Influence of pelagic invertebrate predators on the zooplankton in the Baltic Sea and the North Sea

Einfluss pelagischer wirbelloser Räuber auf das Zooplankton der Ost- und Nordsee

Kristina Barz

Dissertation zur Erlangung des akademischen Grades eines Doktors der
Naturwissenschaften (Dr. rer. nat.)
vorgelegt an der Universität Bremen (Fachbereich 2 - Biologie/Chemie)

Bremen 2006

Stiftung Alfred-Wegener-Institut für Polar- und Meeresforschung in der Helmholtz-Gemeinschaft
Alfred Wegener Institute for Polar and Marine Research
D-27568 Bremerhaven
Bundesrepublik Deutschland - Federal Republic of Germany

Contents

Summary III
Zusammenfassung V
1 Introduction 1
2 Overview 3
2.1 Chaetognatha and Mysidacea 3
2.2 Scyphomedusae 3
2.2.1 Life cycle 4
2.2.2 Mortality 5
2.2.3 Changing abundance and possible causes 6
2.2.4 Regime shifts in the Baltic Sea and North Sea 7
2.2.5 Consequences of high medusae abundance 8
2.3 Objectives of this thesis 9
2.4 Thesis outline 10
3 Study areas 11
3.1 Baltic Sea 11
3.2 North Sea 13
4 Material and Methods 14
4.1 Sampling 14
4.1.1 Sampling dates 14
4.1.2 Central Baltic Sea 15
4.1.3 Southern North Sea 16
5 Results and Discussion 17
5.1 Chaetognatha in the central Baltic Sea – occurrence and impact 17
5.2 Mysidacea in the central Baltic Sea – occurrence and impact 19
5.3 Scyphomedusae 23
5.3.1 Central Baltic Sea 23
5.3.2 Southern North Sea 29
6 Synthesis 31
6.1 Species diversity 31
6.2 Prey and predatory impact 31
6.3 Abundance control by physical forcing? 32
6.4 Future perspectives 34

7 Publications 35

Seasonal development of scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (central Baltic Sea) 36

Scyphozoa in the Bornholm Basin (central Baltic Sea) – The role of advection..............49

Abundance, distribution and prey composition of Scyphomedusae in the southern North Sea 60

8 Acknowledgements 84

9 References.. 86

10 Appendices.. 98

10.1 List of abbreviations..98

Erklärung gem. § 6 (5) Nr. 1-3 Promotionsordnung...99

Summary

Pelagic invertebrates are conspicuous members of the zooplankton in the oceans world wide. They have a wide prey spectrum and may constitute important predators in the pelagial. When reaching high abundance they can affect and reduce the stocks of several zooplankton species and fish larvae considerably. This study analyses the impact of pelagic invertebrate predators in the two connected ecosystems Baltic Sea and North Sea. Both ecosystems have different hydrographic conditions, but also show similarities in their reaction to changing ocean conditions (synchronous regime shifts) and were object of comparative studies in the framework of the German GLOBEC Project.

The main focus of this study was on investigations in the central Baltic Sea (Bornholm Basin) in the years 2002 and 2003. A Major Baltic Inflow event (MBI) of high saline water masses from the North Sea in January 2003 allowed a comparative study of this ecosystem under different hydrographic conditions. The main group of invertebrates investigated in the central Baltic Sea were the Scyphomedusae, but data on Chaetognatha and Mysidacea were also collected and analysed. The study in the southern North Sea was conducted in the years 2004 and 2005 and focused only on Scyphomedusae.

Only two Scyphomedusae species occurred in the central Baltic Sea: *Aurelia aurita* and *Cyanea capillata*. Both species showed the same low abundance in 2002 and 2003. In the North Sea four Scyphomedusae occurred during this investigation in 2004 and 2005: *A. aurita, C. capillata, C. lamarckii* and *Chrysaora hysoscella.* Compared to adjacent areas, abundance of all species was also low. The medusae mainly preyed on crustacean species in both ecosystems. Due to the low medusae and high zooplankton abundance the predatory impact on the zooplankton community in the central Baltic Sea was low. For the southern North Sea, predatory impact was not calculated, but the low medusae abundance lets assume, that the impact was low, too.

In the central Baltic Sea, *A. aurita* did not feed on fish eggs and larvae, as medusae and the eggs and larvae of dominant fish species showed a clear seasonal and vertical mismatch in their patterns of occurrence. These mechanisms prevented fish eggs and fish larvae from predation and competition in this area. In the southern North Sea medusae consumed high numbers of fish eggs and larvae, but it was assumed that medusae did not control the fish populations, due to their low abundance.

Sagitta elegans was the only species of Chaetognatha caught in the central Baltic Sea. It occurred sporadically and was generally low abundant. The abundance maximum was recorded in January 2003 and was clearly related to the MBI. Due to their low abundance, it was assumed that Chaetognatha in the central Baltic Sea had no negative impact on the zooplankton community and fish populations in 2002 and early 2003.

The only species of Mysidacea caught in this investigation was *Mysis mixta*. Swarms of *M. mixta* were found from July to November. They were mainly located at more shallow stations in the north-east and in the south of the study area. Hence, a higher impact on the populations of zooplankton may occur only locally. Although the investigated specimens consumed the same food as fish larvae in this area, no competition for food is expected, as the big swarms of *M. mixta* appeared mainly after the mass occurrence of larvae.

The occurrence patterns of the Scyphomedusae *A. aurita* and *C. capillata* in the central Baltic Sea were completely different in both years. In 2002 first individuals appeared in early July and no ephyrae of either species occurred. These observations were congruent with earlier investigations and suggest, that *A. aurita* and *C. capillata* do not strobilate in this region. In contrast, in 2003 ephyrae were caught in April and small medusae of *A. aurita* and *C. capillata* appeared already in May. The observations in 2002 and 2003 allowed an inter-annual comparison under different hydrographic conditions. Information on strobilation regions and timing in the western Baltic Sea were combined with a 3-dimensional baroclinic model of the Baltic to prove the possibility of advection of medusae from the western to the central parts. For 2002 the model predicted an arrival of medusae in the central Baltic Sea at the end of June. This arrival fits in time exactly with the observations. In 2003 the successive inflow events associated with the MBI most likely caused earlier arrival in the central Baltic. The results explain the absence of ephyrae in the central Baltic Sea in 2002 and in earlier investigations. The ephyrae developed into medusae until late June during their drift before reaching the central Baltic Sea. High transport rates, associated with the inflows in 2003 were necessary to advect ephyrae into the central Baltic, prior to their development into medusae. It is still unclear, whether settlement and strobilation occur in the central Baltic Sea, however, strobilation success would be probably low, and the population is likely to depend on early stages of medusae advected from the western parts of the Baltic Sea. The earlier occurrence of medusae in the central Baltic Sea in 2003 resulted in an overlap of medusae with fish larvae and eggs and may have caused a higher impact on fish populations by predation and competition.

These observations clearly demonstrate the impact of physical forcing on the polyp and ephyrae stages and its effects on abundance and occurrence patterns of medusae, which in turn may affect the populations of zooplankton and fish. Hence, information about the biology and the location of polyp populations is essential to predict the abundance and distribution of medusae to the point of medusae “blooms”.

Zusammenfassung

Pelagische Wirbellose sind ein wichtiger Bestandteil des Zooplanktons in allen Ozeanen weltweit. Da sie ein breites Nahrungsspektrum besitzen, können sie wichtige Räuber im Pelagial darstellen und in hohen Abundanzen die Populationen von Zooplankton und Fischlarven beträchtlich reduzieren. Diese Studie untersucht daher den Einfluss von pelagischen wirbellosen Räubern in den zwei zusammenhängenden Ökosystemen Ost- und Nordsee. Diese Ökosysteme weisen unterschiedliche hydrographische Merkmale auf, reagieren aber ähnlich auf sich verändernde Situationen in den Ozeanen (synchrone „regime shifts“) und sind daher Gegenstand vergleichender Untersuchungen im Rahmen des Projekts GLOBEC Germany.

Das Hauptaugenmerk dieser Untersuchung lag auf der zentralen Ostsee (Bornholm Becken) in den Jahren 2002 und 2003. Ein “Major Baltic Inflow event” (MBI) mit dem Einstrom von salzreichem Wasser aus der Nordsee im Januar 2003 erlaubte eine vergleichende Studie in zwei Jahren mit unterschiedlichen hydrographischen Bedingungen. In der zentralen Ostsee wurden hauptsächlich die Scyphomedusen untersucht, aber auch Daten über Chaetognathen und Mysidaceen gesammelt und analysiert. In der südlichen Nordsee waren hingegen nur die Scyphomedusen Gegenstand der Untersuchungen, die in den Jahren 2004 und 2005 durchgeführt wurden.

In der zentralen Ostsee traten nur zwei Arten von Scyphomedusen auf, *Aurelia aurita* und *Cyanea capillata*. Beide Arten wiesen sowohl 2002 als auch 2003 eine geringe Abundanz auf. In der Nordsee wurden hingegen vier Arten von Scyphomedusen gefangen: *A. aurita, C. capillata, C. lamarckii* and *Chrysaora hysoscella.* Verglichen mit angrenzenden Gebieten war ihre Abundanz in den Jahren 2004 und 2005 ebenfalls gering. In beiden Untersuchungsgebieten fraßen die Medusen überwiegend verschiedene Krebsarten. Aufgrund ihrer geringen Häufigkeit und der hohen Zooplanktondichte in der zentralen Ostsee war der räuberische Einfluss der Medusen nur gering. Für die südliche Nordsee wurde der Einfluss zwar nicht berechnet, wird aber aufgrund der vergleichbar niedrigen Medusenabundanz ebenfalls als gering eingeschätzt.

Die Analyse des Mageninhalts zeigte, dass *A. aurita* in der zentralen Ostsee keine Fischeier und –larven gefressen hat. Medusen und die Eier und Larven dominanter Fischarten kommen in dieser Region zu unterschiedlichen Zeiten und in verschiedenen Tiefenstufen vor. Dieser Versatz schützt Fischeier und –larven in der zentralen Ostsee vor Nahrungskonkurrenz und davor, gefressen zu werden. In der südlichen Nordsee hingegen haben die Medusen eine große Anzahl von Fischeiern und –larven konsumiert. Aufgrund der geringen Medusenabundanz wurde aber wiederum kein Einfluss auf die Fischpopulationen angenommen.

Die einzige Chaetognathenart, die in der zentralen Ostsee gefangen wurde, war *Sagitta elegans*. Sie kam nur sporadisch und in niedriger Abundanz vor. Maximale Mengen wurden im Januar 2003 gefangen. Dieses Abundanzmaximum war eindeutig verbunden mit dem MBI. Wegen ihrer geringen Abundanz hatten Chaetognathen in der zentralen Ostsee in den Jahren 2002 und 2003 wahrscheinlich keinen negativen Einfluss auf die Zooplanktongemeinschaft und die Fischpopulationen.

Mysis mixta war die einzige Mysidaceenart, die in der zentralen Ostsee gefangen wurde. *M. mixta* trat in Schwärmen von Juli bis November auf. Die Schwärme wurden überwiegend auf den flacheren Stationen im Nordosten und Süden des Untersuchungsgebiets gefunden. Ein Einfluss auf die Zooplanktonpopulationen trat daher wahrscheinlich nur lokal auf. Obwohl die untersuchten Tiere das gleiche Beutespektrum wie Fischlarven in dieser Region hatten, ist keine Nahrungskonkurrenz anzunehmen, da die Schwärme von *M. mixta* überwiegend nach dem Abundanzmaximum der Fischlarven auftraten.

Die Vorkommensmuster der Scyphomedusen *A. aurita* und *C. capillata* in der zentralen Ostsee unterschieden sich in den beiden untersuchten Jahren. Im Jahr 2002 erreichten die ersten Tiere das Untersuchungsgebiet Anfang Juli, Ephyren konnten nicht beobachtet werden. Diese Ergebnisse waren in Einklang mit früheren Untersuchungen und führen zu dem Schluss, dass keine der beiden Arten in der zentralen Ostsee strobiliert. Im Jahr 2003 hingegen traten im April die ersten Ephyren auf und im Mai wurden bereits kleine Medusen gefangen. Die Beobachtungen in 2002 und 2003 erlaubten einen Vergleich von zwei Jahren mit unterschiedlichen hydrographischen Bedingungen. Informationen über Strobilationsorte und –zeiten in der westlichen Ostsee wurden in ein 3-dimensionales Modell der Ostsee eingespeist, um die Möglichkeit der Advektion von Medusen aus der westlichen in die zentrale Ostsee zu überprüfen. Für 2002 sagte das Model eine Ankunft der Medusen Ende Juni voraus, was exakt mit unseren Beobachtungen in diesem Jahr übereinstimmte. Im Jahr 2003 bewirkten die mit dem MBI assoziierten Einströme von Nordseewasser höchstwahrscheinlich eine frühere Ankunft der Medusen in der zentralen Ostsee. Die Ergebnisse erklären das Fehlen von Ephyren in der zentralen Ostsee im Jahr 2002 und in früheren Untersuchungen, da die Ephyren bis Ende Juni während ihrer langen Drift in die zentrale Ostsee zu Medusen auswachsen. Höhere Transportraten, wie sie mit dem MBI im Jahr 2003 verbunden waren, sind nötig, um die Ephyren in die zentrale Ostsee zu verbringen, bevor sie zu Medusen auswachsen. Es ist nicht geklärt, ob strobilierende Polypen in der zentralen Ostsee vorkommen. Wahrscheinlich ist der Strobilationserfolg gering und die Medusenpopulationen hängen mit Sicherheit von einem Zustrom aus der westlichen Ostsee ab. Das frühe Auftreten der Medusen in der zentralen Ostsee im Jahr 2003 führte zu einer Überschneidung im Vorkommen mit Fischlarven und –eiern und

könnte daher zu einem größeren Einfluss auf die Fischpopulationen durch direkten Fraß und Nahrungskonkurrenz geführt haben.
Diese Ergebnisse machen deutlich, wie wichtig der Einfluss physikalischer Faktoren auf die Polypen- und Ephyrenstadien ist, und wie er die Abundanz und Verteilung der Medusen beeinflusst. Diese wiederum haben einen wechselnden Einfluss auf Zooplankton- und Fischpopulationen. Es ist daher essentiell, Informationen über das Vorkommen und die Biologie von Polypenpopulationen zu erhalten, um Vorhersagen über die Abundanz und Verteilung von Medusen machen zu können, bis hin zur Vorhersage von „Quallenblüten“.

1 Introduction

Marine ecosystems are mostly self-sustaining systems of life forms and the physical environment. Interactions between species and their environment are correlated in complex food webs. Subsequent advances in the understanding of structure, function and dynamics of the food webs are of vital importance to ecosystem management and conservation (Belgrano et al. 2005). Two main concepts have been proposed to specify the mechanisms regulating the biomass and abundance of organisms in aquatic food webs (e.g. McQueen et al. 1986; Pitta et al. 1998):

1. Resource availability regulates the biomass on a trophic level from the bottom
   ➔ bottom-up force
2. Predation affects the biomass on a trophic level from the top
   ➔ top-down force

Studies of marine pelagic ecology are biased towards bottom-up force, as for a long period of time this was regarded to be a more important factor in ecosystem control than top-down effects. However, in recent years top-down effects were considered to be of equal importance (Verity and Smetacek 1996). Top-down and bottom-up mechanisms interact in concert to determine population size and ecosystem structure (Hunter and Price 1992; Hunt et al. 2002; Sinclair et al. 2003), but their relative importance may vary by location (Hunt and McKinnell 2006). Therefore, a combined investigation of both aspects is necessary in modern large-scale ocean science. In addition, physical effects of changing ocean conditions, often related to "climate change", have to be considered. They may affect the biology and abundance of predators in terms of bottom-up forcing by controlling their reproductive success (Lynam et al. 2004; Hunt and McKinnell 2006) and by regulating plankton abundance as their food (Hays et al. 2005).

GLOBEC Germany combined all these aspects in an interdisciplinary project. The project aims for a better understanding of trophodynamic interactions between zooplankton and planktivorous fish in relation to reproductive success under the impact of physical forcing. Top-down and bottom-up processes were studied comparatively in the Baltic Sea and the North Sea. Several fish and copepod populations have experienced high fluctuations in biomass and recruitment in both ecosystems over the last decades, which were related to climatic induced regime shifts (Alheit et al. 2005; Möllmann et al. 2003; Beaugrand 2004).

Fish are important predators in both ecosystems (Kornilovs et al. 2001; Möllmann et al. 2004; Floeter and Temming 2005), but also pelagic invertebrates may be functionally paramount, as they are conspicuous members of the zooplankton in the oceans world wide. Pelagic invertebrate predators have a wide prey spectrum. When reaching high abundance they can affect and reduce the stocks of several zooplankton species and fish larvae considerably (e.g. Möller 1980a; Purcell 1992; Schneider and Behrends 1998; Baier and Purcell 1997; Tönnesson and Tiselius 2005; Rudstam and Hansson 1990). As they feed on the same kinds of prey, they often directly compete for food with planktivorous adult and larval fish. In addition, many invertebrate species are known to feed on fish eggs and larvae (Purcell 1985; Brodeur et al. 2002; Feigenbaum and Maris 1984; Feigenbaum 1991; Alvarez-Cadena 1993) and thus directly affect the recruitment of fish stocks.

The diversity of pelagic invertebrates in the North Sea and Baltic Sea is different. In the southern North Sea Hydromedusa, Chaetognatha, Appendicularia and Ctenophora are found commonly and may reach high densities during their seasonal cycles (reviewed in Krause et al. 2003). In spring and summer months also meroplanktonic larvae (e.g. Polychaeta and Decapoda) may reach high abundance (Martens 1980; Gerdes 1985). The Baltic Sea has a considerably lower number of species, since compared to freshwater and seawater, brackish waters are characterised by the lowest number of indigenous species (Remane 1934). Hence, the importance of food web complexity for ecosystem functioning can be studied in a comparative manner between the two systems. As scyphozoan medusae were the main obvious pelagic invertebrate predators in both seas, this study concentrated on their predatory impact on the zooplankton communities in the Baltic Sea and the North Sea, with the main focus on the Baltic Sea. Research in the Baltic Sea was completed with investigations on occurrence, abundance and predatory impact of Chaetognatha and Mysidacea, as they were the main additional pelagic invertebrate predators in this area (Mauchline 1980; Salemaa et al. 1990; Margonski and Maciejewska 1999; Maciejewska and Margonski 2001).

2 Overview

This overview will shortly introduce the Chaetognatha and Mysidacea, which played a minor role in this investigation. The main focus is on topics related to Scyphomedusae.

2.1 Chaetognatha and Mysidacea

Chaetognatha occur in nearly every marine habitat. All species are either marine or estuarine. They are strictly carnivorous and may feed on several trophic levels (Feigenbaum and Maris 1984). Planktonic chaetognaths are often abundant and play an important role in the marine food web as the primary predators on copepods. They are thought to be an important link in the energy conversion from primary producers, via copepods, into higher trophic levels (Reeve 1980). In addition Chaetognatha were found to feed on fish larvae (Alvarez-Cadena 1993; Baier and Purcell 1997). *Sagitta elegans* and *S. setosa* are the most abundant chaetognaths in European and boreal waters (Øresland 1987). Both species may occur in the Baltic Sea, but they are most probably allochthonous in this region. Their occurrence depends on advection with saline waters from the Kattegat (Maciejewska and Margonski 2001).

Species of the group Mysidacea occur in vast numbers in coastal regions. There are many brackish water species and a few species that occur in freshwater (Mauchline 1980). Mysidacea are an important element of the food web in the Baltic Sea. They may constitute important competitors with fish larvae (Rudstam and Hansson 1990), but are in turn an essential food source for coastal fish (Mauchline 1980). There are several dominant resident species in the Baltic Sea, whereof *Mysis mixta* is common throughout the whole Baltic Proper (Mauchline 1980).

2.2 Scyphomedusae

Scyphomedusae are probably the most obvious pelagic invertebrate predators in marine ecosystems worldwide. They represent a conspicuous component of the plankton, especially during summer months (Brodeur et al. 2002). In recent years medusae are gaining substantial interest in many aspects, especially related to their increasing abundance observed in several ecosystems (e.g. Mills 2001; Parsons and Lalli 2002; Purcell 2005). The following chapter will introduce some important topics related to Scyphomedusae, starting with basic information about their life cycle and mortality to the point of their role in different ecosystems and factors controlling their abundance.

2.2.1 Life cycle

The life cycle of Scyphozoa is characterised by an alternation of generations (metagenesis). It includes a planula larva that develops into a polyp. The polyp asexually buds more polyps and produces ephyrae by strobilation, which develop into medusae, and finally reproduce sexually. The ephyrae are produced and released from sessile polyps, which are living on hard substrate in coastal areas. Strobilation is triggered by a seasonal progression or combination of environmental changes in sea temperature, salinity, food and light, and may differ among species (e.g. Spangenberg 1965; Russel 1970; Brewer and Feingold 1991; Miyake et al. 2002). The life cycle of Scyphomedusae often leads to transient “blooms”, as the asexual production process is usually seasonal (Mills 2001). The majority of medusae e.g. *Aurelia aurita* and *Cyanea capillata* degenerate and die after the sexual reproduction (Hamner and Jenssen 1974; Möller 1979, 1980a; Hay et al. 1990; Barz and Hirche 2005, PUBLICATION I). However, over-wintering specimens of this species often contributed significantly to the biomass found in spring and early summer (Hay et al. 1990; Barz and Hirche manuscript, PUBLICATION III). A lifespan of two years with a second reproduction phase has been suggested for *A. aurita* in Japanese waters (Omori et al. 1995; Miyake et al. 1997).

Most investigations on Scyphozoa focused on the medusae stage, as it is readily found in conventional plankton samples. Polyp populations are hard to find in the field. They preferentially settle in shaded places, upside down from a hard surface (e.g. Brewer 1976). Studies on polyp behaviour and production of ephyrae therefore are mostly conducted in the laboratory (e.g. Spangenberg 1965, 1967; Brewer 1976, 1978; Svane and Dolmer 1995; Kroiher et al. 2000; Siefker 2004). In the Baltic Sea and the North Sea ephyrae are produced during winter and early spring (Möller 1980a; Schneider and Behrends 1994; Gröndahl and Hernroth 1987; Gröndahl 1988; Olesen et al. 1994). An abundance peak of ephyrae in the western Baltic was found in April (Möller 1980b; Olesen et al. 1994). In the southern North Sea as well as in the central Baltic Sea locations of polyp populations are rarely known. Most reports refer to regions outside the study area or were performed >40 years ago (e.g. Hartlaub 1894; Kühl 1964). In the Skagerrak polyp populations (*A. aurita, C. capillata, C. lamarckii*) are reported from the Gullmar Fjord (Hernroth and Gröndahl 1983; Gröndahl 1988). In the Baltic Sea *A. aurita* polyp populations are known from more recent and older investigations in the Kiel Bight (western Baltic Sea) (Kändler 1961; Thiel 1962; Möller 1980a; Schneider and Behrends 1994) and Kerteminde Fjord (Belt Sea, Denmark) (Olesen et al. 1994). In former publications, the Archipelago of south-west Finland was also mentioned as a strobilation area (Wikström 1932; Palmen 1953). In the central Baltic Sea no locations of large polyp populations are known. This region is characterised by the absence of ephyrae and a late appearance of young medusae (Janas and Witek 1993; Lischka 1999; Barz and Hirche 2005, PUBLICATION I). Knowledge about the location of polyp populations in the southern North Sea is also mostly based on assumptions and historical findings. *A. aurita* populations are known from Helgoland Island (Sabine Holst pers. comm.), Borkum Island and Wilhelmshaven (Kühl 1964). Often the existence of polyp populations was derived from the regional distribution of small ephyrae such as described for *A. aurita* in the Dutch Wadden Sea (van der Veer and Oorthuysen 1985), and *C. hysoscella* in the Elbe Estuary (Kühl and Mann 1967; Merck 1989). The absence of polyps was assumed, when no ephyrae were caught or the ephyrae were too large to have been recently released, as in the northern Wadden Sea of Sylt Island (Kopacz 1994).

2.2.2 Mortality

Scyphozoa are eaten by a wide variety of predators. They are consumed by other jellyfish, planktonic and benthic invertebrates, sharks, bony fish, turtles and birds (e.g. Harrison 1984; Ates 1988, 1991; Arai 1997). In the laboratory, *Aurelia aurita* were eaten by several hydrozoan medusae as well as by *Cyanea capillata* and *Chrysaora hysoscella* (Arai and Jacobs 1980). In the field *A. aurita* may constitute an important prey source for *C. capillata* (Båmstedt et al. 1997; Hansson 1997). Polyps of *C. capillata* and *A. aurita* are subject to predation by nudibranchs, as in the Gullmar Fjord (western Sweden), where the main predator is *Coryphella verrucosa* (Hernroth and Gröndahl 1985; Gröndahl and Hernroth 1987). Beside the natural predation, Scyphozoa are the basis of commercial fisheries in different parts of the world (reviewed in Kingsford et al. 2000). There is an increasing interest in processing and marketing new species, mainly of the rhizostome medusae group, as this contains many large species. However, semaeostome medusae, such as *A. aurita, Cyanea* spp. and *Chrysaora* spp. are of poor quality after processing and therefore of less interest (Sloan and Gunn 1985).

Another mortality factor of Scyphomedusae is the infestation by parasites. A wide range of possible metazoan parasites such as trematode and cestode larvae has been recorded (reviewed in Arai 1997). Hyperiid amphipods are also infesting Scyphomedusae. Thus, *Hyperia galba* is a widespread parasite infesting all large medusae, which occur in the North Sea (Dittrich 1988). It is not known to what extent this parasite reduces the fecundity of the medusae or contributes to their mortality, but according to Dittrich (1988) heavy infestation by *H. galba* may lead to a weakening and progressive breakdown of medusae populations in the North Sea.

2.2.3 Changing abundance and possible causes

In recent times Scyphomedusae attract more attention by unusual “blooms”, non-indigenous species invading new ecosystems (reviewed in Mills 2001) or plagues of giant medusae in Japan (Kawahara et al. 2006). Medusae generally show high inter-annual fluctuations in their abundance (Schneider and Behrends 1994), but native and non-indigenous species have increased in local or regional ecosystems in the last years (reviewed in Mills 2001). Their abundance was increasing in the Bering Sea, Benguela Current and Yangtze Estuary (Brodeur et al. 1999, 2002; Brierley et al. 2001; Purcell 2005; Xiang et al. 2005), but also decreases in medusae populations were reported (Mills 2001; Dawson et al. 2001). Changes are probably caused by pollution or overfishing (Brodeur et al. 1999; Arai 2001; Purcell and Arai 2001). Massive removals of fish from ecosystems open up food sources for gelatinous predators and allow the population to expand (Mills 2001). Also an increase in man-made structures such as floating piers in coastal areas may lead to mass occurrence of medusae (Miyake et al. 2002), as they often provide an adequate hard substrate for polyp settlement. In addition, there is evidence that changes in medusae abundance are indicators of climate induced regional regime shifts (Brodeur et al. 1999; Lynam et al. 2004, 2005a). These climate effected changes in the oceans may be man-made, but also natural climate cycles may affect jellyfish populations. Because of their short generation times, populations of scyphozoan medusae appear to respond to climate forcing without a time lag (Lynam et al. 2005a). To identify the influence of climate variations, records of jellyfish abundance were related to indices of climate oscillations such as El Niño Southern Oscillation or North Atlantic Oscillation (NAO) (reviewed in Purcell 2005). Overlaid on natural climate variation is the potential effect of global warming, which indicates an average warming (0.31°C) in the upper 300m of the world ocean since the mid-1950s (Levitus et al. 2000). The abundance of many jellyfish species may increase in warm conditions (reviewed in Purcell 2005), whereas cold conditions were associated with high medusae abundance in the North Sea (Lynam et al. 2005a).

The abundance of Scyphomedusae in the Baltic Sea and the North Sea showed inter-annual fluctuations and large variability between regions (Hay et al. 1990; Janas and Witek 1993; Schneider and Behrends 1994). Their abundance variability in the North Sea appears to be linked to climatic variations. Lynam et al. (2004, 2005a) found high medusae abundance related to a low NAO Index (NAOI) and vice versa. In the North Sea and also in the Baltic Sea production of ephyrae occurs in autumn and winter, when the NAO has greatest influence. Hence, it might play an important role in mediating the environmental conditions that effect the strobilation of polyps (Lynam et al. 2004, 2005a). In addition, the patterns of abundance and occurrence of *Aurelia aurita* and *Cyanea capillata* in the central

Baltic Sea are related to inflow events, which in turn are also induced by meteorological forcing (Barz et al. 2006, PUBLICATION II).

2.2.4 Regime shifts in the Baltic Sea and North Sea

Climate variability is often associated with “regime shifts” defined as “changes in marine system functioning that are relatively abrupt, persistent, occurring at a large scale, observed at different trophic levels, and related to climate forcing” (deYoung et al. 2004). Changes in the ecosystems of the North Sea and Baltic Sea, especially in their fish stocks, were subject of investigations since the beginning of the last century (Hempel 1978). North Sea fish stocks experienced large fluctuations in abundance and biomass during this time. In the 1960s and 1970s the major gadoid species, cod (*Gadus morhua*), whiting (*Merlangius merlangus*), saithe (*Pollachius virens*) and particularly haddock (*Melanogrammus aeglefinus*) produced some of the largest year classes on record (Hempel 1978a). Cushing (1984) related the “gadoid outburst” to a seasonal delayed peak abundance of *Calanus* sp., leading to a longer temporal overlap of fish larvae with their main prey. In contrast to the development of the gadoids, the pelagic stocks of herring (*Clupea harengus*) and mackerel (*Scomber scombrus*) started to decline sharply in the 1960s (Hempel 1978b). Another ecological regime shift occurred in the North Sea during the period 1982-1988. It has been correlated to a change of the North Atlantic Oscillation Index (NAOI) from a negative to a positive phase (e.g. Reid et al. 2003; Beaugrand 2003, 2004; Beaugrand et al. 2002). Alheit et al. (2005) postulated a teleconnection between regime shifts in the central Baltic Sea and the North Sea. Increasing air and sea surface temperature were the main direct and indirect driving forces, affecting all trophic levels in the pelagial. The composition of phyto- and zooplankton communities in both ecosystems changed conspicuously. Copepod species, which are essential for pelagic invertebrate predators and fish (Purcell 1992; Kornilovs et al. 2001; Voss et al. 2003; Dickmann 2005; Köster et al. 2005), experienced pronounced changes in biomass and recruitment. In the Baltic Sea the dominance of the mesozooplankton community shifted from *Pseudocalanus* sp. to *Temora longicornis* and *Acartia* spp. (Möllmann et al. 2003). In the North Sea the abundance of *Calanus finmarchicus* fell to low levels, whereas *C. helgolandicus* was persistently abundant (Beaugrand 2003). These changes had dramatic consequences on sprat (*Sprattus sprattus*), herring and cod stocks in both ecosystems (Alheit et al. 2005; Möllmann et al. 2005). Due to a combination of high fishing pressure and unfavourable hydrographic conditions (decreasing salinity), Baltic cod stocks declined dramatically at the end of the 1980s (Bagge and Thurow 1993). The concurrent increase in sprat stock is thought to result from the release of predation pressure by cod and a high reproductive success (Parmanne et al. 1994). The high reproductive success was coupled to the direct effect of warmer temperature on sprat egg survival and an increased *Acartia* spp. population, the major food of sprat larvae (Voss et al. 2003; Köster et al. 2005). In addition to overfishing, cod recruitment in the North Sea was negatively affected by higher temperatures and an increasing mismatch between larval cod and its prey, as *C. helgolandicus* appears later in the year than *C. finmarchicus*. Both factors are associated with a high NAO (Beaugrand et al. 2003).

The future state of the Baltic Sea and North Sea ecosystems likely depends not only on the levels of fishing pressure on cod or sprat, but on climate-related changes in biotic and abiotic conditions, with their effects on all members of the ecosystems including the Scyphomedusae.

2.2.5 Consequences of high medusae abundance

High abundance of Scyphomedusae is hindering human activities from the Yangtze Estuary to the Black Sea and the Benguela Current. They hamper fishing activities by clogging and bursting trawl nets or blocking the suction devices in diamond mining industries (Brierley et al. 2001; Graham et al. 2003; Xiang et al. 2005). Medusae interfere with tourism and are medical liabilities for swimmers since their venoms can injure man by allergic or toxic reactions (Burnett 2001).

Scyphomedusae utilize a wide selection of zooplankton prey, but generally, estimated predation rates on copepod populations are too small (e.g. <10% day^{-1}) to cause prey population declines (reviewed in Purcell and Arai 2001). Other studies have shown that they can have a strong impact on zooplankton standing stocks, as suggested for *Chrysaora melanaster* in the Bering Sea (Brodeur et al. 2002) and *Aurelia aurita* in Tokyo Bay (Japan) (Omori et al. 1995; Ishii and Tanaka 2001). *Chrysaora quinquecirrha* may feed a maximum of 94% day^{-1} of the copepod population in Chesapeake Bay (USA) (Purcell 1992). Matsakis and Conover (1991) attributed the population decrease of the hydrozoan *Rathkea octopunctata* to predation by *A. aurita.* The abundance of zooplankton in the Kiel Bight (Germany) was negatively correlated with the density of *A. aurita* (Schneider and Behrends 1994; 1998), which was assumed to be the regulating factor in bloom years (Möller 1980a). In addition, the high prey pressure on zooplankton may result in a negative impact on fish populations. Scyphomedusae and fish larvae as well as planktivorous fish often have an overlapping prey spectrum. If the same prey is utilized it is tempting to assume, that competition occurs, but only a few studies have attempted to directly examine this (Purcell and Sturdevant 2001).

A major source of mortality in fish eggs and larvae is predation. Many scyphozoan species are known to feed on fish larvae and eggs (reviewed in Purcell 1985, Fancett 1988; Purcell et al. 1994). When reaching high abundance they may reduce the stocks of many important fish species. In years with high densities of *A. aurita* in the western Baltic Sea, a decline in the abundance of herring larvae was observed (Möller 1980a, 1984). Lynam et al. (2005b) found a significant negative relationship between the survival of herring larvae and the abundance of *A. aurita* in the North Sea. They postulated an adverse impact of *A. aurita* on the North Sea herring population.

Competition and direct predation on fish eggs and larvae could impact commercial fish stocks in both investigated areas, the central Baltic Sea and the southern North Sea. In the brackish Baltic Sea, spawning of marine fish species with pelagic eggs, such as sprat and cod, occurs in the deep basins (Nissling et al. 2002). The Bornholm Basin, one of the three central Baltic Sea deep basins, is the most important spawning ground for cod and sprat, where both species find adequate hydrographic conditions in different depth levels (Köster et al. 2001). The southern North Sea is an important spawning ground for sprat (Aurich 1941), plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) (Harding et al. 1978). The larvae of both flatfish species migrate into their nursery areas in the adjacent Wadden Sea (Creutzberg et al. 1978). During transport toward the nursery areas, eggs and larvae have high rates of mortality (Harding et al. 1978), partly due to predation by Scyphomedusae (van der Veer 1985). As many North Sea fish stocks are presently in an endangered stage (Lynam et al. 2004) increasing medusae abundance could deteriorate the situation in this area. Therefore, the investigation of the impact of Scyphomedusae on the populations of zooplankton and fish in the central Baltic Sea and the southern North Sea is a main topic in this thesis (Barz and Hirche 2005, PUBLICATION I; Barz and Hirche manuscript, PUBLICATION III).

2.3 Objectives of this thesis

The overview deals with interactive aspects controlling occurrence, abundance and impact of pelagic invertebrate predators on different marine ecosystems. The aim of this thesis was to evaluate the situation in two connected ecosystems, the Baltic Sea and the North Sea. In detail my objectives were to assess:

- Which pelagic invertebrate predators occur in the central Baltic Sea?
- What are their patterns of occurrence in season and space?
- What are they feeding on?
- What is their predatory impact on the zooplankton communities?
- Which physical factors are controlling their occurrence in the central Baltic Sea?
- What are the patterns of occurrence and the prey composition of Scyphomedusae in the southern North Sea?

2.4 Thesis outline

This thesis focuses on the impact of pelagic invertebrate predators on zooplankton compositions in North and Baltic Sea. Therefore, at first the two study areas are shortly introduced. In the following "Material and Methods" section the sampling strategy and handling are described, with focus on the methods not mentioned in the PUBLICATIONS I-III. Chaetognatha and Mysidacea were found to have a low to negligible impact in the central Baltic Sea. Hence, the related results are only shortly presented and discussed in the beginning of the "Results and Discussion" section. Scyphomedusae were the main invertebrate predators in the Baltic Sea. Therefore, the focus of this study was on their seasonal and spatial occurrence and on the estimation of their impact on the populations of zooplankton (Barz and Hirche 2005, PUBLICATION I). The results supported earlier assumptions, that Scyphomedusae do not reproduce in high numbers in that area (Janas and Witek 1993). A 3-dimensional baroclinic model of the Baltic Sea was used to detect the role of advection from the western parts on the occurrence patterns of medusae in the central Baltic Sea (Barz et al. 2006, PUBLICATION II). In addition, the seasonal and spatial occurrence and the prey composition of four medusae species in the southern North Sea were investigated (Barz and Hirche manuscript, PUBLICATION III). The results from both ecosystems are compared in the "Synthesis", which also provides insight in investigations needed in the future.

3 Study areas

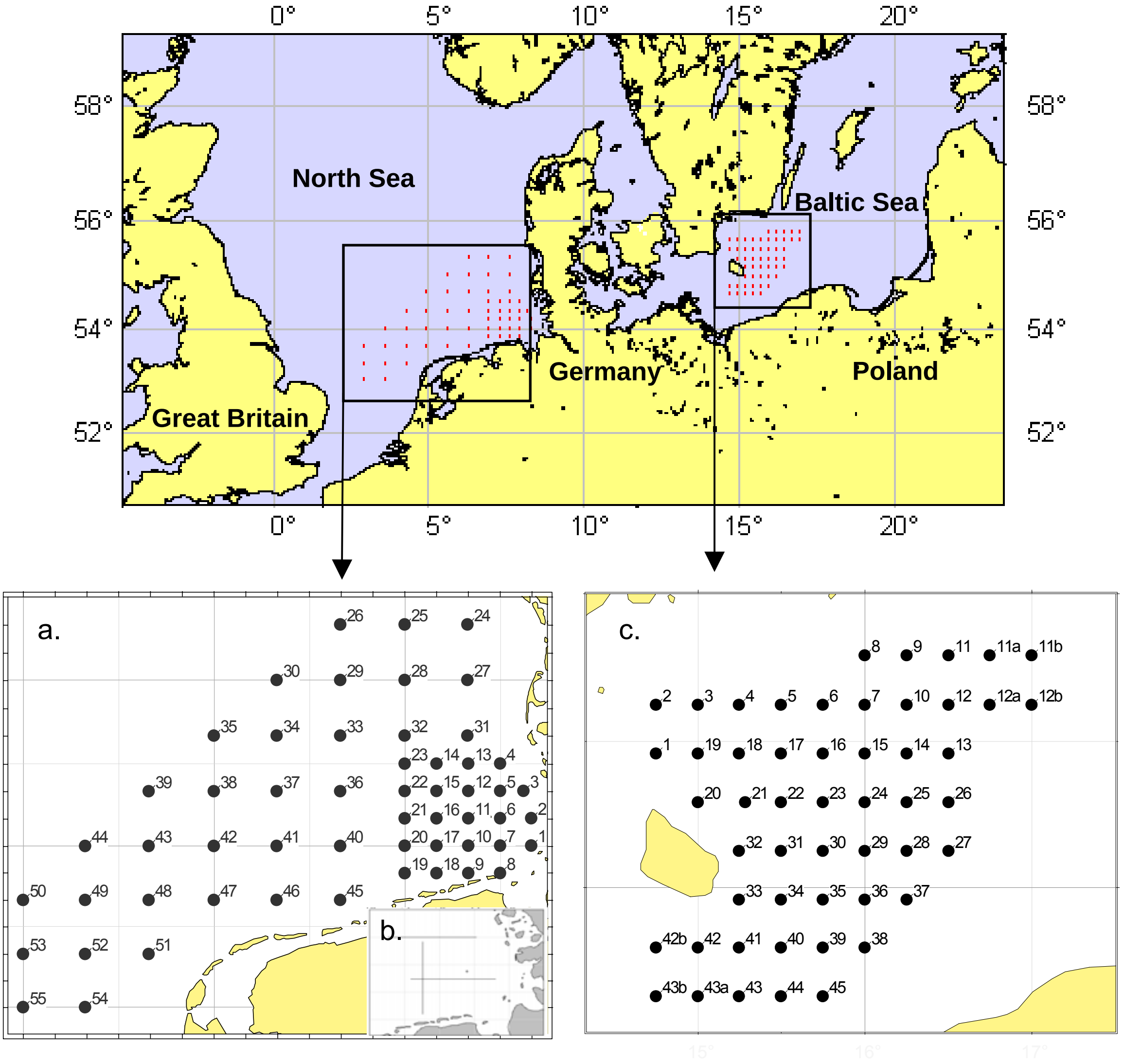


Fig. 1: Sampling areas. Southern North Sea: a. station grid b. transects; c. central Baltic Sea, station grid

3.1 Baltic Sea

The Baltic Sea is the largest brackish water area worldwide. It is connected with the North Sea only via narrow passages and built up by a series of deep basins, which are separated by shallow sills. These narrow passages and the sills limit the inflow of North Sea water masses. Inflows of North Sea water in the entire basins are relatively seldom, and depending on meteorological events in autumn and winter. They are driven by special atmospheric conditions, which cause large and long-lasting sea level differences between the Kattegat and the western Baltic Sea (Mohrholz et al. in press). These inflow events may bring high saline and oxygenated water into the basins and change the hydrographic conditions.

The hydrography of the Baltic Sea is characterised by a clear stratification (Fonselius 1970). The surface water has a low salinity, due to the fresh water discharge of more than 200 rivers. It is separated by a strong pycnocline from the more haline waters in the deep. In summer a thermocline separates the surface layer from the colder intermediate water masses above the halocline. The salinity in the surface layers as well as near the bottom is decreasing from west to east. In the surface layer salinity decreases from 15-25 in the Belt Sea to less than 2 in the Bothnian Bay. Due to these changing salinities from marine, via brackish, to freshwater, animals and plants reach the limits of their distributional and reproductive ranges at the different isohalines and their composition is changing all over the Baltic Sea along this gradient (Rheinheimer 1996).

This study was carried out in the Bornholm Basin (BB) (Fig. 1c; Fig. 1 in PUBLICATION I), which is one of the deep basins in the central Baltic Sea, with a maximum depth of 96m. From July to September 2002 a thermocline was found between 15 and 25m, separating the surface layer from the colder (5-6°C) intermediate water layer. Temperature in the surface layer increased from 16°C in the beginning of July to the maximum summer temperature of 20.8°C in August. In November the surface water had cooled down to 9°C and merged with the intermediate water. Salinity was rather constant between the surface and the halocline (7) and increased beneath the halocline up to 15.5 (Fig. 2). Oxygen concentration decreased rapidly below the halocline to values <2ml l^{-1}.

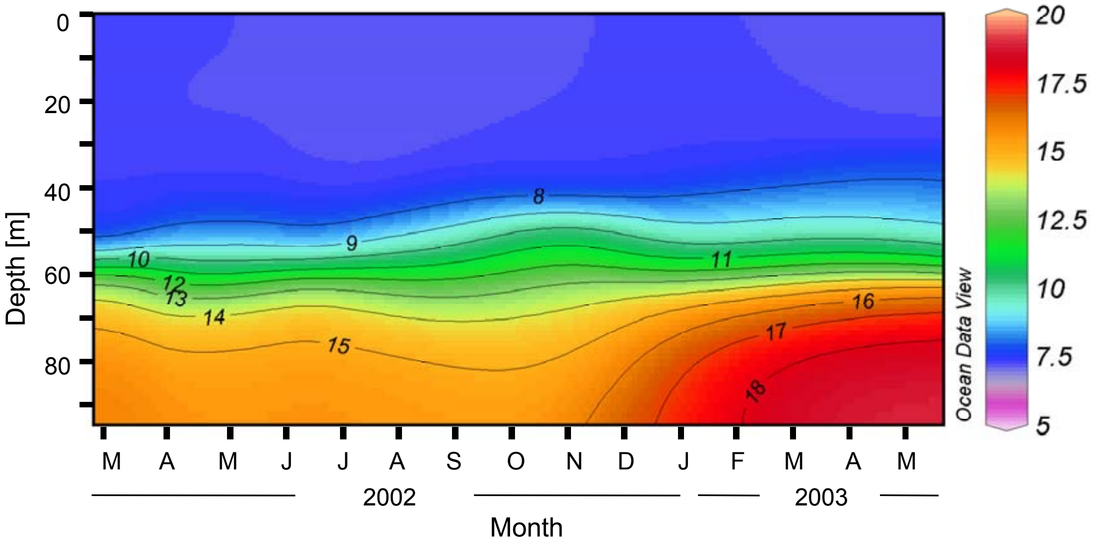


Fig. 2: Salinity in the Bornholm Basin in 2002 and early 2003, with changed salinity signature after the Major Baltic Inflow event in January 2003

In January 2003 a Major Baltic Inflow (MBI) of cold (2°C) and oxygen rich (7ml l^{-1}) water from the Kattegat reached the central Baltic Sea (Feistel et al. 2003) (Fig. 2). It was the first MBI event since 1993 (Mohrholz et al. in press), and was detected in the BB in late January. This large inflow event was followed by two minor inflows: (i) One in March, with the same temperature and oxygen signature as the MBI, and (ii) one in May, which was significantly warmer (Feistel et al. 2003).

3.2 North Sea

The North Sea is a shelf sea adjacent to the Atlantic Ocean. It is connected to the rest of the Atlantic through the English Channel in the south and through the Norwegian Sea in the north. The salinity of the inflowing Atlantic water reaches more than 35.

The study area was located in the southern North Sea, covering the German Bight as well as Dutch and Danish territorial waters (Fig. 1a; Fig. 1 in PUBLICATION 3). The southern North Sea is a temperate shallow shelf sea. It is bordered in the south and east by extensive areas of inter-tidal mudflats (German and Dutch Wadden Sea). In general, two main water masses are found in this area. The Continental Coastal Water, which is a mixture of water from the Atlantic, the English Channel and several rivers, and the central (southern) North Sea Water (Becker et al. 1992). The German Bight is characterised by strong mesoscale variability in physical properties such as fronts and eddies. A permanent feature is the river plume front in the south-east, which is produced by the inflow of fresh water from the river Elbe (Becker et al. 1992). The tides in the southern North Sea are strong and cause turbulent horizontal and vertical exchanges. A tidal mixing front reaches from the surface to the ground and is advected as a whole by the tides (Dippner 1993). Water depth in the investigation area was between 15 and 48m. Due to the shallow depths the water column is mostly completely mixed and well oxygenated. Stratification is sometimes observed during the summer months. The seasonal cycle of water temperature is more pronounced than that of salinity. Around Helgoland Island (Germany) the surface temperature and salinity vary from 2 to 20°C and 28 to 33, respectively.

While temperature was rather uniform across the sampling grids during the cruises, salinity showed a wider variability, with lower values in the eastern part, which is more influenced by freshwater discharge of several rivers (Elbe, Weser, Ems). In April 2004, temperature varied from 6 to 7°C, whereas salinity reached 30.5 in the most eastern part and 34.5 in the western side of the study area, both measured at 10m depth.

4 Material and Methods

In this chapter a short overview on used sampling and analysing strategies is given. For further and subsequent details see related PUBLICATIONS I-III.

4.1 Sampling

4.1.1 Sampling dates

Sampling in the Baltic Sea was performed on cruises in 2002 and 2003. In 2004 and 2005 cruises were only conducted in the North Sea. Table 1 gives the complete cruise schedule.

Table. 1: Cruises in the Baltic Sea and North Sea. Data used for different analyses and publications are marked by ✓. Chaet = Chaetognatha; Drift = Modelling of medusae occurrence; Mysid = Mysidacea; Scyph = Scyphomedusa; PUBL = PUBLICATION

Baltic Sea							**North Sea**		
Year	**Date**	**Chaet**	**Mysid**	**Scyph** Publ. I	**Drift** Publ. II		**Year**	**Date**	**Scyph** Publ. III
2002	12.03.-21.03.			✓	✓		2004	16.02.-05.03.	✓
	02.04.-30.04.	✓	✓	✓	✓			06.04.-27.04.	✓
	05.05.-25.05.			✓	✓			07.05.-26.05.	✓
	15.05.-30.05.			✓	✓			17.06.-06.07.	✓
	11.06.-23.06.	✓	✓	✓	✓			04.08.-23.08.	✓
	22.07.-07.08.	✓	✓	✓	✓			06.09.-12.09.	✓
	12.08.-21.08.	✓	✓	✓	✓		2005	14.04.-21.04.	✓
	22.08.-30.08.	✓	✓	✓	✓			17.05.-24.05.	✓
	03.09.-13.09.			✓	✓			30.06.-08.07.	✓
	30.09.-10.10.	✓	✓	✓	✓				
	11.11.-29.11.	✓	✓	✓	✓				
2003	13.01.-24.01.	✓	✓	✓	✓				
	10.02.-23.02				✓				
	03.03.-22.03	✓	✓		✓				
	17.05.-03.06.				✓				
	01.07.-19.07.				✓				
	07.08.-18.08.				✓				
	24.11.-05.12.				✓				

4.1.2 Central Baltic Sea

Abundance and distribution of zooplankton and pelagic invertebrate predators

The station grid included 52 stations (Fig. 1c). In 2002 and 2003 Scyphomedusae were collected from Bongo net hauls. Their vertical distribution was studied by using a trawled BIOMOC or a trawled multinet on four cruises at station 23. All medusae collected were processed onboard, identified, weighed and measured to the nearest 0.5cm below (for detailed description of sampling see PUBLICATION I and II).

Chaetognatha and Mysidacea were collected in the laboratory from fixed (4% borax-buffered formalin-seawater solution) Bongo net samples (0.6m diameter, 500µm mesh size). Under a dissection microscope they were identified to species level. Abundance and distribution were analysed in 2002 and early 2003 at all grid stations. Samples with high Mysidacea abundance were divided with a plankton splitter until a minimum of 300 individuals contained in the subsample.

Prey analysis, selection and predatory impact

For gut content analysis single *Aurelia aurita* medusae were scooped from the surface water by using a dip net between July and October 2002. In the laboratory the medusae were examined for prey organisms, which were counted and identified to genus or species level.

Prey selection was calculated for *A. aurita* collected from surface waters at station 23 at four cruises from July to October when data on zooplankton abundance were available. Selectivity indices for the zooplankton taxa were calculated from the average numbers of prey in the medusae guts and the corresponding numbers of prey m^{-3}. Statistical significance was based on the χ^2-test as suggested by Pearre (1982). Feeding rates and predatory impact of *A. aurita* were calculated for the focus stations on four cruises from July to October when data on zooplankton abundance were available (for detailed information on prey analyses, selectivity and predatory impact calculations for *A. aurita* see PUBLICATION I)

For easier identification of the gut content of Mysidacea, a digital picture catalogue with fragments (legs, mandibles, characteristic body parts) of potential food items was established.

Mysidacea for gut content analyses were collected from fixed Bongo net samples. The individuals were dissected with a fine scalpel. The separated stomach and gut were transferred to an object slide in a glycerine-water solution (1:1). Under a dissection microscope, the stomachs were opened with fine dissection needles and prey fragments separated. By comparing the fragments with pictures of potential prey, the gut content was mostly identified to species level. When all fragments were associated to single prey individuals, the number of prey in the gut was counted.

Drift-modelling

Numerical simulations of the circulation were performed by application of a 3-dimensional eddy resolving baroclinic model of the Baltic Sea. The model is based on the free surface Bryan-Cox-Semtner model (Killworth et al. 1991) which is a special version of the Cox numerical ocean general circulation model (Bryan 1969; Semtner 1974; Cox 1984). The Baltic Sea model comprises the whole Baltic Sea, including the Gulf of Bothnia, Gulf of Riga as well as the Belt Sea, Kattegat and Skagerrak. It is forced by realistic atmospheric conditions taken from the SMHI (Swedish Meteorological and Hydrological Institute, Norrköping) meteorological data base, which covers the whole Baltic Sea drainage basin on a regular grid of 1°x1°. Calculation of juvenile medusae (ephyrae) drift routes was performed by utilising a Lagrangian particle tracking technique (Hinrichsen et al. 1997) using a 4th order Runge-Kutta scheme (for detailed information on the modelling approach see PUBLICATION II).

4.1.3 Southern North Sea

Abundance and distribution of Scyphomedusae

In 2004 the station grid included 55 stations and was divided in a small grid (10nm distance between stations 1-23) and a large grid (20nm distance between stations 24-55) (Fig. 1a). Scyphomedusae were collected at all grid stations from oblique Bongo net hauls. In 2005 the sampling strategy was different. During three cruises samples were taken with a trawled multinet along a North-South-Transect (T1) and two West-East-Transects (T2, T3) (Fig. 1b). All medusae collected were processed onboard, identified, weighed and measured to the nearest 0.5cm below (for detailed description of sampling see PUBLICATION III).

Prey analysis

For gut content analysis single medusae from Bongo and multinet hauls were measured immediately after collection, weighed and preserved in a 4% borax buffered formalin-seawater solution. In the laboratory the medusae were examined for prey organisms, which were counted and identified to genus or species level (for detailed description of prey analysis see PUBLICATION III).

5 Results and Discussion

In the central Baltic Sea, the most conspicuous invertebrate predators were Scyphomedusae. Therefore, this thesis focused on this group (PUBLICATIONS I and II). In addition the occurrence patterns of Chaetognatha and Mysidacea in the central Baltic Sea were analysed.

For comparative studies in the Baltic Sea and North Sea, additional investigations were conducted on the occurrence and abundance of Scyphomedusae in the North Sea (PUBLICATION III).

The following species were analysed:

	Baltic Sea	**North Sea**
Chaetognatha	*Sagitta elegans*	
Mysidacea	*Mysis mixta*	
Scyphomedusae	*Aurelia aurita*	*Aurelia aurita*
	Cyanea capillata	*Cyanea capillata*
		Cyanea lamarckii
		Chrysaora hysoscella

5.1 Chaetognatha in the central Baltic Sea – occurrence and impact

Chaetognatha are highly abundant in nearly all oceans of the world. They often reach values almost as high as copepods (Feigenbaum and Marris 1984). Chaetognatha are strictly carnivorous and constitute important predators of zooplankton and fish larvae, but the main prey are copepods (Reeve 1980; Feigenbaum and Maris 1984; Feigenbaum 1991; Alvarez-Cadena 1993; Baier and Purcell 1997). When reaching high abundance, Chaetognatha may have a high impact on several zooplankton species (Baier and Purcell 1997; Tönnesson and Tiselius 2005). *Sagitta elegans* is abundant in boreal waters, and one of the dominant species on the European shelf (Øresland 1987). Sameoto (1973) estimated that *S. elegans* consumed 36% of the annual secondary production in Bedford Basin (Canada). It was the most important predator on copepods in this region. In the Gullmar Fjord (Kattegat, Sweden) *S. setosa* reached a peak abundance of 310 ind. m^{-3} in the surface water, whereas *S. elegans* reached maximum values of only 17 ind. m^{-3} in deeper layers. When *S. setosa* was highly abundant, also the predation impact was high, it removed 26 to 48% d^{-1} of the *Pseudocalanus* sp. population. *S. elegans* reached maximum predation rates of 18% d^{-1} on *Calanus finmarchicus* (Tönnesson and Tiselius 2005).

In this study only *S. elegans* was identified in the central Baltic Sea, while also some individuals of *S. setosa* were found in this area in former investigations (Maciejewska and Margonski 2001). *S. elegans* was caught on only five cruises, with a low abundance (Fig. 3). It occurred in April, August, October, November 2002 and January 2003, with an abundance maximum of 1.09 ind. $100m^{-3}$ in January 2003. In March 2003 it had completely disappeared.

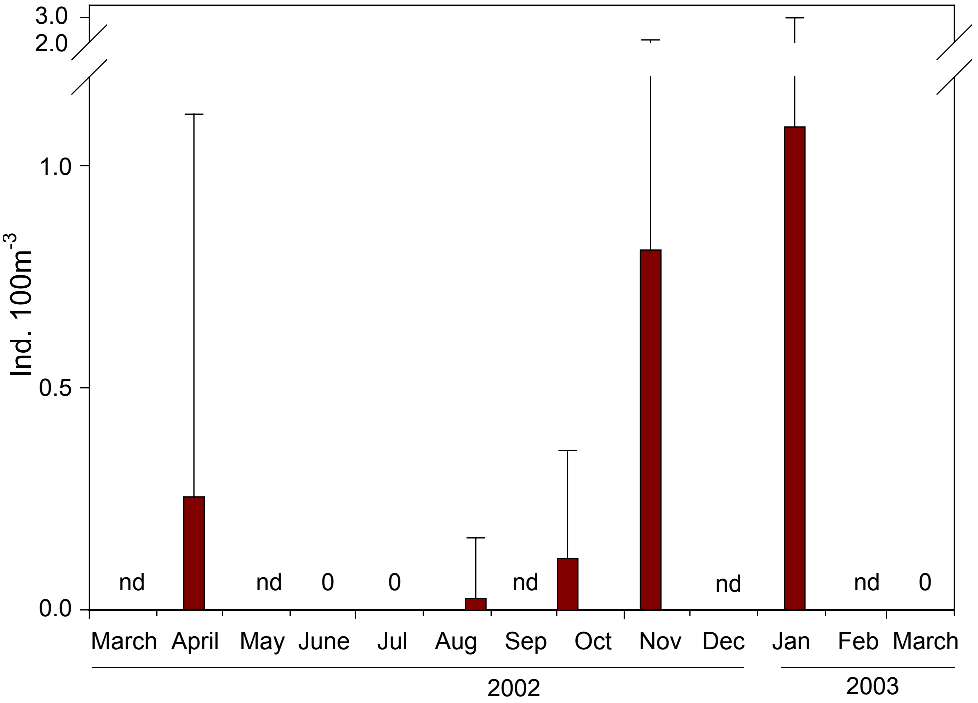


Fig. 3: Seasonal development of *Sagitta elegans* in the central Baltic Sea. nd = no data

Between 1993 and 1996 Maciejewska and Margonski (2001) found a decreasing mean abundance of *S. elegans* in the central Baltic Sea. The abundance dropped from 3 ind. $100m^{-3}$ in August 1994 to 0.01 ind. $100m^{-3}$ in August 1996, and showed a clear dependency on several inflow events. The values in this study in August were at the lower end of the former investigation, but the abundance in January 2003 was the highest since September 1994. Comparable to the results of Maciejewska and Margonski (2001) the high abundance in January was most probably related to a MBI event. The water masses reached the BB at the end of January 2003 (Feistel et al. 2003) and transported the individuals in the high saline waters from the North Sea to the central Baltic Sea. Maciejewska and Margonski (2001) found the maximum abundance of *S. elegans* in 60-80m depth, where the inflow waters with a salinity of 15-17 were located. After the inflow the conditions undergo remarkable changes (decreasing salinity and oxygen). In these unfavourable conditions, combined with the low food abundance, the advected animals probably do not grow and reproduce (Maciejewska and Margonski 2001). These pseudo-populations get extinct sooner or later and have to be renewed with the next inflow from the Kattegat.

Due to the low abundance of *S. elegans* in the central Baltic Sea and the low feeding rates found by Maciejewska and Margonski (2001) (only 3.5% of the analysed chaetognaths had food in their guts), no investigations on gut content were conducted in this study. It is assumed that *S. elegans* in the central Baltic Sea most probably had no negative impact on the zooplankton community and fish populations during this investigation.

Due to their low abundance Chaetognatha had no negative impact on the zooplankton community and fish populations in the central Baltic Sea in 2002 and early 2003.

5.2 Mysidacea in the central Baltic Sea – occurrence and impact

Mysidacea play a significant role in the food web of the Baltic Sea, and may constitute important competitors with fish larvae (Rudstam and Hansson 1990). *Mysis mixta* is one of the major zooplanktivores in coastal areas of the northern Baltic proper. Rudstam et al. (1986) calculated that this species might consume about 20-50% of the zooplankton production in the northern Baltic proper on an annual basis.

In this study only *M. mixta* was identified, and occurred mainly in summer and autumn (Fig. 4). In July and November 2002 mean abundance was about 4 ind. 100m^{-3}. During peak abundance a mean of 9 ind. 100m^{-3} was reached in August. In April and June 2002 individuals were found only sporadically (mean 0.17 und 0.23 ind. 100m^{-3}), and also in January and March 2003 abundance was low (0.66 and 0.16 ind. 100m^{-3}). The life cycle of *M. mixta* in the central Baltic Sea is about the same as in the northern Baltic Sea. The juveniles are released in early spring, grow through the summer and mature in December (Rudstam and Hansson 1990). Males do not survive the winter, therefore, the abundance showed a clear decline from October on (Fig. 4).

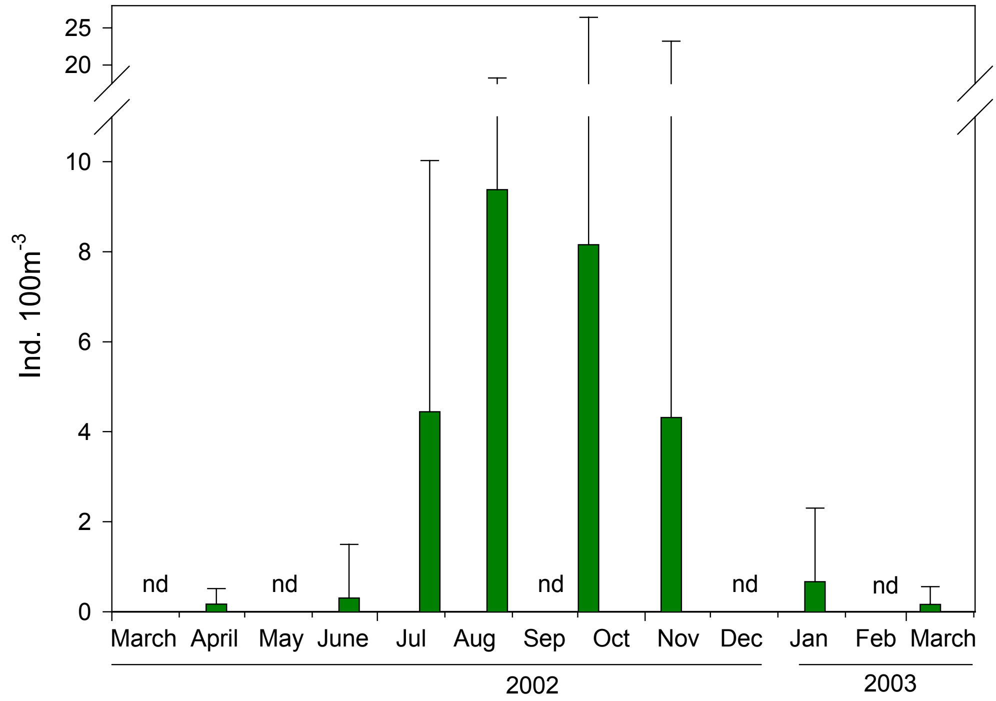


Fig. 4: Seasonal development of *Mysis mixta* in the central Baltic Sea. nd = no data

Swarms of *M. mixta* were found from July to November. They were mainly located at more shallow stations (40-60m) in the north-east and in the south of the investigation area, sometimes obviously related to the coast (Fig. 5). Abundance in the swarms reached a maximum of 203 ind. 100m^{-3} in August. In the deep central basin *M. mixta* were caught only seldom. Salemaa et al. (1990) and Margonski and Maciejewska (1999) found a similar distribution in this area in former investigations.

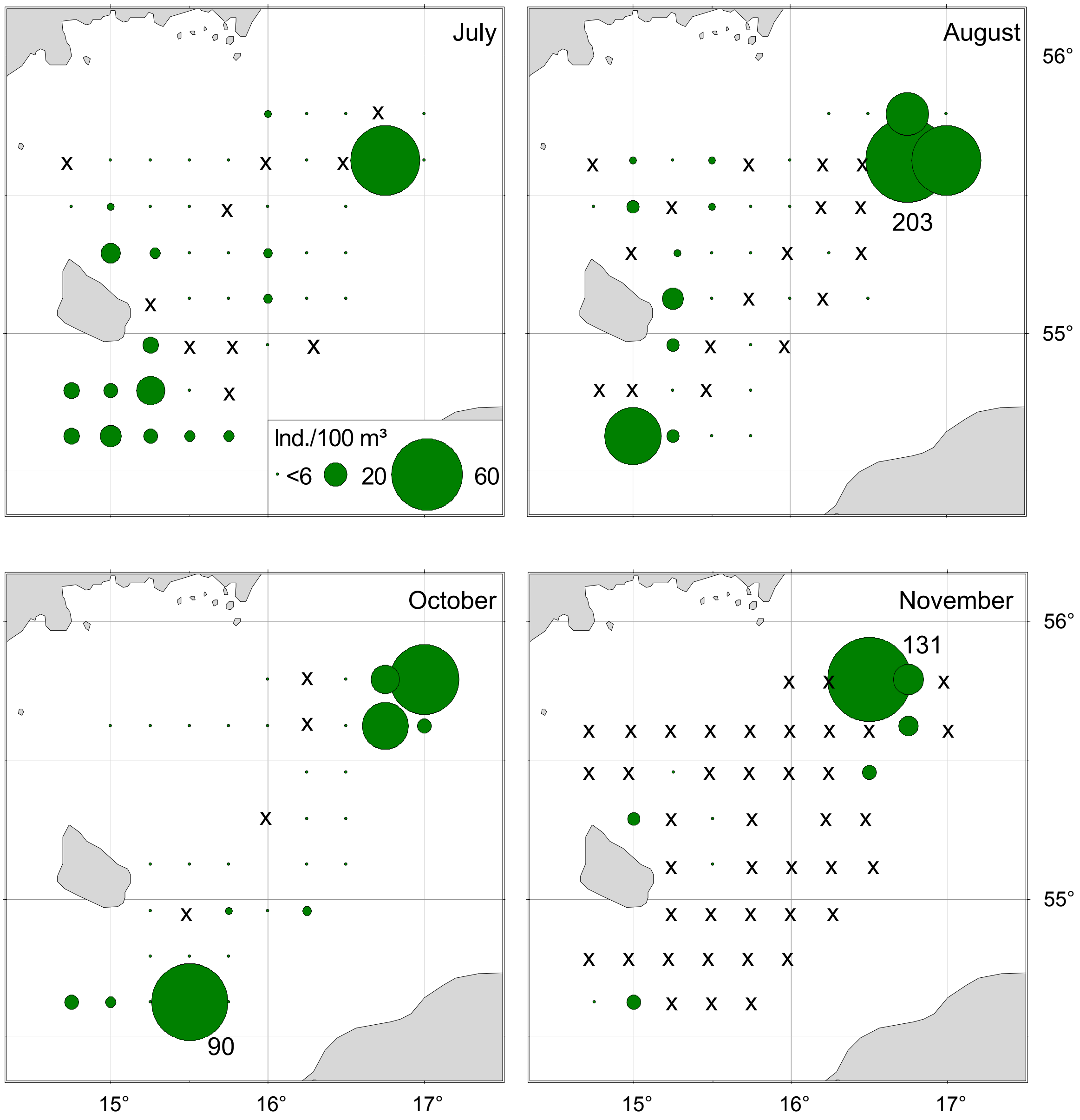


Fig. 5: Horizontal distribution of *Mysis mixta* in the central Baltic Sea in 2002. Numbers next to the plots refer to abundance higher than plot size indicates. x = 0 ind.

Gut content analysis of *M. mixta* was carried out in July 2002. Main food items were the cladocerans *Bosmina coregoni maritima* and *Podon* spp. In addition, fragments (mandibles, legs) of the copepod species *Temora longicornis* and *Centropages hamatus* were identified and also unidentified copepod mandibles were found (Fig. 6). Per individual 6 to 17 prey organisms were found in the guts. In the northern Baltic Sea *M. mixta* was found to be a selective feeder. *M. mixta* preferred the copepod *Eurytemora hirundoides* and cladocerans to other common species (Hansson et al. 1990).

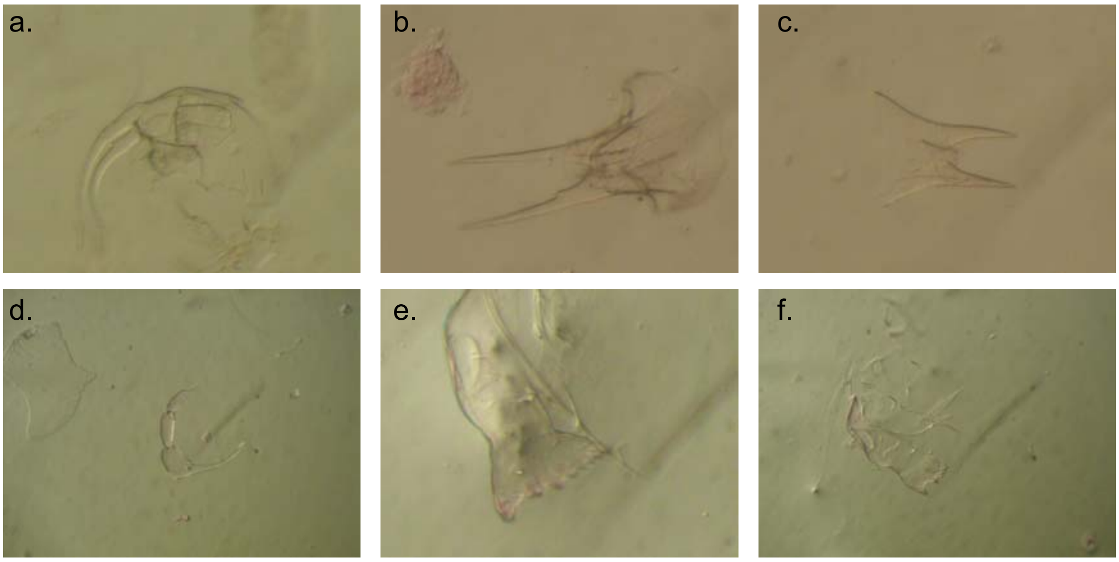


Fig. 6: *M. mixta* gut contents: a.-c. Fragments of cladocerans (a., b. *Bosmina coregoni maritima,* c. *Podon* sp.); d.-f. Leg and mandibles of copepods (d., e. *Temora longicornis*, f. *Centropages hamatus*)

In the northern Baltic Sea *M. mixta* reached an abundance of 50-800 ind. $100m^{-3}$ (Rudstam and Hansson 1990). In this study abundance was much lower in general, and did not exceed 203 ind. $100m^{-3}$ in the only locally found swarms. Therefore, a high impact on the populations of zooplankton as calculated by Rudstam et al. (1986) may occur only locally during the investigated season in the central Baltic Sea. Although there is an overlap in prey with sprat larvae (Voss et al. 2003; Dickmann et al. submitted), no competition for food is expected, as the big swarms of *M. mixta* appeared mainly after the mass occurrence of sprat larvae, which was in June and July (Dickmann 2005).

A negative impact of *Mysis mixta* on the zooplankton community and fish populations in the central Baltic Sea in 2002 and early 2003 may occur only locally.

5.3 Scyphomedusae

5.3.1 Central Baltic Sea

5.3.1.1 Abundance, seasonal occurrence and predatory impact

In the central Baltic Sea only two scyphozoan medusae occurred, *Aurelia aurita* and *Cyanea capillata*. In 2002 the first medusae of both species were caught in July, maximum abundance of *A. aurita* was found in August (2.3 ind. 100m^{-3}), whereas *C. capillata* reached a maximum of only 0.07 ind. 100m^{-3} (Fig. 7a; Fig. 2a in PUBLICATION I). No ephyrae of either species were caught. The horizontal distribution of *A. aurita* showed a maximum abundance of 8 ind. 100m^{-3} on single stations in October and November (Fig. 8).

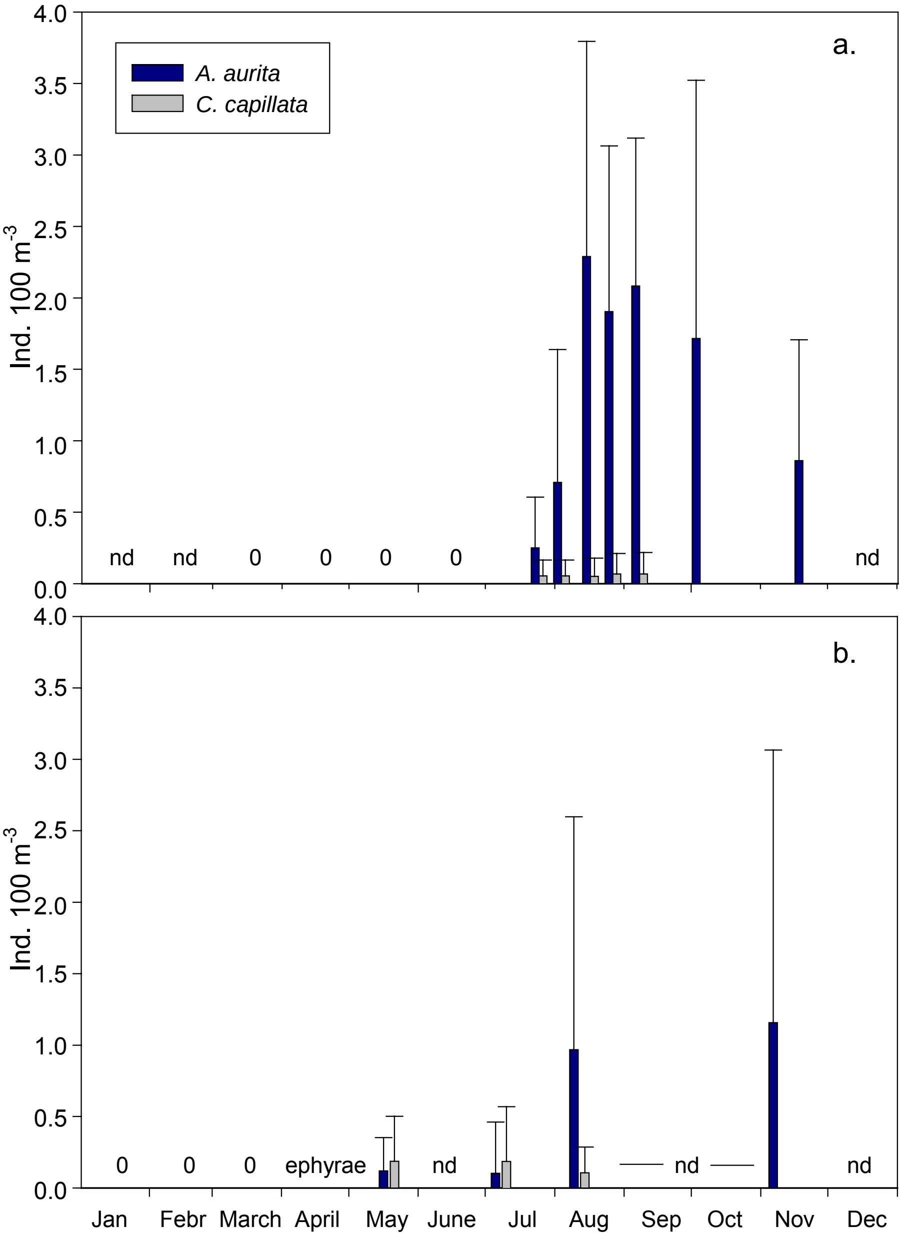


Fig. 7: Mean abundance (±SD) of *Aurelia aurita* and *Cyanea capillata* in the central Baltic Sea in 2002 (a.) and 2003 (b.). nd = no data

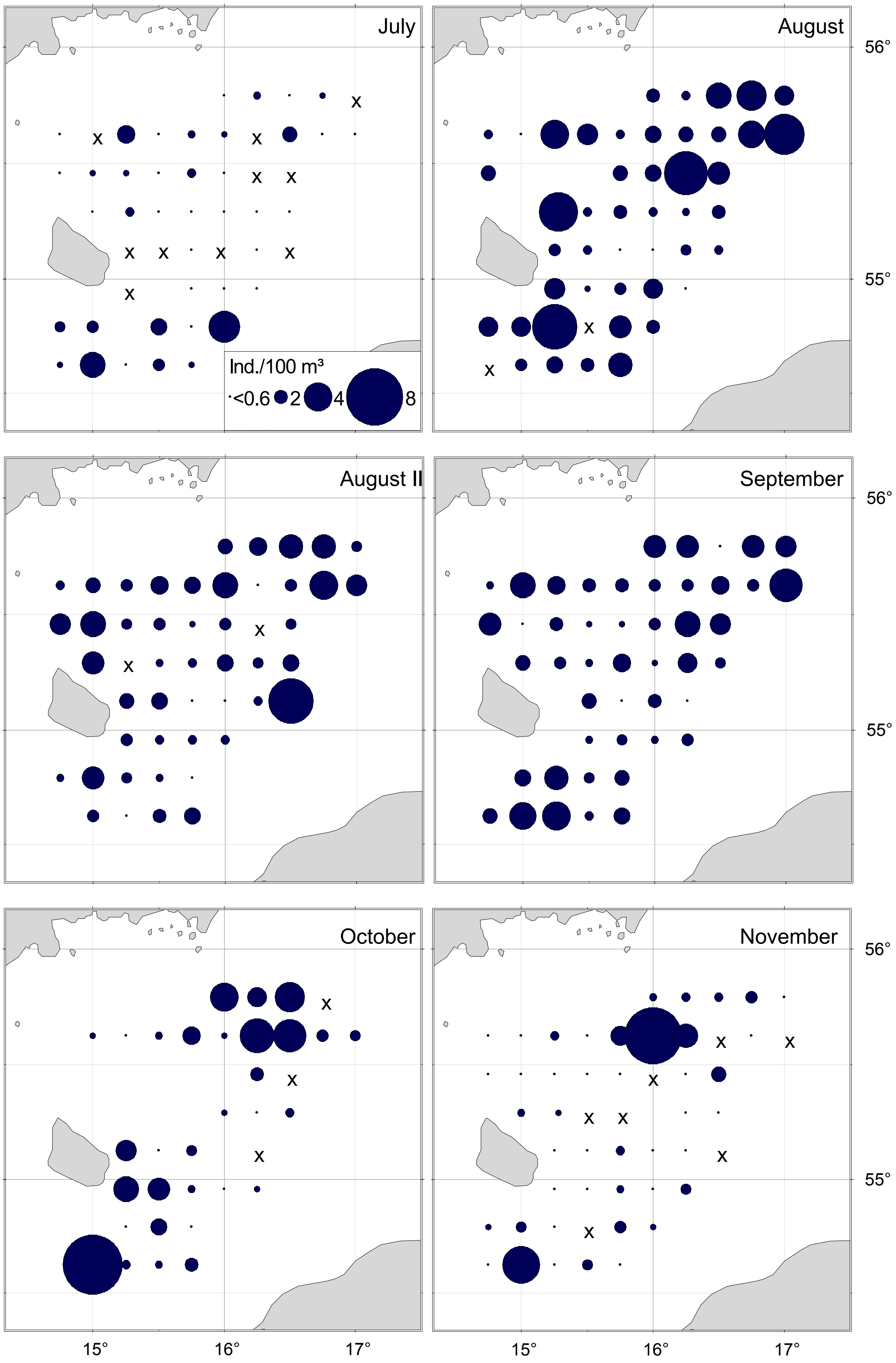


Fig. 8: Horizontal distribution of *Aurelia aurita* in the central Baltic Sea 2002. x = 0 ind.

The abundance of *A. aurita* in this study was at the higher end of values reported for the central Baltic Sea, but lower when compared to the western Baltic Sea (Table 5 in PUBLICATION I). Abundance peaks of 300 ind. m^{-3} were reached in Kerteminde Fjord (Danish Belt Sea), where individuals remained much smaller than in other areas (Olesen et al. 1994). In Tokyo Bay (Japan) highest values of 153 ind. $100m^{-3}$ were found (Omori et al. 1995). In general *A. aurita* abundance is higher in bays and fjords, it is known as a more inshore species (Russel 1970).

From July to September, 80% of *A. aurita* medusae were found in the upper 20m, whereas *C. capillata* showed a dependency on the intermediate water layer and the halocline (50-60m), were salinity increased from 7 to 13 and oxygen was still available (Fig. 3 in PUBLICATION I). Diel vertical migration patterns of *A. aurita* differ geographically (Yasuda 1970, 1973; Mackie et al. 1981; Hamner et al. 1982). However, in the central Baltic Sea no vertical migration was observed during this study. The hydrographic conditions with a stratified water column in summer seem to provide an optimal habitat above the thermocline, with warmer water and high prey availability.

A. aurita fed on several zooplankton species. The guts contained cladocerans and copepods (both groups mainly identified to species and stage level), bivalve and gastropod larvae (Table 2 in PUBLICATION I). Daily feeding rates of medusae were relatively high (up to 4815 cladocerans $medusa^{-1}$ day^{-1}), but due to the low medusae and high zooplankton abundance the predatory impact on the zooplankton community was low. The mean impact on the cladoceran standing stock was always <1.1% day^{-1}, and only a mean of 0.5% day^{-1} of the copepod standing stock were eaten. On stations with high medusae abundance the predatory impact on copepods reached up to 1.2% day^{-1} (station 12 in October 2002) and even 7.8% of the cladoceran standing stock were consumed per day on station 21 in August 2002 (Table 4 in PUBLICATION I). However, these high values were seldom and local events, and are probably still too low to cause prey population declines (Purcell and Arai 2001). The impact rates in the central Baltic Sea were lower compared to other ecosystems. *Chrysaora quinquecirrha* for instance, may feed a maximum of 94% day^{-1} of the copepod population in Chesapeake Bay (USA) (Purcell 1992). In Kiel Bight (western Baltic Sea) *A. aurita* was supposed to be the factor regulating zooplankton density during years of high medusae abundance (Möller 1980a; Schneider and Behrends 1994, 1998). In these and many other ecosystems, *A. aurita* is known to feed mainly on copepod species (Hamner et al. 1982; Matsakis and Conover 1991; Sullivan et al. 1994; Graham and Kroutil 2001; Mutlu 2001). In contrast, in the central Baltic Sea the cladoceran *Bosmina coregoni maritima* was the main prey item. This endemic brackish water cladoceran is the dominating zooplankton species in the upper 20m during the warm months (Hernroth and Ackefors 1979), but in summer 2002, it reached the highest values ever reported in this area (max. 267,000 ind. m^{-3}). With its rapid parthenogenetic reproduction, it can numerically outgrow its predators (Viitasalo et al. 2001).

Low medusae and high zooplankton abundance resulted in a low impact on the zooplankton community in the central Baltic Sea. Higher impact occurred only locally.

A. aurita in the central Baltic Sea did not feed on fish eggs and larvae, although this species is known for high predation rates on several fish species with negative effects on their standing stocks (van der Veer 1985; Purcell 1985). In the western Baltic Sea for example, predation by *A. aurita* resulted in a declining abundance of herring larvae (Möller 1980a, 1984). The BB is an important spawning ground for cod and sprat (Bagge et al. 1994; McKenzie et al. 2000; Köster et al. 2001). Cod eggs occur in the BB mainly from April to July (Nissling 2004). For buoyancy reasons, they are restricted to salinities ≥11, and are therefore distributed below 60m (Nissling et al. 1994). Cod larvae live in nearly all depth layers in the BB, but their abundance peaks are always found deeper than 25m from May to July (Grønkjær and Wieland 1997). During peak spawning in May and June sprat eggs are distributed in and above the halocline from 20-60m depth (Makarchouk and Hinrichsen 1998; Nissling et al. 2003). Sprat larvae co-occurred with medusae in the upper water layers in summer, but reached numbers of only 0-0.3 ind. m^{-2} from August to October 2002, when their peak abundance was already over (Voss et al. 2004). Medusae and sprat larvae in the central Baltic Sea feed on the same species (Voss et al. 2003; Dickmann et al. submitted), but the amount of predation and competition is determined by the spatial and temporal overlap of predator and fish larvae populations. Scyphomedusae and the eggs and larvae of dominant fish species in the central Baltic Sea showed a clear seasonal and vertical mismatch in their occurrence. These mechanisms prevent fish eggs and fish larvae from predation and competition in this area.

The limited seasonal and vertical overlap of fish eggs and larvae with Scyphomedusae in the central Baltic Sea protected them from predation in 2002.

The occurrence patterns of medusae in the central Baltic Sea in 2003 were completely different from 2002. In April ephyrae were caught and small medusae of *A. aurita* and *C. capillata* appeared already in May (Fig. 7b; Fig. 4a in PUBLICATION II). *A. aurita* was caught only in 25m depth and deeper. *C. capillata* showed the same dependency on high salinity as in 2002, it occurred in 40m depth and deeper, where salinity increased from 8 to 19 (Fig. 2 in PUBLICATION II). Abundance of *A. aurita* was about the same in July, early August and

November, with a lack of data in 2003 during the general peak abundance time in mid-August and September.

This different pattern of occurrence in 2003 requires a different impact assessment in this year. Medusae co-occurred with fish eggs and larvae for a longer time in the season. As medusae appeared in May in 25m and deeper they had the opportunity to feed on cod eggs, cod larvae and on sprat eggs. In addition, they co-occurred with sprat larvae in the surface layer during their peak abundance in June and July (Dickmann 2005). Therefore, a higher impact on fish populations was possible by both, direct predation and competition for the same food resources.

Earlier appearance of medusae in the central Baltic Sea in 2003 may have caused a higher impact on fish populations by predation and competition.

5.3.1.2 Origin of medusae in the central Baltic Sea

The occurrence patterns of *Aurelia aurita* and *Cyanea capillata* in the central Baltic Sea found in 2002 were in agreement with earlier observations in this region (Janas and Witek 1993). It was remarkably, that no ephyrae occurred, and medusae appeared later, than in more western parts of the Baltic Sea. In the Gullmar Fjord (western Sweden) ephyrae appeared in October and had developed into medusae already in May (Hernroth and Gröndahl 1983; Gröndahl 1988). Olesen et al. (1994) found ephyrae in Kerteminde Fjord (Danish Belt Sea) in February. In Kiel Fjord first ephyrae appeared in November (Möller 1980b) and entered the medusae stage already in late April. All these areas contain habitats for large polyp populations. Apart from some individual findings (Janas pers. communication), no polyp populations are known in the central Baltic Sea and adjacent areas. Although *A. aurita* medusae live in salinities as low as 3, the limiting salinity for polyps appeared to be about 6 (Russel 1970). The occurrence patterns found in 2002 and in earlier investigations (Janas and Witek 1993) suggest, that *A. aurita* and *C. capillata* do not strobilate in that area. A surface salinity in the central Baltic Sea about 7-8 (Fig. 2; Fig. 3 in PUBLICATION I), as found in this study, seems to inhibit at least strobilation of *A. aurita*. The presence of *C. capillata* is known to be dependent on the inflow of North Sea waters (Möller 1980c; Janas and Witek 1993). Its polyps need a salinity >20 (Cargo 1984), and therefore cannot exist in the central Baltic Sea.

No large polyp populations of Scyphozoa seem to exist in the central Baltic Sea.

The occurrence patterns of medusae in the central Baltic Sea in 2003 were completely different from 2002. In April ephyrae were caught and small medusae of *A. aurita* and *C. capillata* appeared already in May (Fig. 7b; Fig. 4a in PUBLICATION II).

Occurrence of Scyphomedusae is dependent on the existence of polyp populations and advection of ephyrae. As mentioned before, no large polyp populations are known in the central Baltic Sea and adjacent regions and the question arises where the Scyphomedusae appearing in the central Baltic Sea originate.

The data from 2002 and 2003 allowed an inter-annual comparison under different hydrographic conditions. The difference in both years either may originate in a different timing of strobilation or might reflect the inter-annual variability of circulations and currents, which control the transport of ephyrae from the strobilation areas to the central Baltic Sea. In fact, there were remarkable differences in the circulation patterns between the two years. In January 2003 a Major Baltic Sea Inflow (MBI) of cold and oxygen-rich water from the Kattegat reached the central Baltic Sea. The inflow water was detected in the BB in late January (Feistel et al. 2003). It was followed by some minor inflows in March and May, and may have affected the occurrence and distribution of the medusae. To prove this possibility, a 3-dimensional baroclinic model of the Baltic Sea was used to predict the arrival of medusae in the central Baltic Sea. Known strobilation areas in the western Baltic Sea were used as source regions in the model.

The different atmospheric forcing conditions and the corresponding varying hydrographic situations were clearly reflected in the model results. In 2002 nearly all release dates from mid-December 2001 to April 2002 resulted in a medusae arrival in the central Baltic Sea at the end of June (Fig. 3 and Table 2 in PUBLICATION II). This arrival fits in time exactly with the observations, between absence of medusae (end of June) and the first observed individuals (end of July). In 2003 the successive inflow events most likely caused earlier arrival in the central Baltic Sea (Fig. 4 and Table 2 in PUBLICATION II). The model predicted an arrival of medusae in the central Baltic Sea already in January, but no medusae were caught during this time. These results imply that strobilation did not occur that early in the year. As the first ephyrae were caught in April, it was assumed, that they were advected to the central Baltic Sea by the March inflow. The model results indicate a strobilation period from mid-December to April in 2002 and from mid-January to April in 2003, as a release in this time frame produced best agreement with the field observations. A strobilation during this time is congruent with earlier observations (Möller 1980a, b; Olesen et al. 1994). The results explain the lack of ephyrae in the central Baltic in 2002 and in earlier investigations. Ephyrae start growing with an increase in mesozooplankton abundance, depending on water temperature (Möller 1980a; Lucas and Wiliams 1994). Therefore, they develop into medusae until late June during about 90 days of drift before reaching the central Baltic

Sea. High transport rates like the ones associated with the inflows in 2003 are necessary to advect ephyrae into the central Baltic Sea, before they develop into medusae.

It is still unclear, if settlement of larvae and strobilation of polyps occur in the central Baltic Sea and if so, how much they contribute to the population. However, strobilation success is probably low, and the population seems to depend on early stages of medusae advected from the western parts of the Baltic Sea.

The advection of medusae from the western Baltic Sea to the central Baltic Sea is likely.

A Major Baltic Inflow event caused the occurrence of ephyrae and the early appearance of medusae in the central Baltic Sea in 2003.

5.3.2 Southern North Sea

5.3.2.1 Abundance, seasonal occurrence and prey composition

In the southern North Sea four scyphozoan species were caught: *Cyanea lamarckii, C. capillata, Aurelia aurita* and *Chrysaora hysoscella*. Three different patterns of seasonal occurrence were distinguished: (i) The early occurring *C. lamarckii* (February to August), (ii) *C. capillata* and *A. aurita* (April-August) and (iii) the late appearing *C. hysoscella* (Fig. 2 in PUBLICATION III). The seasonal patterns of occurrence of all four species were in the range of former studies in the southern North Sea (Hartlaub 1894; Verwey 1942; Künne 1952; Russel 1970; Möller 1980c; Hay et al. 1990). With a maximum density of 13 ind. $100m^{-3}$ at one station in June 2004 (Fig. 4a in PUBLICATION III) and a maximum mean abundance of 1.8 ± 2.7 ind. $100m^{-3}$ *C. lamarckii* (Fig. 2 in PUBLICATION III) reached the highest abundance of all species during this investigation. The dominance of *C. lamarckii* in the southern North Sea was also described in former studies (Hartlaub 1894; Verwey 1942; Kopacz 1994). In contrast to the Baltic Sea, *A. aurita* was very low abundant in 2004 and was not caught in 2005. The former investigations did not provide abundance data of any species in the southern North Sea. However, Kopacz (1994) found a maximum of 100 *C. lamarckii* $100m^{-3}$ off Sylt Island in the summer of 1991. Van der Veer and Oorthuysen (1985) reported a maximum abundance of 49 *A. aurita* $100m^{-3}$ in a bight of the Dutch Wadden Sea. In comparison with these abundance data (the only available data, but from outside the study area), the abundance during this study in the years 2004 and 2005 was low to medium.

Also in the southern North Sea, knowledge about location of polyp populations is rare. It is mainly based on assumptions (van der Veer and Oorthuysen 1985; Kühl and Mann 1967; Merck 1989) or on investigations performed >40 years ago (Kühl 1964). At least it is not known if polyp populations of *C. hysoscella* really exist in the Elbe Estuary (Kühl and Mann

1967; Merck 1989) or if this species is advected from Spanish and French coasts (http://schutzstation-wattenmeer.de).

The abundance of Scyphomedusae showed inter-annual fluctuations in the North Sea (Hay et al. 1990). Lynam et al. (2004, 2005a) linked the abundance variability between 1971 and 1986 to climatic variations, as quantified by the North Atlantic Oscillation Index (NAOI). In most of the North Sea medusae abundance was generally high when the NAOI was low (Lynam et al. 2004, 2005a). Lynam et al. (2004) generated a conceptual model wherein high a NAOI led to rare *A. aurita* and *C. lamarckii* abundance and vice versa. Deciding parameters were e.g. sea surface temperature as trigger for strobilation (Russel 1970; Omori et al. 1995), and advection, which leads to accumulation or dispersal of ephyrae. According to Lynam et al. (2004) the abundance of *A. aurita* and *C. lamarckii* in the North Sea might be suppressed by the present NAO high. However, the limited duration of this investigation and the lack of long-term studies on medusae abundance in the southern North Sea do not allow an interpretation of the data in relation to climate variability.

The southern North Sea is an important spawning ground for sprat (Aurich 1941), plaice and flounder (Harding et al. 1978). The larvae of both flatfish species then migrate into their nursery areas in the adjacent Wadden Sea (Creutzberg et al. 1978). The investigated medusae in the southern North Sea fed on several copepod and other crustacean species (Table 2 in PUBLICATION III). As this is the same food fish larvae prey on in this area (Dickmann 2005) they have to be considered as competitors. In addition, *C. lamarckii* and *C. capillata* consumed fish larvae and eggs in all months analysed. In June 2004 and July 2005 the investigated *Cyanea* medusae contained a mean of 1-5 fish larvae in their guts (Table 2 in PUBLICATION III). As peak spawning of sprat occurs from May to July (Alheit et al. 1987) when most medusae occur, fish larvae and eggs constitute an important prey for the medusae. Hence, fish larvae in this area may suffer from both, predation and competition, but due to the relative low abundance of Scyphomedusae in this study it was concluded, that they did not control the recruitment of fish in the time frame investigated. However, if a future reversal of the NAO phase provides a more favourable environment for Scyphomedusae (Lynam et al. 2004) the abundance of medusae in the North Sea could increase, and the recruitment of fish stocks may be impacted due to increased competition for prey and predation on eggs and larvae.

Scyphomedusae in the southern North Sea are predators and competitors of fish larvae, but due to their low abundance they had no negative impact on the populations of zooplankton and fish in 2004 and 2005.

6 Synthesis

The comparison of Scyphomedusae related topics in both investigated ecosystems identified similarities as well as differences. Both were expected, as the ecosystems are connected on one hand, but have many differences in hydrography and species composition on the other.

6.1 Species diversity

The Baltic Sea has a considerably lower number of species than the North Sea, since compared to freshwater and seawater, brackish waters are characterised by the lowest number of indigenous species (Remane 1934). According to this only two Scyphomedusae species occurred in the Baltic Sea: *Aurelia aurita*, of which polyps and medusae tolerate less saline waters (Russel 1970) and *Cyanea capillata*, which is bound to higher salinities and therefore distributed only in the halocline (Cargo 1984; Gröndahl and Hernroth 1987; Barz and Hirche 2005 PUBLICATION I). In the southern North Sea four scyphozoan species were found. *A. aurita* is a cosmopolitan species (Russel 1970), but reached much less significance than in the Baltic Sea. *C. capillata* reached higher abundance than in the central Baltic Sea. It might reproduce in the southern North Sea due to the favourable high salinity. In addition *C. lamarckii*, which is common in the southern North Sea (e.g. Verwey 1942; Hay et al. 1990), and *Chrysaora hysoscella* were found. At least five scyphozoan medusae may occur in this area. *Rhizostoma octopus* was found in several investigations (Verwey 1942; Künne 1952; Russel 1970; Hay et al. 1990), but these species generally peaked in September/October and was probably missed during our study.

6.2 Prey and predatory impact

The medusae mainly preyed on crustacean species in both ecosystems. In the Baltic Sea the prey was dominated by the mass occurring, brackish water cladoceran *Bosmina coregoni maritima* (Barz and Hirche 2005, PUBLICATION I), whereas a wider prey spectrum was available and used in the North Sea (Barz and Hirche manuscript, PUBLICATION III).

Selective feeding of Scyphomedusae was demonstrated in several investigations. As Scyphomedusae do not actively attack prey, selection depends on various characteristics of predators and prey (reviewed in Purcell 1997). Large prey is relatively more vulnerable to Scyphomedusae, as found in experiments with copepods and *Aurelia aurita* (Suchman and Sullivan 2000). Also *Cyanea capillata* showed a preference for the larger components of the zooplankton (Fancett 1988). On the other hand small size is suggested to be an effective refuge from predation (Suchman and Sullivan 1998). The findings in the Baltic Sea and the North Sea support these concepts. Nauplii and copepodite stages I-III were not ingested, although they were abundant in the water column (Barz and Hirche 2005, PUBLICATION I; Barz and Hirche manuscript, PUBLICATION III). Although prey selectivity was demonstrated for medusae in the central Baltic Sea (Barz and Hirche 2005, PUBLICATION I), the species investigated are not specialised on specific prey. Therefore, a change in the zooplankton composition associated with the postulated regime shifts in Baltic Sea and North Sea (Alheit et al. 2005; Möllmann et al. 2003) will not negatively affect the medusae as long as enough prey is available.

Due to the low medusae and high zooplankton abundance the predatory impact on the zooplankton community, fish eggs and larvae in both ecosystems was low (Barz and Hirche 2005, PUBLICATION I; Barz and Hirche manuscript, PUBLICATION III). In the central Baltic Sea the seasonal and vertical mismatch in the occurrence of medusae and the larvae and eggs of dominant fish species prevented them from predation. However, an increasing abundance of medusae as anticipated after a reversal of the present NAO (Lynam et al. 2004) may increase their impact on the populations of zooplankton and fish. The changed occurrence patterns, caused by the Major Baltic Inflow event, resulted in a higher overlap of medusae with fish larvae and eggs and may also have caused a higher impact on the populations of important fish species by predation and competition. This factor was not analysed during this study, and needs further attention in future investigations, as a positive selection of fish eggs and larvae was found in earlier studies for many scyphozoan species (reviewed in Purcell and Arai 2001). The positive selectivity may be caused by the little or no escape ability and the relative large size of eggs and yolk-sac larvae (Purcell and Arai 2001). *A. aurita, C. capillata* and *C. hysoscella* are known as predators on ichthyoplankton, at least in laboratory investigations (Möller 1980b, 1984; Lebour 1923; Fancett 1988).

6.3 Abundance control by physical forcing?

Medusae generally show high inter-annual fluctuations in their abundance (Schneider and Behrends 1994), but the reasons for inter-annual differences in population size are often unclear. Although turtles and some fish may eat medusae, top-down control of populations does not seem to be prevalent for most species (Parsons and Lalli 2002). Also in the central Baltic Sea and southern North Sea medusae abundance is probably not controlled by predation, despite the facts: (i) that *Aurelia aurita* might be a substantial food source for *C. capillata* (Båmstedt et al. 1997; Hansson 1997), and (ii) that predation by the ophisthobranch mollusc *Coryphella verrucosa* could drastically affect the growth of polyp colonies (Hernroth and Gröndahl 1985). In fact, abundance of medusae is mostly bottom–up controlled by physical factors (temperature, salinity), food supply and availability of suitable hard substrate for the polyp settlement (Parsons and Lalli 2002). In the Baltic Sea and North Sea the medusae abundance was probably not limited by food availability, as zooplankton was highly abundant during spring and summer and medusae species are not dependent on specific prey species. Most controlling factors affect the polyp generation, influence the ephyrae production and advection, and thus effect variation of the patterns of medusae abundance and occurrence between years and areas. The impact of changing physical conditions (mainly meteorological forcing) on the occurrence and abundance of medusae was already demonstrated. Lynam et al. (2004, 2005a) linked the abundance variability of medusae in the North Sea between 1971 and 1986 to climatic variations, as quantified by the North Atlantic Oscillation Index (NAOI). Lynam et al. (2004) suggested abundance of *A. aurita* and *C. lamarckii* in the North Sea to be suppressed by the present NAO high, which is associated with high sea surface temperatures. A similar mechanism might be valid for the connected Baltic Sea, as it is also affected by the high NAO with an increase in average spring water temperature and decreasing salinities (Hänninen et al. 2000; Fonselius and Valderrama 2003). The limited duration of this investigation and the lack of long-term studies in both regions do not allow an interpretation of the data in relation to climate variability. However, this investigation confirms a low medusae abundance in the Baltic Sea as well as in the North Sea during the presence NAO high.

In addition to abundance, also the occurrence patterns of medusae are controlled by physical forcing. In the western Baltic Sea strobilation of *A. aurita* occurred in winter and spring, but generally peaked in April and first medusae were also found in April (Möller 1980a, b; Olesen et al. 1994). As there is most probably no ephyrae production in the central Baltic Sea (Janas and Witek 1993; Barz and Hirche 2005, PUBLICATION I), *A. aurita* and *C. capillata* strongly depend on advection from the western area and the North Sea. The advection takes a long time and the species appear later in the year compared to the western Baltic Sea. An exceptional Major Baltic Inflow event, which in turn was induced by meteorological forcing, was responsible for completely changed patterns of seasonal occurrence of medusae in this area in 2003 (Barz et al. 2006, PUBLICATION II).

Many factors, mainly controlling the polyp populations, but also affecting the advection of ephyrae, are responsible for abundance and occurrence of medusae in the Baltic Sea and North Sea. Lynam et al. (2004) postulated, that a future reversal of the NAO (from high to low) could release the environmental inhibition of Scyphomedusae. A following increase of medusae abundance could cause strong impacts on the populations of zooplankton and fish in the southern North Sea and the central Baltic Sea. For a successful monitoring and eventual forecast of medusae blooms in an area it is critical to learn more about their complete life history dynamics (Mills 2001) and the locations of polyp populations. In the Baltic Sea, as well as in the North Sea, the main problem arises, where medusae are produced at all. Without knowledge about the origin of medusae it is impossible to link their patterns of occurrence to the local or remote polyp populations.

6.4 Future perspectives

Major Baltic Inflow events are relatively seldom and mostly induce remarkable changes in the whole Baltic environment. They may affect all communities from the benthal to the pelagial (Wasmund et al. 2004) and several changes still have to be expected after the last MBI. Therefore the occurrence patterns of Scyphomedusae need to be monitored during the next years, as e.g. changes in the salinity probably open up new habitats for polyp settlement.

A major goal of future investigations on Scyphozoa in the Baltic Sea and the North Sea should be the detection of polyp populations of all species in both ecosystems. The located populations need to be observed the whole year round, and a simultaneous recording of physical conditions has to be conducted. Only this combination of observation with abiotic conditions allows a direct connection of strobilation to physical forcing. In addition, local currents need to be revealed and inserted in drift models, as they may affect advection of all free-swimming scyphozoa stages to other regions. This information will provide tools to predict when and how many ephyrae will be released in one year, and where they might be advected. Hence, they are basic for a prediction of medusae “blooms”.

7 Publications

PUBLICATION I

Barz, K. and Hirche, H.-J. 2005 Seasonal development of scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (central Baltic Sea). Mar. Biol. 147: 465-476 DOI 10.1007/s00227-005-1572-2

The initial idea originates from the co-author and myself. Sampling, analysing and interpretation of the data was done by myself. I wrote the manuscript, which was improved by the co-author.

PUBLICATION II

Barz, K. Hinrichsen, H.-H. and Hirche, H.-J. (2006) Scyphozoa in the Bornholm Basin (central Baltic Sea) – The role of advection. J. Mar. Syst. 60 (1-2): 167-176 DOI 10.1016/j.jmarsys.2006.01.002

The initial idea originates from the third author and myself. Sampling, analysing and interpretation of the data was done by myself. The second author developed and run the model. I wrote the manuscript, which was improved by the second and the third author.

PUBLICATION III

Barz, K. and Hirche, H.-J. Abundance, distribution and prey composition of Scyphomedusae in the southern North Sea. Manuscript

The initial idea originates from the co-author and myself. Sampling, analysing and interpretation of the data was done by myself. I wrote the manuscript, which was improved by the co-author.

Seasonal development of scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (central Baltic Sea)

Kristina Barz and Hans-Jürgen Hirche

Marine Biology 2005

Marine Biology (2005) 147: 465–476
DOI 10.1007/s00227-005-1572-2

RESEARCH ARTICLE

K. Barz · H.-J. Hirche

Seasonal development of scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (central Baltic Sea)

Received: 6 September 2004 / Accepted: 24 January 2005 / Published online: 4 March 2005

Abstract The annual cycle of abundance and distribution of the scyphozoan medusae *Aurelia aurita* and *Cyanea capillata* was studied in the Bornholm Basin (central Baltic Sea) in 2002. Seasonal changes in prey composition and predatory impact were investigated by analyzing stomach contents. *A. aurita* occurred from July to November, with a maximum mean abundance of 2.3 ind. per 100 m^3 in August, whereas *C. capillata* was caught in much smaller numbers from July to September. No ephyrae of either species were found; therefore, advection of medusae from the western Baltic Sea is assumed. From July to October, ~80% of *A. aurita* medusae was distributed in the upper 20 m above the thermocline, whereas *C. capillata* occurred only in the halocline below 45 m. *A. aurita* did not migrate vertically and fed mainly on the most abundant cladoceran species *Bosmina coregoni maritima*. Further prey organisms were the cladocerans *Evadne nordmanni* and *Podon* spp., mollusk larvae and copepods. Copepod nauplii and copepodite stages I–III were not eaten by the medusae, neither were fish eggs and larvae used as prey. Based on mean medusa and zooplankton abundance from the upper 20 m, the predatory impact was very low. In August, when mean abundance of *A. aurita* was highest, only 0.1% of the copepod and 0.5% of the cladoceran standing stock were eaten per day. However, in regions with higher medusa or lower zooplankton abundance, up to 7.9% of the cladoceran standing stock was consumed per day. Hence, *A. aurita* did not regulate the zooplankton community in the Bornholm Basin, and fish larvae did not suffer from competition with and predation by the medusae.

Communicated by O. Kinne, Oldendorf/Luhe

K. Barz (✉) · H.-J. Hirche
Alfred-Wegener-Institute for Polar and Marine Research,
Columbusstrasse, 27568 Bremerhaven, Germany
E-mail: kbarz@awi-bremerhaven.de
Tel.: +49-471-48311324
Fax: +49-471-48311918

Introduction

Scyphomedusae are conspicuous members of marine pelagic ecosystems. When reaching high abundance, they can reduce the stocks of zooplankton communities considerably (e.g. Möller 1980b; Matsakis and Conover 1991; Purcell 1992; Olesen 1995; Omori et al. 1995; Lucas et al. 1997; Schneider and Behrends 1998). The most important effects of predation by medusae are summarized by Purcell (1997): top-down control of zooplankton populations and competition for food with fish, consumption of fish eggs and larvae, and changes in the zooplankton community through predation on organisms in various trophic levels. In the Baltic Sea only two scyphozoan medusae occur. *Cyanea capillata* is found only sporadically. Its abundance in the Bornholm Basin (central Baltic Sea) is very low, alternating with years of complete absence (Janas and Witek 1993; Lischka 1999). In contrast, *Aurelia aurita* occurs continuously in the Baltic Sea. In Kiel Bight (western Baltic Sea) it was observed all year round (Möller 1980a), sometimes reaching high densities. In such "bloom" years (Schneider and Behrends 1994), a decline in the abundance of herring (*Clupea harengus*) larvae and copepods was observed there (Möller 1980b; Schneider and Behrends 1998).

While the western Baltic Sea is a relatively shallow area, where copepods dominate the zooplankton, the central Baltic is a highly stratified, brackish body of water, with a permanent halocline and a summer thermocline in the deep basins. These conditions affect the composition and distribution patterns of the zooplankton community, which, especially in summer, is dominated by cladocerans above the thermocline and copepods below it (Schulz and Hirche, personal communication). During an intensive field study in the Bornholm Basin in the framework of the German GLOBEC, which focuses on the interactions between zooplankton and fish under the influence of physical processes, it was our aim to assess the role of scyphozoan medusae in the pelagic food web. As they are the only invertebrate predators in the plankton besides chaetognaths and mysids, they may constitute an important factor controlling zooplankton mortality, although Janas and Witek (1993), from estimates of the food requirements of medusae, did not find a significant impact. In addition medusae compete for zooplankton with the commercially important planktivorous fish species sprat (*Sprattus sprattus*) and herring, but also may prey on fish eggs and larvae and thus directly affect their recruitment. Margonski and Horbowa (1995) mentioned feeding of *A. aurita* and *C. capillata* on cod (*Gadus morhua*) eggs in the Bornholm Basin. In order to answer these questions, seasonal and vertical distributions of the two scyphomedusae were described, and their abundances were estimated. From gut content analysis of *A. aurita*, predation rates were estimated and the impact on the zooplankton community was calculated.

Materials and methods

Sampling location, dates and hydrography

The study area was located in the Bornholm Basin, central Baltic Sea. The station grid included 52 stations with 9 focus stations (Fig. 1). The water depth varied between 30 and 90 m. Samples were taken during 12 cruises from March 2002 to January 2003, with a maximum time interval of 2 weeks between the sampling events from July to October (Table 1). Five cruises between March and July 2002 are not listed in Table 1, because no medusae occurred. The cruise in July included two complete grid investigations (Jul. and Aug. I), which were presented separately for medusa abundance and size. Salinity, temperature and dissolved oxygen were recorded on every station with a standard CTD probe (SBE 911+, ME).

Abundance and distribution of zooplankton and scyphomedusae

Zooplankton samples were collected at nine focus stations using a multinet (0.25-m^2 opening, 55-μm-mesh size), vertically towed in 10-m intervals from near bottom to surface. Samples were preserved in a 4% borax-buffered formalin-seawater solution. At all grid stations scyphomedusae were collected from oblique Bongo net hauls (0.6-m diameter, 335- and 500-μm-mesh size). As 335- and 500-μm Bongo showed no difference for the abundance of *A. aurita* ($P=0.5$–0.9; Mann–Whitney rank sum test), the average values of both nets were used for the distribution and abundance of the medusae. Additional oblique hauls with an Isaacs–Kidd midwater trawl (IKMT, 6-m^2 opening, 1,000-μm-mesh size) were used at the focus stations to validate the sampling efficiency of the Bongo net for scyphomedusae. Comparison of both net types showed that the Bongo net worked well for scyphomedusae in the study area ($P=0.4$–0.6; Mann–Whitney rank sum test).

The vertical distribution of the scyphomedusae was studied by using a trawled BIOMOC (1-m^2 opening, 55-μm-mesh size) or a trawled multinet (0.25-m^2 opening, 335-μm-mesh size) on four cruises at stn 23. On each cruise during 24 h, three day and three night hauls were taken in 5-m (July–September) or 10-m (November) intervals from bottom (90 m) to surface. The depths shown in Fig. 3 are mean trawling depths. All medusae collected were processed onboard, identified, weighed and measured to the nearest 0.5 cm below.

Prey analysis

For gut content analysis, single *A. aurita* medusae were scooped from the surface water by using a dip net between July and October. After collection medusae were immediately measured, weighed and preserved in a 4% borax-buffered formalin-seawater solution. To investigate the predation in different depth strata, medusae from BIOMOC hauls were preserved for prey analysis. In the laboratory the medusae were dissected, and canals, stomach and gastric pouches were examined for prey organisms, which were counted and identified to genus or species level. Copepods were determined to stage level.

Prey selection

Prey selection was calculated for *A. aurita* medusae collected from surface waters at stn 23 on four cruises from July to October when data on zooplankton abundance were available. Selectivity indices (*C*) for the zooplankton taxa were calculated from the average numbers of prey in the medusa guts and the corresponding numbers of prey per cubic meter in the upper 20 m. Statistical significance was based on chi-square, as suggested by Pearre (1982). Selectivity values range from –1 to +1, with 0 indicating no selection.

Feeding rates and predatory impact

Feeding rates and predatory impact were calculated for the focus stations on four cruises from July to October when data on zooplankton abundance were available. Individual feeding rates were expressed as numbers of prey consumed per medusa per day:

$$F = C\mathrm{m} \div D \times 24\ \mathrm{h} \qquad (1)$$

where F is the number of prey consumed per medusa per day, C_m is the number of prey in the medusa and D is digestion time (h), 24-h feeding is assumed. Digestion time of *A. aurita* depends on temperature, prey size and numbers of prey in the gut (Matsakis and Conover

1991; Martinussen and Båmstedt 1999, 2001; Båmstedt and Martinussen 2000). Purcell (2003) found a digestion time of 3 h at 14°C for *Aurelia labiata* in Prince William Sound, Alaska, while Kerstan (1977) measured a digestion time of 4 ± 2 h for *A. aurita* in the western Baltic at 14–15°C. As during our study the number of prey per medusae were similar to Purcell's and warmer water in August and September may have accelerated digestion, we used a digestion time of 3 h in our calculations.

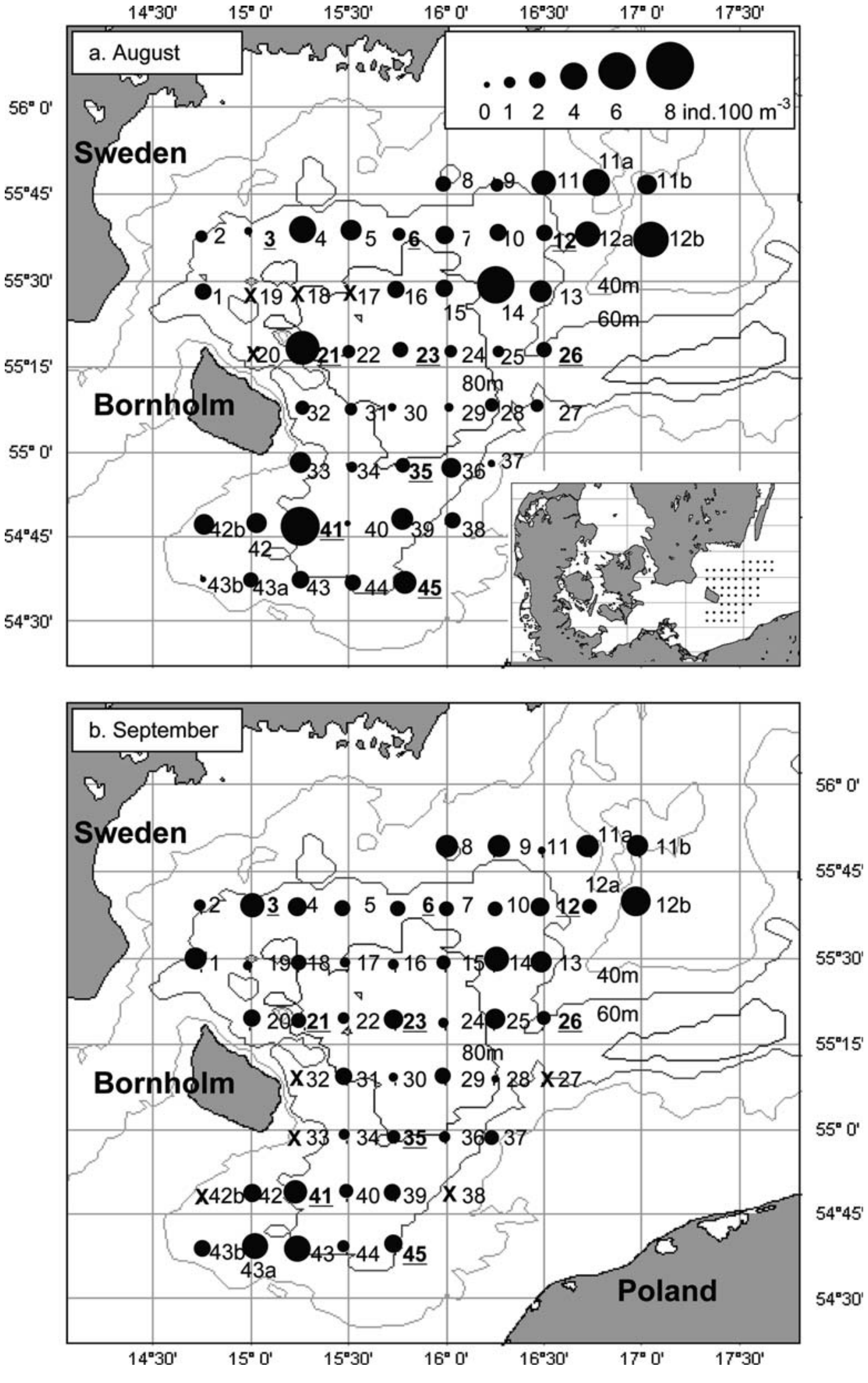


Fig. 1 Study site in the Bornholm Basin with names of stations and spatial distribution of *Aurelia aurita* in August (**a**) and September (**b**) 2002. *Size of circles* indicates abundance (ind. per 100 m^3) (*X* no data on cruise). Focus stations *bold* and *underlined*

Table 1 Cruise dates, parameters and nets for scyphomedusa investigations in 2002–2003 (*MN* Multinet; *PC* prey composition; *PI* predatory impact; *PS* prey selectivity; *SD* spatial distribution; *VD* vertical distribution). Sampling stations: Bongo on whole grid; dip net, IKMT and MN on focus stations; BIOMOC and trawled MN on stn 23; zooplankton was sampled on all cruises except Aug. III with MN on focus stations

Cruise date	Scyphomedusae	
	Parameter	Net
22 Jul–7 Aug (Jul., Aug. I)	SD, VD, PC, PS PI	Bongo, IKMT, BIOMOC, dip net
12–21 Aug (Aug. II)	SD, PC, PS PI	Bongo, IKMT, dip net
22–30 Aug (Aug. III)	SD, VD, PC	Bongo, IKMT, trawled MN, dip net
3–13 Sep	SD, VD, PC, PS PI	Bongo, IKMT, BIOMOC, dip net
30 Sep–10 Oct	SD, PC, PS PI	Bongo, IKMT, dip net
11–29 Nov	SD, VD	Bongo, IKMT, trawled MN
13–24 Jan, 2003	No medusae	Bongo, IKMT

The predatory impact of the medusae on the populations of copepods and cladocerans was calculated according to the equation:

$$P = F \times M \div C \times 100 \qquad (2)$$

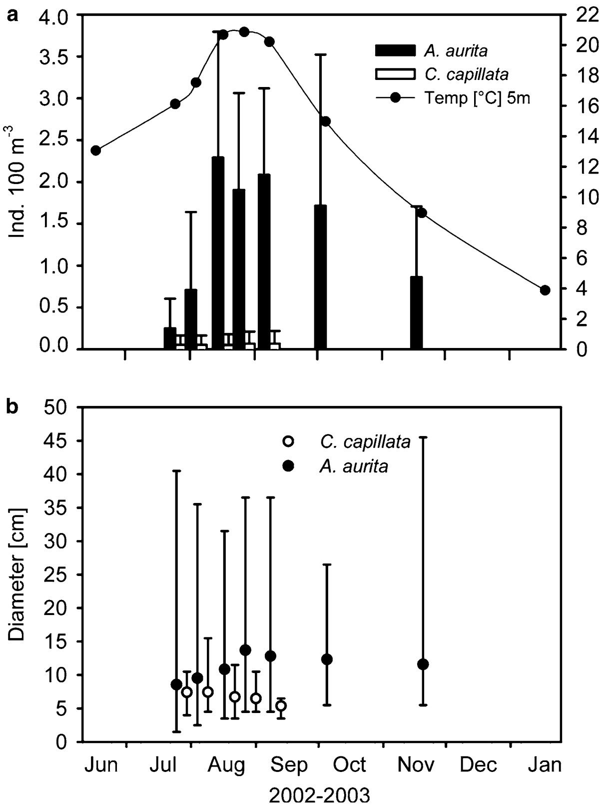


Fig. 2a, b *Aurelia aurita*, *Cyanea capillata*. **a** Mean abundance (± SD) and water temperature in 5 m in 2002–2003. **b** Mean diameter (cm) with min. and max. values shown as *vertical lines*

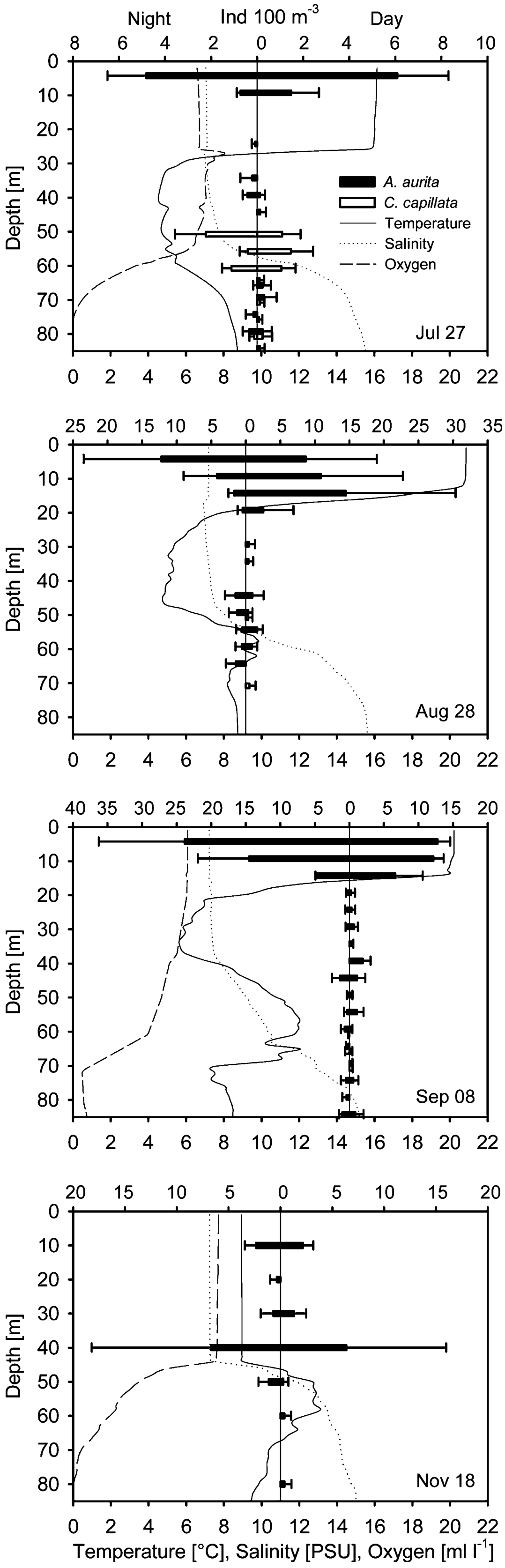


Fig. 3 *Aurelia aurita*, *Cyanea capillata*. Vertical distribution (mean abundance ± SD) in relation to hydrography (temperature, salinity, oxygen) from July to November 2002

where P is the percentage of prey standing stock consumed per day, F is the number of prey consumed per medusa per day, M is the abundance of medusae per cubic meter and C is the abundance of prey per cubic meter.

Results

Hydrography

The hydrography of the central Baltic Sea is characterized by clear stratification (see Fig. 3). From July to September the thermocline was found between 25 and 15 m, separating the surface layer from the colder (5–6°C) intermediate water layer. Temperature in the surface layer is shown in Fig. 2. It increased from 16°C in the beginning of July to the maximum summer temperature in August (20.8°C). In November the surface water had cooled down to 8.9°C and merged with the intermediate water. Below a halocline, which varied between 55 m in July and 45 m in November, oxygen-depleted bottom water reached to the ground. Salinity was rather constant between the surface and the halocline (7 PSU) and increased thereafter up to 15.5 PSU. Oxygen concentration decreased rapidly below the halocline to values <2 ml l^{-1}. In September a warm North Sea water body originating from an exceptional summer inflow event reached the Bornholm Basin (Fig. 3). With a temperature of 12–13°C it resided in the halocline between the intermediate water and the bottom water (Feistel et al. 2003).

Medusa abundance and size

Aurelia aurita and *Cyanea capillata* were the only scyphozoan species caught in the Bornholm Basin. The first medusae of both species were observed at the end of July (Fig. 2). In Fig. 2 mean abundance is shown for all stations per cruise, integrated over the whole water column. Highest abundance of *A. aurita* was found in August and the beginning of September, with 2.3 and 2.1 ind. per 100 m^3, respectively. In November still 0.9 ind. per 100 m^3 were observed, but in mid-January no medusae were found. Mean medusa size varied only slightly between 8.5 cm in July and 13.7 cm in August; the size range, however, was almost constant during the whole investigation period (Fig. 2).

C. capillata occurred only between July and September and in much smaller numbers than *A. aurita*. Abundance varied between 0.05 ind. per 100 m^3 in July and August and 0.07 ind. per 100 m^3 in late August and early September (Fig. 2). Mean medusa size showed a decreasing trend from 7 cm in July to 5 cm in September. No ephyrae of either species were caught during the whole investigation period.

Vertical distribution

A. aurita and *C. capillata* showed a pronounced vertical separation over the water column during the 24-h sampling (Fig. 3). From July to September *A. aurita* had its highest abundance in the upper water layers. About 80% of the medusae was present in the upper 20 m, the rest was spread over the remaining water column. In contrast, in November most medusae were caught in 40 m.

A large patch of *C. capillata* was caught in July above and in the halocline between 50 and 60 m, where salinity increased from 7 to 13 PSU, temperature was 5°C and oxygen content was >2 ml l^{-1} (Fig. 3). This patch probably does not reflect the general abundance of *C. capillata* in this month (Fig. 2). In August and September *C. capillata* was only found sporadically; in November it was absent.

No significant difference between day and night samples of either species was detected ($P=0.18$–1.00, Mann–Whitney rank sum test).

Horizontal distribution

Two examples of the horizontal distribution of *A. aurita* in the Bornholm Basin are presented in Fig. 1. Values were integrated over the whole water column. In August some larger patches of medusae were encountered where abundance reached >6 ind. per 100 m^3 (stns 14 and 41), but also areas with no medusae were found (stns 40 and 43b). In September the distribution was rather homogenous, abundance varied between 0.3 and 4 ind. per 100 m^3. The highest concentration of medusae was 8 ind. per 100 m^3, found at stn 43a in October and stn 7 in November. A study examining medusa distribution in relation to circulation patterns is under way.

Zooplankton abundance

Data on seasonal and vertical zooplankton abundance and distribution at the focus stations were provided by Schulz and Hirche (personal communication). In brief, during medusa occurrence, cladocerans and copepods dominated the zooplankton. Between July and September the most abundant species above the thermocline was the cladoceran *Bosmina coregoni maritima*, which reached a maximum density of 267,000 ind. m^{-3} at stn 23 in August (Schulz and Hirche, personal communication). Abundance of *Podon intermedius* peaked in July/August (800 ind. m^{-3} at stn 41), followed by a smaller peak in October. *Evadne nordmanni* reached its maximum abundance already in May; the highest numbers during medusa occurrence were caught in October (7,000 ind. m^{-3}). Abundant copepods were *Acartia bifilosa*, *A. longiremis*, *Temora longicornis*, *Pseudocalanus acuspes* and *Centropages hamatus*, but their maximum abundance was usually confined to the waters between 20 and 70 m. During the warm months only *A. bifilosa* was found, mostly above the thermocline (Dutz, in preparation).

Table 2 *Aurelia aurita*. Composition of gut contents (%) from July to October 2002, with sampling depth (m), number (*n*) and mean size (cm) of analyzed medusae (*0 m* caught by dip net from surface; *all others* caught by BIOMOC)

Month	Depth (m)	Medusae (*n*)	Size (cm) (mean ± SD)	*Bosmina coregoni maritima*	*Evadne nordmanni*	*Podon* spp.	*Pseudocalanus acuspes*	*Acartia* spp.	*Temora longicornis*	*Centropages hamatus*	*Eurytemora hirundoides*	Bivalve larvae	Gastropod larvae
Jul.	0	10	8.7 ± 2.1	87.5	1.4	4.0	0.1	0.4	1.9	3.9	0.0	0.8	0.0
	0–5	10	7.9 ± 0.9	48.2	1.7	36.4	1.1	0.0	11.5	1.1	0.0	0.0	0.0
	0–10	20	6.6 ± 1.8	46.5	1.7	37.6	1.2	0.1	11.7	1.2	0.0	0.0	0.0
	30–40	6	7.0 ± 3.3	75.8	1.5	16.6	0.6	0.9	2.2	2.5	0.0	0.0	0.0
	70–80	9	9.9 ± 2.5	64.0	1.2	19.3	3.2	1.8	6.0	3.6	0.0	0.9	0.0
Aug. II	0	10	10.8 ± 3.0	87.6	0.5	1.9	0.0	0.3	0.2	0.5	0.0	9.0	0.0
Aug. III	0	10	14.4 ± 0.7	67.2	1.5	1.0	1.2	1.0	3.9	1.7	0.0	21.2	1.3
Sep.	0	10	15.2 ± 1.6	75.1	9.8	0.3	0.1	0.3	1.5	1.3	0.0	11.2	0.4
	0–5	10	10.9 ± 1.6	78.8	5.2	6.9	1.6	0.3	4.2	2.0	0.0	1.2	0.0
	10–15	10	11.9 ± 1.1	26.4	21.9	13.5	2.3	1.1	23.0	9.6	0.0	2.3	0.0
	40–45	10	13.6 ± 1.6	28.1	10.9	6.3	1.0	3.3	38.6	6.9	0.0	4.6	0.3
	80–85	6	14.7 ± 4.7	55.8	8.0	5.1	5.8	4.4	15.9	5.1	0.0	0.0	0.0
Oct.	0	10	14.0 ± 3.0	75.4	1.8	6.2	0.4	9.1	1.2	0.8	2.8	2.3	0.0

Gut content

Gut content of *A. aurita* from five cruises was analyzed in specimens collected individually with a dip net from the surface layer. Due to limitations in time for sampling and appropriate sampling conditions (calm sea), only the most abundant size class was collected (compare Fig. 2b and Table 2). The larger specimens were always damaged, while the small ones were out of reach. Their food consisted of cladocerans, copepods, bivalve and gastropod larvae and varied only slightly in species composition and abundance during the study period. The cladoceran *Bosmina coregoni maritima* was the most abundant prey item during the whole investigation (Table 2). In July cladocerans made up 93% of the gut content. The copepod fraction included copepodites IV–V (CIV–CV) and adults of *Acartia* spp., *Pseudocalanus acuspes*, *Temora longicornis*, *Centropages hamatus* and *Eurytemora hirundoides* and varied from 1% to 14% of the prey items. The highest value was found for *Acartia* spp. in October (9%). A further important group of food items was bivalve larvae, with up to 21% in late August (Aug. III). The guts of *A. aurita* caught by dip net near the surface contained many more prey items than those caught by BIOMOC in deeper water layers. The comparison of total prey in specimens collected by dip net to those caught by BIOMOC in 0–5 m, which are supposed to feed in the same depth, suggests that medusae lose once ingested prey items during the haul, which may lead to an underestimation of daily ration. Therefore, gut contents of medusae caught by BIOMOC are listed for information (Table 2), but are not used for calculation of impact.

Prey selectivity

The selectivity values for *A. aurita* ranged around zero (Table 3), indicating low prey selection. However, the values were always significantly positive for *Podon* sp. ($P < 0.001$); bivalve larvae were significantly positively selected in August and September ($P < 0.001$). In contrast, prey selection values for *Acartia* spp. were always negative and significantly different from 0 in July and September ($P < 0.001$). Nauplii and CI–CIII were always available, but never eaten by *A. aurita*.

Predatory impact

The effect of predation by *A. aurita* on the zooplankton community was calculated for all focus stations on four cruises from July to October. As the major portion (80%) of *A. aurita* lived in the upper 20 m from July to September (Fig. 3), calculations for prey selection and

Table 3 *Aurelia aurita*. Prey selectivity values from July to October 2002 according to Pearre (1982). *Asterisk* denotes significant selection ($P < 0.05$) (*dash* prey not present in guts)

Month	*Bosmina coregoni maritima*	*Evadne nordmanni*	*Podon* spp.	*Pseudocalanus acuspes*	*Acartia* spp.	*Temora longicornis*	*Centropages hamatus*	*Eurytemora hirundoides*	Bivalve larvae	Gastropod larvae
Jul.	0.022*	0.010	0.044*	0.009	−0.017*	0.010	0.022*	–	−0.007	–
Aug. II	−0.007	0.004	0.011*	−0.002	−0.001	−0.004	0.000	–	0.148*	–
Sep.	0.014	0.095*	0.032*	−0.003	−0.028*	−0.026*	0.006	–	0.056*	0.002
Oct.	0.047*	−0.002	0.054*	0.027	−0.006	−0.006	0.003	0.000	−0.007	–

predatory impact were made for the 0- to 20-m layer only. Furthermore, all calculations were related to the mean size and biomass of the medusae for each cruise, as only such medusae were analyzed. Thus, it is possible that size-related differences were ignored. In Table 4, the impact in the upper 20 m is shown for stn 23 and other stations having high medusa abundance, with mean values for all focus stations per cruise. Because of their low importance as prey (Table 2), all copepod species were pooled for impact calculations. *Bosmina coregoni maritima*, *Evadne nordmanni* and *Podon* spp. were pooled as "cladocerans". From July to September, a maximum impact of 0.28% day^{-1} on the copepod standing stock was observed (stn 41 in July; Table 4); the highest mean consumption per cruise was 0.10% day^{-1} in August. In October, medusae fed on more copepods and the predatory effects reached a maximum of 1.15% day^{-1} of the standing stock at stn 12, but the mean value for all focus stations in October was only 0.41% day^{-1}. The mean impact on the cladoceran stock was comparably low, but some stations were stressed by a higher predation effect. In August, 7.87% day^{-1} of the cladoceran stock was eaten at stn 21, whereas the large patch of medusae at stn 41 (Fig. 1) ingested only 0.9% day^{-1} of the cladocerans, due to their extremely high abundance. The highest mean impact per cruise was found in October (1.09% day^{-1}), when abundance of cladocerans in the upper 20 m was lowest.

Discussion

Seasonal distribution and life cycle

The two scyphozoan medusae *Aurelia aurita* and *Cyanea capillata* are found regularly in the Bornholm Basin, but are not present all year round. Our collection of *A. aurita* from July to November is in the range of the observations by Janas and Witek (1993) in the Polish fisheries zone (southern/central Baltic) between 1983 and 1991, where it was found from July to January, with highest numbers between August and November.

The life cycle of *A. aurita* in the Bornholm Basin in 2002 started with the appearance of medusae ≥1.5 cm in diameter in July and closed in November, when the main abundance of medusae was found in 45–35 m depth (Fig. 3). This life cycle is characterized by the absence of ephyrae, a later appearance of young medusae and a

Table 4 *Aurelia aurita*. Feeding rate (prey consumed $\text{medusa}^{-1}\text{day}^{-1}$) and predatory impact (% prey standing stock consumed day^{-1}) on copepod and cladoceran standing stock from July to October 2002 at stn 23 and stations having high medusa abundance, with mean values (±SD) and range for all focus stations. Calculated with abundance of medusae and prey in the upper 20 m (ind. m^{-3}). For size and number of analyzed medusae see Table 2

Month	Station	Abundance (ind. m^{-3})			Feeding rate (prey med.^{-1} day^{-1})		Predatory impact (% consumed day^{-1})	
		Medusae	Copepoda	Cladocera	Copepoda	Cladocera	Copepoda	Cladocera
Jul.	23	0.02	4,267	43,280	163.2	2,420.8	0.08	0.11
	41	0.04	2,358	32,154	163.2	2,420.8	0.28	0.30
	Mean ± SD	0.01 ± 0.01	5,028 ± 5,695	43,812 ± 19,278	163.2	2,420.8	0.03	0.05
	Range						0.00–0.28	0.00–0.30
Aug. II	23	0.07	9,139	174,118	55.2	4,815.2	0.04	0.19
	21	0.15	3,078	9,178	55.2	4,815.2	0.27	7.87
	41	0.18	4,192	95,501	55.2	4,815.2	0.24	0.91
	Mean ± SD	0.09 ± 0.06	4,601 ± 2,855	75,749 ± 67,946	55.2	4,815.2	0.10	0.54
	Range						0.03–0.27	0.13–7.87
Sep.	23	0.10	5,971	6,384	59.2	1,559.2	0.10	2.44
	03	0.11	3,101	12,954	59.2	1,559.2	0.21	1.32
	41	0.09	3,450	3,392	59.2	1,559.2	0.15	4.14
	Mean ± SD	0.07 ± 0.03	5,328 ± 7,198	17,716 ± 10,088	59.2	1,559.2	0.07	0.58
	Range						0.01–0.21	0.19–4.14
Oct.	23	0.03	19,328	37,965	385.6	2,245.6	0.06	0.18
	12	0.12	4,013	6,656	385.6	2,245.6	1.15	4.05
	Mean ± SD	0.05 ± 0.03	6,144 ± 5,517	12,862 ± 11,261	385.6	2,245.6	0.41	1.09
	Range						0.06–1.15	0.18–4.05

smaller mean diameter than in adjacent areas. In the Gullmar Fjord (western Sweden) ephyrae occurred from October on, and already in May all specimens had developed into medusae (Hernroth and Gröndahl 1983; Gröndahl 1988). Olesen et al. (1994) found ephyrae in Kertinge Nor and Kerteminde Fjord in the Danish Belt Sea in February. In the western Baltic (Kiel Fjord) first ephyrae appeared in November (Möller 1980a) and entered the medusa stage (> 1 cm) already in late April. The mean diameter of *A. aurita* during our investigation varied only slightly between 8.5 and 13.7 cm, with a minimum diameter of 1.5 and a maximum of 45.5 cm. The greatest mean diameter of *A. aurita* from Kiel Fjord between 1978 and 1979 was larger (19.7 cm, Möller 1980a).

In fall, *A. aurita* is found in deeper waters, similar to in the Black Sea (Vinogradov and Shushkina 1982). It is unclear whether this is part of a seasonal migration (Yasuda 1970) or whether they follow their prey. In the Bornholm Basin, prey abundance was not greater at the depth of their occurrence (Schulz and Hirche, personal communication). The majority of medusae seem to degenerate and die after reproduction (Hamner and Jenssen 1974; Möller 1979, 1980a; Hay et al. 1990). Therefore, the deep-dwelling medusae found in November in the Bornholm Basin are probably degenerating animals accumulating on the pycnocline. However, a life span of 2 years and a second reproduction phase have been suggested for Japanese waters from laboratory observations and field studies by Omori et al. (1995) and Miyake et al. (1997).

The absence of ephyrae, the later appearance and the smaller size than in adjacent areas indicate that *A. aurita* does not reproduce successfully in the study area. Janas and Witek (1993) proposed that reproduction of *A. aurita* may occur in Polish waters, locally and in small numbers, but the majority of medusae is transported by surface currents from the western Baltic. Möller (1980c) suggested the Kiel Bight and waters around the Danish Isles as the main areas of *A. aurita* production, where polyps find sheltered bays and fjords with their preferred conditions (Möller 1979; Gröndahl 1988). A study dedicated to medusa abundance and distribution patterns combined with circulation models should help in identifying the origin of *A. aurita* in the central Baltic.

C. capillata is usually much less abundant in the central Baltic than *A. aurita* (Janas and Witek 1993; Margonski and Horbowa 1995; Lischka 1999). It shows a considerable interannual variability in its seasonal occurrence in the Bornholm Basin. First appearance varied from February to August, alternating with years of complete absence (Janas and Witek 1993; Lischka 1999); our observations of occurrence from July to September fit into this range. In Kiel Bight it occurred from June to September in 1976/1977 and already in April during 1978/1979 (Möller 1984). First ephyrae appeared in Gullmar Fjord in February; medusae appeared from June until December (Gröndahl 1988). The origin of *C. capillata* in the Bornholm Basin is also unclear, as the absence of ephyrae and the generally low abundance indicate that there was no reproduction in the study area either. The Gullmar Fjord (Sweden) is known as one production area of *C. capillata* near the Baltic, where the polyps find favorable salinity (> 20 PSU, Cargo 1984), although the low abundance of ephyrae there indicates the geographical boundary for production (Gröndahl and Hernroth 1987; Gröndahl 1988). The vast majority of individuals of this species probably drifts into the Baltic from the North Sea, which makes it an indicator of North Sea water masses in the Baltic Sea (Möller 1980c; Gröndahl and Hernroth 1987).

Vertical distribution

The two medusa species showed marked differences in their vertical distribution in the Bornholm Basin (Fig. 3). From July to September 2002 the vast majority of *A. aurita* were collected in the upper 15 m, whereas *C. capillata* was only found below 45 m. In August and September the lower boundary for the largest part of the population of *A. aurita* at 15 m depth coincided with the thermocline, where temperature dropped from 20°C to 6°C. Previous studies in this area also found highest numbers of *A. aurita* in August and September in the upper 20 m at temperatures around 17°C and a salinity of 7 PSU (Margonski and Horbowa 1995; Lischka 1999). While Margonski and Horbowa (1995) explained an unusual peak abundance in August 1993 at 50–60 m by a warm water intrusion in this depth, the warm water inflow during our study in September 2002 (Fig. 3) apparently did not affect vertical distribution. Diel vertical migration patterns of *A. aurita* differ geographically (e.g. Yasuda 1970, 1973; Mackie et al. 1981; Hamner et al. 1982). In Kiel Bight medusae approached the surface at midday and midnight, possibly following their copepod food (Möller 1984). In the Black Sea, on the other hand, *A. aurita* were restricted to the surface layers and did not migrate (Kideys and Romanova 2001). In the Bornholm Basin diel vertical migration has not been studied before. At 24-h stations between July and November, no diel vertical migration was observed in our study (Fig. 3). The hydrographic situation in the Bornholm Basin, with a stratified water column from July to September, seems to provide an optimal habitat for *A. aurita* above the thermocline, with warmer water and high prey availability.

C. capillata was never observed above 40 m in the central Baltic (Hernroth und Ackefors 1979; Margonski and Horbowa 1995; Lischka 1999). In contrast to *A. aurita*, it seemed to prefer the intermediate water layer and the adjacent halocline. The higher salinity found below 60 m, which is closer to the oceanic conditions under which *C. capillata* is usually found (Gröndahl and Hernroth 1987), does not seem to be accessible in the Bornholm Basin due to low oxygen concentrations. Although scyphozoan medusae in general seem to tolerate low oxygen conditions (Arai 1997), they moved to upper layers when oxygen content was ≤ 2 mg l^{-1}, as found by Keister et al. (2000) for *Chrysaora quinquecirrha*. Negative effects of oxygen depletion upon the predation capacity or the absence of prey could be the reason for this avoidance (Keister et al. 2000).

As *A. aurita* may be a substantial food source for *C. capillata* (Båmstedt et al. 1994, 1997; Hansson 1997), its absence at 50–60 m in July could be explained as a result of predation by the large patch of *C. capillata* (up to 2 ind. per 100 m^3) caught at this depth. In Lischka's study (1999), *A. aurita* was also absent at 55–75 m, where *C. capillata* occurred in August 1998, but she could not detect *A. aurita* in the guts of *C. capillata*. The exclusive occurrence of *C. capillata* at ≥70 m in August could also be predation related, whereas both species co-occurred in July and September in deeper layers (>60 m).

Abundance

The abundance of *A. aurita* during this study is at the higher end of the values reported for the central Baltic, but lower when compared to the western Baltic (Table 5). Average numbers of *A. aurita* found by Lischka (1999) in 1998 in the same area showed similar values for July and August, with 0.31 and 2.18 ind. per 100 m^3, respectively (Table 5). In contrast, Margonski and Horbowa (1995) caught only about 0.8 ind. per 100 m^3 in the Bornholm Basin in August 1994 (abundance estimated from their Fig. 2). Average biomass values for *A. aurita* caught by Janas and Witek (1993) during the years 1983–1991 were only 50% of our values, indicating large interannual variability. In the western Baltic, often much higher numbers of medusae were found. Thus, in Kiel Fjord abundance of *A. aurita* medusae reached a maximum of 12.1 ind. per 100 m^3 in September 1978 and 1979 (Möller 1980a). In Kiel Bight and Eckernförde Bay medusa abundance also showed high interannual variability (Schneider 1989; Schneider and Behrends 1994). Years with high numbers alternated with years of lower concentrations, such as those in our study, especially in August 1983 in Eckernförde Bay (Schneider 1989).

The abundance of *C. capillata* was characterized as occasional in the central Baltic Sea by Hernroth and Ackefors (1979). Maximum abundance of 0.07 ind. per 100 m^3 in September during our study compares well with the earlier study by Margonski and Horbowa (1995), but is much lower than the values reported for July by Lischka (1999) (Table 5). Möller (1979) classified *C. capillata* as secondary in importance among coelenterates in Kiel Bight. Due to the scarcity of abundance data and the absence of predation rates, it is impossible at present to judge the role of *Cyanea* predation for the *A. aurita* population in the Baltic.

Predation

Medusae used for gut analysis in this study usually represented the mean size of the population. Graham and Kroutil (2001) reported a tendency towards a greater variety of prey in the guts of larger medusae. In our study the portion of medusae larger than the ones analyzed for gut content varied between 3% and 28% (mean 14%) for the 4 months investigated. Therefore, the effect on overall impact should be rather small. The gut content of

Table 5 *Aurelia aurita*,*Cyanea capillata*. Mean abundance (ind. per 100 m^3) and biomass (g wet weight per 100 m^3) in the Baltic in various years (*BB* Bornholm Basin; *EB* Eckernförde Bay; *KB* Kiel Bight; *KF* Kiel Fjord; *PF* Polish Fisheries Zone; *dash* no data)

Area	Year	July		August		September		Author
		Abundance	Biomass	Abundance	Biomass	Abundance	Biomass	
A. aurita								
BB	2002	0.25	18	2.30	159	2.10	281	Present paper
BB	1998	0.31	–	2.18	–	–	–	Lischka (1999)
BB	1994	–	–	~0.80	–	~0.40	–	Margonski and Horbowa (1995)
PF	1983–1991	–	–	–	84	–	132	Janas and Witek (1993)
KF	1978/1979	9.70	~2,320	6.90	~2,396	12.10	~2,740	Möller (1980a, 1984)
EB	1982	15.00	–	14.00	–	14.00	–	Schneider (1989)
EB	1983	0.78–2.40	–	2.30	–	0–1.50	–	Schneider (1989)
KB	1993	~14.00	–	~7.00	–	–	–	Schneider and Behrends (1994)
KB	1990/1991	~1.00	–	~1.00	–	~0.50	–	Schneider and Behrends (1994)
C. capillata								
BB	2002	0.05	1.00	0.05	1.25	0.07	0.51	Present paper
BB	1998	~0.22	–	–	–	–	–	Lischka (1999)
BB	1994	–	–	~0.09	–	~0.09	–	Margonski and Horbowa (1995)
KF	1978/1979	0.00	–	0.05	–	0.02	–	Möller (1980a, 1984)

A. aurita consisted of cladocerans, copepods and mollusk larvae, reflecting closely the food availability in the upper 20 m during the investigation. However, some interesting aspects were found in prey composition and prey selection. As scyphomedusae do not actively attack prey, selection depends on various characteristics of predators and prey (reviewed in Purcell 1997). Large prey is relatively more vulnerable to scyphomedusae, as found in experiments with copepods and *A. aurita* (Suchman and Sullivan 2000). Vice versa, small size is suggested to be an effective refuge from predation (Suchman and Sullivan 1998). Our findings support these concepts. Small nauplii and CI–CIII were not ingested by *A. aurita*, although they were available in the water column, with abundances reaching 29,000 nauplii m^{-3} and 8,600 CI–III m^{-3} in the upper 20 m in October. On the other hand, there was a significant positive selection for *Podon* spp., the biggest prey item found in the medusa guts, during the whole study period (Table 3). Other remarkable findings were a conspicuous number of *Evadne nordmanni* in the guts in September (9.8%), which could not be explained from the perspective of measured abundance. Possibly, *A. aurita* met an *E. nordmanni* patch, which was not detected with our zooplankton hauls. Significant positive selection was found for bivalve larvae in August and September, when they were the second most abundant prey item in the medusa guts, although their abundance in the water column was lower than in other months. Hamner et al. (1982) described bivalve larvae as a relatively easier prey to catch for *A. aurita* compared to active copepods with elaborate sensory organs. However, the predatory impact on the bivalve population may have been negligible, as they were shown to avoid digestion and survive gut passage (Purcell et al. 1991). The high numbers of *Acartia* spp. in the guts in October correspond to the extreme increase in individuals of *Acartia* species in the upper 20 m, from 3,200 ind. m^{-3} in July to 12,600 in October at stn 23 (Dutz, in preparation). *A. aurita* could not be verified as a predator on cod eggs, as described by Margonski and Horbowa (1995) for the Bornholm Basin, or on fish larvae, as found by Möller (1980b, 1984), Purcell (review 1985) and van der Veer (1985). Cod eggs are restricted to salinities ≥11 PSU, and were therefore distributed in the Bornholm Basin below 60 m (Nissling et al 1994). Sprat eggs in general were also found in deeper waters (Makarchouk and Hinrichsen 1998; Nissling et al. 2003). The absence of fish eggs in medusa guts can therefore be explained by a limited spatial overlap in the water column. Loss of already ingested prey during the haul could cause the absence of fish eggs and larvae in medusae caught by BIOMOC in deeper layers. Sprat larvae were present in the upper water layers, but reached numbers of only 0–0.3 ind. m^{-2} from August to October 2002, when peak abundance was already over (Voss et al. 2004). Thus, their absence in the medusa guts could be caused by the limited seasonal overlap. While copepods were described as the main food of *A. aurita* in other regions (Möller 1980b; Hamner et al. 1982; Matsakis and Conover 1991; Sullivan et al. 1994; Graham and Kroutil 2001; Mutlu 2001), in the Bornholm Basin *Bosmina coregoni maritima* was the most ingested prey item from July to October. This endemic brackish water cladoceran was the most abundant species in the upper 20 m from July to October. During the warm months, it is the dominant zooplankton species (Hernroth and Ackefors 1979), but, in summer 2002, it reached the highest values ever reported in this area (Schulz and Hirche, personal communication).

Scyphomedusae can have a strong impact on zooplankton standing stocks. Purcell (1992) estimated for *Chrysaora quinquecirrha* a maximum consumption of 94% day^{-1} of the copepod population in Chesapeake Bay (USA). Matsakis and Conover (1991) attributed the population decrease of *Rathkea octopunctata* (hydrozoan) to predation by *A. aurita*. Schneider and Behrends (1998) correlated zooplankton abundance to medusa densities in Kiel Bight, and concluded that the stocks of most zooplankton species were negatively affected in *A. aurita* bloom years. Möller (1980b) also suggested that *A. aurita* is the dominant factor in regulating plankton dynamics in Kiel Bight during summer. In contrast Purcell (1997) suggested that predation on copepods usually is inadequate to reduce populations. For *Aurelia labiata* she found only low predation rates, with a maximum of 0.08% day^{-1} of the copepod stock in Prince William Sound, Alaska (Purcell 2003). In the Bornholm Basin in 2002, copepods were only of secondary importance as food in general and only a maximum of 1.15% day^{-1} of the standing stock of the upper 20 m was consumed (Table 4). The main prey species, *B. coregoni maritima*, was very abundant, and only the combination of high medusa densities and lower prey abundance at some stations resulted in a higher impact, as found for stn 21 in August (7.87% day^{-1} of the standing stock consumed). As *B. coregoni maritima* has rapid parthenogenetic reproduction, it can numerically outgrow its predators (Viitasalo et al. 2001).

In conclusion we suggest that predation by *A. aurita* did not regulate the zooplankton community in the Bornholm Basin during this investigation. Although both *A. aurita* and sprat larvae fed on cladocerans and CIV–CVI (Voss et al. 2003; Dickmann and Voss, submitted), fish larvae should not suffer from competition with *A. aurita*. Limited spatial and seasonal overlap of fish eggs and larvae with medusae protect them from predation.

Acknowledgements This study would not have been possible without the support of many colleagues and students who helped in collecting and analyzing medusae. We thank the crews of R.V. “Alkor”, “Heincke” and “A. v. Humboldt”. This research was funded by GLOBEC Germany, BMBF 03F0320D.

References

Arai MN (1997) A functional biology of Scyphozoa. Chapman and Hall, London

Båmstedt U, Martinussen MB (2000) Estimating digestion rate and the problem of individual variability, exemplified by a scyphozoan jellyfish. J Exp Mar Biol Ecol 251:1–15

Båmstedt U, Martinussen MB, Matsakis S (1994) Trophodynamics of the two scyphozoan jellyfishes, *Aurelia aurita* and *Cyanea capillata*, in western Norway. ICES J Mar Sci 51:369–382

Båmstedt U, Ishii H, Martinussen MB (1997) Is the scyphomedusa *Cyanea capillata* (L.) dependent on gelatinous prey for its early development? Sarsia 82:269–273

Cargo DG (1984) Some laboratory techniques for the culture of Scyphozoa. In: Workshop on jellyfish blooms in the Mediterranean. UNEP, Athens, pp 129–138

Feistel R, Nausch G, Mohrholz V, Lysiak-Pastuszak E, Seifert T, Matthäus W, Krüger S, Hansen IS (2003) Warm waters of summer 2002 in the deep Baltic Proper. Oceanologia 45:571–592

Graham WM, Kroutil RM (2001) Size-based prey selectivity and dietary shifts in the jellyfish, *Aurelia aurita*. J Plankton Res 23:67–74

Gröndahl F (1988) A comparative ecological study on the scyphozoans *Aurelia aurita*, *Cyanea capillata* and *C. lamarckii* in the Gullmar Fjord, western Sweden, 1982 to 1986. Mar Biol 97:541–550

Gröndahl F, Hernroth L (1987) Release and growth of *Cyanea capillata* (L.) ephyrae in the Gullmar Fjord, western Sweden. J Exp Mar Biol Ecol 106:91–101

Hamner WM, Jenssen RM (1974) Growth, degrowth and irreversible cell differentiation in *Aurelia aurita*. Am Zool 14:833–849

Hamner WM, Gilmer RW, Hamner PP (1982) The physical, chemical, and biological characteristics of a stratified, saline, sulfide lake in Palau. Limnol Oceanogr 27:896–909

Hansson LJ (1997) Capture and digestion of the scyphozoan jellyfish *Aurelia aurita* by *Cyanea capillata* and prey response to predator contact. J Plankton Res 19:195–208

Hay SJ, Hislop JRG, Shanks AM (1990) North Sea Scyphomedusae: summer distribution, estimated biomass and significance particularly for 0-group gadoid fish. Neth J Sea Res 25:113–130

Hernroth L, Ackefors H (1979) The zooplankton of the Baltic proper: a long-term investigation of the fauna, its biology and ecology. Rep Fish Board Swed Inst Mar Res 2:1–60

Hernroth L, Gröndahl F (1983) On the biology of *Aurelia aurita* (L.). 1. Release and growth of *Aurelia aurita* (L.) ephyrae in the Gullmar Fjord, western Sweden, 1982–83. Ophelia 22:189–199

Janas U, Witek Z (1993) The occurrence of medusae in the Baltic and their importance in the ecosystem, with special emphasis on *Aurelia aurita*. Oceanologia 34:69–84

Keister JE, Houde ED, Breitburg DL (2000) Effects of bottom-layer hypoxia on abundances and depth distributions of organisms in Patuxent River, Chesapeake Bay. Mar Ecol Prog Ser 205:43–59

Kerstan M (1977) Untersuchungen zur Nahrungsökologie von *Aurelia aurita* Lam. Diplom thesis, Kiel University, Kiel

Kideys AE, Romanova Z (2001) Distribution of gelatinous macrozooplankton in the southern Black Sea during 1996–1999. Mar Biol 139:535–547

Lischka M (1999) Abundanz, Verteilung und Nahrungsökologie von Scyphomedusen in der zentralen Ostsee. Diplom thesis, Kiel University, Kiel

Lucas CH, Hirst AG, Williams JA (1997) Plankton dynamics and *Aurelia aurita* production in two contrasting ecosystems: comparisons and consequences. Estuar Coast Shelf Sci 45:209–219

Mackie GO, Larson KS, Larson RJ, Passano LM (1981) Swimming and vertical migration of *Aurelia aurita* (L.) in a deep tank. Mar Behav Physiol 7:321–329

Makarchouk A, Hinrichsen HH (1998) The vertical distribution of ichthyoplankton in relation to the hydrographic conditions in the eastern Baltic. Int Counc Explor Sea Comm Meet 1998/R:11

Margonski P, Horbowa K (1995) Vertical distribution of cod eggs and medusae in the Bornholm basin. Medd Havsfiskelab Lysekil 327:7–17

Martinussen MB, Båmstedt U (1999) Nutritional ecology of gelatinous planktonic predators. Digestion rate in relation to type and amount of prey. J Exp Mar Biol Ecol 232:61–84

Martinussen MB, Båmstedt U (2001) Digestion rate in relation to temperature of two gelatinous planktonic predators. Sarsia 86:21–35

Matsakis S, Conover RJ (1991) Abundance and feeding of medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during spring. Can J Fish Aquat Sci 48:1419–1430

Miyake H, Iwao K, Kakinuma Y (1997) Life history and environment of *Aurelia aurita*. South Pac Stud 17:273–285

Möller H (1979) Significance of coelenterates in relation to other plankton organisms. Meeresforschung 27:1–18

Möller H (1980a) Population dynamics of *Aurelia aurita* medusae in Kiel Bight, Germany (FRG). Mar Biol 60:123–128

Möller H (1980b) Scyphomedusae as predators and food competitors of larval fish. Meeresforschung 28:90–100

Möller H (1980c) A summer survey of large zooplankton, particularly scyphomedusae, in North Sea and Baltic. Meeresforschung 28:61–68

Möller H (1984) Data on the biology of jellyfish and youngfish in Kiel Bight. Möller, Kiel

Mutlu E (2001) Distribution and abundance of moon jellyfish (*Aurelia aurita*) and its zooplankton food in the Black Sea. Mar Biol 138:329–339

Nissling A, Kryvi H, Vallin L (1994) Variation in egg buoyancy of Baltic cod *Gadus morhua* and its implications for egg survival in prevailing conditions in the Baltic Sea. Mar Ecol Prog Ser 110:67–74

Nissling A, Müller A, Hinrichsen H-H (2003) Specific gravity and vertical distribution of sprat eggs in the Baltic Sea. J Fish Biol 63:280–299

Olesen N (1995) Clearance potential of jellyfish *Aurelia aurita*, and predation impact on zooplankton in a shallow cove. Mar Ecol Prog Ser 124:63–72

Olesen NJ, Frandsen K, Riisgård HU (1994) Population dynamics, growth and energetics of jellyfish *Aurelia aurita* in a shallow fjord. Mar Ecol Prog Ser 105:9–18

Omori M, Ishii H, Fujinaga A (1995) Life history strategy of *Aurelia aurita* (Cnidaria, Scyphomedusae) and its impact on the zooplankton community of Tokyo Bay. ICES J Mar Sci 52:597–603

Pearre SJ (1982) Estimating prey preference by predators: uses of various indices, and a proposal of another based on χ^2. Can J Fish Aquat Sci 39:914–923

Purcell JE (1985) Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. Bull Mar Sci 37:739–755

Purcell JE (1992) Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay, USA. Mar Ecol Prog Ser 87:65–76

Purcell JE (1997) Pelagic cnidarians and ctenophores as predators: selective predation, feeding rates, and effects on prey populations. Ann Inst Oceanogr 73:125–137

Purcell JE (2003) Predation on zooplankton by large jellyfish, *Aurelia labiata*, *Cyanea capillata* and *Aequorea aequorea*, in Prince William Sound, Alaska. Mar Ecol Prog Ser 246:137–152

Purcell JE, Cresswell FP, Cargo DG, Kennedy VS (1991) Differential ingestion and digestion of bivalve larvae by the scyphozoan *Chrysaora quinquecirrha* and the ctenophore *Mnemiopsis leidyi*. Biol Bull (Woods Hole) 180:103–111

Schneider G (1989) Estimation of food demands of *Aurelia aurita* medusae populations in the Kiel Bight/western Baltic. Ophelia 31:17–27

Schneider G, Behrends G (1994) Population dynamics and the trophic role of *Aurelia aurita* medusae in the Kiel Bight and western Baltic. ICES J Mar Sci 51:359–367

Schneider G, Behrends G (1998) Top-down control in a neritic plankton system by *Aurelia aurita* medusae—a summary. Ophelia 48:71–82

Suchman CL, Sullivan BK (1998) Vulnerability of the copepod *Acartia tonsa* to predation by the scyphomedusa *Chrysaora quinquecirrha*: effect of prey size and behaviour. Mar Biol 132:237–245

Suchman CL, Sullivan BK (2000) Effect of prey size on vulnerability of copepods to predation by the scyphomedusae *Aurelia aurita* and *Cyanea* sp. J Plankton Res 22:2289–2306

Sullivan BK, Garcia JR, Klein-MacPhee G (1994) Prey selection by the scyphomedusan predator *Aurelia aurita*. Mar Biol 121:335–341

van der Veer HW (1985) Impact of coelenterate predation on larval plaice *Pleuronectes platessa* and flounder *Platichthys flesus* stock in the western Wadden Sea. Mar Ecol Prog Ser 25:229–238

Viitasalo M, Flinkman J, Viherluoto M (2001) Zooplanktivory in the Baltic Sea: a comparison of prey selectivity by *Clupea harengus* and *Mysis mixta*, with reference to prey escape reactions. Mar Ecol Prog Ser 216:191–200

Vinogradov ME, Shushkina EA (1982) Estimate of the concentration of Black Sea jellyfish, ctenophores and *Calanus* based on observations from the Argus submersible. Oceanology 22:351–355

Voss R, Köster FW, Dickmann M (2003) Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. Fish Res (Amst) 63:97–111

Voss R, Clemmesen K, Baumann H, Dickmann M (2004) Recruitment success in Baltic sprat: coupling of food availability, larval condition and survival. Int Counc Explor Sea Comm Meet 2004/O:02

Yasuda T (1970) Ecological studies on the jelly-fish *Aurelia aurita* (L.) in Urazoko Bay, Fukui Prefecture. 5. Vertical distribution of the medusa. Annu Rep Noto Mar Lab 10:15–22

Yasuda T (1973) Ecological studies on the jelly-fish *Aurelia aurita* in Urazoko Bay, Fukui Prefecture. 9. Diel vertical migration of the medusa in late spring, 1970. Bull Jpn Soc Sci Fish 39:1145–1150

Scyphozoa in the Bornholm Basin (central Baltic Sea) – The role of advection

Kristina Barz, Hans-Harald Hinrichsen and Hans-Jürgen Hirche

Journal of Marine Systems 2006

Available online at www.sciencedirect.com
SCIENCE DIRECT®
Journal of Marine Systems 60 (2006) 167 – 176
JOURNAL OF MARINE SYSTEMS
www.elsevier.com/locate/jmarsys

Scyphozoa in the Bornholm Basin (central Baltic Sea)–The role of advection

Kristina Barz [a,*], Hans-Harald Hinrichsen [b], Hans-Jürgen Hirche [a]

[a] *Alfred Wegener Institute for Polar and Marine Research, Columbusstrasse, D-27568 Bremerhaven, Germany*
[b] *Leibniz Institute of Marine Sciences, Düsternbrooker Weg 20, D-24105 Kiel, Germany*

Received 7 November 2005; received in revised form 11 January 2006; accepted 12 January 2006
Available online 21 February 2006

Abstract

The usual absence of ephyrae and late appearance of medusae of the Scyphozoa *Aurelia aurita* and *Cyanea capillata* in the Bornholm Basin (BB; central Baltic Sea) indicate that these species are not strobilating in the region and their presence depends on advection. To study their potential origin we compared drift from historically known strobilation areas derived from a circulation model with spatial distributions observed during 19 cruises in the BB during 2002 and 2003. The model results are in good accordance with the field observations. According to the model results inter-annual differences in the timing of first appearance and life stage at appearance of *A. aurita* were clearly related to differences in the hydrodynamic regime during the investigation periods. During the stagnation regime in 2002 young medusae occurred first in June in the BB. In contrast, in 2003 fast transport due to several inflow events advected ephyrae released between January and March in the western Baltic already in April to the BB. Although the Gullmar Fjord (western Sweden) is the nearest known strobilation area for *C. capillata*, the model did not support advection from there in numbers explaining the occurrence of this species in the BB in 2002 and 2003. If the model works adequately in this regions we have to assume that the Gullmar Fjord is not a main source region of *C. capillata* in the BB, but other strobilation areas in the Kattegat or the North Sea appear more important.

Our results imply that advection and inflow events are critical for the occurrence and distribution of early stages of jellyfish in the central Baltic Sea. They demonstrate the potential of circulation models as tools to study the effect of long-range transport on the spatial composition of these organisms.

Keywords: *Aurelia aurita*; *Cyanea capillata*; Scyphozoa; Strobilation area; Circulation model; Advection; Baltic Sea; Bornholm Basin

1. Introduction

The abundance of scyphomedusae is increasing in many marine pelagic ecosystems, perhaps as a result of regime shifts (Brodeur et al., 1999; Brierley et al., 2001; Mills 2001; Lynam et al., 2004). It has been shown that medusae can reduce the stocks of mesozooplankton communities considerably in years of high abundance (e.g. Möller, 1980a; Matsakis and Conover, 1991; Purcell, 1992; Olesen, 1995; Omori et al., 1995; Lucas et al., 1997; Schneider and Behrends, 1998). They compete for zooplankton with commercially important planktivorous fish species, but they may also prey on fish eggs and larvae and thus directly affect their recruitment.

The deep basins in the Baltic Sea, including the Bornholm Basin (BB, central Baltic), are significant

---

* Corresponding author. Tel.: +49 471 4831 1324; fax: +49 471 4831 1918.
E-mail address: kbarz@awi-bremerhaven.de (K. Barz).

0924-7963/$ - see front matter © 2006 Elsevier B.V. All rights reserved.
doi:10.1016/j.jmarsys.2006.01.002

spawning grounds for cod (*Gadus morhua*) (Bagge et al., 1994; McKenzie et al., 2000) and sprat (*Sprattus sprattus*) (Köster et al., 2001). Therefore, the patterns of medusae abundance and occurrence and the factors regulating them are of special interest to assess, for instance, the impact of medusae on the populations of zooplankton and fish.

In the Baltic Sea only the scyphozoan medusae *Aurelia aurita* and *Cyanea capillata* are found. They are observed regularly in the BB, but are not present all year round (Janas and Witek, 1993; Barz and Hirche, 2005). Both species perform a typical cnidarian life cycle, including a planula which develops into a polyp. The polyp asexually produces medusae by strobilation, which in turn reproduce sexually (metagenesis). However, it is unclear if the species complete their whole life cycle in the BB. The facts that ephyrae are not found regularly and medusae appear later and were smaller than in adjacent seas suggest that *A. aurita* does not strobilate in this area (Janas and Witek, 1993; Barz and Hirche, 2005). *C. capillata* is usually much less abundant in the central Baltic than *A. aurita* (Janas and Witek, 1993; Margonski and Horbowa, 1995; Barz and Hirche, 2005). The absence of ephyrae and generally low abundance suggest that there is no strobilation area either (Barz and Hirche, 2005). Therefore, the question arises where the scyphomedusae appearing in the BB originate.

Large *A. aurita* polyp populations are reported from Kiel Bight (western Baltic) (Kändler, 1961; Thiel, 1962; Möller, 1979, 1980a,b; Schneider and Behrends, 1998), Kerteminde Fjord (Belt Sea, Denmark) (Olesen et al., 1994) and Gullmar Fjord (Skagerrak, Sweden) (Hernroth and Gröndahl, 1983; Gröndahl 1988). In older publications, the archipelago of S. W. Finland is also mentioned as a strobilation area (Wikström, 1932; Palmen, 1953). The Gullmar Fjord is the nearest known production area of *C. capillata*, although the low abundance of ephyrae there was interpreted as an indication for marginal living conditions by Gröndahl and Hernroth (1987) and Gröndahl (1988). The vast majority of this species is probably advected into the Baltic from the North Sea, which accordingly makes it an indicator of North Sea water masses in the Baltic Sea (Möller, 1980c; Gröndahl and Hernroth, 1987).

During an intensive field study in the BB, within the framework of German GLOBEC, which focused on the interactions between zooplankton and fish under the influence of physical processes, the seasonal and spatial occurrence patterns of *A. aurita* and *C. capillata* were

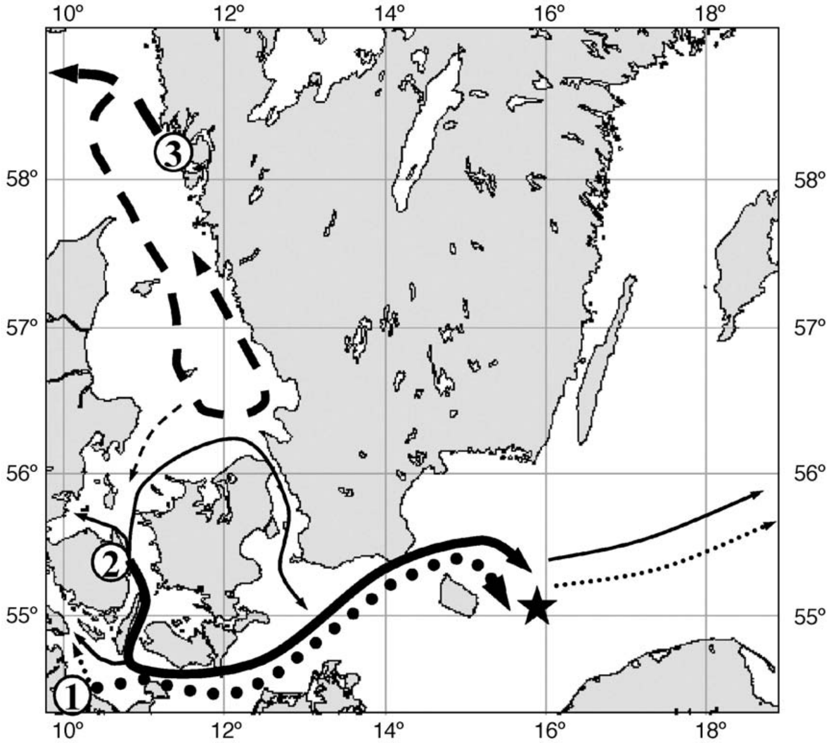


Fig. 1. Study area (Bornholm Basin = ★), release areas and main drift routes of medusae derived from the circulation model: 1 = Kiel Bight, dotted lines; 2 = Kerteminde area, solid lines; 3 = Gullmar Fjord area, dashed lines. Width of lines indicates significance of drift route.

Table 1
Time schedule of GLOBEC cruises 2002 and 2003

2002	2003
12–21 Mar	13–24 Jan
02–30 Apr	10–23 Feb
05–25 May	3–22 Mar
15–30 May	17–28 Apr
11–23 Jun	15 May–03 Jun
22 Jul–07 Aug	01–19 Jul
12–21 Aug	07–18 Aug
22–30 Aug	24 Nov–05 Dec
03–13 Sep	
30 Sep–10 Oct	
11–29 Nov	

investigated. Detailed data on medusa abundance and distribution in 2002 are already published (Barz and Hirche, 2005). Combined with new data from 2003 they allowed an inter-annual comparison under different hydrographic conditions. Thus, a Major Baltic Inflow event was recorded in the beginning of 2003 (Feistel et al., 2003), which may have affected the occurrence and distribution patterns of the medusae. Johnson et al. (2001) have shown how inter-annual variability of current patterns can produce remarkable fluctuations in jellyfish populations.

In order to study the advection of medusae from the known strobilation areas we used a three-dimensional eddy resolving baroclinic circulation model of the Baltic Sea. The modelled arrival of medusae in the BB was then compared with our observations in 2002 and 2003. The major aim was to identify the potential sources of the scyphomedusae in the central Baltic Sea, and to evaluate the processes controlling their occurrence and distribution in the area.

2. Material and methods

2.1. Sampling location, dates and hydrography

The study was carried out in the Bornholm Basin, central Baltic Sea (Fig. 1). Samples were taken during 19 cruises from March 2002 to December 2003 (Table 1), on a station grid of 52 stations. Water depth varied between 30 and 90 m. Salinity, temperature and dissolved oxygen were recorded on every station with a standard CTD probe.

2.2. Abundance and vertical distribution of scyphomedusae

Scyphomedusae were collected at all grid stations from oblique Bongo net hauls (0.6 m diameter, 335 and 500 μm mesh size). The average values of both nets were used for the distribution and abundance of the medusae, as 335 and 500 μm Bongo showed no difference for the abundance of *A. aurita* (p=0.5–0.9; Mann–Whitney Rank Sum Test). Sampling efficiency of the Bongo net was validated using additional oblique

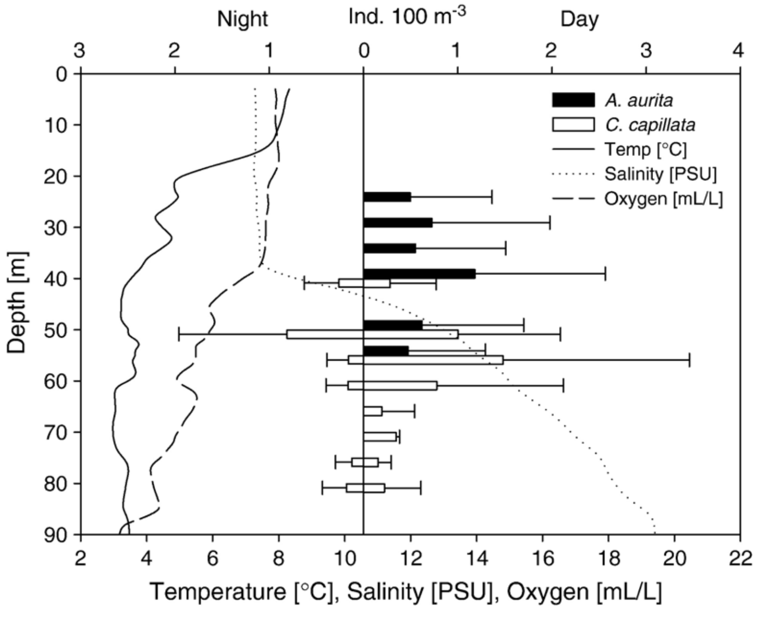


Fig. 2. Vertical distribution (mean abundance ± S.D.) of *Aurelia aurita* and *Cyanea capillata* and hydrography (temperature, salinity, and oxygen) in May 2003 on Station 23 in the central Bornholm Basin.

hauls with an Isaacs–Kidd midwater trawl (IKMT, 6 m^2 opening, 1000 μm).

In May 2003 the vertical distribution of the scyphomedusae was studied by using a trawled BIOMOC (1 m^2 opening, 55 μm) on Station 23 in the central BB. During 24-h three days and three nights, hauls were taken in 5-m intervals from bottom (90 m) to surface. The depths shown in Fig. 2 are mean trawling depths.

All medusae collected were processed onboard, identified and measured to the nearest 0.5 cm below.

2.3. Baltic Sea model

Numerical simulations of the circulation were performed by application of a three-dimensional eddy resolving baroclinic model of the Baltic Sea. The model is based on the free surface Bryan–Cox–Semtner model (Killworth et al., 1991) which is a special version of the Cox numerical ocean general circulation model (Bryan, 1969; Semtner, 1974; Cox, 1984). A detailed description of the equations and modifications made, necessary to adapt the model to the Baltic Sea, can be found in Lehmann (1995). The Baltic Sea model comprises the whole Baltic Sea, including the Gulf of Bothnia, Gulf of Riga as well as the Belt Sea, Kattegat and Skagerrak. The horizontal resolution is 5 km (eddy-permitting) with 60 vertical levels specified, which enables us to resolve the upper 100 m with levels of 3-m thickness.

The model is forced by realistic atmospheric conditions taken from the SMHI (Swedish Meteorological and Hydrological Institute, Norrköping) meteorological data base, which covers the whole Baltic drainage basin on a regular grid of 1° × 1°. The temporal increment of data records is 3 h. Additionally, river runoff has been evaluated from a monthly mean runoff data set (Bergstrøm and Carlsson, 1994). Runoff data are specified for 42 individual rivers distributed around the Baltic and the Kattegat.

Prognostic variables of the hydrodynamic model are: the oceanic baroclinic current field, the 3-D temperature, salinity and oxygen distributions, the 2-D surface elevation and the barotropic transport. These prognostic variables have been extracted from the model every 6 h and formed the database for the subsequent analysis.

Calculation of juvenile medusae (ephyrae) drift routes was performed by utilising a Lagrangian particle tracking technique (Hinrichsen et al., 1997) using a 4th-order Runge–Kutta scheme. Simulated three-dimensional velocity fields were extracted in order to develop a database for Lagrangian particle tracking exercises. The data set offers the possibility to derive drift trajectories by calculating the advection of “marked” water particles.

Simulations of within and between year variation in the drift patterns of ephyrae were performed for the years 2002 and 2003. For both years, the initial conditions of the model are realistic three-dimensional distributions of temperature and salinity, taken during several quasi-synoptic hydrographic surveys throughout the years. During simulations, ephyrae were prescribed as Lagrangian drifters, which were released into the modelled Eulerian flow fields at 10-day intervals, i.e., every 10 days a new batch of ephyrae was inserted. The release dates commenced November 12th of the foregoing year and ended April 21st.

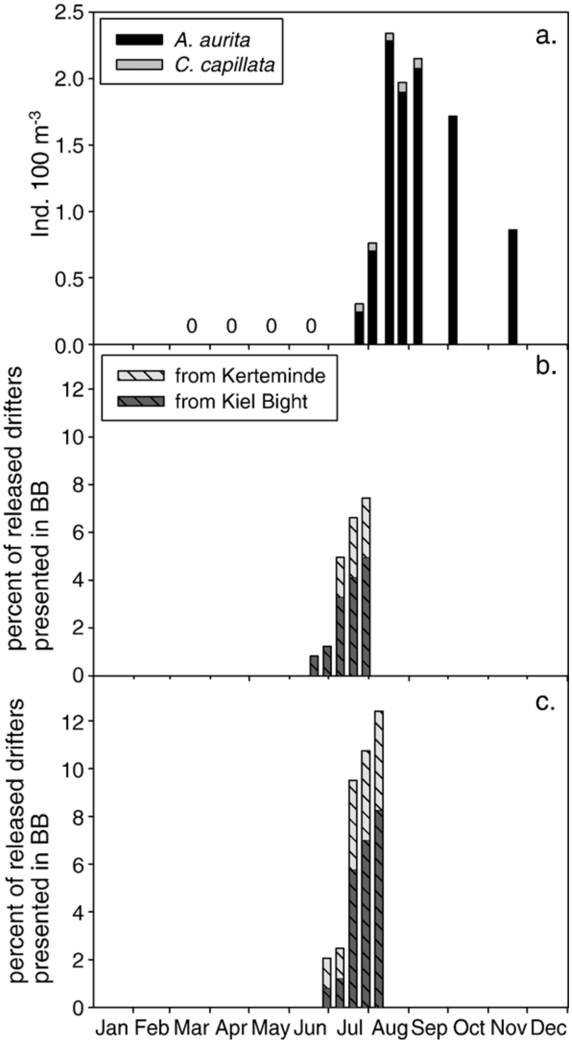


Fig. 3. (a) Observed medusae occurrence in 2002 (Ind. 100 m^{-3}); (b, c) modelled medusae arrival (% of 242 released drifters per source region presented in BB) from release date 12th of December 2001 (b) and 10th of February 2002 (c).

All drifters were tracked until August 20th. The drifters were deployed in the model in historical regions of peak reproduction of *A. aurita* in the Kiel Bight (Thiel, 1962; Möller, 1980b; Schneider and Behrends, 1994) and near Kerteminde (Olesen et al., 1994) as well as of *C. capillata* near the Gullmar Fjord in the Skagerrak (Gröndahl and Hernroth, 1987; Gröndahl, 1988) (Fig. 1). A total of 242 drifters were released on a regular spaced grid in each subarea in near surface waters (5 and 8 m deep). The drifters were allowed to leave the layers where they originally were launched. The positions of the drifters varied over time, as a result of the three-dimensional velocities that they experienced.

3. Results

3.1. Field observations

In 2002, the first medusae of both species were observed in the BB at the end of July (Fig. 3a). *A. aurita* was caught until November, *C. capillata* only to September. No ephyrae of either species were caught during the investigation period. Mean size of first caught medusae in July was 85±70 mm for *A. aurita* and 70±20 mm for *C. capillata* (Barz and Hirche, 2005). More detailed information about medusae abundance and distribution in 2002 has been provided by Barz and Hirche (2005).

In 2003 ephyrae of *A. aurita* were first detected in April, and small medusae of *A. aurita* and *C. capillata* were first caught in May (Fig. 4a). *A. aurita* was found in May in the central BB only between 25 and 55 m depth during day, no individuals were caught during night (Fig. 2). *C. capillata* occurred from 40 to 80 m during day and night. Abundance of both species was low in May and July (<0.2 ind. per 100 m^3). Whereas abundance of *C. capillata* remained low in August and the species was completely absent in November, *A. aurita* abundance increased to 1 ind. per 100 m^3 (August). In November, still 1.2 ind. per 100 m^3 were caught, note the lack of data between September and October (Fig. 4a). Size of ephyrae in April was not measured, mean medusa size in May was 12±3 mm (max. 20 mm) for *A. aurita* and 23±17 mm (max. 95 mm) for *C. capillata*.

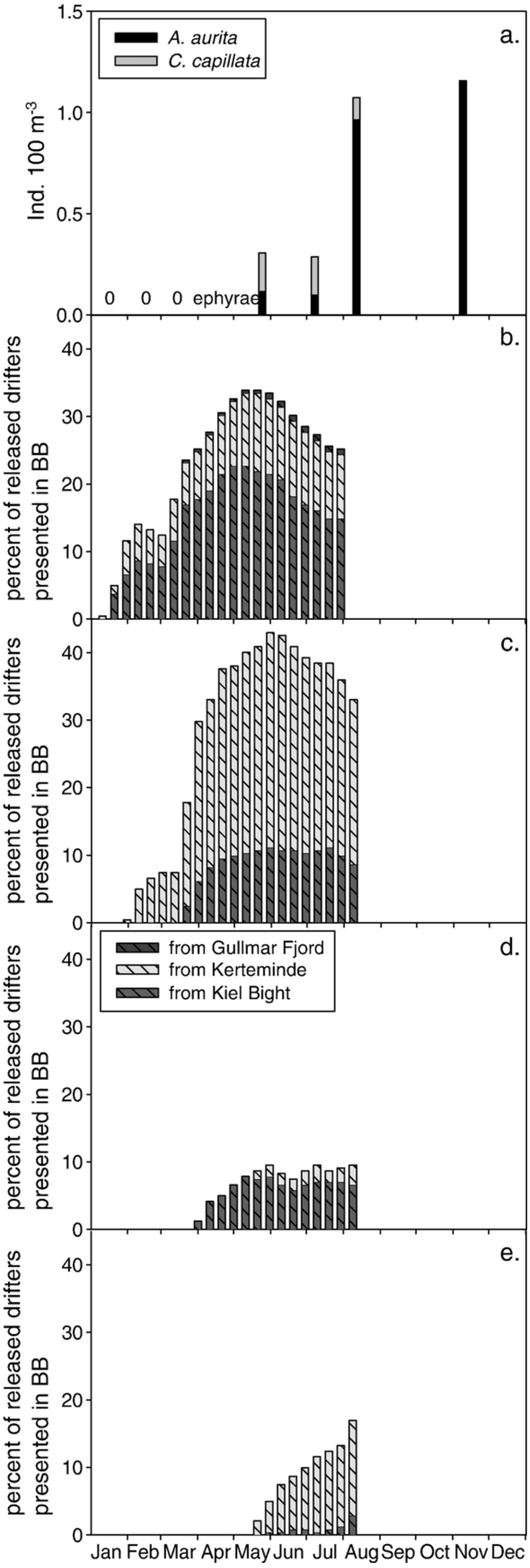


Fig. 4. (a) Observed medusae occurrence in 2003 (Ind. 100 m^{-3}); (b–e) modelled medusae arrival (% of 242 released drifters per source region presented in BB) from release date 2nd of December 2002 (b), 1st of January (c), 10th of February (d) and 12th of March 2003 (e).

3.2. Model results

The model does not distinguish between *A. aurita* and *C. capillata*; therefore, the drifters were treated as "medusae" in general. The main drift routes are shown in Fig. 1, drifters reached the BB with the water body in 40 m depth and deeper. The modelled number of "medusae" in the graphs (Figs. 3 and 4) is always a snapshot of percentage of medusae from the release areas present in the BB on that particular date. When medusae leave the BB after that date (Fig. 1), the numbers can decrease again (Fig. 4b, c).

The number of "medusae" reaching the BB in 2002 was very low in general, but always higher for those from Kiel Bight (KB) than from Kerteminde (KM) (Table 2). The most "medusae" reached the BB when released on the 1st of April in KB (17% of all drifters arrived). From the Gullmar Fjord area (GF) "medusae" arrived in the BB only from release date 11th of January (0.4% arrived on 30th of June). In general, most drifters from GF stayed near the release area or drifted towards the Kattegat or Skagerrak (Fig. 1). From all 17 release dates at KB and KM, first "medusae" mainly arrived in BB on 20th or 30th of June (Table 2). Only when released on 22nd of

Table 2
Modelled first arrival date, minimum drift duration in days and total percent of medusae arrived from single release dates and areas

Release area	Kiel Bight			Kerteminde			Gullmar Fjord		
Release date	First arrival	Min. drift duration (day)	Total arrived (%)	First arrival	Min. drift duration (day)	Total arrived (%)	First arrival	Min. drift duration (day)	Total arrived (%)
Nov 12 2001	Jun 30	230	2.9	Jun 30	230	2.1			
Nov 22	Mar 02	100	4.5	Jun 20	210	2.5			
Dec 02	Feb 20	80	5.8	Jun 30	210	5.4			
Dec 12	Jun 20	190	5.0	Jul 10	210	2.5			
Dec 22	Jun 30	190	5.8	Jun 20	180	3.3			
Jan 01 2002	Jun 30	180	3.7	Jul 20	200	3.3			
Jan 11	Jun 30	170	4.5	Jun 30	170	5.0	Jun 30	170	0.4
Jan 21	Jun 30	160	9.9	Jun 30	160	6.6			
Jan 31	Jun 30	150	6.6	Jun 30	150	3.7			
Feb 10	Jun 30	140	8.3	Jun 30	140	4.1			
Feb 20	Jun 30	130	7.9	Jun 30	130	5.0			
Mar 02	Jun 30	120	9.1	Jul 20	140	1.7			
Mar 12	Jun 30	110	11.0	Jul 30	140	0.8			
Mar 22	Jun 30	100	9.5	Jul 20	120	1.2			
Apr 01	Jun 30	90	17.0						
Apr 11	Jun 30	80	13.0	Jul 20	100	0.8			
Apr 21	Jul 30	70	1.2						
Nov 12 2002	Jan 11	60	18.6	Dec 22	40	16.1			
Nov 22	Jan 11	50	12.0	Jan 11	50	7.0			
Dec 02	Jan 21	50	22.7	Jan 11	40	11.6	Mar 22	110	0.8
Dec 12	Jan 31	50	24.4	Jan 21	40	33.5			
Dec 22	Jan 31	40	17.4	Feb 10	50	12.8			
Jan 01 2003	Mar 22	80	11.2	Jan 31	30	31.8			
Jan 11	Mar 22	70	11.6	Feb 10	30	21.9			
Jan. 21	Apr 01	70	3.7	Apr 11	80	2.9			
Jan 31	Apr 01	60	9.9	May 11	100	0.4			
Feb 10	Apr 01	50	7.9	May 21	100	2.9			
Feb 20	Apr 21	60	3.3	May 01	70	3.3			
Mar 02	Apr 21	50	21.1	Apr 21	50	13.6			
Mar 12	May 31	80	2.9	May 21	70	14.0			
Mar 22									
Apr 01									
Apr 11	Aug 09	120	0.8						
Apr 21									

Light grey rows indicate possible strobilation time. Dark grey rows are displayed in Figs. 3b, c and 4b–e.

November and 2nd of December 2001 from KB "medusae" arrived in the BB already in March and February, respectively.

Comparing the model results with the observations in 2002, there is a high concordance in the arrival time of "medusae" in the BB. Two examples (release date 12th of December 2001 and 10th of February 2002) represent the modelled arrival on 20th and 30th of June (Fig. 3b, c). The modelled first arrival fits exactly in time between absence of medusae (end of June) and first observed individuals (end of July) (Fig. 3a).

The modelled number of "medusae" arriving in the BB was obviously higher in 2003 than in 2002. Highest numbers of "medusae" reached the BB when released on 12th of December 2002 (24% from KB, 33.5% from KM) (Table 2). Drifters from GF were found in the BB only when released on 2nd of December 2002 (Fig. 4b), as most of them remained in the Kattegat and Skagerrak (Fig. 1). The time of first arrival of "medusae" from the 17 release dates was more heterogeneous in 2003 than in 2002. First arrival was observed on several dates from December 2002 to May 2003 and on August 9th (Table 2).

For comparing the modelled first arrival with the field observations in 2003 four examples were chosen (Fig. 4b–e). Release dates 2nd of December 2002, 1st of January, 10th of February and 12th of March 2003 represent different first arrival dates (11th of January, 31st of January, 1st of April, 21st of May, respectively). As first ephyrae in 2003 were caught in April, the modelled arrival of medusae fits our observations, when release date was later than the 11th of January and earlier than the 12th of March (Fig. 4 and Table 2).

4. Discussion

The occurrence patterns of *A. aurita* and *C. capillata* in the BB were quite different in 2002 and 2003. Our observations in 2002 show a complete absence of ephyrae of *A. aurita* and the appearance of *A. aurita* and *C. capillata* medusae from July onwards (Barz and Hirche, 2005). These findings were in agreement with earlier investigations between 1983 and 1991 in this area (Janas and Witek, 1993). However, in 2003, the appearance of ephyrae of *A. aurita* in April and the occurrence of medusae of both species already in May was unusual. These deviations either may originate in a different timing of strobilation or might reflect the inter-annual variability of circulation patterns which control the transport of ephyrae from the strobilation area to the BB.

We have no detailed information on the timing of strobilation in the source regions. According to Möller (1980a,b) and Olesen et al. (1994) it should be in the same time range over the years. However, there were remarkable differences in the circulation patterns between the two years. In January 2003 a Major Baltic Inflow of cold and oxygen-rich water from the Kattegat reached the central Baltic Sea, considered the most important inflow since 1993 (Feistel et al., 2003). The inflow water was detected in the BB in late January. This large inflow was followed by minor ones in March and May 2003, which also reached the BB (Feistel et al., 2003).

The different atmospheric forcing conditions and the corresponding varying hydrographic situations are clearly reflected in the model results. In 2002, nearly all release dates from the middle of December 2001 to April 2002 resulted in a "medusae" arrival in the BB between June 20th and 30th (Fig. 3b,c and Table 2). This is exactly the time between a cruise in June, when no medusae were found, and a cruise in July when first medusae occurred (Fig. 3a). In 2003, the successive inflow events most likely caused earlier arrival and higher numbers of drifter in the BB. Thus, the Major Baltic Inflow in January 2003 probably advected the "medusae" released in November, December 2002 and early January 2003 to the BB already at the end of January (Fig. 4b,c and Table 2). The arrival of the second group of "medusae" released in January, February and early March 2003 in the BB in March and April may be related to the later inflow in March (Fig. 4d and Table 2). In the field, no ephyrae were found in the BB during the Major Baltic Inflow in January 2003 (Fig. 4a). Hence we assume that the first ephyrae observed in April were advected to the BB by the March inflow (Fig. 4a,d).

As the model results suggest, the medusae arrived in the BB in a depth of 40 m and deeper. This would explain why *A. aurita* in May 2003 was distributed in deeper layers compared to 2002, where they were caught mainly in the upper 20 m (Barz and Hirche, 2005). Probably medusae arrived in the same depth in 2002, but already raised to the surface before the cruise in July started. *C. capillata* showed the same dependency on high salinity as in 2002 (Barz and Hirche, 2005). It occurred at 40 m depth and deeper, where salinity increased from 8 up to 19 PSU (Fig. 2).

The model results indicate a strobilation period of *A. aurita* from mid-December to April in 2002 and from mid-January to April in 2003 (Table 2), as a release in this time-frame produced best agreement with our field observations. A strobilation during that time span is congruent with earlier observations in the western Baltic (Möller, 1980a,b; Olesen et al., 1994). It would also explain the lack of ephyrae in 2002 and in earlier investigations, and supports the assumption that there is no strobilation in or near the central Baltic. In laboratory experiments (15 °C) ephyrae grew in 10 d from 4 to 9 mm with high food supply (growth rate of 0.22/day), but size decreased with low food concentration (Olesen et al., 1994). In the field, the newly released ephyrae measure about 2 mm in diameter, and do not grow during winter and early spring in KB (Möller, 1980b). Growth of *A. aurita* increases rapidly with an increase in mesozooplankton abundance. Depending on water temperature, the growth rates may vary from year to year (Möller, 1980b; Lucas and Williams, 1994). For example, in KB, *A. aurita* grew from 3 mm in April to 49 mm in June 1979 (Möller, 1980b). Thus, when ephyrae start growing in April they would develop into medusae until late June during ~90 days of drift before reaching the BB (Table 2). Therefore, high transport rates like the ones associated with the inflows in 2003 are necessary to advect ephyrae into the central Baltic, before they develop to medusae.

The model results are in good agreement with our field observations, and clearly suggest that advection of medusae from the western Baltic is the main source for *A. aurita* in the BB.

The polyps of *C. capillata* cannot settle in the central Baltic, if they really need salinities >20 PSU as suggested by Cargo (1984). The nearest known area of strobilation is the Gullmar Fjord on the west coast of Sweden (Gröndahl and Hernroth, 1987; Gröndahl, 1988). However, the model did not support advection from the Gullmar Fjord area in numbers explaining the occurrence of this species in the BB in 2002 and 2003 (Figs. 3 and 4). This suggests that the Gullmar Fjord is probably not the main source region of *C. capillata* in the BB. More likely is the advection of this species from elsewhere in the Skagerrak, the Kattegat or the North Sea (Möller, 1980c; Gröndahl and Hernroth, 1987).

Although the model results presented here match field observations very well, certain aspects have to be considered. Due to the lack of knowledge, vertical migration and growth of the medusae were not included in the model. The drifters were allowed to leave the layers where they were launched, but active vertical movements could affect the drift trajectories. In addition, changing size of medusae during growth could affect the drift. As there were no recent publications about polyp populations in the Baltic Sea, we had to use historical data about strobilation areas and times. However, there could be other areas with *A. aurita* polyp populations. For example, Wikström (1932) found polyps in the Tvärminne area (Gulf of Finland, eastern Baltic), and Janas and Witek (1993) mentioned possible local production in the central Baltic. Polyps and ephyrae of *A. aurita* were also observed in the Gulf of Gdansk (southern Baltic) (Janas, personal communication), but Hinrichsen et al. (2005), using a similar model, found only low probability of mixing sprat between the BB and the Gotland Basin. The same might be valid for medusae.

Hence, the question arises: why do *A. aurita* so rarely or not at all settle and strobilate in the central Baltic? Planulae require sheltered bights and fjords (Möller, 1979; Gröndahl, 1988), where they settle on the underside of rough or grooved surfaces (Brewer, 1978). The downward settling is controlled by negative phototaxis and geotaxis as found for *C. capillata* planulae (Brewer, 1976; Svane and Dolmer, 1995) and might explain the difficulty to find the cryptic polyp populations in the field. Adequate substrates for *A. aurita* polyps are shells, algae, rocks, barnacles and human buildings (Wikström, 1932; Verwey, 1942; Thiel, 1962; Hernroth and Gröndahl, 1985; Gröndahl 1989), and their settlement here is probably gregarious (Gröndahl, 1989). The strobilation of *A. aurita* polyps is controlled by endo- and exogenous factors, such as iodinated compounds, polypeptides, temperature, light and nutrition (e.g. Thiel, 1962; Spangenberg, 1965; 1967; Kakinuma, 1975; Omori et al., 1995; Kroiher et al., 2000), which were not investigated in this study. For *A. aurita*, direct development from planulae to single ephyrae has also been recorded (Kakinuma, 1975, Yasuda, 1975).

So far, it is unclear if settlement and strobilation of *A. aurita* occur in the BB and, if so, how much it contributes to the population. When planulae find adequate substrate in the Gulf of Gdansk area, they are expected to do so also around the BB. However, strobilation success in the BB is probably low, and the found population is much dependent on early stages of medusae transported by advection from more western parts of the Baltic, and from the Kattegat and the North Sea.

Acknowledgements

We like to thank all colleagues and students for their support in collecting and analysing medusae. Furthermore, we thank the crews of RV *Alkor, Heincke* and *A. v. Humboldt*. This research was funded by GLOBEC Germany, BMBF 03F0320D.

References

Bagge, O., Thurow, F., Steffensen, E., Bray, J., 1994. The Baltic cod. Dana 10, 1–28.

Barz, K., Hirche, H.-J., 2005. Seasonal development of scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (central Baltic Sea). Mar. Biol. 147, 465–476.

Bergstrøm, S., Carlsson, B., 1994. River runoff to the Baltic Sea: 1950–1990. Ambio 23, 280–287.

Brewer, R.H., 1976. Larval settling behaviour in *Cyanea capillata* (Cnidaria: Scyphozoa). Biol. Bull. 150, 183–199.

Brewer, R.H., 1978. Larval settlement behavior in the jellyfish *Aurelia aurita* (Linnaeus) (Scyphozoa: Semaeostomeae). Estuaries 1, 120–122.

Brierley, A.S., Axelsen, B.E., Buecher, E., Sparks, C.A.J., Boyer, H., Gibbons, M.J., 2001. Acoustic observations of jellyfish in the Namibian Benguela. Mar. Ecol., Prog. Ser. 210, 55–66.

Brodeur, R.D., Mills, C.E., Overland, J.E., Walters, G.E., Schumacher, J.D., 1999. Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. Fish. Oceanogr. Transl. 8, 296–306.

Bryan, K., 1969. A numerical method for the study of the circulation of the world ocean. J. Comput. Phys. 4, 347–376.

Cargo, D.G., 1984. Some laboratory techniques for the culture of Scyphozoa. Workshop on jellyfish blooms in the Mediterranean. UNEP, Athens, pp. 129–138.

Cox, M.D., 1984. A primitive equation 3-dimensional model of the ocean. GFDL Ocean Group Tech. Rep., vol. 1. Geophysical Fluid Dynamics Laboratory, Princeton Univ., Princeton, NJ.

Feistel, R., Nausch, R., Matthäus, G., Hagen, W., 2003. Temporal and spatial evolution of the Baltic deep water renewal in spring 2003. Oceanologia 45, 623–642.

Gröndahl, F., 1988. A comparative ecological study on the scyphozoans *Aurelia aurita*, *Cyanea capillata* and *C. lamarckii* in the Gullmar Fjord, western Sweden, 1982 to 1986. Mar. Biol. 97, 541–550.

Gröndahl, F., 1989. Evidence of gregarious settlement of planula larvae of the scyphozoan *Aurelia aurita*: an experimental study. Mar. Ecol., Prog. Ser. 56, 119–125.

Gröndahl, F., Hernroth, L., 1987. Release and growth of *Cyanea capillata* (L.) ephyrae in the Gullmar Fjord, western Sweden. J. Exp. Mar. Biol. Ecol. 106, 91–101.

Hernroth, L., Gröndahl, F., 1983. On the biology of *Aurelia aurita* (L.): 1. Release and growth of *Aurelia aurita* (L.) ephyrae in the Gullmar Fjord, western Sweden, 1982–83. Ophelia 22, 189–199.

Hernroth, L., Gröndahl, F., 1985. On the biology of *Aurelia aurita* (L.): 2. Major factors regulating the occurrence of ephyrae and young medusae in the Gullmar Fjord, western Sweden. Bull. Mar. Sci. 37, 567–576.

Hinrichsen, H.-H., Lehmann, A., St.-John, M., Brügge, B., 1997. Modeling the cod larvae drift in the Bornholm Basin in summer 1994. Cont. Shelf Res. 17, 1765–1784.

Hinrichsen, H.-H., Kraus, G., Voss, R., Stepputtis, D., Baumann, H., 2005. The general distribution pattern and mixing probability of Baltic sprat juvenile populations. J. Mar. Syst. 58, 52–66.

Janas, U., Witek, Z., 1993. The occurrence of medusae in the Baltic and their importance in the ecosystem, with special emphasis on *Aurelia aurita*. Oceanologia 34, 69–84.

Johnson, D.R., Perry, H.M., Burke, W.D., 2001. Developing jellyfish strategy hypotheses using circulation models. Hydrobiologia 451, 213–221.

Kakinuma, Y., 1975. An experimental study of the life cycle and organ differentiation of *Aurelia aurita* Lamarck. Bull. Mar. Biol. Stat. Asamushi 15, 101–117.

Kändler, R., 1961. Über das Vorkommen von Fischbrut, Decapodenlarven und Medusen in der Kieler Förde. Kieler Meeresforsch. 17, 48–64.

Killworth, P.D., Stainforth, D., Webb, D.J., Paterson, S.M., 1991. The development of a free-surface Bryan–Cox–Semtner ocean model. J. Phys. Oceanogr. 21, 1333–1348.

Köster, F.W., Möllmann, C., Neuenfeldt, S., St.-John, M., Plikshs, M., Voss, R., 2001. Developing Baltic recruitment models: I. Resolving spatial and temporal dynamics of spawning stock and recruitment for cod, herring and sprat. Can. J. Fish. Aquat. Sci. 58, 1516–1533.

Kroiher, M., Siefker, B., Berking, S., 2000. Induction of segmentation in polyps of *Aurelia aurita* (Scyphozoa, Cnidaria) into medusae and formation of mirror-image medusa anlagen. Int. J. Dev. Biol. 44, 485–490.

Lehmann, A., 1995. A three-dimensional baroclinic eddy-resolving model of the Baltic Sea. Tellus 47A, 1013–1031.

Lucas, C.H., Williams, J.A., 1994. Population dynamics of the scyphomedusa *Aurelia aurita* in Southampton water. J. Plankton Res. 16, 879–895.

Lucas, C.H., Hirst, A.G., Williams, J.A., 1997. Plankton dynamics and *Aurelia aurita* production in two contrasting ecosystems: comparisons and consequences. Estuar. Coast. Shelf Sci. 45, 209–219.

Lynam, C.P., Brierley, A.S., Hay, S.J., 2004. Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. Limnol. Oceanogr. 49, 637–643.

Margonski, P., Horbowa, K., 1995. Vertical distribution of cod eggs and medusae in the Bornholm Basin. Medd. Havsfiskelab. Lysekil 327, 7–17.

Matsakis, S., Conover, R.J., 1991. Abundance and feeding of medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during spring. Can. J. Fish. Aquat. Sci. 48, 1419–1430.

McKenzie, B.R., Hinrichsen, H.-H., Plikshs, M., Wieland, K., Zezera, A.S., 2000. Quantifying environmental heterogeneity: habitat size necessary for successful development of cod *Gadus morhua* eggs in the Baltic Sea. Mar. Ecol., Prog. Ser. 193, 143–156.

Mills, C.E., 2001. Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451, 55–68.

Möller, H., 1979. Significance of coelenterates in relation to other plankton organisms. Meeresforschung 27, 1–18.

Möller, H., 1980a. Scyphomedusae as predators and food competitors of larval fish. Meeresforschung 28, 90–100.

Möller, H., 1980b. Population dynamics of *Aurelia aurita* medusae in Kiel Bight, Germany (FRG). Mar. Biol. 60, 123–128.

Möller, H., 1980c. A summer survey of large zooplankton, particularly Scyphomedusae, in North Sea and Baltic. Meeresforschung 28, 61–68.

Olesen, N.J., 1995. Clearance potential of jellyfish *Aurelia aurita*, and predation impact on zooplankton in a shallow cove. Mar. Ecol., Prog. Ser. 124, 63–72.

Olesen, N.J., Frandsen, K., Riisgard, H.U., 1994. Population dynamics, growth and energetics of jellyfish *Aurelia aurita* in a shallow fjord. Mar. Ecol., Prog. Ser. 105, 9–18.

Omori, M., Ishii, H., Fujinaga, A., 1995. Life history strategy of *Aurelia aurita* (Cnidaria, Scyphomedusae) and its impact on the zooplankton community of Tokyo Bay. ICES J. Mar. Sci. 52, 597–603.

Palmen, E., 1953. Seasonal occurrence of ephyrae and subsequent instars of *Aurelia aurita* (L.) in the shallow waters of Tvärminne. S. Finland. Arch. Soc. 'Vanamo' 8, 122–131.

Purcell, J.E., 1992. Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay, USA. Mar. Ecol., Prog. Ser. 87, 65–76.

Schneider, G., Behrends, G., 1994. Population dynamics and the trophic role of *Aurelia aurita* medusae in the Kiel Bight and western Baltic. ICES J. Mar. Sci. 51, 359–367.

Schneider, G., Behrends, G., 1998. Top-down control in a neritic plankton system by *Aurelia aurita* medusae–a summary. Ophelia 48, 71–82.

Semtner, A.J., 1974. A general circulation model for the world ocean. Tech. Rep., vol. 9. Dep. of Meteorology, Univ. California, Los Angeles.

Spangenberg, D.B., 1965. A study of strobilation in *Aurelia aurita* under controlled conditions. J. Exp. Zool. 160, 1–10.

Spangenberg, D.B., 1967. Iodine induction of metamorphosis in *Aurelia*. J. Exp. Zool. 165, 441–449.

Svane, I., Dolmer, P., 1995. Perception of light at settlement: A comparative study of two invertebrate larvae, a scyphozoan planula and a simple ascidian tadpole. J. Exp. Mar. Biol. Ecol. 187, 51–61.

Thiel, H., 1962. Untersuchungen über die Strobilisation von *Aurelia aurita* LAM. An einer population der Kieler Förde. Kieler Meeresforsch. 18, 198–230.

Verwey, J., 1942. Die periodizität im Auftreten und die aktiven und passiven Bewegungen der Quallen. Arch. Neerl. Zool. 6, 363–468.

Wikström, D.A., 1932. Beobachtungen über die Ohrenqualle (*Aurelia aurita* L.) in den Schären SW-Finnlands. Mem. Soc. Pro Fauna Flora Fennica 8, 14–17.

Yasuda, T., 1975. Ecological studies on the jellyfish, *Aurelia aurita* (Linne), in Urazoko Bay, Fukui Prefecture: 2. An observation on ephyra formation. Publ. Seto Mar. Biol. Lab. 22, 75–80.

Abundance, distribution and prey composition of Scyphomedusae in the southern North Sea

Kristina Barz and Hans-Jürgen Hirche

Manuscript

Abundance, distribution and prey composition of Scyphomedusae in the southern North Sea

Kristina Barz and Hans-Jürgen Hirche

Alfred Wegener Institute for Polar and Marine Research
Columbusstrasse, D-27568 Bremerhaven, Germany
Email: kbarz@awi-bremerhaven.de
Tel.: +49-471-48311324
Fax.: +49-471-48311918

Abstract

The annual cycle of abundance and distribution of the scyphozoan medusae *Aurelia aurita*, *Cyanea lamarckii*, *C. capillata* and *Chrysaora hysoscella* were studied in the southern North Sea in 2004 and 2005. Three different patterns of seasonal occurrence of medusae were distinguished: (i) The early occurring *C. lamarckii* (February-August), (ii) *C. capillata* and *A. aurita* (April-August) and (iii) the late appearing *C. hysoscella* (July/August-September). *C. lamarckii* was the most frequently encountered species in this study, its highest mean abundance was 1.8 ± 2.7 ind. 100m^{-3}. The food of *C. lamarckii*, *C. capillata* and *C. hysoscella* contained several copepod and other crustacean species. The prey spectra of these species make them potential competitors with fish larvae. Medusae in this study also consumed fish eggs and larvae, including clupeids, in all months analysed. Although peak spawning by sprat (*Sprattus sprattus*) coincides with the maximum abundance of medusae (May to June) the relative low abundance of all medusae species in this study makes jellyfish predation unlikely to be a factor controlling sprat recruitment during the time frame investigated.

Keywords: Jellyfish, German Bight, *Aurelia aurita*, *Cyanea capillata, Cyanea lamarckii, Chrysaora hysoscella*

Introduction

Scyphomedusae are probably the most obvious pelagic invertebrate predators in marine ecosystems worldwide. They represent a conspicuous component of the plankton, especially during the summer months (Brodeur et al. 2002). In recent years studies have focused on the trophodynamic role of medusae due to their increased abundance in many systems (e.g. Mills 2001; Parsons and Lalli 2002; Purcell 2005). For example, their abundance has increased in the Bering Sea, Benguela Current and Yangtze Estuary (Brodeur et al. 1999, 2002; Brierley et al. 2001; Purcell 2005; Xiang et al. 2005), but decreases have also been reported (Mills 2001; Dawson et al. 2001). The focus of interest has thus shifted from general investigations about scyphozoa occurrence, distribution or predatory impact to an examination of the causes and consequences of changing ocean conditions on changes in medusae abundance. Changes have been related to pollution or overfishing (Brodeur et al. 1999; Arai 2001; Purcell and Arai 2001), but also to climate-induced regional regime shifts (Brodeur et al. 1999; Lynam et al. 2004, 2005a). The abundance of many jellyfish species may increase in warm conditions (reviewed in Purcell 2005), whereas cold conditions have been associated with high medusae abundance in the North Sea (Lynam et al. 2005a).

The North Atlantic Oscillation Index (NAOI), the dominant mode of climate variability in the North Atlantic region, changed in the late 1980s from a negative to a positive phase (e.g. Reid et al. 2003; Beaugrand 2003, 2004; Beaugrand et al. 2002). This was correlated to an ecological regime shift, involving all pelagic trophic levels. Increases in air and sea surface temperatures were the main direct and indirect driving forces. The composition of phyto- and zooplankton communities changed conspicuously. Copepod species which are essential for medusae and fish, experienced pronounced changes in biomass and recruitment. These changes had dramatic consequences on North Sea cod (*Gadus morhua*) stocks (Alheit et al. 2005). Also the abundance of Scyphomedusae showed inter-annual fluctuations and large variability between regions in the North Sea (Hay et al. 1990). Lynam et al. (2004, 2005a) correlated variability in the abundance of Scyphomedusae to changes in the NAOI. They found high medusae abundance related to a low NAOI and vice versa.

Scyphomedusae utilize a wide spectrum of zooplankton prey and can have a strong impact on zooplankton standing stocks in all parts of the world (Omori et al. 1995; Ishii and Tanaka 2001; Brodeur et al. 2002). For example maximum feeding rates by *Chrysaora quinquecirrha* were estimated to be 94% day^{-1} of the copepod population in Chesapeake Bay (USA) (Purcell 1992). The abundance of zooplankton in Kiel Bight (Germany) was negatively correlated with the density of *Aurelia aurita* (Schneider and Behrends 1994, 1998), which was assumed to be the regulating factor in medusae “bloom” years (Möller

1980a, b). In addition, the high predation pressure on zooplankton may negatively impact fish populations due to the fact that Scyphomedusae, fish larvae and all stages of planktivorous fish often have an overlapping prey spectrum. If the same prey is utilized it is tempting to assume, that competition occurs, but only a few studies have attempted to directly examine this (Purcell and Sturdevant 2001).

Many scyphozoan species are known to feed on fish larvae and eggs (reviewed in Purcell 1985; Fancett 1988; Purcell et al. 1994). When reaching high abundance these medusae may reduce the recruitment potential of many important fish species. For example, years with high densities of *A. aurita* in the western Baltic Sea coincided with low abundances of herring (*Clupea harengus*) larvae (Möller 1980a, 1984). Lynam et al. (2005b) observed a significant negative relationship between the survival of herring larvae and the abundance of *A. aurita* in the North Sea. They postulated an adverse impact of *A. aurita* on North Sea herring populations.

Competition and direct predation on fish eggs and larvae could impact commercial fish stocks in the southern North Sea due to the importance of this region as a spawning ground for sprat (*Sprattus sprattus*) (Aurich 1941), plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) (Harding et al. 1978). Due to these negative effects, it is important to understand which environmental factors may cause increases in jellyfish populations (Purcell 2005), but information on medusae abundance in the southern North Sea is scarce. Most investigations on Scyphomedusae in the southern North Sea were qualitative, lacking data on abundance, and were performed >40 years ago (Hartlaub 1894; Verwey 1942; Künne 1952; Kühl 1964; Thiel 1966). These studies provide lists of species that sometimes include information on seasonal patterns in occurrence. A recent study was conducted around Sylt Island, and provides data about seasonal occurrence and abundance of species in this region (Kopacz 1994). Moreover knowledge about the location of polyp populations is mostly based on assumptions and historical findings (Hartlaub 1894; Kühl 1964; Kühl and Mann 1967; van der Veer and Oorthuysen 1985; Merck 1989; Kopacz 1994).

This investigation provided a new inventory of scyphozoan species, including seasonal and spatial occurrence patterns, abundance and diet composition in the southern North Sea. During a field study on a highly resoluted station grid in the years 2004 and 2005, intensive sampling of Scyphomedusae was conducted. The study was part of the German GLOBEC project, which focuses on the interactions between zooplankton and fish under the influence of physical processes. Here we provide information on the trophodynamic roles of scyphozoan medusae in the southern North Sea.

Material and methods

Sampling location, dates and hydrography

The 2004 station grid with 55 stations included a more highly resolved grid (8nm between stns 1-23) that was embedded within the larger grid (20nm between stns 24-55) (Fig. 1). The water depth varied between 13 and 48m. Samples were taken during cruises from February to September (Table 1). In 2005 the sampling strategy was different and consisted of three cruises (April, May and July) that repeatedly sampled a North-South-Transect (T1) and two West-East-Transects (T2, T3) (Fig. 5a). Salinity, temperature and dissolved oxygen were recorded in both years on every station with a standard CTD probe.

Abundance and distribution of Scyphomedusae

In 2004 Scyphomedusae were collected at all grid stations from oblique Bongo net hauls (0.6m diameter; 335 and 500µm mesh size; trawling speed 0.5m s^{-1}). The two meshes 335 and 500µm did not show any difference in the abundance of medusae ($p = 0.6$-0.9; Mann-Whitney Rank Sum Test), therefore average values of both nets were used. Occurrence of ephyrae was analysed in 2004 on nine focus stations (7, 20, 22, 31, 32, 35, 42, 47, 49). In 2005 a trawled multinet (0.5m² opening; 335µm mesh size; trawling speed 0.5m s^{-1}) was used to analyse the spatial and vertical distribution along the three transects. The transects were mostly sampled twice per cruise during daytime in 7 depth layers from 5 to 35m. For vertical distribution the sampled medusae were separated for stations ≤22m depth and 23-48m depth. The depths shown in Fig. 6 are mean trawling depths. All medusae collected were processed onboard, identified, weighed and measured to the nearest 0.5cm below.

Prey analysis

For gut content analysis, single medusae from Bongo and multinet hauls were measured immediately after collection, weighed and preserved in a 4 % borax buffered formalin-seawater solution. In the laboratory the medusae were dissected and canals, stomach and gastric pouches were examined for prey organisms, which were counted and identified to genus or species level. Copepods were identified to stage level.

Since quantification of gut contents in medusae caught by a trawled net is problematic due to cod end feeding and the loss of gut contents, this analysis was not considered to be quantitative. In total, 49 specimens from three cruises were examined in 2004 and 33 specimens from two cruises were examined in 2005.

Results

Hydrography

The southern North Sea is a temperate shallow shelf sea. In the investigation area, depth varied from 13 to 48m. While temperature was rather uniform across the sampling grids, salinity was more variable, with lower values in the eastern part, resulting from the freshwater discharge of several rivers (Elbe, Weser, Ems). Due to the shallow depths, the water column was mostly completely mixed; stratification was sometimes observed during the summer months. In April 2004, temperature at 10m depth was between 6 and 7 °C. Salinity at 10m depth reached 30.5 in the most eastern part and 34.5 in the western end of the study area. Around Helgoland Island, the seasonal cycle of surface temperature and salinity ranged between 2 and 20°C and 28 to 33, respectively.

Seasonal abundance and size

Four species of Scyphozoan medusae were caught in the southern North Sea during this investigation: *Cyanea lamarckii, C. capillata, Aurelia aurita* and *Chrysaora hysoscella*. Ephyrae were caught in February 2004 only on station 42 (3.2 ind. m^{-3}) and in April on stations 22, 31, and 49 (3.2, 6.4 and 1.6 ind. m^{-3}, respectively), but were not further specified. In Fig. 2 the seasonal development of mean abundance of medusae (all grid stations in 2004, all transect stations in 2005, whole water column in both years) is shown for all species. In February 2004 only a few individuals of *C. lamarckii* were collected on stations 12, 13, 17 and 20 (mean abundance 0.09 ± 0.37 ind. $100m^{-3}$) (Fig. 2). Starting in April, *C. capillata* was also encountered. *C. lamarckii* and *C. capillata* showed a similar trend in their abundance. They were most abundant in June (1.79 ± 2.75 and 0.68 ± 1.05 ind. $100m^{-3}$, respectively), thereafter abundance dropped until August, and both species had completely disappeared by September. *A. aurita* also appeared first in April. Its abundance was very low and reached a maximum in August with 0.06 ± 0.39 ind. $100m^{-3}$. Similar to both *Cyanea* species *A. aurita* was not found in September. In contrast, *C. hysoscella* was observed only in August and September (0.22 ± 0.63 and 0.16 ± 0.45 ind. $100m^{-3}$, respectively).

In 2005 medusae were collected in April, May and early July on three transects. No data on ephyrae occurrence were available for this year. The seasonal occurrence patterns of medusae were different to 2004. In April only *C. lamarckii* was found, *C. capillata* appeared not until May. Abundance of both species was low in May and increased in early July. In July also some individuals of *C. hysoscella* occurred, whereas *A. aurita* was not observed in 2005.

The development of mean size of medusae was relatively similar in both years (Fig. 3). In 2004, mean size of *C. lamarckii* increased from 4.8 ± 3.1cm in February to 9.5 ± 3.3cm in

August, *C. capillata* measured 4.8 ± 2.7cm in April and reached 9.8 ± 5.0cm in August. Mean size of *A. aurita* increased from April (3.8 ± 2.3cm) to June (12.5 ± 0.5cm), and then decreased until August. *C. hysoscella* showed about the same size in August (9.9 ± 4.1cm) and September (8.5 ± 1.5cm). In 2005 *C. lamarckii* was smaller in April (3.9 ± 1.8cm), but also reached 9.5 ± 2.1cm in July. *C. hysoscella* reached a mean size of 10.5 ± 0.5cm in July. The smallest medusae of *C. lamarckii* were caught in February 2004 (1cm), whereas the biggest in the same month reached 17cm. This diameter was only excelled by individuals of 20cm caught in June 2004. Smallest medusae of C*. capillata* were found in April 2004 (1cm). The largest individuals of this species reached 28cm diameter in August 2004.

Horizontal distribution

In 2004 the horizontal distribution of all four species was analysed in detail for all month to illustrate spatial variability (Fig. 4a-d). The two congeners, *C. lamarckii* and *C. capillata,* showed a predominant easterly distribution in April and May and appeared later in the more western parts of the station grid. In general, more individuals were caught near shore than offshore. *A. aurita* was caught sporadically only on one or two stations per cruise and had its highest abundance in August on station 1. *C. hysoscella*, only found in August and September, was also distributed near shore on the eastern station grid.

For 2005 all transects sampled were plotted separately (Fig. 5b). In April only *C. lamarckii* was caught. The distribution showed no shore-related trend, only on the second sampling of T3 more individuals were caught near Helgoland Island. Compared to April, less medusae were caught in May, but *C. capillata* and *C. lamarckii* were distributed more near shore on all three transects. In July this trend was continued. On T3 *C. hysoscella* appeared and was caught mainly near Helgoland Island.

Vertical distribution

Vertical distribution was analysed in April, May and July 2005 (Fig. 6). The distribution was separately analysed for stations ≤22m depth (shallow) and 23-48m depth (deep). Maximum trawling depth on the shallow stations was about 15m, and about 38m on the deep ones. In April, only *C. lamarckii* was found and individuals were caught between 5 and 25m. On the shallow stations, medusae were caught only in 5 and 10m depth, whereas at the deeper stations medusae were mainly distributed in the deeper layers. Fewer *C. lamarckii* were caught in April and in addition *C. capillata* occurred. Both species were found only in the upper 15m, with higher abundance at the shallow stations. In early July, abundance of *C. lamarckii* was generally higher, especially in the upper 5m of the shallow stations. *C.*

capillata was still less abundant and occurred only in the upper 10m. In addition, some individuals of *C. hysoscella* were caught in 15 and 20m on the deep stations.

Gut content

The sampling method used here (towed plankton net) did not allow quantitative analysis of daily rations and predatory impact, as loss of prey during capture or cod end feeding were possible sources of errors. In this study, many food items in the guts, especially copepods and fish larvae, were partly digested. In these cases it was assumed that they were eaten prior to capture, rather than in the net. Larson (1987a, b) and Matsakis and Conover (1991) also found net feeding by gelatinous predators to be negligible. Loss of gut content is a source of error, and has been observed for medusae caught by a trawled BIOMOC (Barz and Hirche 2005). Therefore, no calculation of daily rations and predatory impact was made with these gut content data, only the mean abundance of each prey species per medusae was tabulated (Table 2).

In 2004 *C. lamarckii* and *C. hysoscella*, in 2005 *C. lamarckii* and *C. capillata* were analysed. Prey items of the three species could be summarised using 17 groups. The copepod species included males, females and copepodite stages IV and V. *Centropages* sp. included *C. hamatus* and *C. typicus*, decapod larvae included zoea and megalopa of the taxa Brachyura and Caridea, Echinodermata larvae included Brachiolaria and Ophiuroidea, fish larvae included Syngnathidae, Clupeidae and horse mackerel (*Trachurus trachurus*).

All three species fed mainly on the same prey, however *C. lamarckii* had a higher prey diversity than the other two species, and was the only one found to feed on fish eggs. Most groups of prey items were found for *C. lamarckii* in June 2004 and July 2005. Highest prey numbers per taxon in one medusae during these months was for *Temora* sp., decapod larvae and fish larvae (Table 2).

Discussion

Abundance and distribution

Little is known about the occurrence and distribution of Scyphomedusae in the North Sea and even less about the location of their polyp populations. Some investigations covered the whole North Sea, but provided only limited information on the southern regions (Möller 1980c; Hay et al. 1990), others focused on the Dutch coast (Verwey 1942) and the British Isles (Russel 1970). Studies on Scyphozoa in the southern North Sea (Hartlaub 1894; Künne 1952; Kopacz 1994) and the Elbe Estuary (Kühl 1964; Thiel 1966) were mainly conducted >40 years ago. Most investigations focused on the medusa stage, as they are readily found in conventional plankton samples. Polyp populations are hard to find in the field, as they preferentially settle upside-down from a hard surface in shaded places (e.g. Brewer 1976). Therefore, the location of polyp populations in the southern North Sea is mostly unclear, apart from individual findings. Their existence was mostly derived from the regional distribution of small ephyrae such as described for *A. aurita* in the Dutch Wadden Sea (van der Veer and Oorthuysen 1985), and *C. hysoscella* in the Elbe Estuary (German Bight) (Merck 1989). The absence of polyps was assumed, when no ephyrae were caught or the ephyrae were too large, to have been recently released, as in the northern Wadden Sea of Sylt Island (Kopacz 1994).

Three different patterns of seasonal occurrence of medusae were distinguished in this study: (i) The early occurring *C. lamarckii* (February-August), (ii) *C. capillata* and *A. aurita* (April-August) and (iii) the late appearing *C. hysoscella* (July/August-September). These observations are comparable to earlier investigations. In all former studies *C. lamarckii, C capillata, A. aurita* and *C. hysoscella* were commonly found, but the species were of variable importance (Hartlaub 1894; Verwey 1942; Künne 1952; Russel 1970; Möller 1980c; Hay et al. 1990).

C. lamarckii was the most abundant species observed during this investigation. The dominance of this species in the southern North Sea was also described in former studies (Hartlaub 1894; Verwey 1942; Kopacz 1994). *C. lamarckii* was usually much more abundant in the southern parts than in the rest of the North Sea (Hay et al. 1990). The first individuals of *C. lamarckii* appeared in February 2004. In 1933-39 it was also first present within samples collected in February, reached highest abundance from May to early August and disappeared in October (Verwey 1942). In this investigation this species was absent from samples collected in September. Strobilation off the Dutch coast may occur from December to June (Verwey 1942). Künne (1952) observed ephyrae of *Cyanea* sp. in the German Bight from March until May. The ephyrae caught in this study during February 2004 were most probably *C. lamarckii*, but could also have been *C. capillata* or *A. aurita*. The large individuals of *C. lamarckii* (17cm in diameter) caught in February were most likely survivors of the preceding year.

C. capillata was described as a northern boreal species (Russel 1970). In agreement with this study, previous reports observed that it appeared mostly later and was less abundant in the southern North Sea than *C. lamarckii* (Hartlaub 1894; Verwey 1942; Kopacz 1994). In 2004, *C. capillata* were caught from April to August and a peak in its abundance was observed in June. In contrast, Verwey (1942) found this species until October. The more offshore distribution of *C. capillata*, described by Hay et al. (1990), was not observed in this study until August. *C. capillata* has been described as the larger of the two *Cyanea* species and may reach a diameter of >40 cm in the North Sea (Verwey 1942). In this investigation

C. capillata reached 28cm, a larger maximum diameter than *C. lamarckii* (max. 20cm). Strobilation may occur from March to June off the Dutch coast (Verwey 1942), and therefore fits the observations.

From February to May 2004 medusae of both *Cyanea* species were more abundant at stations near the south-east coast. In 2005 their distribution was clearly related to the coast, including Helgoland Island, until July. Due to the dependence on hard substrate (Brewer 1976) *Cyanea* polyps live most probably somewhere at the coast in this region, but were only found once on a granite block near Helgoland Island (Hartlaub 1894). The polyps of *C. capillata*, were found on stones, shells and algae (Verwey 1942). They are common in the Gullmar Fjord (Skagerrak, Sweden) but at lower abundance than those of *A. aurita* (Gröndahl and Hernroth 1987; Gröndahl 1988).

A. aurita was described as rare on one hand (Merck 1989; Niermann et al. 1998) and as the most abundant species in coastal waters in the North Sea on the other (Hay et al. 1990). In August 1987, it was restricted to the north-western area (Möller 1980c) and, in many years, was caught only sporadically in the waters around Helgoland Island (Hartlaub 1894; Künne 1952) and Sylt Island (Kopacz 1994). The complete absence of *A. aurita* in the investigation period in 2005 was therefore, not unusual. In addition, *A. aurita* is a potential food source for *C. capillata* (Båmstedt et al. 1994, 1997; Hansson 1997), and its population dynamics might be controlled by predation. The occurrence of *A. aurita* off the Dutch coast from April to August (Verwey 1942; van der Veer and Oorthuysen 1985) and off Helgoland Island in 1984 and 1985 from May on (Dittrich 1988) fits the patterns observed in 2004 in this study. The strobilation period may start in November/December (Künne 1952) or in February/March (Verwey 1942; van der Veer and Oorthuysen 1985) and last until June. Polyp populations are known from Helgoland Island (Sabine Holst pers. comm.), Borkum Island and Wilhelmshaven (Kühl 1964) and have been reported to exist in the Dutch Wadden Sea (van der Veer and Oorthuysen 1985). They are also found in the Gullmar Fjord (Skagerrak, Sweden) (Hernroth and Gröndahl 1983; Gröndahl 1988) and the western Baltic (e.g. Kändler 1961; Möller 1980a; Olesen et al. 1994; Schneider and Behrends 1998).

C. hysoscella occurs mainly in the southern North Sea (Hay et al. 1990). The late appearance of this species in both years of this study is consistent with former studies. It occurred mainly from August to October off the Dutch coast and around Helgoland Island (Hartlaub 1894; Verwey 1942; Künne 1952). In August 2004 it was the most frequent species sampled in the study area, similar to the results of Möller (1980c) who sampled the region in 1978. The more south-easterly distribution in this investigation was almost identical with observations by Merck (1989). High abundance of this species in and near the Elbe Estuary led to the conclusion that polyp populations and strobilation may occur there (Kühl and Mann 1967; Merck 1989).

In some investigations, *Rhizostoma octopus* has been observed (Verwey 1942; Künne 1952; Russel 1970; Hay et al 1990). This species might be indigenous to the German Bight since about 1920 (Thiel 1966). From the occurrence of small ephyrae the existence of polyp populations in the Elbe Estuary was suggested (Kühl 1964; Thiel 1966). As this species was found to be most abundant in September/October by some authors (Verwey 1942; Künne 1952), it may have been missed in this study in 2004 and was definitely missed in 2005. *C. hysoscella* and *R. octopus* appear later in the year because their polyps require warmer water to initiate strobilation (Verwey 1942). As polyp populations of *C. hysoscella* and *R. octopus* were never found in the field, it is doubtful that their complete life cycle occurs in the German Bight or in North Sea waters. Instead, they are most likely advected into this region from Spanish and French coasts (*C. hysoscella*) or the English Channel and North Atlantic (*R. octopus*) (http://schutzstation-wattenmeer.de).

Controls of medusae distribution

The life cycle of Scyphozoa often leads to the transient appearance of “medusa blooms” due to the seasonality in asexual production (Mills 2001). Furthermore, medusae generally show high inter-annual fluctuations in their abundance (Schneider and Behrends 1994), but native and non-indigenous species have increased in abundance in local habitats or regional ecosystems in the last years (reviewed in Mills 2001). In the North Sea, the abundance of Scyphomedusae showed inter-annual fluctuations (Hay et al. 1990). Lynam et al. (2004, 2005a) linked the inter-annual variability in abundance between 1971 and 1986 to changes in the North Atlantic Oscillation Index (NAOI). In most of the North Sea, the abundance of medusae was generally high when the NAOI was low (Lynam et al. 2004, 2005a). Lynam et al. (2004) generated a conceptual model wherein high NAOI led to rare *A. aurita* and *C. lamarckii* abundance and vice versa. Important environmental factors included sea surface temperature, as trigger for strobilation (Russel 1970; Omori et al. 1995), and advection, which leads to accumulation or dispersal of ephyrae. As strobilation takes place in winter and spring, when the NAO has greatest influence in the North Sea, it might have a high impact on environmental conditions that effect strobilation e.g. changes in temperature (Lynam et al. 2004). According to Lynam et al. (2004) abundance of *A. aurita* and *C. lamarckii* in the North Sea might be suppressed by the present high state of NAOI. The limited duration of this investigation and the lack of long-term studies in the southern North Sea do not allow us to interpret the data in relation to climate variability. Unfortunately, most of the former studies did not provide abundance data. *C. lamarckii,* the most frequent species in this study, reached a maximum abundance of 13 ind. 100m^{-3} at one station in June 2004. Its highest mean abundance was 1.8 ± 2.7 ind. 100m^{-3}. However, Kopacz (1994) found a maximum of 100 ind. 100m^{-3} off Sylt Island in the summer of 1991. Van der Veer and Oorthuysen (1985) found a maximum abundance of 49 *A. aurita* ind. 100m^{-3} in a bight of the Dutch Wadden Sea. Compared to this data the years 2004 and 2005 were characterised by a low to medium abundance.

Scyphomedusae might have a negative impact on recruitment of several fish stocks as a result of competition for the same food (Purcell and Sturdevant 2001) and in terms of direct predation on fish eggs and larvae (reviewed in Purcell 1985). The Scyphomedusae in the southern North Sea fed on several copepod and other crustacean species. As this is the same food that fish larvae prey upon in this area (Dickmann 2005) they have to be considered as competitors. In the western Wadden Sea (Dutch coast) *A. aurita* was found to feed on larvae of plaice and flounder (van der Veer 1985). Lynam et al. (2005b) suggested, that *A. aurita* could have an adverse impact on North Sea herring populations. Herring is the most important commercial fish species taken in the North Sea (http://www.ices.dk). Furthermore, the southern North Sea is an important spawning ground for sprat (Aurich 1941), plaice and flounder (Harding et al. 1978). The larvae of both flatfish species migrate into their nursery areas in the adjacent Wadden Sea (Creutzberg et al. 1978). During transport toward the nursery areas, eggs and larvae have high rates of mortality (Harding et al. 1978), partly due to predation by Scyphomedusae (van der Veer 1985). In contrast to investigations in the central Baltic Sea (Barz and Hirche 2005), and in agreement with investigations in other areas (e.g. Möller 1980b, 1984; Purcell 1985), partially digested fish eggs and larvae, including clupeids, were found in the gut contents in all months analysed. The peak spawning of sprat occurs from May to June (Alheit et al. 1987) when most medusae occur. However, due to the relative low abundance of all species in this study, we have concluded, that predation by medusae was not among the important factors affecting recruitment of fish in the time frame investigated. However, if a future reversal of the NAO phase provides a more favourable environment for Scyphomedusae (Lynam et al. 2004) the abundance of medusae in the North Sea could increase and the recruitment of fish stocks may be impacted due to increased competition for prey and predation on eggs and larvae. For a better management of North Sea Herring stocks, Lynam et al. (2005b) suggested to include a monitoring of jellyfish. However, bottom–up processes influenced by physical factors (temperature, salinity), food availability, and the availability of suitable hard substrate for the polyp settlement mostly control the abundance of medusae (Parsons and Lalli 2002). Hence, for a successful monitoring and eventual forecast of medusae blooms in the southern North Sea it is critical to locate the polyp populations of all species and to learn more about their complete life history dynamics (Mills 2001). With this information a prediction on numbers of released ephyrae and their advection to other regions might be possible.

Acknowledgements

This study would not have been possible without the support of many colleagues and students in collecting and analysing medusae. We thank the crews of RV Alkor, Heincke and A. v. Humboldt. Many thanks also to Ulrike Holtz and Adrian Basilico for their help in examination of medusae and Dr. Rainer Knust and Inken Suck for provide and support the MapIt programme. This research was funded by GLOBEC Germany, BMBF 03F0320D.

References

Alheit J, Wahl E, Cihangir B (1987) Distribution, abundance, development rates, production and mortality of sprat eggs. ICES CM 1987/H:45

Alheit J, Möllmann C, Dutz J, Kornilovs G, Loewe P, Mohrholz V, Wasmund N (2005) Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. ICES J Mar Sci 62: 1205-1215

Arai MN (2001) Pelagic coelenterates and eutrophication: A review. Hydrobiologia: 451: 69-87

Aurich HJ (1941) Die Verbreitung der pelagischen Fischbrut in der südlichen Nordsee während der Frühjahrsfahrten 1926-1937 der deutschen Forschungsschiffe Poseidon und Makrele. Helgol wiss Meeresunters 2: 184-225

Båmstedt U, Martinussen MB, Matsakis S (1994) Trophodynamics of the two scyphozoan jellyfishes, *Aurelia aurita* and *Cyanea capillata*, in western Norway. ICES J Mar Sci 51: 369-382

Båmstedt U, Ishii H, Martinussen MB (1997) Is the scyphomedusa *Cyanea capillata* (L.) dependent on gelatinous prey for its early development? Sarsia 82: 269-273

Barz K, Hirche H-J (2005) Seasonal development of scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (central Baltic Sea). Mar Biol 147: 465-476

Beaugrand G (2003) Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. Fish Oceanogr 12: 270-283

Beaugrand G (2004) The North Sea regime shift: Evidence, causes, mechanisms and consequences. Prog Oceanogr 60: 245-262

Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296: 1692-1694

Brewer RH (1976) Larval settling behaviour in *Cyanea capillata* (Cnidaria: Scyphozoa). Biol Bull 150: 183-199

Brierley AS, Axelsen BE, Buecher E, Sparks CAJ, Boyer H, Gibbons MJ (2001) Acoustic observations of jellyfish in the Namibian Benguela. Mar Ecol Prog Ser 210: 55-66

Brodeur RD, Sugisaki H, Hunt GLJ (2002) Increases in jellyfish biomass in the Bering Sea: Implications for the ecosystem. Mar Ecol Prog Ser 233: 89-103

Brodeur RD, Mills CE, Overland JE, Walters GE, Schumacher JD (1999) Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. Fish Oceanogr 8: 296-306

Creutzberg F, Eltink ATGW, Noort GJv (1978) The migration of plaice larvae *Pleuronectes platessa* into the western Wadden Sea. In: McLusky DS, Berry AJ (ed) Physiology and behaviour of marine organisms, Proc 12th Europ Mar Biol Symp Pergamon Press, Oxford, New York, p 243-251

Dawson MN, Martin LE, Penland LK (2001) Jellyfish swarms, tourists, and the Christ-child. Hydrobiologia 451: 131-144

Dickmann M (2005) Feeding ecology of sprat (*Sprattus sprattus* L.) and sardine (*Sardina pilchardus* W.) larvae in the Baltic Sea and the North Sea. PhD thesis, University of Rostock, Germany

Dittrich B (1988) Studies on the life cycle and reproduction of the parasitic amphipod *Hyperia galba* in the North Sea. Helgol Meeresunters 42: 79-98

Fancett MS (1988) Diet and prey selectivity of scyphomedusae from Port Phillip Bay, Australia. Mar Biol 98: 503-509

Gröndahl F (1988) A comparative ecological study on the scyphozoans *Aurelia aurita, Cyanea capillata* and *C. lamarckii* in the Gullmar Fjord, western Sweden, 1982 to 1986. Mar Biol 97: 541-550

Gröndahl F, Hernroth L (1987) Release and growth of *Cyanea capillata* (L.) ephyrae in the Gullmar Fjord, western Sweden. J Exp Mar Biol Ecol 106: 91-101

Hansson LJ (1997) Capture and digestion of the scyphozoan jellyfish *Aurelia aurita* by *Cyanea capillata* and prey response to predator contact. J Plankton Res 19: 195-208

Harding D, Nichols JH, Tungate DS (1978) The spawning of plaice (*Pleuronectes platessa* L.) in the southern North Sea and English Channel. Rapp P-V Réun Cons Int Explor Mer 172: 102-113

Hartlaub C (1894) Die Coelenteraten Helgolands. Beiträge zur Meeresfauna von Helgoland 4, Wiss Meeresunters, N.F. 1: 161-206

Hay SJ, Hislop JRG, Shanks AM (1990) North Sea Scyphomedusae: Summer distribution, estimated biomass and significance particularly for 0-group gadoid fish. Neth J Sea Res 25: 113-130

Hernroth L, Gröndahl F (1983) On the biology of *Aurelia aurita* (L.). 1. Release and growth of *Aurelia aurita* (L.) ephyrae in the Gullmar Fjord, western Sweden, 1982-83. Ophelia 22: 189-199

Ishii H, Tanaka F (2001) Food and feeding of *Aurelia aurita* in Tokyo Bay with an analysis of stomach contents and a measurement of digestion times. Hydrobiologia 451: 311-320

Kändler R (1961) Über das Vorkommen von Fischbrut, Decapodenlarven und Medusen in der Kieler Förde. Kiel Meeresforsch 17: 48-64

Kopacz U (1994) Gelatinöses Zooplankton (Scyphomedusae, Hydromedusae, Ctenophora) und Chaetognatha im Sylter Wattgebiet. PhD thesis, University of Göttingen, Germany

Kühl H (1964) Die Scyphomedusen der Elbemündung. Veröff Inst Meeresforsch Bremerh 9: 84-94

Kühl H, Mann H (1967) Untersuchungen über das Plankton der Aussenelbe. Gewäss Abwäss 44/45: 7-36

Künne C (1952) Untersuchungen über das Grossplankton der Deutschen Bucht und im Nordsylter Wattenmeer. Helgol Wiss Meeresunters 4: 1-54

Larson RJ (1987a) Daily ration and predation by medusae and ctenophores in Saanich Inlet, B.C., Canada. Neth J Sea Res 21: 35-44

Larson RJ (1987b) Trophic ecology of planktonic gelatinous predators in Saanich Inlet, British Columbia: Diets and prey selection. J Plankton Res 9: 811-836

Lynam CP, Brierley AS, Hay SJ (2004) Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. Limnol Oceanogr 49: 637-643

Lynam CP, Brierley AS, Hay SJ (2005a) Jellyfish abundance and climatic variation: Contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. J Mar Biol Ass UK 85: 435-450

Lynam CP, Brierley AS, Heath MR, Hay SJ (2005b) Evidence for impacts by jellyfish on North Sea herring recruitment. Mar Ecol Prog Ser 298: 157-167

Matsakis S, Conover RJ (1991) Abundance and feeding of medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during spring. Can J Fish Aquat Sci 48: 1419-1430

Merck T (1989) Untersuchungen zur ökologischen Nische von *Chrysaora hysoscella*. Jahresbericht der Biologischen Anstalt Helgoland: 53-54

Mills CE (2001) Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451: 55-68

Möller H (1980a) Scyphomedusae as Predators and Food Competitors of Larval Fish. Rep Mar Res 28: 90-100

Möller H (1980b) Population Dynamics of *Aurelia aurita* Medusae in Kiel Bight, Germany (FRG). Mar Biol 60: 123-128

Möller H (1980c) A summer survey of large zooplankton, particularly Scyphomedusae, in North Sea and Baltic. Rep Mar Res 28: 61-68

Möller H (1984) Data on the biology of jellyfish and youngfish in Kiel Bight. H. Möller, Kiel, Germany

Niermann U, Bingel F, Ergün G, Greve W (1998) Fluctuation of dominant mesozooplankton species in the Black Sea, North Sea and the Baltic Sea: is a general trend recognisable? Turkish J Zool 22: 63-81

Omori M, Ishii H, Fujinaga Ai (1995) Life history strategy of *Aurelia aurita* (Cnidaria, Scyphomedusae) and its impact on the zooplankton community of Tokyo Bay. ICES J Mar Sci 52: 597-603

Olesen NJ, Frandsen K, Riisgard HU (1994) Population dynamics, growth and energetics of jellyfish *Aurelia aurita* in a shallow fjord. Mar Ecol Prog Ser 105: 9-18

Parsons TR, Lalli CM (2002) Jellyfish population explosions: Revisiting a hypothesis of possible causes. La mer 40: 111-121

Purcell JE (1985) Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. Bull Mar Sci 37: 739-755

Purcell JE (1992) Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay, USA. Mar Ecol Prog Ser 87: 65-76

Purcell JE (2005) Climate effects on formation of jellyfish and ctenophore blooms: A review. J Mar Biol Ass UK 85: 461-476

Purcell JE, Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451: 27-44

Purcell JE, Sturdevant MV (2001) Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. Mar Ecol Prog Ser 210: 67-83

Purcell JE, Nemazie DA, Dorsey SE, Houde ED, Gamble JC (1994) Predation mortality of bay anchovy *Anchoa mitchilli* eggs and larvae due to scyphomedusae and ctenophores in Chesapeake Bay. Mar Ecol Prog Ser 114: 47-58

Reid PC, Edwards M, Beaugrand G, Skogen M, Stevens D (2003) Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. Fish Oceanogr 12: 260-269

Russel FS (1970) The medusae of the British Isles. II Pelagic Scyphozoa with a supplement to the first volume on hydromedusae. Cambridge University Press, London

Schneider G, Behrends G (1994) Population dynamics and the trophic role of *Aurelia aurita* medusae in the Kiel Bight and western Baltic. ICES J Mari Sci 51: 359-367

Schneider G, Behrends G (1998) Top - down control in a neritic plankton system by *Aurelia aurita* medusae - a summary. Ophelia 48: 71-82

Thiel ME (1966) Untersuchungen über die Herkunft, das Auftreten, das Wachstum und die Fortpflanzung von *Rhizostoma octopus* im Elbmündungsgebiet. Abh Verhand Naturwissensch Ver Hamburg 10: 59-88

van der Veer HW (1985) Impact of coelenterate predation on larval plaice *Pleuronectes platessa* and flounder *Platichthys flesus* stock in the western Wadden Sea. Mar Ecol Prog Ser 25: 229-238

van der Veer HW, Oorthuysen W (1985) Abundance, growth and food demand of the scyphomedusa *Aurelia aurita* in the western Wadden Sea. Neth J Sea Res 19: 38-44

Verwey J (1942) Die Periodizität im Auftreten und die aktiven und passiven Bewegungen der Quallen. Arch Neerl Zool 6: 363-468

Xiang W, Kang B, Liu R (2005) Jellyfish blooms in the Yangtze Estuary. Science 307: 41

Tables

Table 1: Cruise dates and measured parameters in 2004-2005. Spatial = spatial distribution; vertical = vertical distribution; food = gut content

Year	Date	Parameter		
		spatial	vertical	food
2004	16.02.-05.03.	+		+
	06.04.-27.04.	+		
	07.05.-26.05.	+		
	17.06.-06.07.	+		+
	04.08.-23.08.	+		+
	06.09.-12.09.	+		
2005	14.04.-21.04.	+	+	
	17.05.-24.05.	+	+	+
	30.06.-08.07.	+	+	+

Table 2: Gut content of *C. lamarckii* (*C. lam*), *C. capillata* (*C. cap*) and *C. hysoscella* (*C. hys*). Mean abundance of prey items per medusae += <1; ++ = 1-5; +++ = > 5

	2004				2005			
	Feb	Jun	Aug		May		Jul	
Species	*C. lam*	*C.lam*	*C. lam*	*C. hys*	*C. lam*	*C. cap*	*C. lam*	*C. cap*
Analysed guts	23	15	5	6	7	8	10	8
Empty guts	13	4	1	1	1	4	3	3
Temora sp.	+	++			+	+	+++	+
Acartia spp.	+	+	+	+	++	++	++	
Centropages spp.		+	+	+	+	+	++	
Pseudocalanus sp.		+					+	
Calanus helgolandicus		+					+	
Harpacticoida		+					+	
Podon		++	+		+	+	++	
Evadne		+					+	
Penilia		+	++	+				
Polychaeta larvae		+					++	
Appendicularia		++						
Decapoda larvae		+++	++	+	+		++	++
Mysidacea	++	+						
Fish eggs	++	+			+		+	
Fish larvae		++	+		+		++	++
Echinodermata larvae		+					+	
others	+	+	++	+		+	++	+

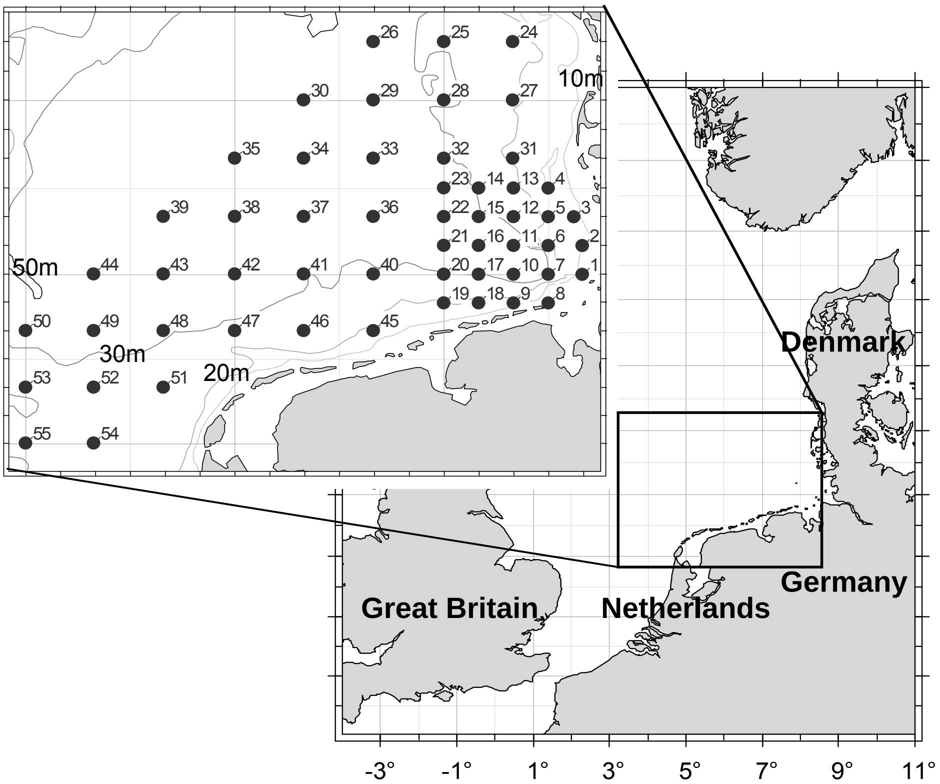


Fig. 1: Station grid in the southern North Sea in 2004.

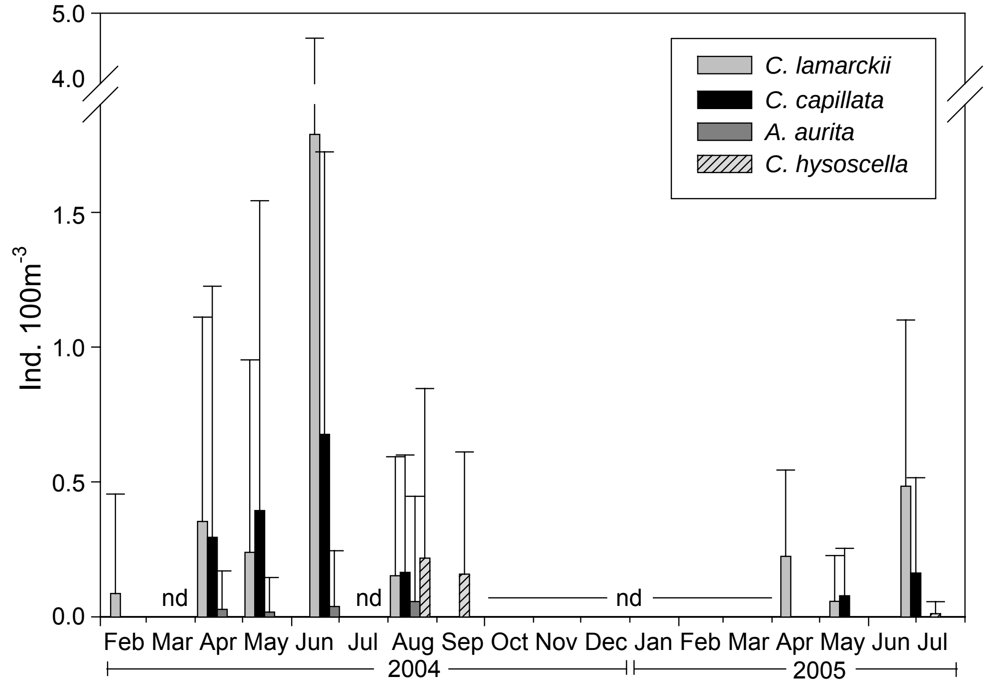


Fig. 2: Mean abundance (± SD) of Scyphomedusae in 2004 and 2005. 2004 from Bongo net hauls on the station grid, 2005 from multinet hauls on the transects.

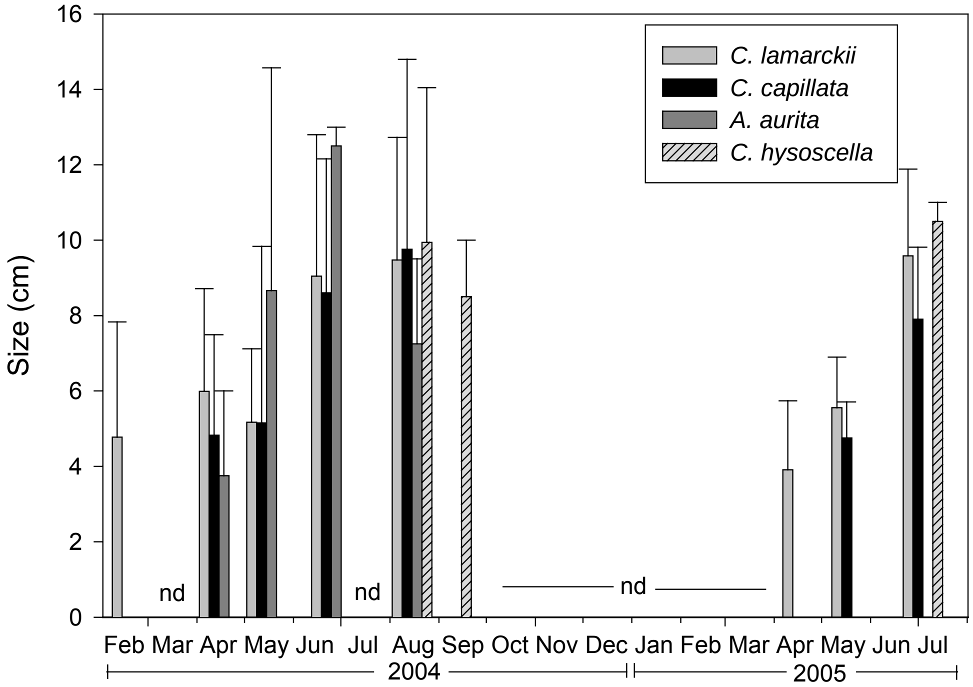
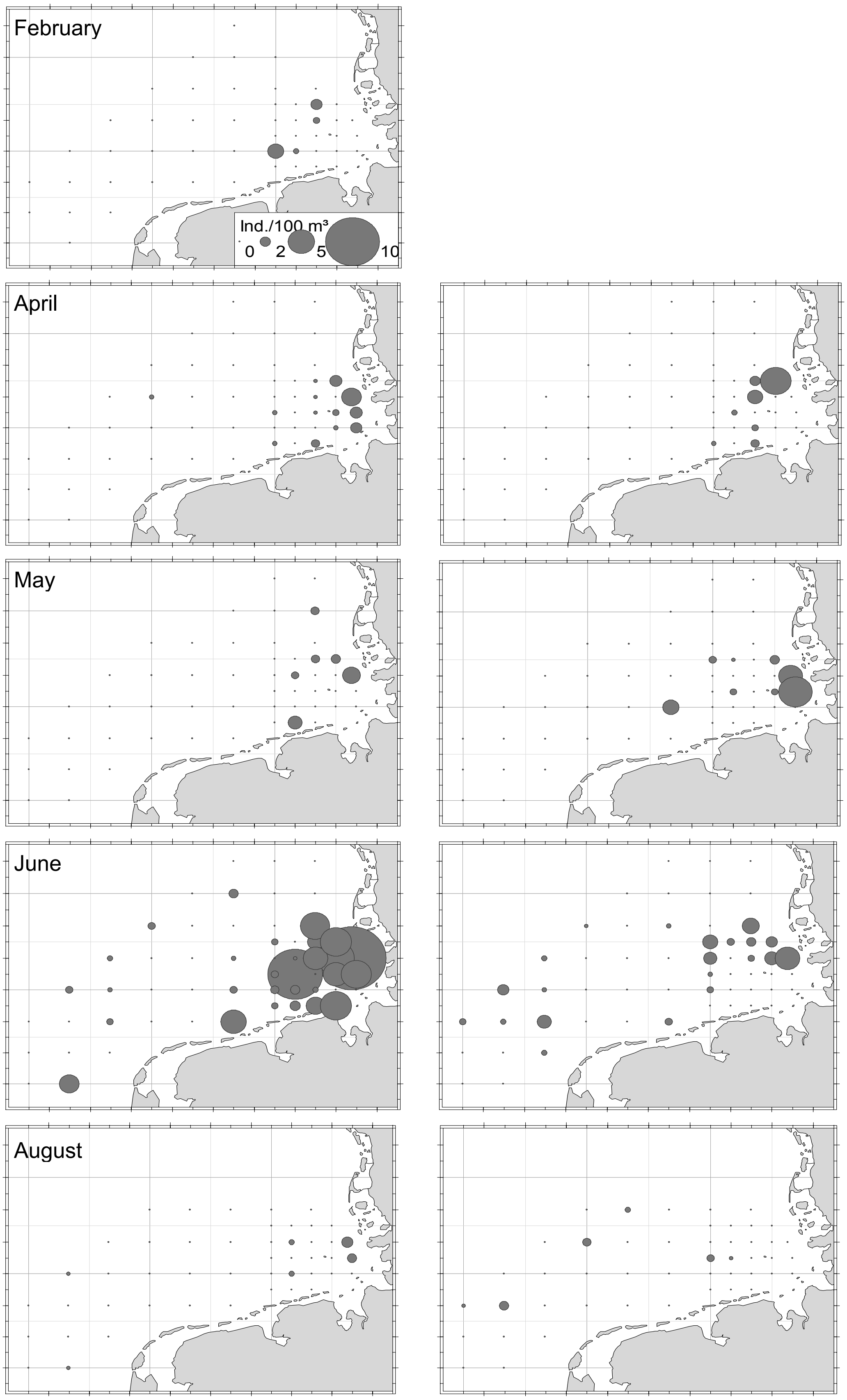
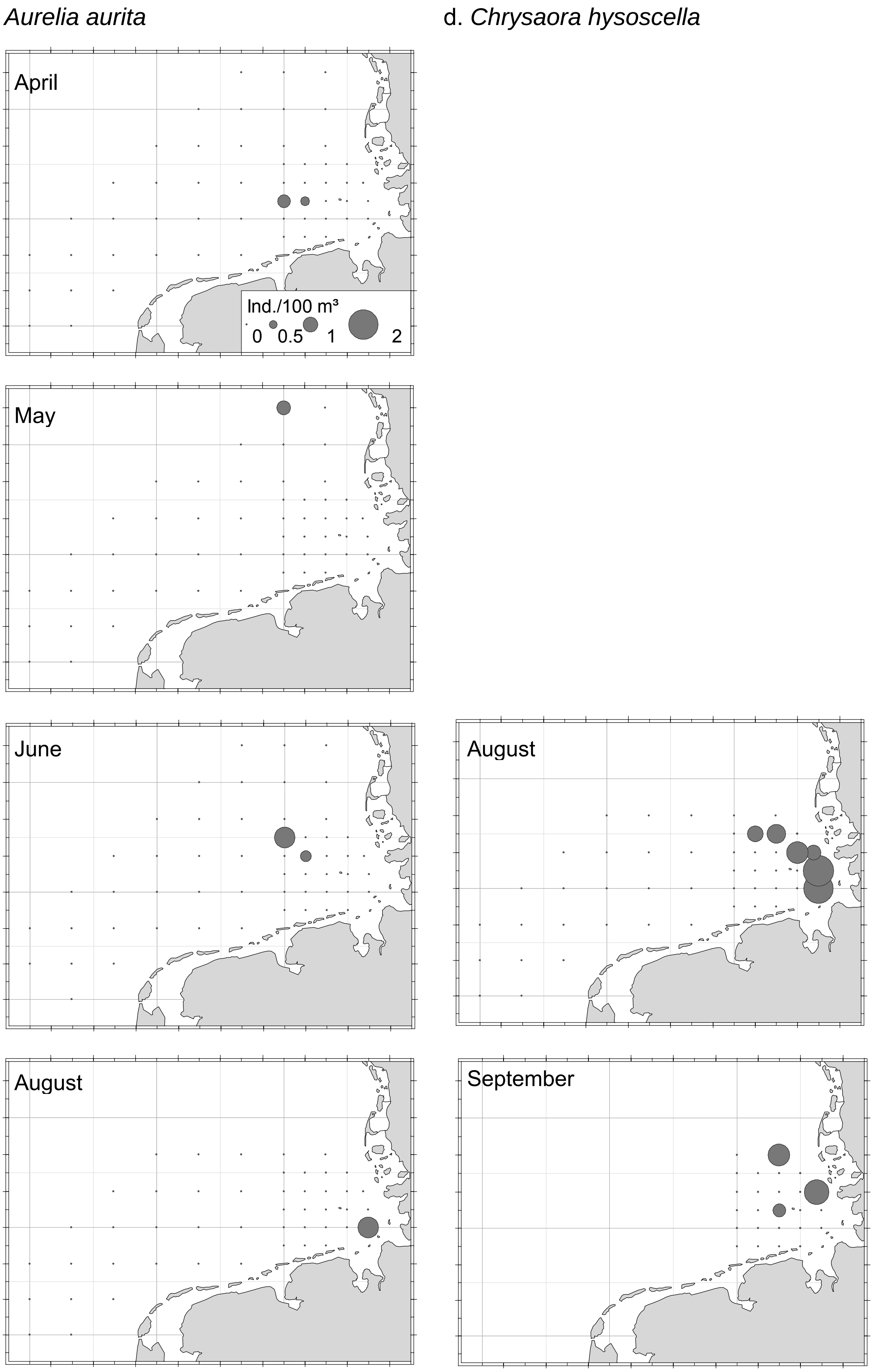


Fig. 3: Mean size (± SD) of Scyphomedusae in 2004 and 2005. 2004 from Bongo net hauls on the station grid, 2005 from multinet hauls on the transects.


a. *Cyanea lamarckii*

b. *Cyanea capillata*

Fig. 4a-b: Spatial distribution of a. *Cyanea lamarckii* and b. *C. capillata* (ind. $100m^{-3}$) in 2004 from Bongo net hauls.


c. *Aurelia aurita*

d. *Chrysaora hysoscella*

Fig. 4c-d: Spatial distribution of c. *Aurelia aurita* and d. *Chrysaora hysoscella* (ind. 100m^{-3}) in 2004 from Bongo net hauls.

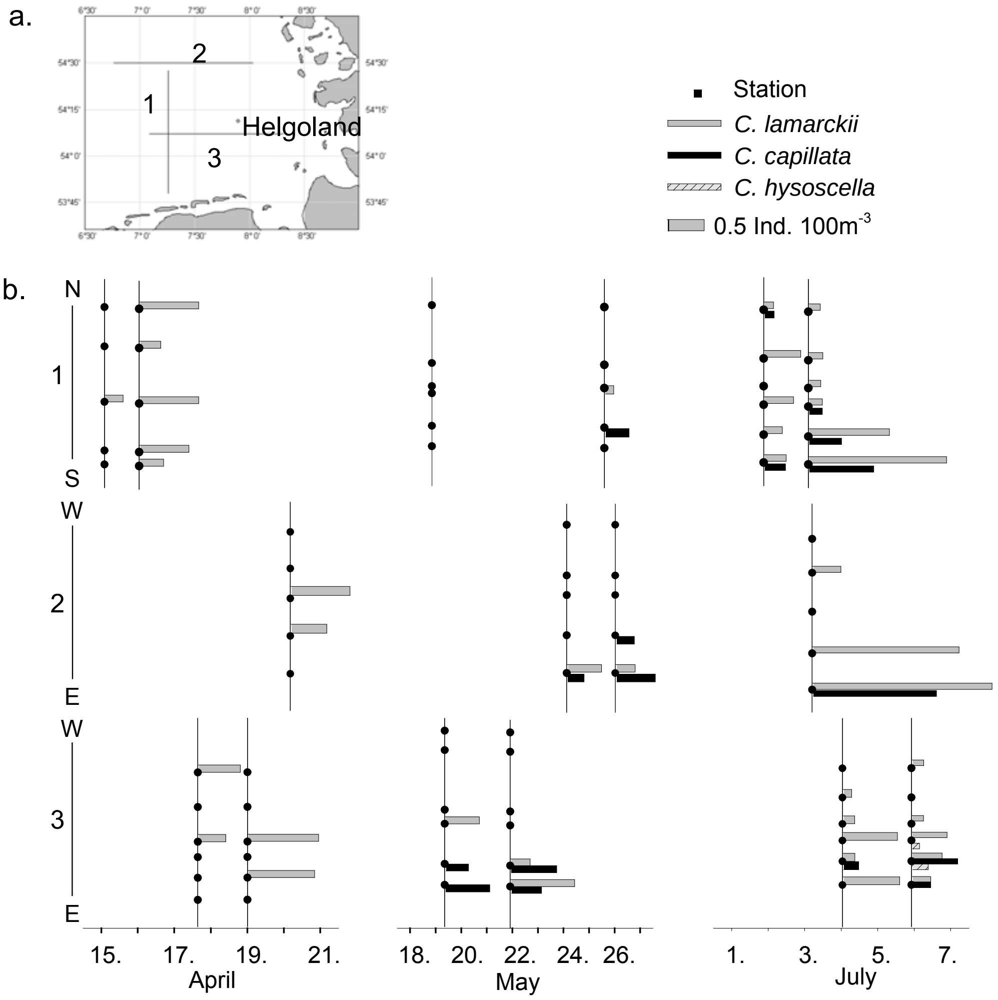


Fig. 5a-b Spatial distribution of Scyphomedusae (ind. $100m^{-3}$) in 2005 on transects. a. Location of transects; b. Abundance from samplings on transects 1-3. N = north; S = south, W = west, E = east.

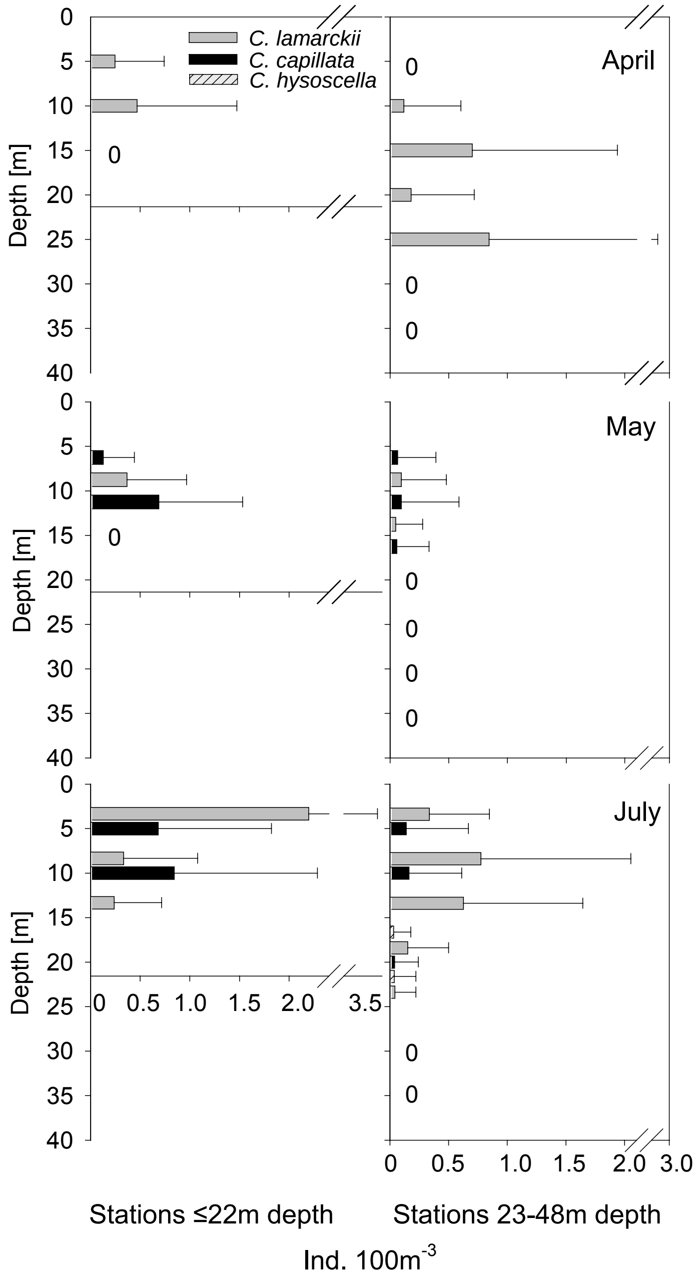


Fig. 6: Vertical distribution (mean abundance ± SD) in April, May and July 2005. Distribution is separately analysed for stations ≤22m depth (left, max. trawling depth ~15m) and 23-48m depth (right, max. trawling depth ~38m).

8 Acknowledgements

Viele Menschen haben mich auf verschiedenste Art und Weise beim Erstellen dieser Arbeit unterstützt. Bei allen möchte ich mich ganz herzlich bedanken und hoffe, dass ich im folgenden niemanden vergesse.

Ich danke Herrn Prof. Dr. Wolf Arntz für die Betreuung und Begutachtung dieser Arbeit.

Vielen Dank an Frau Prof. Dr. Sigrid Schiel ebenfalls für die Begutachtung dieser Arbeit.

Vielen Dank an Dr. Hans-Jürgen Hirche, für die Betreuung der Arbeit und die Unterstützung während meiner Promotionszeit am AWI.

Herrn Prof. Dr. Wilhelm Hagen, vielen Dank für die Teilnahme als Prüfer an meinem Dissertationskolloquium.

Einen herzlichen Dank möchte ich der gesamten GLOBEC Gemeinde aussprechen, besonders den Kieler Jungs Rudi Voss, Gerd Kraus, Hans-Harald Hinrichsen und Jörn Schmidt, die auf meine Anrufe, meistens beginnend mit „Ich hab da mal ne kurze Frage“, immer lieb und hilfsbereit reagierten.

Vielen lieben Dank an die beste Arbeitsgruppe von allen: Jasmin Renz, Diak Mengedoht, Anne Wesche, Jan Schulz, Marcus Engel, Michael Potthoff und Jan Michels (euch zwei zähl ich einfach mal mit dazu). Irgendjemand hatte immer Kaffee, Milch, Schokolade, ein offenes Ohr……………Euch allen vielen Dank auch für das „Schönmachen“ von Grafiken und Karten, für das Korrekturlesen, für das Beisitzen und für die tolle Zeit überhaupt.

Vielen Dank an all diejenigen, die Teil der unzähligen, gemeinsamen Ausfahrten waren. Besonders an die Leute, die an Bord freudig Quallen sortiert und eingemacht haben ☺. Daniel, danke für den Käscher.

Ein Dank gebührt auch den Besatzungen der Forschungsschiffe „Heincke“, „Alkor“ und „Alexander von Humboldt“.

Vielen Dank an Ulrike Holtz, Adrian Basilico, Sabine Lenk und Johanna Silber, die fleißig Quallen und Mysis auseinander genommen bzw. deren Mageninhalt bestimmt haben.

Ein Dankeschön auch an Rainer Knust für die Bereitstellung des MapIt Programms und Inken Suck für die Einführung in selbiges.

Vielen Dank an Frau Helga Kapp (DZMB, Hamburg), die mich in die Geheimnisse der Chaetognathen-Bestimmung eingeweiht hat.

Many thanks to Dr. Myron Peck (IHF, Hamburg) for proof reading of the third manuscript.

Vielen lieben Dank an das AWI Haus G. Besonders natürlich an meine WG, die einen ganz wichtigen Überlebensfaktor darstellt. Es ist schön, dass immer jemand da ist zum Schnacken, Rotwein trinken, Rumhängen vor dem Fernseher……. Danke für Eure Freundschaft: Inken, Hinnerk, Ewoud, Michelle, Corinna.

Danke an Jenny (Goldschühchen) und Nicole, die besten Laufpartnerinnen der Welt, ihr wollt es doch auch! Und danke an die Caipi-Milchbar-Gang (5 sind genug!!).

Ganz besonders möchte ich mich bei meiner Familie bedanken. Ihr habt mich immer unterstützt und brav abgewartet, dass ich endlich fertig werde. Schwesterchen: “…und danke für den Fisch“.

Einen besonders lieben Dank an Matthias. Du hast mir extrem geholfen, indem du einfach da warst und meine zum Ende hin immer schlechtere Laune ertragen hast. Danke für die schöne Zeit (immer 1000 mal mehr ☺).

9 References

Alheit J, Wahl E, Cihangir B (1987) Distribution, abundance, development rates, production and mortality of sprat eggs. ICES CM 1987/H:45

Alheit J, Möllmann C, Dutz J, Kornilovs G, Loewe P, Mohrholz V, Wasmund N (2005) Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. ICES J Mar Sci 62: 1205-1215

Alvarez-Cadena JN (1993) Feeding of the chaetognath *Sagitta elegans* Verrill. Estuar Coast Shelf Sci 36: 195-206

Arai MN (1997) A Functional Biology of Scyphozoa. Chapman and Hall, London

Arai MN (2001) Pelagic coelenterates and eutrophication: A review. Hydrobiologia 451: 69-87

Arai MN, Jacobs JR (1980) Interspecific predation of common Strait of Georgia planktonic coelenterates: Laboratory evidence. Can J Fish Aquat Sci 37: 120-123

Ates RML (1988) Medusivorous fishes, a review. Zoologische Mededeelingen 62: 29-42

Ates RML (1991) Predation on Cnidaria by vertebrates other than fishes. Hydrobiologia 216/217: 305-307

Aurich HJ (1941) Die Verbreitung der pelagischen Fischbrut in der südlichen Nordsee während der Frühjahrsfahrten 1926-1937 der Deutschen Forschungsschiffe Poseidon und Makrele. Helgol Wiss Meeresunters 2: 184-225

Bagge O, Thurow F (1994) The Baltic cod stock: Fluctuations and possible causes. ICES Mar Sci Symp 198: 254-268

Bagge O, Thurow F, Steffensen E, Bay J (1994) The Baltic cod. Dana 10: 1-28

Baier CT, Purcell JE (1997) Trophic interactions of chaetognaths, larval fish, and zooplankton in the South Atlantic Bight. Mar Ecol Prog Ser 146: 43-53

Båmstedt U, Ishii H, Martinussen MB (1997) Is the scyphomedusa *Cyanea capillata* (L.) dependent on gelatinous prey for its early development? Sarsia 82: 269-273

Barz K, Hirche H-J (2005) Seasonal development of scyphozoan medusae and the predatory impact of *Aurelia aurita* on the zooplankton community in the Bornholm Basin (central Baltic Sea). Mar Biol 147: 465-476

Barz K, Hinrichsen H-H, Hirche H-J (2006) Scyphozoa in the Bornholm Basin (central Baltic Sea) - The role of advection. J Mar Syst 60: 167-176

Beaugrand G (2003) Long-term changes in copepod abundance and diversity in the north-east Atlantic in relation to fluctuations in the hydroclimatic environment. Fish Oceanogr 12: 270-283

Beaugrand G (2004) The North Sea regime shift: Evidence, causes, mechanisms and consequences. Progr Oceanogr 60: 245-262

Beaugrand G, Reid PC, Ibaňez F, Lindley JA, Edwards M (2002) Reorganization of North Atlantic marine copepod biodiversity and climate. Science 296: 1692-1694

Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. Nature 426: 661-664

Becker GA, Dick S, Dippner JW (1992) Hydrography of the German Bight. Mar Ecol Prog Ser 91: 9-18

Belgrano A, Scharler UM, Dunne J, Ulanowicz RE (2005) Aquatic food webs, An ecosystem approach. Oxford University Press, New York

Brewer RH (1976) Larval settling behavior in *Cyanea capillata* (Cnidaria: Scyphozoa). Biol Bull 150: 183-199

Brewer RH (1978) Larval settlement behavior in the jellyfish *Aurelia aurita* (Linnaeus) (Scyphozoa: Semaeostomeae). Estuaries 1: 120-122

Brewer RH, Feingold JS (1991) The effect of temperature on the benthic stages of *Cyanea* (Cnidaria: Scyphozoa), and their seasonal distribution in the Niantic River estuary, Connecticut. J Exp Mar Biol Ecol 152: 49-60

Brierley AS, Axelsen BE, Buecher E, Sparks CAJ, Boyer H, Gibbons MJ (2001) Acoustic observations of jellyfish in the Namibian Benguela. J Exp Mar Biol Ecol 210: 55-66

Brodeur RD, Sugisaki H, Hunt GLJ (2002) Increases in jellyfish biomass in the Bering Sea: Implications for the ecosystem. Mar Ecol Prog Ser 233: 89-103

Brodeur RD, Mills CE, Overland JE, Walters GE, Schumacher JD (1999) Evidence for a substantial increase in gelatinous zooplankton in the Bering Sea, with possible links to climate change. Fish Oceanogr 8: 296-306

Bryan K (1969) A numerical method for the study of the circulation of the world ocean. J Comput Phys 4: 347-376

Burnett JW (2001) Medical aspects of jellyfish envenomation: Pathogenesis, case reporting and therapy. Hydrobiologia 451: 1-9

Cargo DG (1984) Some laboratory techniques for the culture of Scyphozoa Workshop on jellyfish blooms in the Mediterranean. UNEP, Athens, pp 129-138

Cox MD (1984) A primitive equation 3-dimensional model of the ocean. GFDL Ocean Group Tech., vol. 1, Geophysical Fluid Dynamics Laboratory, Princeton University, NJ

Creutzberg F, Eltink ATGW, Noort GJ v (1978) The migration of plaice larvae *Pleuronectes platessa* into the western Wadden Sea. In: McLusky DS, Berry AJ (ed) Physiology and behaviour of marine organisms, Proc 12th Europ Mar Biol Symp Pergamon Press, Oxford, New York, pp 243-251

Cushing DH (1984) The gadoid outburst in the North Sea. J Cons Int Explor Mer 41: 159-166

Dawson MN, Martin LE, Penland LK (2001) Jellyfish swarms, tourists, and the Christ-child. Hydrobiologia 451: 131-144

deYoung B, Harris R, Alheit J, Beaugrand G, Mantua N, Shannon L (2004) Detecting regime shifts in the ocean: Data considerations. Prog Oceanogr 60: 143-164

Dickmann M (2005) Feeding ecology of sprat (*Sprattus sprattus* L.) and sardine (*Sardina pilchardus* W.) larvae in the Baltic Sea and the North Sea. PhD thesis, Univ. Rostock, Germany

Dippner JW (1993) A frontal-resolving model for the German Bight. Cont Shelf Res 13: 49-66

Dittrich B (1988) Studies on the life cycle and reproduction of the parasitic amphipod *Hyperia galba* in the North Sea. Helgol Meeresunters 42: 79-98

Fancett MS (1988) Diet and prey selectivity of scyphomedusae from Port Phillip Bay, Australia. Mar Biol 98: 503-509

Feigenbaum D (1991) Food and feeding behaviour. In: Bone Q, Kapp H, Pierrot-Bults AC (eds) The Biology of chaetognaths. Oxford University Press, New York, pp 45-54

Feigenbaum DL, Maris RC (1984) Feeding in the Chaetognatha. Oceanogr Mar Biol Annu Rev 22: 343-392

Feistel R, Nausch G, Matthäus W, Hagen E (2003) Temporal and spatial evolution of the Baltic deep water renewal in spring 2003. Oceanologia 45: 623-642

Floeter J, Temming A (2005) Analysis of prey size preference of North Sea whiting, saithe, and grey gurnard. ICES J Mar Sci 62: 897-907

Fonselius S (1970) On the stagnation and recent turnover of the water in the Baltic. Tellus 22: 533-543

Fonselius S, Valderrama J (2003) One hundred years of hydrographic measurements in the Baltic Sea. J Sea Res 49: 229-241

Gerdes D (1985) Zusammensetzung und Verteilung von Zooplankton sowie Chlorophyll- und Sestongehalte in verschiedenen Wassermassen der deutschen Bucht in den Jahren 1982/83. Veröff Inst Meeresforsch Bremerh 20: 119-139

Graham WM, Kroutil RM (2001) Size-based Prey Selectivity and Dietary Shifts in the Jellyfish, *Aurelia aurita*. J Plankton Res 23: 67-74

Graham WM, Martin DL, Felder DL, Asper VL, Perry HM (2003) Ecological and economic implications of a tropical jellyfish invader in the Gulf of Mexico. Biol Invasions 5: 53-69

Grønkjær P, Wieland K (1997) Ontogenetic and environmental effects on vertical distribution of cod larvae in the Bornholm Basin, Baltic Sea. Mar Ecol Prog Ser 154: 91-105

Gröndahl F (1988) A comparative ecological study on the scyphozoans *Aurelia aurita, Cyanea capillata* and *C. lamarckii* in the Gullmar Fjord, western Sweden, 1982 to 1986. Mar Biol 97: 541-550

Gröndahl F, Hernroth L (1987) Release and growth of *Cyanea capillata* (L.) ephyrae in the Gullmar Fjord, western Sweden. J Exp Mar Biol Ecol 106: 91-101

Hamner WM, Jenssen RM (1974) Growth, Degrowth and Irreversible Cell Differentiation in *Aurelia aurita*. Amer Zool 14: 833-849

Hamner WM, Gilmer RW, Hamner PP (1982) The physical, chemical, and biological characteristics of a stratified, saline, sulfide lake in Palau. Limnol Oceanogr 27: 896-909

Hänninen J, Vuorinen I, Hjelt P (2000) Climatic factors in the Atlantic control the oceanographic and ecological changes in the Baltic Sea. Limnol Oceanogr 45: 703-710

Hansson LJ (1997) Capture and digestion of the scyphozoan jellyfish *Aurelia aurita* by *Cyanea capillata* and prey response to predator contact. J Plankton Res 19: 195-208

Hansson S, Larsson U, Johansson S (1990) Selective predation by herring and mysids, and zooplankton community structure in a Baltic Sea coastal area. J Plankton Res 12: 1099-1116

Harding D, Nichols JH, Tungate DS (1978) The spawning of plaice (*Pleuronectes platessa* L.) in the southern North Sea and English Channel. Rapp P-v Réun Cons Int Explor Mer 172: 102-113

Harrison NM (1984) Predation on jellyfish and their associates by seabirds. Limnol Oceanogr 29: 1335-1337

Hartlaub C (1894) Die Coelenteraten Helgolands. Beiträge zur Meeresfauna von Helgoland 4, Wiss Meeresunters, N.F. 1: 161-206

Hay SJ, Hislop JRG, Shanks AM (1990) North Sea Scyphomedusae: Summer distribution, estimated biomass and significance particularly for 0-group gadoid fish. Neth J Sea Res 25: 113-130

Hays GC, Richardson AJ, Robinson C (2005) Climate change and marine plankton. Trends Ecol Evol 20: 337-344

Hempel G (1978a) Symposium on North Sea fish stocks – Recent changes and their causes. Introduction and historical background. Rapp P-v Réun Cons Int Explor Mer 172:5-9

Hempel G (1978b) Synopsis of the symposium on North Sea fish stocks – Recent changes and their causes. Rapp P-v Réun Cons Int Explor Mer 172: 445-449

Hernroth L, Ackefors H (1979) The zooplankton of the Baltic proper: a long-term investigation of the fauna, its biology and ecology. Report, Fish Bd Sweden, Inst Mar Res (no. 2)

Hernroth L, Gröndahl F (1983) On the biology of *Aurelia aurita* (L.). 1. Release and growth of *Aurelia aurita* (L.) ephyrae in the Gullmar Fjord, western Sweden, 1982-83. Ophelia 22: 189-199

Hernroth L, Gröndahl F (1985) On the biology of *Aurelia aurita* (L.). 3. Predation by *Coryphella verrucosa* (Gastropoda, Opisthobranchia), a major factor regulating the development of *Aurelia* populations in the Gullmar Fjord, western Sweden. Ophelia 24: 37-45

Hinrichsen H-H, Lehmann A, St John M, Brügge B (1997) Modeling the cod larvae drift in the Bornholm Basin in summer 1994. Cont Shelf Res 17: 1765-1784

Hunt Jr. GL, McKinnell S (2006) Interplay between top-down, bottom-up, and wasp-waist control in marine ecosystems. Prog Mar Oceanogr 68: 115-124

Hunt Jr. GL, Stabeno P, Walters G, Sinclair E, Brodeur RD, Napp JM, Bond NA (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep-Sea Res Part II 49: 5821-5853

Hunter MD, Price PW (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. Ecology 73: 724-732

Ishii H, Tanaka F (2001) Food and feeding of *Aurelia aurita* in Tokyo Bay with an analysis of stomach contents and a measurement of digestion times. Hydrobiologia 451: 311-320

Janas U, Witek Z (1993) The occurrence of medusae in the Baltic and their importance in the ecosystem, with special emphasis on Aurelia aurita. Oceanologia 34: 69-84

Kändler R (1961) Über das Vorkommen von Fischbrut, Decapodenlarven und Medusen in der Kieler Förde. Kiel Meeresforsch 17: 48-64

Kawahara M, Uye S-I, Ohtsu K, Iizumi H (2006) Unusual population explosion of the giant jellyfish *Nemopilema nomurai* (Scyphozoa: Rhizostomeae) in East Asian waters. Mar Ecol Prog Ser 307: 161-173

Killworth PD, Stainforth D, Webb DJ, Paterson SM (1991) The development of a free-surface Bryan-Cox-Semtner ocean model. J Phys Oceanogr 21: 1333-1348

Kingsford MJ, Pitt KA, Gillanders BM (2000) Management of jellyfish fisheries, with special reference to the order Rhizostomeae. Oceanogr Mari Biol Annu Rev 38: 85-156.

Kopacz U (1994) Gelatinöses Zooplankton (Scyphomedusae, Hydromedusae, Ctenophora) und Chaetognatha im Sylter Wattgebiet, PhD thesis, Univ. Göttingen, Germany

Kornilovs G, Sidrevics L, Dippner JW (2001) Fish and zooplankton interaction in the Central Baltic Sea. ICES J Mar Sci 58: 579-588

Köster FW, Möllmann C, Hinrichsen H-H, Wieland K, Tomkiewicz J, Kraus G, Voss R, Makarchouk A, MacKenzie BR, St. John MA, Schnack D, Rohlf N, Linkowski T, Beyer JE (2005) Baltic cod recruitment - The impact of climate variability on key processes. ICES J Mar Sci 62: 1408-1425

Köster FW, Möllmann C, Neuenfeldt S, St. John MA, Plikshs M, Voss R (2001) Developing Baltic cod recruitment models. I. Resolving spatial and temporal dynamics of spawning stock and recruitment for cod, herring, and sprat. Can J Fish Aquat Sci 58: 1516-1533

Krause M, Fock H, Greve W, Winkler G (2003) North Sea Zooplankton: A review. Senckenbergiana Maritima 33: 71-204

Kroiher M, Siefker B, Berking S (2000) Induction of segmentation in polyps of *Aurelia aurita* (Scyphozoa, Cnidaria) into medusae and formation of mirror-image medusa anlagen. Internat J Develop Biol 44: 485-490

Kühl H (1964) Die Scyphomedusen der Elbemündung. Veröff Inst Meeresforsch Bremerh 9: 84-94

Kühl H, Mann H (1967) Untersuchungen über das Plankton der Aussenelbe. Gewäss Abwäss 44/45: 7-36

Künne C (1952) Untersuchungen über das Grossplankton der Deutschen Bucht und Im Nordsylter Wattenmeer. Helgol Wiss Meeresunters 4: 1-54

Lebour MW (1923) The food of plankton organisms II. J Mar Biol Assoc UK 13: 70-92

Levitus S, Anotonov JI, Boyer TP, Stephens C (2000) Warming of the world ocean. Science 287: 2225-2229

Lischka M (1999) Abundanz, Verteilung und Nahrungsökologie von Scyphomedusen in der zentralen Ostsee. MS thesis, Univ. Kiel, Germany

Lucas CH, Williams JA (1994) Population dynamics of the scyphomedusa *Aurelia aurita* in Southampton Water. J Plankton Res 16: 879-895

Lynam CP, Brierley AS, Hay SJ (2004) Interannual variability in abundance of North Sea jellyfish and links to the North Atlantic Oscillation. Limnol Oceanogr 49: 637-643

Lynam CP, Brierley AS, Hay SJ (2005a) Jellyfish abundance and climatic variation: Contrasting responses in oceanographically distinct regions of the North Sea, and possible implications for fisheries. J Mar Biol Assoc UK 85: 435-450

Lynam CP, Brierley AS, Heath MR, Hay SJ (2005b) Evidence for impacts by jellyfish on North Sea herring recruitment. Mar Ecol Prog Ser 298: 157-167

Maciejewska K, Margonski P (2001) Status of arrow worms (Chaetognatha) in the southern Baltic Sea. Bull Sea Fish Inst Gdynia 152: 15-29

Mackie GO, Larson KS, Larson RJ, Passano LM (1981) Swimming and vertical migration of *Aurelia aurita* (L.) in a deep tank. Mar Behav Physiol 7: 321-329

Makarchouk A, Hinrichsen HH (1998) The vertical distribution of ichthyoplankton in relation to the hydrographic conditions in the Eastern Baltic. ICES CM 1998/R:11

Margonski P, Horbowa K (1995) Vertical distribution of cod eggs and medusae in the Bornholm basin. Medd Havsfiskelab Lysekil 327: 7-17

Margonski P, Maciejewska K (1999) The distribution, abundance and biomass of *Mysis mixta* and *Neomysis integer* (Crustacea: Mysidacea) in the open waters of the southern Baltic Sea. Bull Sea Fish Inst Gdynia 147: 23-35

Marques AC, Collins AG (2004) Cladistic analysis of Medusozoa and cnidarian evolution. Invertebrate Biol 123: 23-42

Martens P (1980) Beiträge zum Mesozooplankton des Nordsylter Wattenmeeres. Helgol Meeresunters 34: 41-53

Matsakis S, Conover RJ (1991) Abundance and feeding of medusae and their potential impact as predators on other zooplankton in Bedford Basin (Nova Scotia, Canada) during spring. Can J Fish Aquat Sci 48: 1419-1430

Mauchline J (1980) The biology of mysids and euphausids. Adv Mar Biol 18: 1-369

McKenzie BR, Hinrichsen HH, Plikshs M, Wieland K, Zezera AS (2000) Quantifying environmental heterogeneity: Habitat size necessary for successful development of cod *Gadus morhua* eggs in the Baltic Sea. Mar Ecol Prog Ser 193: 143-156

McQueen DJ, Post JR, Mills EL (1986) Trophic relationships in freshwater pelagic ecosystems. Can J Fish Aquat Sci 43: 1571-1581

Merck T (1989) Untersuchungen zur ökologischen Nische von *Chrysaora hysoscella*. Jahresbericht der Biologischen Anstalt Helgoland: 53-54

Mills CE (2001) Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? Hydrobiologia 451: 55-68

Miyake H, Iwao K, Kakinuma Y (1997) Life history and environment of *Aurelia aurita*. South Pacific Study 17: 273-285

Miyake H, Terazaki M, Kakinuma Y (2002) On the polyps of the common jellyfish *Aurelia aurita* in Kagoshima Bay. J Oceanogr 58: 451-459

Mohrholz V, Dutz J, Kraus G (in press) The impact of exceptionally warm summer inflow events on the environmental conditions in the Bornholm Basin. J Mar Syst, DOI: 10.1016/j.jmarsys.2005.10.002

Möller H (1979) Significance of coelenterates in relation to other plankton organisms. Rep Mar Res 27: 1-18

Möller H (1980a) Scyphomedusae as Predators and Food Competitors of Larval Fish. Rep Mar Res 28: 90-100

Möller H (1980b) Population Dynamics of *Aurelia aurita* Medusae in Kiel Bight, Germany (FRG). Mar Biol 60: 123-128

Möller H (1980c) A summer survey of large zooplankton, particularly Scyphomedusae, in North Sea and Baltic. Rep Mar Res 28: 61-68

Möller H (1984) Data on the biology of jellyfish and youngfish in Kiel Bight. H. Möller, Kiel, Germany

Möllmann C, Köster FW, Kornilovs G, Sidrevics L (2003) Interannual variability in population dynamics of calanoid copepods in the central Baltic Sea. ICES Mar Sci Symp 219: 220-230

Möllmann C, Kornilovs G, Fetter M, Köster FW (2004) Feeding ecology central Baltic Sea herring and sprat. J Fish Biol 65: 1563-1581

Möllmann C, Kornilovs G, Fetter M, Köster FW (2005) Climate, zooplankton, and pelagic fish growth in the central Baltic Sea. ICES J Mar Sci 62: 1270-1280

Mutlu E (2001) Distribution and abundance of moon jellyfish (*Aurelia aurita*) and its zooplankton food in the Black Sea. Mar Biol 138: 329-339

Nissling A (2004) Effects of temperature on egg and larval survival of cod (*Gadus morhua*) and sprat (*Sprattus sprattus*) in the Baltic Sea - implications for stock development. Hydrobiologia 514: 115-123

Nissling A, Kryvi H, Vallin L (1994) Variation in egg buoyancy of Baltic cod *Gadus morhua* and its implications for egg survival in prevailing conditions in the Baltic Sea. Mar Ecol Prog Ser 110: 67-74

Nissling A, Westin L, Hjerne O (2002) Reproductive success in relation to salinity for three flatfish species, dab (*Limanda limanda*), plaice (*Pleuronectes platessa*), and flounder (*Pleuronectes flesus*), in the brackish water Baltic sea. ICES J Mar Sci 59: 193-108

Nissling A, Müller A, Hinrichsen HH (2003) Specific gravity and vertical distribution of sprat eggs in the Baltic Sea. J Fish Biol 63: 280-299

Øresland V (1987) Feeding of the chaetognaths *Sagitta elegans* and *S. setosa* at different seasons in Gullmarsfjorden, Sweden. Mar Ecol Prog Ser 39: 69-79

Olesen NJ, Frandsen K, Riisgård HU (1994) Population dynamics, growth and energetics of jellyfish *Aurelia aurita* in a shallow fjord. Mar Ecol Prog Ser 105: 9-18

Omori M, Ishii H, Fujinaga A (1995) Life history strategy of *Aurelia aurita* (Cnidaria, Scyphomedusae) and its impact on the zooplankton community of Tokyo Bay. ICES J Mar Sci 52: 597-603

Palmen E (1953) Seasonal occurrence of ephyrae and subsequent instars of *Aurelia aurita* (L.) in the shallow waters of Tvärminne, S. Finland. Arch Soc 'Vanamo' 8: 122-131

Parmanne R, Rechlin O, Sjöstrand B (1994) Status and future of herring and sprat stocks in the Baltic Sea. Dana 10: 29-59

Parsons TR, Lalli CM (2002) Jellyfish population explosions: Revisiting a hypothesis of possible causes. La Mer 40: 111-121

Pearre SJ (1982) Estimating Prey Preference by Predators: Uses of various indices, and a proposal of another based on χ^2. Can J Fish Aquat Sci 39: 914-923

Pitta P, Giannakourou A, Divanach P, Kentouri M (1998) Planktonic food web in marine mesocosms in the Eastern Mediterranean: Bottom-up or top-down regulation? Hydrobiologia 363: 97-105

Purcell JE (1985) Predation on fish eggs and larvae by pelagic cnidarians and ctenophores. Bull Mar Sci 37: 739-755

Purcell JE (1992) Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay, USA. Mar Ecol Prog Ser 87: 65-76

Purcell JE (1997) Pelagic cnidarians and ctenophores as predators: Selective predation, feeding rates, and effects on prey populations. Ann Inst Oceanogr 73: 125-137

Purcell JE (2005) Climate effects on formation of jellyfish and ctenophore blooms: A review. J Mar Biol Ass UK 85: 461-476

Purcell JE, Arai MN (2001) Interactions of pelagic cnidarians and ctenophores with fish: a review. Hydrobiologia 451: 27-44

Purcell JE, Nemazie DA, Dorsey SE, Houde ED, Gamble JC (1994) Predation mortality of bay anchovy *Anchoa mitchilli* eggs and larvae due to scyphomedusae and ctenophores in Chesapeake Bay. Mar Ecol Prog Ser 114: 47-58

Purcell JE, Sturdevant MV (2001) Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska. Mar Ecol Prog Ser 210: 67-83

Reeve MR (1980) Comparative experimental studies on the feeding of chaetognaths and ctenophores. J Plankton Res 2: 381-393

Reid PC, Edwards M, Beaugrand G, Skogen M, Stevens D (2003) Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. Fish Oceanogr 12: 260-269

Remane A (1934) Die Brackwasserfauna. Verh dt zool Ges 36: 34-74

Rheinheimer (1996) Biologie und Ökologie. In: Rheinheimer (ed) Meereskunde der Ostsee. Springer, Berlin, pp 113-115

Rudstam LG, Hansson S (1990) On the ecology of *Mysis mixta* (Crustacea, Mysidacea) in a coastal area of the northern Baltic proper. Ann Zool Fenn 27: 259-263

Rudstam LG, Hansson S, Larsson U (1986) Abundance, species composition and production of mysid shrimps in a coastal area of the northern Baltic Proper. Ophelia Suppl. 4: 225-238

Russel FS (1970) The medusae of the British Isles. II. Pelagic Scyphozoa with a supplement to the first volume on Hydromedusae. Cambridge University Press, Cambridge

Salemaa H, Vuorinen I, Vaelipakka P (1990) The distribution and abundance of *Mysis* populations in the Baltic Sea. Ann Zool Fenn 27: 253-257

Sameoto DD (1973) Annual life cycle and production of the chaetognath *Sagitta elegans* in Bedford Basin, Nova Scotia. J Fish Res Board Can 30: 333-344

Schneider G (1989) Estimation of food demands of *Aurelia aurita* medusae populations in the Kiel Bight/western Baltic. Ophelia 31: 17-27

Schneider G, Behrends G (1994) Population dynamics and the trophic role of *Aurelia aurita* medusae in the Kiel Bight and western Baltic. ICES J Mar Sci 51: 359-367

Schneider G, Behrends G (1998) Top - down control in a neritic plankton system by *Aurelia aurita* medusae - a summary. Ophelia 48: 71-82

Semtner AJ (1974) A general circulation model for the world ocean. Tech. Rep., vol. 9 Dep. of Meteorology, Univ. California, Los Angeles

Siefker B (2004) Kontrolle von Metamorphose und Strobilation bei Scyphozoen, PhD thesis, Univ. Köln, Germany

Sinclair ARE, Mduma S, Brashares JS (2003) Patterns of predation in a diverse predator-prey system. Nature 425: 288-290

Sloan NA, Gunn CR (1985) Fishing, processing, and marketing of the jellyfish, *Aurelia aurita* (L.) from southern British Columbia. Canadian Industry Report of Fisheries and Aquatic Sciences 157: 1-29

Spangenberg DB (1965) A study of strobilation in *Aurelia aurita* under controlled conditions. J Exp Zool 160: 1-10

Spangenberg DB (1967) Iodine induction of metamorphosis in *Aurelia*. J Exp Zool 165: 441-449

Suchman CL, Sullivan BK (1998) Vulnerability of the copepod *Acartia tonsa* to predation by the scyphomedusa *Chrysaora quinquecirrha*: Effect of prey size and behavior. Mar Biol 132: 237-245

Suchman CL, Sullivan BK (2000) Effect of prey size on vulnerability of copepods to predation by the scyphomedusae *Aurelia aurita* and *Cyanea* sp. J Plankton Res 22: 2289-2306

Sullivan BK, Garcia JR, Klein-MacPhee G (1994) Prey selection by the scyphomedusan predator *Aurelia aurita*. Mar Biol 121: 335-341

Svane I, Dolmer P (1995) Perception of light at settlement: A comparative study of two invertebrate larvae, a scyphozoan planula and a simple ascidian tadpole. J Exp Mar Biol Ecol 187: 51-61

Thiel H (1962) Untersuchungen über die Strobilisation von *Aurelia aurita* LAM. an einer Population der Kieler Förde. Kiel Meeresforsch 18: 198-230

Tönnesson K, Tiselius P (2005) Diet of the chaetognaths *Sagitta setosa* and *S. elegans* in relation to prey abundance and vertical distribution. Mar Ecol Prog Ser 289: 177-190

van der Veer HW (1985) Impact of coelenterate predation on larval plaice Pleuronectes platessa and flounder *Platichthys flesus* stock in the western Wadden Sea. Mar Ecol Prog Ser 25: 229-238

van der Veer HW, Oorthuysen W (1985) Abundance, growth and food demand of the scyphomedusa *Aurelia aurita* in the western Wadden Sea. Neth J Sea Res 19: 38-44

Verity PG, Smetacek V (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. Mar Ecol Prog Ser 130: 277-293

Verwey J (1942) Die Periodizität im Auftreten und die aktiven und passiven Bewegungen der Quallen. Archiv Neerland Zool 6: 363-468

Viitasalo M, Flinkman J, Viherluoto M (2001) Zooplanktivory in the Baltic Sea: A comparison of prey selectivity by *Clupea harengus* and *Mysis mixta*, with reference to prey escape reactions. Mar Ecol Prog Ser 216: 191-200

Voss R, Clemmesen K, Baumann H, Dickmann M (2004) Recruitment success in Baltic sprat: Coupling of food availability, larval condition and survival. ICES CM 2004/O:02

Voss R, Koester FW, Dickmann M (2003) Comparing the feeding habits of co-occurring sprat (*Sprattus sprattus*) and cod (*Gadus morhua*) larvae in the Bornholm Basin, Baltic Sea. Fish Res 63: 97-111

Wasmund N, Pollehne F, Postel L, Siegel H, Zettler ML (2004) Biologische Zustandseinschätzung der Ostsee im Jahre 2003. Mar Sci Rep 60: 1-94

Wikström DA (1932) Beobachtungen über die Ohrenqualle (*Aurelia aurita* L.) in den Schären SW-Finnlands. Mem Soc Pro Fauna Flora Fennica 8: 14-17

Xiang W, Kang B, Liu R (2005) Jellyfish blooms in the Yangtze Estuary. Science 307: 41

Yasuda T (1970) Ecological studies on the jellyfish *Aurelia aurita* (L.) in Urazoko Bay, Fukui Prefecture - 5. Vertical distribution of the Medusa. Ann Rep Noto Mar Lab 1970. 10: 15-22

Yasuda T (1973) Ecological studies on the jelly-fish, *Aurelia aurita* in Urazoko Bay, Fukui-Prefecture. 9. Diel vertical migration of the medusa in late spring, 1970. Bull Jap Soc Sci Fish 39: 1145-1150

10 Appendices

10.1 List of abbreviations

Abbreviation	Description
BB	Bornholm Basin
MBI	Major Baltic Inflow
C. cap	*Cyanea capillata*
C. hys	*Chrysaora hysoscella*
C. lam	*Cyanea lamarckii*
NAO(I)	North Atlantic Oscillation (Index)
nd	no data
nm	Nautical miles
SD	Standard Deviation

Anlage zur Dissertation

Kristina Barz
Gildemeisterstr. 4
27568 Bremerhaven

Erklärung gem. § 6 (5) Nr. 1-3 Promotionsordnung

Ich erkläre hiermit, dass ich

1. die Arbeit ohne unerlaubte fremde Hilfe angefertigt habe,

2. keine anderen, als die von mir angegebenen Quellen und Hilfsmittel benutzt habe und
3. die den benutzten Werken wörtlich oder inhaltlich entnommenen Stellen als solche kenntlich gemacht habe.

Kristina Barz