which is most likely too early for the two other common scyphozoans, *Chrysaora hysoscella* and *Rhizostoma octopus* (Holst, 2012a, 2012b; Vansteenbrugge et al., 2015; Van Walraven et al., 2014). Also, sampling sites may have been too far North in order to catch these species during this season (Van Walraven et al., 2014). The holoplanktonic scyphozoan *Pelagia noctiluca* has recently not been found in the North Sea, only time series suggest it to be abundant in very low numbers and rather infrequently in the 1960 (Van Walraven et al., 2014) and the 1970/80s (Hay et al., 1990).

The general occurrence of species largely agrees with earlier reported distributions patterns. The “southern boreal” (Russell, 1970) species *C. lamarckii* occurred in high numbers in the warmer coastal parts of the southern North Sea, being the largest (max. 23 cm) and most abundant species in 2012, with no presence at the northern sampling points. This species was considerable less abundant and smaller (max 18.5 cm) in 2013. This is in line with findings of this species (20 cm) in the German Bight by Barz and Hirche (2007) and its absence from the central North Sea (Möller, 1980). Still, it has been found in large numbers in the northeastern part of the North Sea (Hay et al., 1990). Whether they were transported there or they originated from a local source polyp population is not determinable.

Cyanea capillata, often referred to as “northern boreal” (Russell, 1970), was found at almost every station in both years in more or less equal shares of the catch and comparable abundance. This agrees well with previous findings, where it was present all over the North Sea (Möller, 1980), particularly on the northwestern coast of Ireland,

the southern North Sea (Hay et al., 1990) and the German Bight (Barz and Hirche, 2007). Alike *C. lamarckii,* also *C. capillata* is absent from the central North Sea (Möller, 1980).

Aurelia aurita, however, known to be ubiquitous rather than being restricted to certain areas (Russell, 1970), was more abundant in the central North Sea than in coastal areas in 2012. In 2013, the picture changed and *A. aurita* was found at most stations sampled especially in the coastal areas. The considerable alternation from low abundances of *A. aurita* (0.001±0.002 Ind. $100 \cdot m^{-3}$, max diameter 19.5 cm) in 2012 to much higher abundances in 2013 (0.03±0.03 Ind. $100 \cdot m^{-3}$, max diameter 26.0 cm), reflect findings of *A. aurita* reaching maximum abundances of 0.06±0.39 Ind. $100 \cdot m^{-3}$ in August 2004 and not being observed at all in 2005 (Barz and Hirche, 2007). The findings from 2013 confirm what is known about this species in the North Sea, being common in the German Bight (Barz and Hirche, 2007; Hay et al., 1990), aggregate close to shore (Russell, 1970) and being found in the northwestern areas of the North Sea (Möller, 1980). *Aurelia aurita* is the most abundant jellyfish species in the North Sea (Hay et al., 1990).

Results from this and earlier studies showed that identifying clear distribution ranges or seasons is difficult partly due to the low sample numbers and observations but also due to the high intra- and interannual variability, as can be seen in *A. aurita* (this study). Inter-annual fluctuations have been reported to be common in various species of scyphozoan jellyfish (Schneider and Behrends, 1994), also, climate related changes associated with the North Atlantic Oscillation (NAO) may be influencing abundances of scyphozoan jellyfish (Lynam et al., 2010). Various approaches to collect data on jellyfish using different sampling gears have been made. Trawls originally designed to sample fish (Hay et al., 1990), plankton bongo nets (Barz and Hirche, 2007) or complex trap-like nets like the kom-fyke (Van Walraven et al., 2014) were used to sample jellyfish. Also, data collection by observing and counting patches of scyphozoans from boats (Bastian et al., 2011) or airplanes (Houghton et al., 2006) is becoming more common together with active involvement of citizens by evaluating questionnaires completed by bathers (Baumann and Schernewski, 2012) or providing online platforms where citizens can report sights of jellyfish (Pikesley et al., 2014).

When using trawls as we did in our study, gelatinous zooplankton may be injured or pressed through the net, which may oblige scientists to only work on fragments of captured animals (Raskoff et al., 2003). Additionally, their fragile nature as well as problems when fixating medusae, raises the urge for specialists identifying the animals as they are caught. Furthermore the rather large mesh sizes in comparison to plankton nets do not quantitatively catch small individuals bearing the risk of underestimation. The length frequency distributions (not shown) peaked at 11, 6 and 4 cm for *A. aurita*, *C. capillata* and *C. lamarckii*, respectively, indicating a minimum full retention diameter of 3-4 cm.

We suggest previous studies from the North Sea to overestimate abundances of scyphozoan jellyfish, rather than underestimating them. With mean abundances of 0.08±0.13 (mean±SD) Ind. $100 \cdot m^{-3}$ and maximum abundances of 0.66 Ind. $100 \cdot m^{-3}$ of *C. lamarckii* at one station in 2012, our results show lowest abundances ever reported on scyphomedusae in the North Sea. Mean abundances of 6.6±12.0 Ind. $100 \cdot m^{-3}$ (Vansteenbrugge et al., 2015) and 1.8±2.7 Ind. $100 \cdot m^{-3}$ (Barz and Hirche, 2007) as well as maximum abundances of 13 Ind. $100 \cdot m^{-3}$ of *C. lamarckii* at one station (Barz and Hirche, 2007) and 49 Ind. $100 \cdot m^{-3}$ of *A. aurita* in the Dutch Wadden Sea (Van Der Veer and Oorthuysen, 1985) were much higher than our findings. Barz and Hirche (2007) assumed to underestimate abundances of scyphomedusae due to their patchy distribution (Graham et al., 2001), furthermore, mesh- and jellyfish size also may have lead to an underestimation of abundance (Hay et al., 1990). A pelagic trawl used in the North Sea described a filter volume of 65,000 m^3 of water h^{-1} (Hay et al., 1990). The data collected in this study are based on a flow of ~500,000 m^3 of water h^{-1}, varying with the speed of the boat. In the Northern California current, abundances of 0.0063±0.046 Ind. $100 \cdot m^{-3}$ of *Chrysaora fuscescens* were reported, using a surface trawl with a mean net opening of 123 m^3 with consequently filter volumes of >500,000 m^3 of water h^{-1} (Suchman and Brodeur, 2005). These findings suggest large nets to display lower abundances, at the same time the sampled water body is much larger. Grand pelagic trawls with large mouth openings may lead to more quantitative sampling than smaller nets. We suggest establishing regular surveys and sample jellyfish with large trawls to ensure quantitative comparability of jellyfish in the North Sea and elsewhere. As mentioned before, large interannual variation can be expected

for scyphozoans, partly due to the discussed sampling bias or undersampling but also due to the generally low understanding of what drivers determine size and abundance in these species.

Our findings based on the principal component analysis revealed that abundances of scyphozoan jellyfish always appeared in mixed sizes and species composition indicating either a highly divers cohort, different origins or different strobilation times. We were not able to detect any kind of pattern, relating jellyfish size or abundance to present abiotic factors such as temperature, salinity or stratification. The results suggest that scyphomedusae grow and endure very well, with an impeccable ability to survive anywhere. The species distribution, composition and size seem rather random. When looking at the large numbers accumulating close to the shore of the German Bight, aggregations due to physiological barriers such as fronts are becoming more likely (Graham et al., 2001; Hay et al., 1990). Ocean currents generally are homogenous still, vertical movement of scyphomedusae may influence their drift trajectories, as has been shown in fish larvae (Bolle et al., 2009; Fiksen et al., 2007). Nevertheless, the effect of vertical transport may be minor on larval fish (Dickey-Collas et al., 2009; Hufnagl et al., 2014a) and consequently on scyphomedusae, as the southern North Sea is well-mixed during fall and winter. We suggest the appearances of scyphomedusae to be primarily dependent on the hydrodynamic (currents and streams) conditions of the North Sea.

Not finding significant environmental influence on size and abundance is partly due to the snapshot type sampling, which is not reflecting earlier conditions experienced by the individual. Comparably, we did not find clear drivers for strobilation time or one dominating potential polyp habitat within the model analysis. The results of the drift study indicated that a variety of possible start dates and temperatures might exist and that these might differ considerably between years and species, which fits the observed interannual variability. Some bias can be expected in the model study as sampling locations in close proximity to potential polyp habitats, here defined as rocky gravelly grounds, received drifters more often and within a shorter time frame than more distant located areas. Thus the results were partly biased by the chosen sampling points and dates as well as by ignoring other potential polyp habitats like platforms,

offshore construction, floating plastic or wood (Holst and Jarms, 2007). As long as no reliable data on drift times, age or growth of the scyphomedusae or observation on strobilation dates exist, a more precise analysis is not possible. Still, some of the results fit actual reported features of the life cycle quite well.

Most likely strobilation dates of *A. aurita* were either November, December in 1978 and 2011, April, May in 1982 or January, February and May in 1983, respectively. These findings correspond with results from long-term laboratory experiments, showing *A. aurita* to reproduce asexually through strobilation November through May at 10°C (Holst, 2012a), matching the range of the model which estimates strobilation temperatures to vary between 8 and 14°C. *Cyanea capillata* most likely strobilated in November and December of 1978 and 2011, April and May 1982 and basically all winter and spring 1982 / 1983 at temperatures up to 17°C in 1979. These findings suggest potential misclassification of *C. capillata* as *C. lamarckii* (Holst and Laakmann, 2013), as strobilation in *C. capillata* is reported to be inhibited at 15°C and above (Holst, 2012a). Strobilation is reported to occur from March through May at 10°C, and from February to April at 5°C, with no strobilation at all at 15°C (Holst, 2012a), indicating an upper thermal boundary of this species, which corresponds to the northern boreal description as reported by Russell (1970). This nevertheless does not explain our findings and suggests potential errors when identifying the animals as well as errors deriving from the simulation conducted in this study. According to the model, *C. lamarckii* strobilated in late spring and early summer of 1979, almost not at all in 1982 and early in 1983 and 2012. In support of our findings, the southern boreal species (Russell, 1970) strobilated November through August at 10°C, with high possibilities of migrating further north with warming waters in the North Sea (Holst, 2012a). In summary, Holst (2012a) showed that *A. aurita* and *C. lamarckii* will benefit from rising temperatures, whereas *C. capillata* will not. The benefiting species will not only produce more ephyrae, strobilation will also occur much faster and possibly more often (Holst, 2012a; Lucas et al., 2012), which in turn may impact abundances of large medusae, given high numbers of ephyrae to survive.

Recently it has been suggested, that the metagenetic life cycle displays a rather multi-modal lifecycle than an alternation of sexual- and asexual reproduction, depending on

the season (Ceh et al., 2015). Also, it is suggested that ephyrae released in winter may be overwintering in deeper layers (Holst, 2012a) before maturing into medusae. Furthermore, adult medusae may not die by the end of the season, but overwinter as well (Hay et al., 1990). These findings suggest the possibility of strobilation and consequent production of ephyrae all year round, even in the North Sea. Unfortunately, the compelling lack of knowledge about the ecology of scyphozoan polyps (Lynam et al., 2010) is hindering any progress concerning these matters. Although strobilation may potentially occur all year in areas like the German Bight, ephyrae may only survive under specific hydrographical conditions, as it was the case in 2012. Even though drifters from all habitats were distributed over the whole North Sea, only drifters from the earliest release dates were transported into the German Bight, which does not preclude strobilation to occur at other points in time. Since *C. capillata* is known as northern boreal species (Russell, 1970), the likelihood of polyps being found in the warm waters of the English channel is low. Most likely medusae caught in 2012 were misclassified as *C. capillata*, while most of them were actually *C. lamarckii*.

Our findings underline the urgent need for reporting gelatinous species from sampling campaigns with a high spatial coverage and resolution, like e.g. the International Bottom Trawl Survey. Furthermore, reliable growth estimates would sharpen the results as they allow for the use of size at catch and back-calculation to further rule out unlikely strobilation dates and conditions, given the availability of known prey conditions, as it is well known that size of scyphozoan medusae highly depend on food supply and possibly temperature (Båmstedt et al., 1999; Ishii and Båmstedt, 1998; Møller and Riisgård, 2007).

The model results along with the field observations in 2012 and 2013 and the broad distribution observed by several authors across the North Sea (Barz and Hirche, 2007; Hay et al., 1990), indicate that the observed species are generally not bound to or restricted by environmental factors, but rather dependent on hydrodynamic conditions and transport (Graham et al., 2001; Hay et al., 1990). Also, strobilation may occur over a broad range of environmental conditions and throughout the year. Nevertheless, it is unclear whether jellyfish abundances in the North Sea are increasing

rather than declining, which is mainly resulting from few publications which allow quantitative comparison (Barz and Hirche, 2007; Hay et al., 1990; Möller, 1980; Vansteenbrugge et al., 2015). Additionally, our results may indicate jellyfish abundances to have been overestimated in the last 50 years.

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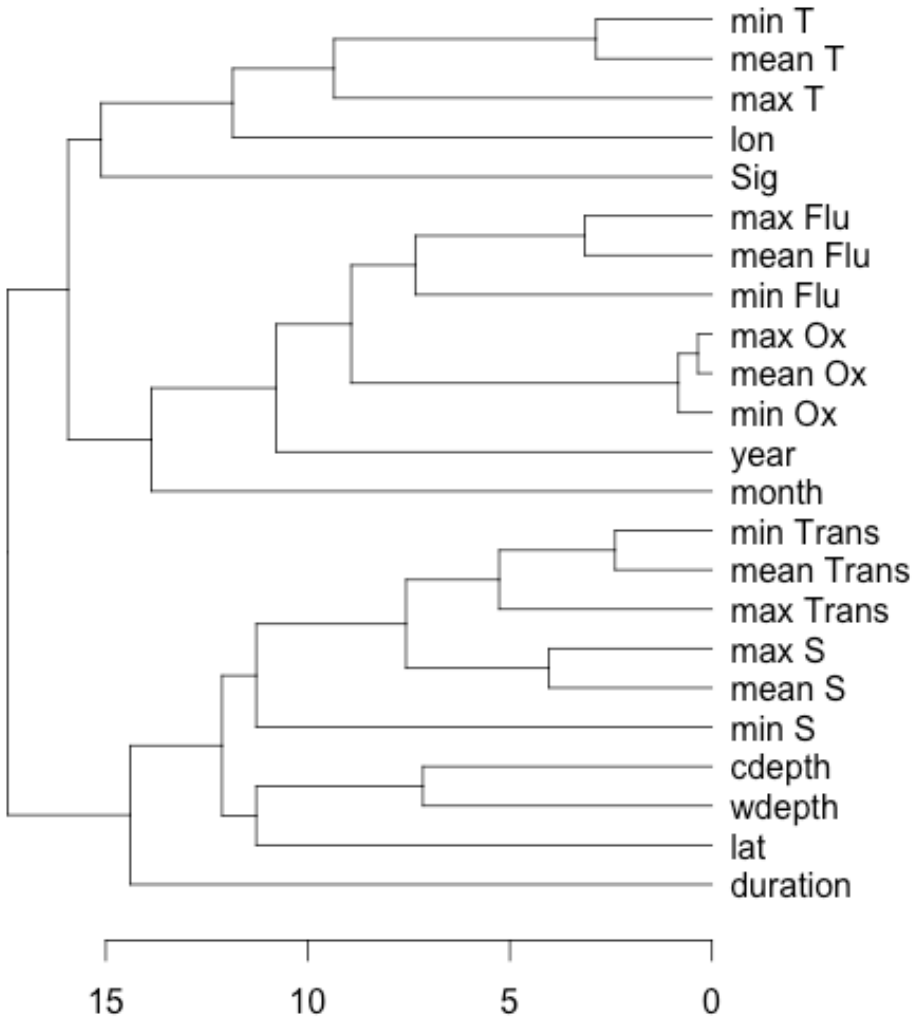
5.7 Supplementary Material



Supplementary Figure S5.8: Hirarchical Cluster Analysis of abiotic factors

CHAPTER 6

General Discussion

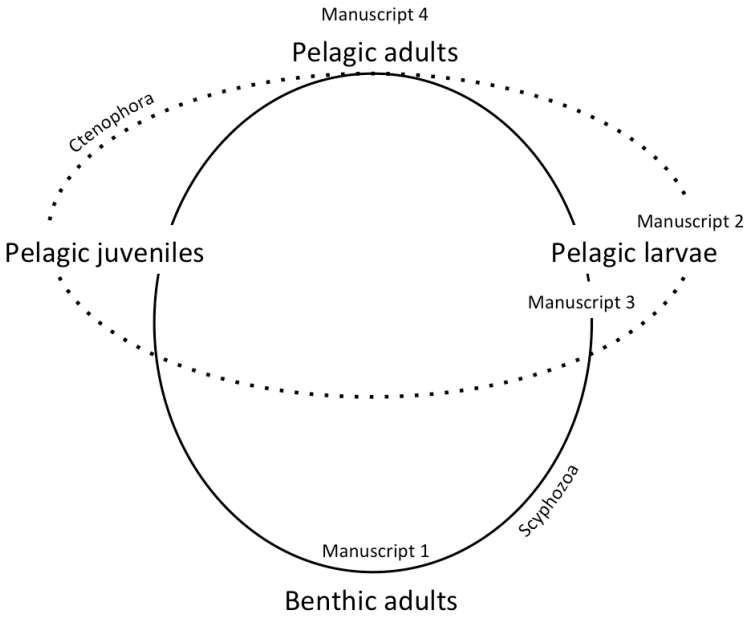
6 General Discussion

Jellyfish blooms are a recurring phenomenon reported from all over the globe. Irrespective of whether numbers of jellyfish are generally increasing or jellyfish simply accumulate in response to hydrodynamic conditions and thus appear to become more dominant, reports of gelatinous zooplankton blooms are rising. Changing environmental conditions such as temperature may impact life cycle dynamics and physiological response in jellyfish. Additionally, reliable information on abundances of pelagic stages and potential habitats of polyps need to be investigated more thoroughly in order to derive causal inference on mass occurrences of gelatinous zooplankton.

In this thesis, thermal windows of different life stages of bloom forming gelatinous zooplankton, as well as abundance and possible habitats for source populations in the North Sea were analyzed. The results contribute to the growing body of information identifying potential causes for jellyfish blooms (Fig. 6.1).

When looking at survival, boundaries of thermal windows in scyphozoan polyps are highly variable, depending on species and geographical range (reviewed in Lucas et al., 2012). Respiration as a key metabolic function is highly dependent on temperature. To date, thermal windows determining the survival of polyps have received little attention (Mangum et al., 1972). Results from *Manuscript 1* display threshold-like changes in respiration rates of scyphozoan polyps with warming temperatures between 7 and 20°C. Significant increase of routine respiration rate (R_R) between 12 and 15°C in three of the five groups tested (*Aurelia aurita, Cyanea capillata, Aurelia labiata*) might reflect a shift in metabolic strategy, similar to the effect reported in ephyrae of *A. aurita* (Møller and Riisgård, 2007). Declines in R_R at temperatures above 18°C were related to the collection locations of the polyps, where monthly mean temperatures never exceeded this value. *Aurelia aurita* polyps from higher latitudes (37°N) displayed thermal boundaries at 12 and 32°C (Mangum et al., 1972). In contrast, while R_R were similar between 12 and 18°C, polyps including *A. aurita* from temperate (lower) latitudes showed upper thermal boundaries around 18°C, while lower boundaries could not be detected in the tested temperature range of 7-20°C

(*Manuscript 1*). These findings confirm differences in thermal windows to be strongly dependent not only on species, but also on geographical range and thus may differ on a population-specific level. Conversion of R_R and weights from the literature into the same units at 15°C showed similarities in metabolic scaling in all life stages. Ephyrae and polyps displayed nearly identical R_R, which is interesting as usually differences between pelagic and benthic stages are expected (Glazier, 2006). Isometric or close to isometric scaling seems common in pelagic and benthic stages of scyphozoan jellyfish at 15°C (*Manuscript 1*).



Manuscript 1: Polyp R_R displayed theshold-like changes with warming temperatures from 7-20°C. Hypoxia reduced R_R at <25% O_2 saturation.

Manuscript 2: Growth and ingestion of larval *M. leidyi* from the North Sea at 8 different temperatures revealed thermal boundaries to be between 7-25°C

Manuscript 3: Settlement dynamics of scyphozoan planula larvae from the North Sea were highly dependent on temperature. Temperature ranges did not cover thermal boundaries of these species. A drift model was used to anticipate potential settling grounds of planulae, thus obtaining information on potential habitats of polyps.

Manuscript 4: Abundances of scyphozoan medusae in the North Sea seem lower than reported. Outputs of hydrodynamic drift models based on catches of medusae suggest potential habitats of polyp populations.

Figure 6.1: Schematic representation of the metagenetic life cycle in scyphozoa and the life cycle in ctenophores, with conclusions of each chapter assigned to the corresponding life stage.

When looking at responses to low oxygen conditions, R_R in *A. aurita* remained constant, until critical oxygen tension was reached, where R_R started to decline monotonically with oxygen concentration. This process was dependent on temperature, displaying the highest threshold to be <25% oxygen saturation at 15.5°C (*Manuscript 1*). These results are in support of findings, describing low oxygen conditions to be favorable for the survival, growth and reproduction of scyphozoan polyps and planula larvae (Condon et al., 2001; Ishii et al., 2008). Also, the gelatinous intragel layer in pelagic stages is reported to function as a storage for oxygen, which

enables medusae to keep metabolism running under hypoxic conditions (Rutherford and Thuesen, 2005; Thuesen et al., 2005).

In several pelagic scyphozoan stages such as ephyrae and medusae, respiration rates displayed strong effects of temperature and high tolerance to low oxygen conditions (Møller and Riisgård, 2007; Rutherford and Thuesen, 2005; Thuesen et al., 2005). Also, respiration rates in ctenophores have been examined, with results suggesting temperature to impact respiration rates in *Mnemiopsis leidyi* as well (Kremer, 1977; Lilley et al., 2014; Purcell et al., 2001). This ctenophore has been reported to show high growth rates together with high feeding rates in adults as well as in larval stages (Costello et al., 2012; Jaspers et al., 2015; Rapoza et al., 2005; Sullivan and Gifford, 2007). When studying these metabolic functions, only few studies considered thermal boundaries in adult organisms (Finenko et al., 2014; Reeve and Baker, 1975; Robinson and Graham, 2014), none of them included larvae of *M. leidyi*.

The results from *Manuscript 2* showed changes in clearance, ingestion and growth rate as a function of temperature in larvae of *M. leidyi* from the North Sea (Fig. 6.1). After identifying optimal prey concentration for maximum growth of 1.5 mm larvae, exponential increases of clearance and ingestion were shown in temperatures between 6 and 25°C, as well as strong linear increase of growth, peaking at 25°C followed by a rapid decrease of rates at higher temperatures (*Manuscript 2*). Rates of ingestion and clearance in larval *M. leidyi* measured in *Manuscript 2* were similar to those reported between 18 and 22°C (Sullivan and Gifford, 2004). Maximum growth rates of 0.87 d^{-1} at 27°C for larval *M. leidyi* (*Manuscript 2*) were in the same range as previously reported growth rates for newly hatched larvae (0.83 d^{-1} at 21°C, Stanlaw et al., 1981) and larvae of 6 mm diameter (0.8 d^{-1} at 26°C; Reeve et al., 1989).

The lack of data concerning thermal windows including all life stages of *M. leidyi* is surprising considering the importance of temperature on the life cycle dynamics of this ctenophore (*Manuscript 2*). Warm temperatures support high rates of growth and feeding. Furthermore, temperatures between 8°C and 25°C were shown to be optimal for *M. leidyi,* corresponding to the monthly mean temperatures in the North Sea, and thus to their habitat (*Manuscript 2*).

When studying the effects of temperature on different types of larvae it is critical to identify whether these effects are genuine or specific in their nature. Planula larvae, a life stage within bloom forming scyphozoans, have received little attention concerning the effects of temperature. Temperature showed accelerating effects on metabolism and settlement of planulae of *Cyanea lamarckii* and *Chrysaora hysoscella* from the North Sea (*Manuscript 3*). Since metabolic needs in planulae are not covered as they have no mouth or gastric system and therefore do not feed, a close relationship between metabolism and settlement was expected. No preference in substrate (concrete, PET, wood) was detected. This was probably due to not providing undersides of substrates, which has repeatedly been reported as preferred area for settlement (Brewer, 1976; Holst and Jarms, 2007; Miyake et al., 2002; Willcox et al., 2008). Rising temperature and light availability showed significant positive effects on settlement success of planula larvae of *Chrysaora hysoscella* (*Manuscript 3*). Darkness previously has been shown to enhance mortality rates in *C. capillata* (Brewer, 1976). In correspondence with recent findings of Mayorova et al. (2014), serotonin-like immunoreactive cells in planulae may inhibit settlement due to the lack of serotonin in darkness. Increasing metabolic costs at warmer temperatures (O'Connor et al., 2007; Schneider and Weisse, 1985) may explain declining numbers of settlers at darkness as opposed to a general increase at better light conditions for *C. hysoscella* (*Manuscript 3*).

Temperatures increasing from 9.4 through 26.8°C showed accelerating effects on settlement of planulae of *C. lamarckii* with stressful conditions presumably around 21°C. Four studies, covering larvae of semaeostomeaen as well as rhizostomeaen jellyfish from various latitudes, did not report similar patterns in temperature responses suggesting general statements concerning the magnitude of larval settlement at rising temperatures to be unwarranted (Fitt and Costley, 1998; Prieto et al., 2010; Riascos et al., 2013; Webster and Lucas, 2012). These findings rather suggest species-specific if not population-specific responses to rising temperatures, pointing out the strong impact of geographical distribution (*Manuscript 3*). The time required for 95% of the larvae to settle (*Manuscript 3*) agreed well with previous estimates made for the rhizostome *Cotylorhiza tuberculata* (Prieto et al., 2010) and the semaeostome *A. aurita* (Webster and Lucas, 2012). With increasing time spent in the

water column, the ability to settle decreased in planula, critically affected by rising temperatures (11.3-19.4°C). However, the final cumulative number of successfully settled individuals was highest at 19.4°C, indicating effects of warming waters to increase settlement speed with simultaneous shortening of the time frame available to find substrate and settle (*Manuscript 3*).

This measure of the ability to settle, commonly referred to as pelagic larval duration (PLD), was calculated to be at 250-300 degree days (*Manuscript 3)*. In contrast, previous findings on *C. lamarckii* from the North Sea suggested PLD to be lower (108°d; Holst and Jarms, 2007). In this study the crucial dependence of this ability on time was not accounted for. The PLD is also highly variable and dependent on temperature and geographical range, as reported in the literature (Brewer, 1978; Calder, 1982; Conley and Uye, 2015; Ishii and Båmstedt, 1998; Lotan et al., 1992; Pitt, 2000; Prieto et al., 2010).

When evaluating data of PLD, it is important to distinguish between survival, swimming, and the ability to complete settlement and metamorphosis, since these features were not taken into consideration when running a model to identify potential habitats of polyps (*Manuscript 3*). Results showed upper thermal limits for *C. lamarckii* planulae to be between 18 and 21°C, whereas lower boundaries exceeded the temperatures tested (*Manuscript 3*). The model, estimating drift distances of larval dispersal in the North Sea, suggested larvae to be transported 50-100 km from release areas, identifying potential source locations of polyps (*Manuscript 3*).

Locating habitats of polyps is a crucial step towards understanding dynamics of jellyfish blooms. It would allow studying populations *in situ*, and thus provide an opportunity to estimate possible consequences of changing environmental condition on jellyfish blooms in a natural environment, as they are the source of the blooming pelagic stages. Unfortunately, the whereabouts of the benthic scyphozoan polyps are mainly unknown (Di Camillo et al., 2010). Based on data of scyphozoan jellyfish in the North Sea in 2012, potential habitats of polyps were identified, using a drift model. Data on the abundance and distribution of *A. aurita*, *C. lamarckii* and *C. capillata* were collected in two consecutive years (2012 and 2013), using a large young fish trawl (YFT), with net openings between 60 and 100 m^2, depending on the speed of the boat

(*Manuscript 4*). Annual fluctuations in species composition have been reported (Barz and Hirche, 2007 and references therein), as well as distinct distribution patterns of both *Cyanea* species (Russell, 1970). Using a statistical approach, results from *Manuscript 4* did not display any relationship of distribution with abiotic factors such as temperature or salinity, supporting the notion of patchy areas of medusae to derive from hydrodynamic conditions (Graham et al., 2001; Hay et al., 1990). Abundances of jellyfish seemed to be lower with larger nets (*Chapter 4*; Suchman and Brodeur, 2005) compared to abundances obtained from smaller trawls (Hay et al., 1990) or plankton nets (Barz and Hirche, 2007; Vansteenbrugge et al., 2015). For the North Sea, only little data is available and was obtained with various sampling techniques (Barz and Hirche, 2007; Hay et al., 1990; Möller, 1980; Vansteenbrugge et al., 2015; Van Walraven et al., 2014).

The hydrodynamic model conducted in order to identify potential habitats of polyps (*Manuscript 4*), provided indications of periods and temperatures at which recruitment to the pelagic life stage due to strobilation could occur. The model output is largely supported by Holst (2012), who identified possible seasons and temperatures for the induction of strobilation and consequent release of the pelagic stage.

Recently, the validity of the metagenetic life cycle has been questioned, proposing a multi-modal approach involving ideas such as overwintering in medusae, and strobilation throughout the year (Ceh et al., 2015). Thus, conclusions drawn to explain dynamics behind blooms involving the timing of the metagenetic life cycle should be reevaluated. Additionally, the availability of literature covering abundances of scyphozoan jellyfish in the North Sea exemplify the necessity for standard protocols and regular surveys in order to make reliable statements on jellyfish dynamics, and also to eventually find habitats of polyps.

6.1 Conclusion and Outlook

Examining thermal windows of different life stages of bloom forming jellyfish (*Manuscripts 1, 2, 3*) revealed no universal effect of temperature or general thermal boundaries, but largely population-specific effects of temperature on metabolism of jellyfish. Respiration rates of scyphozoan polyps from temperate latitudes revealed thermal boundaries at 7 and 18°C. The lower boundary was not necessarily reached, as

temperatures below 7°C were not included in the experiment (*Manuscript 1*). Interestingly, the lower thermal boundary restricting ingestion and growth, but not survival in larval *Mnemiopsis leidyi* from the North Sea was around 7-8°C, with an upper boundary around 25°C (*Manuscript 2*). Settlement speed of planula larvae of *C. lamarckii* from the North Sea suggested upper thermal limits to be at 18-21°C, whereas lower boundaries could not be detected, as the lowest test temperature of at 9.4°C did not threaten survival. Temperature dependent pelagic larval duration was around 250-300 degree days, implying larval drift distances of up to 100 km in the North Sea after release (*Manuscript 3*). These findings display how diverse life stages react differently to changing temperature conditions, pointing out population-specific metabolic responses particularly when including findings from the literature (e.g. Fitt and Costley, 1998; Lilley et al., 2014; Mangum et al., 1972; Møller and Riisgård, 2007; Prieto et al., 2010; Riascos et al., 2013; Webster and Lucas, 2012).

Understanding physiological responses of different life stages to changing temperatures (*Manuscripts 1, 2, 3*) is only one part when trying to comprehend mechanisms behind jellyfish blooms. The habitats of the benthic bloom forming life stage need to be identified in order to learn more about their ecology (*Manuscripts 3, 4*). To answer the question whether numbers of jellyfish in the North Sea are rising, regular jellyfish surveys need to be conducted on a large scale, using standard protocols. As long as this is not the case, it will not be possible to make valid statements on whether jellyfish blooms in the North Sea are expected to be accompanied by successively growing numbers of medusae, or if blooms are just a phenomenon of hydrodynamic conditions (*Manuscript 4*).

The findings obtained in this thesis suggest several directions of future research. More research on metabolism considering all life stages of bloom forming species need to be conducted in order to understand the full magnitude behind blooms. Evaluating effects of environmental changes on metabolism within and across species from different latitudes is important to gain a full picture of population-specific responses. Additionally, standard protocols need to be established to obtain reliable insight on abundances. Misclassification of species may lead to false conclusions, considering large differences in life cycle dynamics of jellyfish and resulting mass occurrences. The

results from this thesis cover various life stages of bloom forming gelatinous zooplankton and thus add to the growing body of information. Still, more research needs to be conducted in order to comprehend the life cycle dynamics of jellyfish and consequently, blooms.

Judging cause-and-effect mechanisms behind jellyfish blooms is not an easy task, as the underlying structures are very complex. The source of jellyfish blooms may not be medusae, but rather other life stages such as polyps, larvae, or even joint contributions. Rising temperatures accelerate metabolic processes in all life stages of jellyfish. Gelatinous zooplankton is experiencing an advantage with warming waters over other species (such as fish), which can be explained by their large thermal windows. In evolution, conquering different ecological niches molds species differentiation, which makes species highly adapted to certain environmental and geographical conditions. Gelatinous zooplankton, however, are not specialized to certain ecological niches, including temperature, which allows them to survive and reproduce under circumstances deadly to other species in the ocean. On top of that, predation pressure on gelatinous zooplankton is minor and jellyfish are not being economically exploited such as fish, which allows them to flourish unimpeded. Thus, changing environmental conditions may be threatening to various species in the ocean, but not to gelatinous zooplankton. These opportunistic species may conquer the oceans and survive through mass. We better start knowing them.

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Outline of Publications

The following overview outlines the four manuscripts included in this thesis, as well as the contributions from co-authors. This thesis was funded by the European Community's Seventh Framework Program (FP7/2007-2013) under Grant Agreement No. 266445 for the project Vectors of Change in Oceans and Seas Marine Life, Impact on Economic Sectors (VECTORS). Funding was also received from the German Science Foundation (DFG, Physi2CoGel, Grant No. PE1157/3-1).

Manuscript 1

Respiration rates of the polyps of four jellyfish species: Potential thermal triggers and limits – Journal of Experimental Marine Biology and Ecology (2014) 459: 17-22

Maria Gambill and Myron A. Peck

MG and MAP designed the experiments. MG conducted the experiments under supervision of MAP. MG conducted the data analysis and wrote the text under close supervision of MAP, who critically reviewed the manuscript and provided valuable comments

Manuscript 2

Effects of temperature on the feeding and growth of the larvae of the invasive ctenophore *Mnemiopsis leidyi* – Journal of Plankton Research (2015) 37(5): 1001-1005

Maria Gambill, Lene Friis Møller, Myron A. Peck

MG and LFM designed and conducted the experiment. MG, LFM and MAP conducted the data analysis and wrote the manuscript.

Manuscript 3

Temperature-dependent settlement of planula larvae of two scyphozoa jellyfish from the North Sea – re-submitted to Estuarine, Coastal and Shelf Science (in revision)

Maria Gambill, Sadie L. McNaughton, Markus Kreus, Myron A. Peck

This manuscript was re-submitted to Estuarine, Coastal and Shelf Science in November 2015 after revision. No final decision was made until this thesis was finished. MG and MAP designed the experiments. MG and SLM conducted the experiments under

supervision of MAP. MG conducted the data analysis and wrote the text under supervision of MAP, who critically reviewed the Manuscript and provided valuable comments. MK ran the model and wrote the text concerning the model.

Manuscript 4

Abundance of large bloom forming semaeostomeaen jellyfish in the southern North Sea and potential habitats of scyphistomae – Manuscript in preparation

Maria Gambill, Myron A. Peck, Marc Hufnagl

MG and MAP designed the sampling protocol. MG and students from the Institute of Hydrobiology and Fisheries Science, University of Hamburg collected the data onboard the RV Heincke. MG and MH evaluated the data and wrote the Manuscript. MAP critically reviewed the Manuscript and provided valuable comments.

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Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift

„Ecophysiology and Life Cycle Dynamics of North Sea Gelatinous Zooplankton“

selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

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Hamburg, den 23. November 2015 Maria Gambill