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Ecological assessment of the Ctenophore Invader
Mnemiopsis leidyi in the Western Baltic Sea

Dissertation

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by

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Summary

Species invasion is a conspicuous phenomenon in today's human-dominated biosphere. With the changing configuration of marine ecosystems, the barriers limiting the range of species are changing, too. Studing species invasions allows scientists to observe and measure many ecological processes (such as spatial distribution, genetic changes) directly, which are difficult to study with long-established native species. Therefore the study of invasion ecology gained the name of "an experiment in nature" (Grinnel 1919 as referred in Sax et al. 2005). Because the frequency of gelatinous zooplankton increases globally, their future ecological role is a matter of concern for marine invasion ecologists. The Baltic Sea is a recipient of species from several different donor systems and referred to as 'a sea of invaders' by Leppaekoski et al. (2002). The recent invasion by the comb jelly *Mnemiopsis leidyi* became a topic of major concern after its appearance in the Baltic Sea because of the vast ecological and economic impacts it had in its previously invaded habitats such as the Black Sea.

In the first chapter, we established a morphological key to distinguish *Mnemiopsis leidyi* from *Bolinopsis infundibulum.* Both species are very similar. This key enabled us to identify this species from time series data of Helgoland Road station where *B. infundibulum* naturally occurs.

A permanent weekly sampling in the Western Baltic Sea provided the basic knowledge on *M. leidyi* seasonal dynamics and ability of being established. In chapter II we show the late summer outbreak in 2007 with a 10 fold increase in abundance in a short time that coincided with high reproduction activity. The drop of mesozooplankton prey in late spring was due to predatory control of fish larvae and no seasonal overlap between *M. leidyi* and fish eggs or larvae could be detected. We have also provided data on the main environmental conditions which might trigger the outbreaks of *M. leidyi* population in the Western Baltic Sea.

In chapter III, we simulated the drift pattern of *M. leidyi* during its first year of observation in 2007 by using a hydrographical model. The model illustrated the possible advection route of *M. leidyi* through the Baltic Sea. It is hardly possible that *M. leidyi* has penetrated from Kategat Skagerak as a single source of spread. Instead ballast water release and the subsequent spread away from different recipient harbors might have led to the concentration of its population in the deep basin of North and Central Baltic Sea.

In the last chapter we show the predatory impact of *M. leidyi* on mesozooplankton population of Western Baltic Sea was measured. During cold season this species showed a high preference for small sized and slow swimming prey. Copepods were preferred just for a short time in August. The most abundant prey in summer were planula larvae of the other gelatinous carnivore in the Baltic Sea, *Aurelia aurita.* However adults of *M. leidyi* got their major energy intake via cannibalism on their own larvae.

Zusammenfassung

Invasion von Arten ist ein auffallendes Phänomen in der heutigen vom Menschen beherrschten Biosphäre. Durch das Verschwinden von natürlichen Barrieren, welche die Verbreitung von Arten in der vergangenheit bestimmt haben, ändert sich die gesamte Artenzusammensetzung. Das Untersuchen von einwandernden Arten erlaubt es Wissenschaftlern direkt viele ökologische Prozesse wie Raumausbreitung, genetische Änderungen zu beobachten und zu messen, welches mit lang etablierten einheimischen Arten nicht möglich ist. Deshalb wird das Untersuchen von einwandernden Arten auch als „natürliches Experiment" (Grinnel 1919 als reffered in Sax et al. 2005) bezeichnet. In Anbetracht der globalen Zunahme von gallertartigem Zooplankton sind Invasionsökologen besonders daran interessiert, die zukünftige ökologische Rolle dieser Gruppe zu verstehen. Die Ostsee beherbergt eine große Anzahl von eingewanderten Arten aus benachbarten aquatischen Systemen und wird daher als ‚Meer der Einwanderer' bezeichnet (Leppaekoski u. a. 2002). Die Invasion der Ostsee durch die Rippenqualle *Mnemiopsis leidyi* hat Besorgnis hervorgerufen, da diese Art in den vorher besiedelten Gebieten großen ökologischen wie ökonomischen Einfluss geommen hat.

Im ersten Kapitel, habe ich einen morphologischen Bestimmungsschlüssel entwickelt, um *Mnemiopsis leidyi* von der sehr ähnlichen *Bolinopsis infundibulum* zu unterscheiden. Dieser Schlüssel ermöglichte uns, *B. infundibulum* in der Helgoland Reede Zeitreihe zu idenzifizieren. *B. infundibulum* kommt natürlicherweise vor Helgoland vor.

Ein dauerhaftes wöchentliches Monitoring von *M. leidyi* in der Westlichen Ostsee stellte die Datengundlage her, mit der die saisonalen Dynamiken und die Etablierung der Art in der Ostsee erklärt werden kann. Im zweiten Kapitel zeigen wir, dass die 10fache Zunahme von *M. leidyi* im Sommer 2007 mit ihrer hohen Reproduktionsaktivität korreliert. Die Abnahme der Mesozooplankton-Beute gegen Ende des Frühlings war dem Konsum der Fischlarven zuzuschreiben und es gab keine zeitliche Überlappung zwischen *M. leidyi* und Fischeiern oder -larven. Weiterhin haben wir Daten der wichtigsten Umweltbedingungen erhoben, welche für die Massenvermehrung der *M. leidyi* Population in der Westlichen Ostsee verantwortlich sein könnten.

In Kapitel III haben wir mit Hilfe eines hydrographischen Modells das Antrieb-Muster von *M. leidyi* während ihres ersten Jahres (2007) der Etablierung simuliert. Das Modell illustriert die mögliche advektive Route von *M. leidyi* durch die Ostsee. Die Ergebnisse zeigen, dass es kaum möglich ist, dass *M. leidyi* vom Kategat-Skagerak als eine einzige Quelle die Ostsee besiedelt hat. Dahingegen ist es eher wahrscheinlich, dass die Art sich durch Ballastwassereintrag von verschiedenen Häfen aus in die tiefen Becken der nördlichen und zentralen Ostsee verbreitet hat.

In Kapitel IV haben wir den räuberischen Einfluß von *M. leidyi* auf das Mesozooplankton der Westlichen Ostsee untersucht. Während der kalten Jahreszeit zeigte diese Art eine Vorliebe für kleine und langsam schwimmende Beute. Copepoden wurden nur für kurze Zeit im August bevorzugt. Die Haupbeute im Sommer waren Planulalarven der zweiten Quallenart der Ostsee, *Aurelia aurita*. Die Hauptkohlenstoff-Quelle der adulten *M. leidyi* wurde durch Kannibalismus auf ihre eigenen Larven gedeckt.

Introduction

Global importance of gelatinous zooplankton

Gelatinous plankton organisms are ancient organisms (Pagès 2001) and known as the earliest multicellular animals radiating at the base of animal tree of life (Dunn et al. 2008). They are very plastic, adaptable, and opportunistic. By simply reducing their body size, they can survive for long periods of time without food. In many areas of the world where the natural species diversity has been affected by pollution (Romeo et al. 1992), over-fishing (Lynam et al. 2006) and, now, climate change (Lynam et al. 2005; Purcell 2005) and eutrophication (Arai 2001), gelatinous plankton organisms may be becoming the dominant predator species. These organisms may significantly mediate the transport and the cycling of carbon fluxes in oceanic waters (Gorsky et al. 1984; Sommer et al. 2002).

Gelatinous zooplankton populations are most likely to further increase both in frequency and intensity due to global anthropogenic changes leading an increase in surface seawater temperature of ~2 to 5°C in European shelf seas by 2100, (IPCC 2007, Purcell 2005). This may have profound effects on pelagic food webs and fisheries, as jellyfish are known to feed voraciously on fish eggs, fish larvae and the prey organisms of fish (Mills 2001). Nevertheless, unequivocal proof of sustained increases of jellyfish populations over recent years is lacking (Purcell et al. 2007). Historical plankton records, in fact, indicate that presumed exceptional jellyfish outbreaks of the present day (e.g. *Pelagia noctiluca* on the North Ireland coasts, see Sharrock 2007) were already described more than 100 years ago (Boero et al. 2008; Goy et al. 1989).

Furthermore, other anthropogenic perturbations, such as overfishing and eutrophication or even increase of available hard substrates (enhancing the chance for suitable planula settlement) are known to cause unexpected jellyfish outbreaks (Arai 2001; Holst and Jarms 2007; Kideys 2002; Lynam et al. 2006; Pearsons and lalli 2002; Tatsuki 2005) and may shift the ecosystem from fish dominance towards jellyfish dominance (Boero et al. 2008; Mills 2001) (Fig.1). (Boero et al. 2008) suggested that: human made disturbances like overfishing and clime change affects the evolutionary chain to a way that suppresses high-energy (fish and whales) food chains with a possible

subsequent de-evolution of the pelagic marine ecosystem that leads to degradation back to the Cambrian era, when jellyfish dominated the world's oceans.

The role of gelatinous predators for the function of food web

Fraser (1970) was one of the first to describe the ecological significance of gelatinous carnivores in the pelagic food web. In recent years the role of gelatinous zooplankters has received considerable attention. They are ubiquitous in coastal ecosystems and can prey voraciously on co-occurring zooplankton and ichthyoplankton. When abundant, gelatinous predators can have profound effects on the plankton community through direct predation and competition for food (Alldredge et al. 1984; Behrends and Schneider 1995; Nicholas and Frid 1999) as well as trophic cascading effects (Malej et al. 2007; Verity and Smetacek 1996). Although the role of predators in influencing zooplankton community structure is well established for freshwater lakes (Brook & Dodson 1965), top-down effects are not as well established as a primary factor structuring marine ecosystems (Suchman et al. 2008). Nevertheless, several studies have shown inverse relationships between medusa densities and their prey (e.g. (Behrends and Schneider 1995; Brewer 1989; Moller 1984). Therefore there is a need to consider both changes in populations and predation impact of gelatinous predators if we want to understand or predict marine ecosystem dynamics fully. Most of our knowledge about jellyfish predation comes from studies of relatively small medusae in semi-enclosed bays or estuaries, or under experimental conditions. Gut content analyses of larger individuals (Graham and Kroutil 2001; Purcell et al. 1993; Uye and Shimauchi 2005) show that, like smaller medusae, larger forms can feed across a broad range of zooplankton, including copepods, other gelatinous taxa, and fish eggs. Reports on predation impact by large medusae vary widely. In the Bering Sea, (Brodeur et al. 2002) estimated that *Chrysaora melanaster* consumed one-third of the standing stock of zooplankton during the summer season. In subregions of Prince William Sound, Alaska, (Purcell 2003) calculated predation by scyphomedusae on copepod standing stock to be at most 0.3% d^{-1} and on larvaceans up to 7% d^{-1}, although stations with the largest jellyfish aggregations were excluded from her analysis. (Uye and Shimauchi 2005) reported the *Aurelia aurita* population in the Sea of Japan could consume 26% d^{-1} of the available net zooplankton biomass.
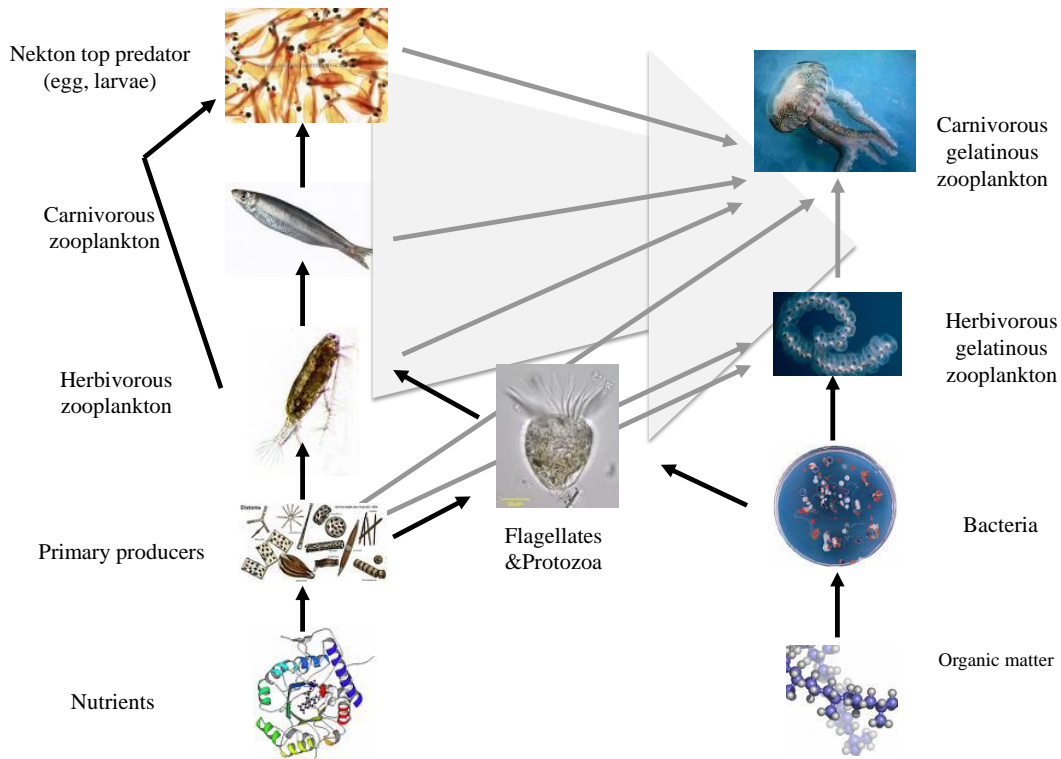
Fig.1- Simplified trophic pathways with and without gelatinous zooplankton. By relying on different compartments of the pelagic food web, gelatinous animals act as 'sinks' for transfer of energy and matter.

Moreover in eutrophicated areas, outbreak of jellyfish can reduce or eliminate the grazing of zooplankton which results in an increased sedimentation of phytoplankton and may cause severe oxygen depletion and release of nutrients from the anoxic sediment "vicious circle" (Riisgard 1996).

This group has the potential to reach very high densities in a short time thus influencing pelagic energy pathways (Sommer et al. 2002). The food web configuration of this group is multifold. The gelatinous carnivores might channel the secondary and tertiary production, competing for food with other zooplankton and with planktivorous fish. They act also as predators on many fish species feeding on their eggs and larvae. Thus they might exert a major disruption on the whole food web (see Fig.1) and disrupt the transfer of matter and energy by acting as sink in the pelagic food web.

Transport

Transport

Death,captivity   Introduction

Establishment

Fail   Establish

Spraed

Remain local   Spread

Impact

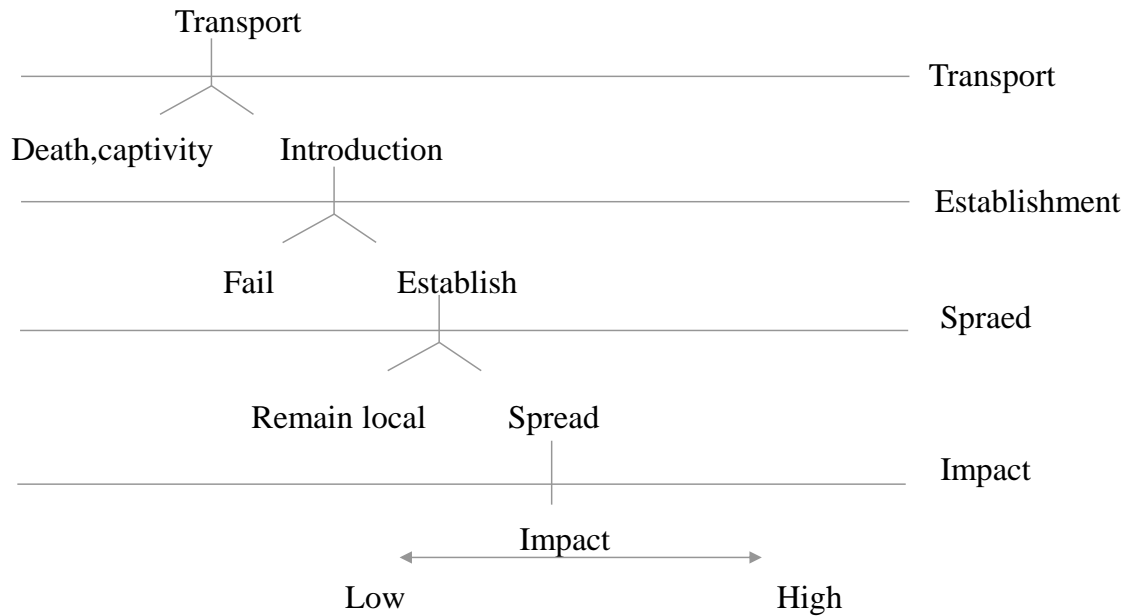Impact

Low   High

Fig.2- Invasion process model illustrates the different stages an invasive species passes through as well as alternative outcomes at each stage (after Lockwood, 2007)

In spite of its overall importance, the irregular occurrence of gelatinous carnivores and the fact that the physical forcing affects their spatial distribution represents a critical point to the investigation of food web interactions. In contrast to the almost regular occurrence of blooms of crustacean plankton, the pulses of gelatinous zooplankton often last for rather short times (CIESM 2001; Kawahara et al. 2006). Therefore their structuring effect on the pelagic community is often temporary (Lebedeva 1998; Matsakis and Conover 1991).

All gelatinous plankters, however, regardless of their trophic status, neither store much energy in the form of reserves nor do they generally perform, in the presence of currents, active migrations other than vertical. Thus their representatives can play overwhelming roles with their pulses for much longer than they actually occur: ''irregularities (sometimes) rule the world'' (Boero et al. 2008)

Biological invasion and jellyfish

In the aquatic systems, non-indigenous species (NIS), are occurring at an alarming rate and are causing global concern (Mack et al. 2000; Occhipinti-Ambrogi and Savini 2003; Reusser and Lee 2008).Yet the consequences, or ecological impacts, of NIS are not always well understood, especially in plankton system (Parker et al. 1999).

Typically it is only when the NIS is widespread and abundant that it will cause some sort of ecological or economic harms, and thus earn the name ''invasive''. However, there are several complicated stages along the path to becoming a successful invader (Fig.2). Several life cycle (i.e. quantitative shifts at the individual level) and life history (i.e. quantitative fluctuations at the population level) adaptations enable gelatinous zooplankton to pass between each of invasion stages and overcome several ecological barriers (Boero et al. 2008).

Over recent decades several cases of invasions of gelatinous plankters (medusae and/or ctenophores) have been documented and/or reviewed (Greve 1994; Shiganova et al. 2001a; Shiganova et al. 2001b; Zhilyakova et al. 2004; Purcell 2005; Xian et al. 2005; Kawahara et al. 2006; Link and Ford 2006).The impact of gelatinous plankton predation on marine biota became too obvious to be neglected when *Mnemiopsis leidyi*, an Atlantic ctenophore, was brought to the Black Sea, presumably by the ballast waters of oil tankers, and developed huge populations. Its massive occurrence was held responsible for the collapse of fisheries in the whole basin, impairing fish recruitment via predation on fish larvae and on their food (Belyaev and Solov'eva 1995; Avsar 1997; Berdnikov et al. 1999; Brodeur et al. 2002). This example indicated how a combination of environmental disturbances like eutrophication, overfishing of competing pelagic species and the absence of natural controls may have interacted to create an opening for gelatinous invader.

The case study of the Baltic Sea

Baltic Sea is known as a young sea considering both geological and hydrographical aspects. Therefore there are few and perhaps no truly endemic species in the Baltic. The spatio-temporal heterogeneity of its environment not only strongly

influences the native biotic communities, but also provide a broad pool of NIS of different origins (from cold stenothermal to eurythermal species). The flora and fauna consist mainly of euryhaline species that have extended their natural range from the North Atlantic, relicts from previous periods of sea history, brackish and freshwater species, as well as species recently introduced by humans (see Segerstråle 1957 for a comprehensive review).

In recent decades, the Baltic Sea ecosystem has been exposed to an ever increasing rate of bioinvasions mainly as a consequence of global climate change and the intensified shipping trade in the region. It is expected that the risk of successful alien species establishment originating from warmer regions may increase (Leppaekoski et al. 2002; Gollasch and E.Leppaekoski 2007). The ongoing eutrophication which alters Baltic ecosystems and makes it more suitable for species that prosper in nutrient-rich, turbid waters of coastal lagoons, inlets and port areas and opens new niches for present and future species invasions. The alterations in major circulation patterns of the Baltic Sea and subsequent changes of environmental factors may also affect dispersal patterns of alien species and subsequent impact on the native species (Leppaekoski and Olenin 2000)

In the Baltic Sea, environmental degradation has led to a gradual reduction of the main top- predator (the piscivorous cod) and a multi level trophic cascade down to primary producers (Alheit et al. 2005; Casini et al. 2008). A major concern of ecologists and fishery biologists now would be the threat of jellyfish on commercially important fish stocks through direct predation on fish early life stages or through indirect competition on available food sources, mainly mesozooplankton. Unfortunately there are only a few attempts to estimate the ecological role of jellyfish predators in the Baltic Sea. Barz and Hirche (2005) estimated a low predatory impact of *Aurelia aurita* on the zooplankton community in the central Baltic Sea. However the pattern of *A. aurita* predation seems to be different in the local scale in which a top-down effect by mesozooplankton predation would be considered (Moller 1984; Schneider and Behrends 1998).

Thesis outline

This thesis is divided into four chapters representing more or less independent studies addressing the ecological importance of the recent invasion of the comb jelly *Mnemiopsis leidyi* into the Baltic Sea.

Chapter I addresses the first records of comb jelly occurrence in the Baltic and North Sea. I provided a simple explanation on the main morphological characters of this species which was neglected in the previous sampling attempts.

In chapter II the aim was to describe both the establishment of the invader and the main factors that might influence *M. leidyi* establishment after its first observation. This chapter contains information on the annual population dynamics, seasonality and timing of *M. leidyi* in the Western Baltic Sea.

Chapter III addresses the spreading route of *M. leidyi* through the Baltic Sea. This was assessed by using a hydrographical model (Lagrangian particle tracking model). Due to lack of biologically identifiable data on the life history and reproductive potential of *M. leidyi* from different parts of the Baltic Sea, this model might be considered as the best-first option for tracking the invader spreading route in the Baltic Sea.

The last chapter shows the predation potential of *M. leidyi* on mesozooplankton community of the Kiel Fjord. It provides the first set of quantitative data on seasonal diet composition, size structure and life history traits of *M. leidyi* and its predatory role in the pelagic ecosystem of the Western Baltic Sea. We have discussed the influence of adverse environmental conditions on this species fitness and the consequence reduction of its potential predatory impact in the new invaded environment.

Chapter I

First record of Mnemiopsis leidyi A. Agassiz 1865 in the Baltic Sea

Jamileh Javidpour, Ulrich Sommer and Tamara Shiganova

Abstract

The invasive ctenophore *Mnemiopsis leidyi* was first recorded in the Kiel Bight (western Baltic Sea) on 17 October 2006 during a regular weekly sampling program. The *M. leidyi* abundance gradually increased from 29.5±12.7 ind.m-3 in mid-October to 92.3±22.4 ind.m-3 in late November 2006. The occurrence of *M. leidyi* in the Baltic Sea is of great concern as this invader has caused negative impacts in the southern seas of Europe.

Key words: ctenophores, alien species, *Mnemiopsis leidyi*, *Bolinopsis infundibulum*, ballast water, first record

The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 was introduced into the Black Sea in the 1980s (Vinogradov et al. 1989). It showed an explosive mass development there since 1988 and expanded to the Azov, Marmara, and eastern Mediterranean Seas and in 1999 it was introduced into the Caspian Sea likely with ballast water of oil tankers (Studenikina et al. 1991; Shiganova 1993; Ivanov et al. 2000; Shiganova et al. 2001b).

Fig. 1-*Mnemiopsis leidyi* from the Baltic Sea (Photograph by J.Javidpour)

The native habitat of *M. leidyi* includes estuaries and coastal regions along the eastern coast of North and South America (GESAMP 1997). *M. leidyi* is a polymorphic species with wide tolerance to environmental factors and high phenotypic variability (reviewed in GESAMP 1997). Therefore it could establish in different environmental conditions of the southern Eurasian seas. *M. leidyi* strongly affected all levels of ecosystems and fishery in the productive Black, Azov and Caspian; however no remarkable effects were recorded in the oligotrophic Aegean Sea (Shiganova et al. 2001b; Shiganova et al. 2004a, Shiganova et al. 2004b). *M. leidyi* has not been observed along western and northern European waters until recently, although its wide
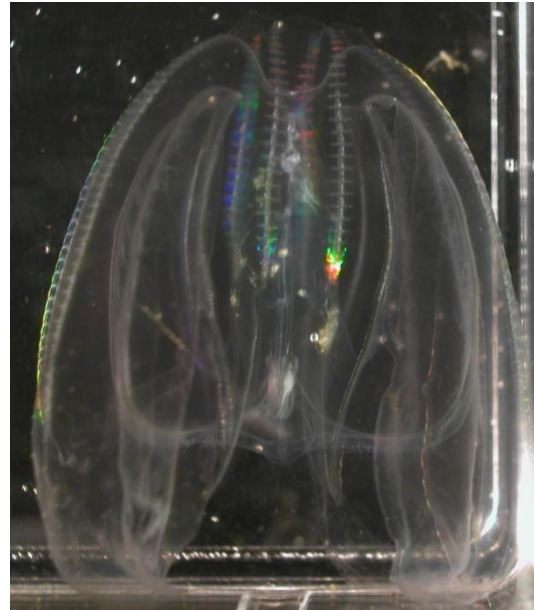

Fig. 2- *Mnemiopsis leidyi* from the Black Sea (Photograph by T. Shiganova)

tolerance to salinity (4-38‰) and temperature (4-32°C) (reviewed in GESAMP, 1997) make most of the Baltic Sea a suitable environment.

Low water temperature in winter and a relatively low temperature in summer may negatively impair its reproduction. On 17 October 2006 J. Javidpour and U. Sommer observed swarms of *M. leidyi* for the first time in the Kiel Bight (western Baltic Sea). The ctenophores were collected during a regular weekly sampling program in the Kiel Bight, which started in February 2005. The sampling station is located in the Kiel Fjord (54°19.7' N, 10°09.5' E). Vertical hauls from 10 m depth were carried out with plankton net (openingdiameter 80 cm, mesh size 500 µm). The collected animals were determined and counted alive. The preliminary identification of *M. leidyi* was confirmed by T.A. Shiganova and also DNA sequencing was carried out by the private lab AGOWA (www.agowa.de/struktur/newsbasis.html).

M. leidyi (Fig. 1) can morphologically be distinguished from the native ctenophore *Bolinopsis infundibulum*. The main difference is the position of the oral lobes. In *M. leidyi*, the oral lobes originate near the infundibulum, in *B. infundibulum* the oral lobes originate approx. half-way between the mouth and the infundibulum (Mayer 1912), see also (Faasse and Bayha 2006). Individuals of *M. leidyi* from the Baltic Sea are more similar to specimens caught in the Sea of Azov and the Caspian Sea compared to individuals from the Black Sea (Shiganova et al. 2004a; Shiganova et al. 2004b). The Baltic Sea individuals are smaller and adult individuals do not have oral lobes as long as the Black Sea individuals (Fig. 2).

During weekly surveys *M. leidyi* was found in high numbers first on 17 October 2006 (29.5±12.7 ind.m-3). Its abundance gradually increased to 92.3±22.4 ind.m-3 in the sample taken on 28 November 2006 (Fig. 3).
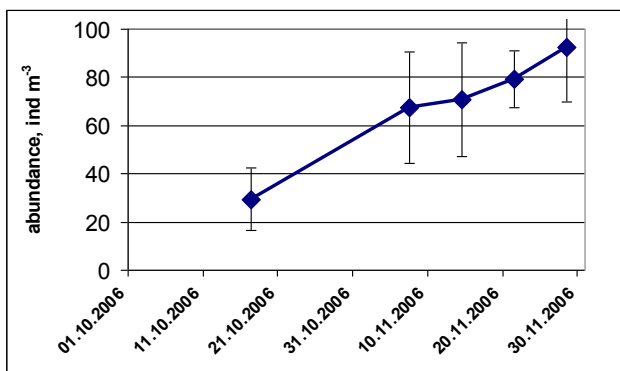

Fig. 3- Temporal abundance (individuals per cubic meter) of *M. leidyi* in 2006 in the Kiel Bight

This very high density is comparable with the density of *M. leidyi* during the first years of its outbreak in the Black Sea (Vinogradov et al. 1989). During the first observation more than 80 % of individuals were equal or smaller than 5 mm in total length, the maximal length was 5 cm. The surface water temperature in the Kiel Bight reached 22.6°C in July 2006, which was 1.7oC higher than in the same period in 2005 (Fig. 4). The water temperature was 5°C higher in October and November 2006 compared to 2005. The salinity ranged from 13.1 to 22.2‰ which is comparable with the Black Sea salinity (14-22‰) (Ovchinnikov and Titov 1990). These conditions are optimal for *M. leidyi* reproduction (Kremer 1994). In the Black Sea *M. leidyi* begins to reproduce at water temperatures above 21°C, reaches a peak at 23°C and continues until the water temperature drops below 14°C in autumn (Shiganova et al. 2001b). The main factors to control the *M. leidyi* population size are temperature and prey availability (Kremer 1982, 1994; Sullivan et al. 2001).
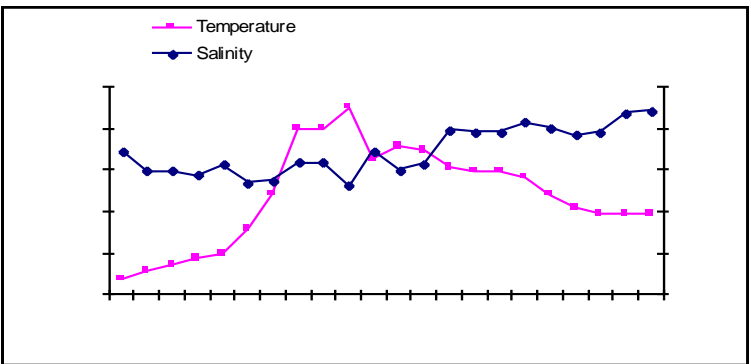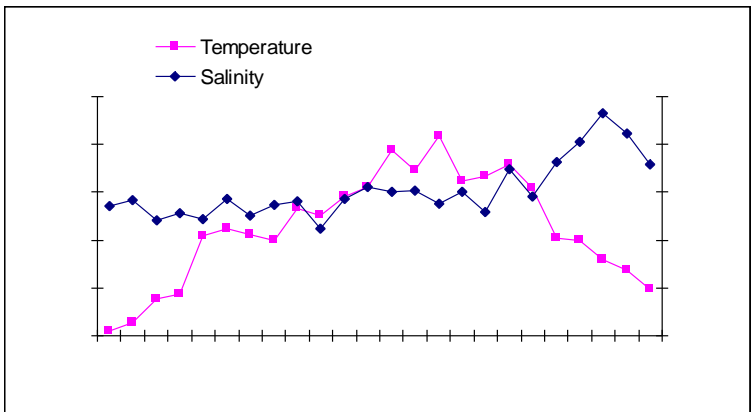

Fig.4- Seasonal temperature and salinity variations in 2005 and 2006 in the Kiel Bight.

The southwestern Baltic is considered as a high productive area during winter and a high abundance of copepods has been investigated in winter months compared to the summer mesozooplankton community (Schneider 1987). It is therefore assumed that the *M. leidyi* population in the Baltic Sea developed high densities in October 2006, although it may have arrived earlier.

Two pathways could have brought *M. leidyi* into the Kiel Fiord. Firstly, Kiel is one of the busiest ports in the Baltic Sea and therefore *M. leidyi* may have been released with ballast water from America or the Black Sea region. Secondly, *M. leidyi* could have been transported into the Baltic by currents from the North Sea, where *M. leidyi* was observed earlier (Hansson 2006; Boersma et al. 2007; Faasse and Bayha 2006).

It is unknown if the *M. leidyi* population is able to survive in winter in the Baltic Sea. However, the Kiel Bight temperature is very low in winter (0.4 to 2°C in March 2005 and 1.7 to 2°C in February and March 2006 (Figure 4) and we assume that it will probably not survive such temperatures at the rather low salinities. In contrast, *M. leidyi* survives winter temperatures <4°C in its native range if salinities are higher, but it does not survive colder temperatures in low salinity waters of the Black, Azov and the Caspian Seas (Purcell et al. 2001). However *M. leidyi* may be re-introduced into the Baltic Sea with water currents from the North Sea next year. The expansion of *Mnemiopsis leidyi* in the Baltic Sea is of great concern as this aggressive invader has already damaged several productive ecosystems of the southern seas of Europe. Its high density in the Baltic Sea as well as in the North Sea estuaries in 2006 is an indication of a possible *M. leidyi* establishment in northern European coastal waters.

Acknowledgements

The first occurrence of the ctenophore Mnemiopsis leidyi in the North Sea

Maarten Boersma, Arne M. Malzahn, Wulf Greve, Jamileh Javidpour

Abstract

After the discovery of large densities of Mnemiopsis leidyi in the Baltic Sea near Kiel by Javidpour et al. (submitted) in October 2006, we investigated the gelatinous zooplankton in the North Sea near Helgoland, and recorded Mnemiopsis leidyi for the first time in the North Sea, albeit in much lower densities than those recorded in the Baltic Sea.

Key words: Neozoa, Invasive species, German Bight, Helgoland Roads, *Beroe,* Black Sea

Introduction

On the 17th of October 2006, a swarm of the lobate ctenophore *Mnemiopsis leidyi* was observed for the first time during regular sampling of the Baltic Sea near Kiel, Germany (Javidpour et al. 2006). This news was met with a combination of scepticism and apprehension, as *Mnemiopsis leidyi* has gathered quite a reputation as a biological invader. Originally a species from the Western Atlantic (Purcell et al. 2001), occupying coastal waters over a wide latitudinal range (40°N–46°S), it invaded the Black Sea in the 1980s, followed by subsequent invasions of the other large water bodies in the Mediterranean Basin (Shiganova et al. 2001a). The consequences of these invasions for the systems were drastic. Predators of *Mnemiopsis leidyi* were not present in these seas, and as a result populations developed to very high densities (Kideys et al. 2000). *Mnemiopsis leidyi* is a voracious predator on zooplankters, as well as on fish eggs and larvae (Reeve et al. 1978; Kremer 1979). The mass occurrence of *Mnemiopsis leidyi* in the Black Sea and Caspian Sea coincided with a sharp decline in the fisheries yields (Bilio and Niermann 2004).

As there is intense water exchange between the North Sea and the Western Baltic Sea, and another ctenophore *Pleurobrachia pileus* is known to be transported into the Baltic from the Belt Sea or Skagerak (Schneider 1987), it is of utmost importance to assess whether *Mnemiopsis leidyi* has also invaded the North Sea.

Methods

We sampled the gelatinous zooplankton on the Helgoland Roads station (54°11.18′N and 07°54.00′E); the same station that has been sampled for the long-term series of zooplankton (Greve et al. 2004), phytoplankton and nutrients (Wiltshire and Manly 2004) for the last 30-40 years. The sampling station is located between the Island of Helgoland and the adjacent sandy island in the German Bight, North Sea. The water depth at the station is approximately 10 m and the water column is mixed throughout the year due to strong tidal currents (up to 1.5 knots). After subtraction of tidal currents, the counter clock-wise residual flow direction in the area is northerly from the English Channel

to the northern North Sea. Salinity is fairly constant, varying between 30 and 33, temperature ranges from 2-20°C.

Lobate ctenophores such as *Mnemiopsis leidyi* and the naturally occurring *Bolinopsis infundibulum* are notoriously difficult to fixate, as they disintegrate rapidly as a result of fixation. Therefore, in the standard long-term zooplankton samplings these organisms were recorded only until the early 1980s. *Bolinopsis* was found almost exclusively in the months July-September.

A CalCOFI ring trawl with a 500 µm mesh net (aperture 100 cm, length 400 cm, equipped with a flowmeter) was towed for 15 min from a research vessel, resulting in a sampled volume of water of around 500 m^3. The samples were transferred to the laboratory, and the ctenophores were sorted out immediately.

Results and Discussion

On November 30th 2006, our first day of sampling following the discovery of *Mnemiopsis leidyi* in the Kiel Bight, we caught several ctenophores in the North Sea near Helgoland, which were identified as *Mnemiopsis leidyi*. Weather conditions prevented quantitative sampling. Quantitative sampling on December 5th and 6th 2006 yielded densities of around 0.1 individuals of *Mnemiopsis leidyi* m^{-3}, mostly in the size range of 1-2.5 cm. These densities were much lower than the ones reported for the Baltic Sea (80 m^{-3} Javidpour et al. *2006*). Nevertheless *Mnemiopsis leidyi* has also reached the southern North Sea.

At this moment it is not possible to assess the potential impact of *Mnemiopsis leidyi* on the plankton community of the southern North Sea, as we do not know how the density of this organism is going to change. Most likely, however, the impact on the system will be less than in the Black and Caspian Seas. First of all, two species of the ctenophore genus *Beroe* occur in the German Bight. This genus is known to feed selectively on other ctenophores with which they co-evolved (Greve et al. 1976). *Beroe ovata* is the major predator of *Mnemiopsis leidyi* in the native habitat, and since the accidental introduction of *Beroe ovata* into the Black Sea population densities of *Mnemiopsis leidyi* have decreased and seem to be under predation control. *Beroe*

cucumis, the predator of *Bolinopsis infundibulum* in the North Sea, will probably feed on *M. leidyi,* and so may *Beroe gracilis*, the predator of *Pleurobrachia pileus* in the North Sea. This should constrain mass development of *Mnemiopsis leidyi* populations to some extent. Secondly, according to Shiganova et al. (2001a) *Mnemiopsis leidyi* does not survive temperatures lower that 4 °C in the Black Sea. Water temperature at Helgoland Roads at the moment of sampling was 10 °C, but typically goes to 2-3 °C in February (Wiltshire and Manly 2004). This would mean that local survival of the populations at least in the surface waters of the southern North Sea at may not be likely (see also Esser et al 2004), and that future populations either need to find appropriate winter refugia, or need to be seeded by overwintering populations from somewhere else. However, global warming may prevent this control of the invader, which in turn could result in elevated grazing pressure on overwintering holoplankters.

Even though predation rates of *Mnemiopsis leidyi* are large, and they certainly gravely affected zooplankton densities in the Black Sea (Kideys 2002) and Caspian Sea some authors suggest that the fisheries yields in the Black Sea primarily declined as a result of overfishing, which freed up the zooplankton production to be used by *Mnemiopsis* rather than the reverse (Gucu 2002). This means that *Mnemiopsis leidyi* in the Black Sea could have been present long before actually reaching the high densities. Only when conditions were favourable, *i.e.* less competition by juvenile fish, high primary production as a result of eutrophication, did the mass development occur (Gucu 2002). This mass development of *Mnemiopsis leidyi* then decreased the fish stocks even more. A similar phenomenon might have occurred in the North Sea. It is most likely that *Mnemiopsis leidyi* has also been present in the North Sea at low densities for quite some time, and used a loophole opened recently by historically low stock sizes of one of the most important planktivorous fish in the North Sea, lesser sandeel (*Ammodytes marinus*). Sandeel plays a pivotal role as prey for piscivorous fish, sea birds and marine mammals. On top of that, a large fisheries exists for this species, which until fairly recently was classified as sustainable by ICES (ICES 2002). Sandeel is responsible for around 1/3 of the commercial fish landings from the North Sea, with landings increasing from 0.2 million tons y^{-1} to over 1 million tons y^{-1} in the 1990s. The enormous increase in fisheries on this important planktivore has caused the stocks to decline dramatically (Arnott and Ruxton 2002), causing a closure of the fisheries for 2005. It is possible that the decrease in sandeel standing stock and the other planktivorous fish stocks that had been depleted

before in the North Sea has released the competitive pressure on *Mnemiopsis leidyi* to an extent which allows this species to develop densities high enough to be noticed in sampling. This all needs further research.

Mnemiopsis leidyi has arrived in the North Sea; we do at this moment not know how and wherefrom. The densities observed by us as and especially those in the Baltic Sea (Javidpour et al. 2006) are, however, so high that we can exclude a single recent ballast water release event. It is another example of biological species invasions in this part of the world that might severely affect the ecosystem (Diederich 2006). We will have to keep the finger at the pulse of this sensitive ecosystem to be able to make predictions of the impact of this new species in the North Sea.

Chapter II

Seasonal changes and population dynamics of the ctenophore Mnemiopsis leidyi after its first year of invasion in the Kiel Fjord, Western Baltic Sea

Jamileh Javidpour, Juan Carlos Molinero, Jesco Peschutter & Ulrich Sommer

Abstract

We analyzed the seasonal variations of the ctenophore *Mnemiopsis leidyi* weekly collected since its first record in the western Baltic Sea in October 2006. The distribution pattern, together with the seasonal dynamics and population outbreaks late summer 2007 indicate recent successfully establishment of *M. leidyi* in this area. Seasonal changes showed two periods of high reproductive activity characterized by a population structure dominated by small size classes, followed by an increase of larger ones. These results further revealed that the bulk of the population remains in deep layers during the periods of low population density, whereas it appeared situated in upper layers during the proliferation of the species. We further emphasized the strength of the population outbreaks, which can reach abundances > 10-fold higher in time periods shorter than a week. The predatory impact this species may have in pelagic ecosystems warns on the importance of its recent range of expansion.

Key words: Biological invasions, ctenophores, Mnemiopsis leidyi, population structure, Baltic Sea

Introduction

Biological invasions are currently one of the leading threats to the diversity of aquatic ecosystems worldwide. Through competition, predation, and habitat alteration, invaders can radically change both the species composition and functioning of invaded ecosystems (Levine 2008). Concerns of biological invasions in marine ecosystems relate to the serious ecological and economical menace, which lead to biodiversity loss, ecosystem unbalancing, fishery and tourism impairment. Furthermore, in the ecological theory framework, biological invasions are of great interest since they represent unique natural experiments for understanding the structure and functioning of ecological communities (Occhipinti-Ambrogi and Savini 2003).

The Baltic Sea is one of the largest brackish water bodies on earth and is possibly one of the most exposed European areas to global warming (IPCC 2007). In addition, the 16 million people living in immediate vicinity of the coast and the 85 million within the catchment's area make the Baltic Sea highly vulnerable to human-induced ecological impacts (Leppaekoski et al. 2002). In the last century, the Baltic Sea has undergone drastic perturbations related to ecosystem-wide structural changes, i.e. a shift from a system with seals to cods as top-predators followed by a shift to an eutrophic sea, and during the recent decades a shift from cod to clupeids as dominant fish (Alheit et al. 2005; Österblom et al. 2007). Hence, human induced impacts (i.e. overfishing, eutrophication) as well as natural factors (broad salinity-temperature gradients), made the Baltic Sea an unstable ecosystem, which could be extremely favorable for invasion of non-indigenous species (Paavola et al. 2005). This may explain the large number of alien species reported in the Baltic Sea during the last two centuries (~100 species; Leppakoski et al. 2002). Consequently, the Baltic Sea represents an important node in global aquatic invasive species (Gollasch and E.Leppäkoski 2007).

One of the most dramatic and serious effects of alien species in European seas so far has been the introduction of *Mnemiopsis leidyi* in the Black Sea, where it showed an explosive outbreak and expanded into the Azov, Marmara, and Caspian Seas (Shiganova 1998). *M. leidyi* is widely recognized as a harmful invader and ranked among the world's 100 worst invasive species (http://www.issg.org/). It became particularly infamous for causing major ecological and economic damage to the Black Sea ecosystem after its
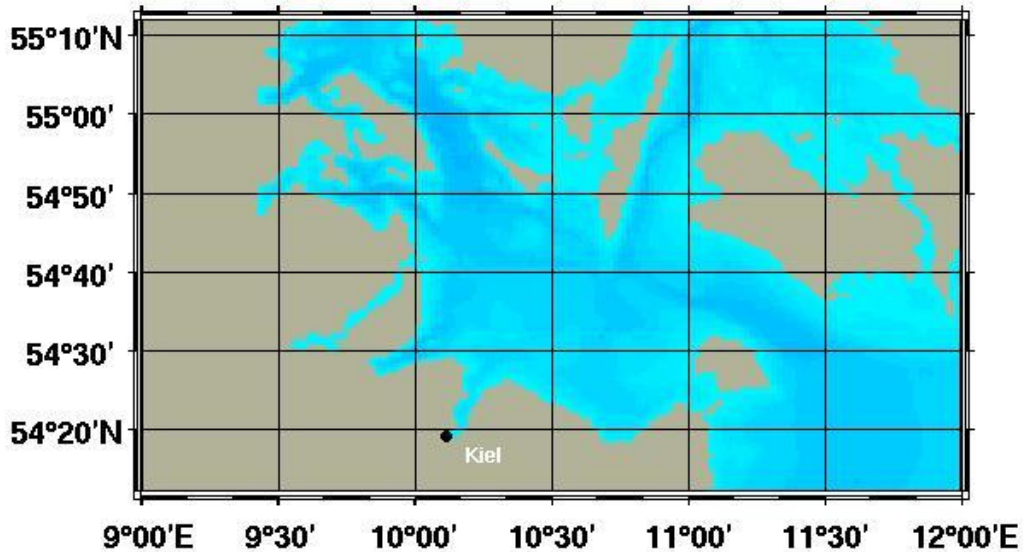
Fig.1- Map of the Western Baltic Sea showing the location of the Kiel Fjord

introduction in the 1980s (Shiganova et al. 2001a; Stone 2005). Its presence in northern European waters has been reported in some Netherlands estuaries where it probably existed already since several years (Faasse and Bayha 2006), and recent records indicate a progressive eastward spread (Janas and Zgrundo 2007, Javidpour et al. 2006; Kube et al. 2007; Lehtiniemi et al. 2007). In the southwest Baltic Sea, the first record of *M. leidyi* was October 2006 (Javidpour et al. 2006). Concerns about this invasion have led to the systematic monitoring to track population density variations of this species and the physical factors that favor its development.

The strong ecological impact of *M. leidyi* on marine food webs stems from both the direct feeding on fish larvae and eggs and resource competition with zooplanktivourus fish due to its voracious feeding on mesozooplankton. Recent investigations, however, reveal that cause and effect relationships between *M. leidyi* and fish are controversial since pelagic fish stocks were already declining prior to the advent of *M. leidyi* in the Black Sea (Bilio and Niermann 2004; Oguz and Gilbert 2007). While a potential effect on the ecosystem structure of the pelagic Baltic ecosystem including impacts on fisheries

remains an open question, a prior understanding of the seasonal variations and population dynamics of *M. leidyi* is required to evaluate and potentially prevent any possible effect of this species in the marine ecosystem of the Baltic Sea. Here we provide the first data on the annual cycle, seasonal changes and population dynamics of *M. leidyi* in the southwestern Baltic Sea after its first occurrence, and discuss the possible mechanisms underlying its establishment in the Baltic ecosystem.

Methods

The study area - The sampling station is located in the inner part of Kiel Fjord (south-west Baltic Sea, Fig.1), which with a mean depth of about 13 m, constitutes a small extension of the Kiel Bight in the Belt Sea. The Belt Sea area is a transition zone between the higher saline water masses from the Kattegat and brackish waters from the central Baltic Sea, separated by the Belt Sea front. Mainly under the influence of the wind, this frontal zone moves back and forth through Great Belt and Fehmarn Belt. Salinity changes in Kiel Bight directly influence the salinity in the Kiel Fjord by baroclinic exchange. Under strong wind conditions Kiel Fjord can be completely flushed within a few days (Lehmann, pers. comm.).

Sampling – Plankton sampling covered the period of October 2006 to December 2007 and was performed at weekly intervals during most of the year Microplankton composition and abundance was quantified from water samples taken with a free flow sampler at 0 m, 8 m and 18 m depth at a central station in Kiel Fjord. These samples were merged to obtain an estimate of the microplankton composition in the entire water column. Samples were fixed by Lugol's iodine solution and analyzed under an inverse microscope later in the laboratory. Mesozooplankton was sampled at the same station with a plankton net (0.6 m diameter opening, 200 µm mesh size) from integrated vertical tows of 18 m depth to the surface. Samples were preserved in 5 % buffered formaldehyde-seawater mixture for later quantification. All mesozooplankton in the samples were identified at least to genus level under a dissecting microscope. In addition, ichthyoplankton and scyphomedusae samples were collected with the same frequency using a paired bongo net (335µm and 500µm mesh size, 0.6 m mouth diameter) towed for 5 minutes on depth-integrated oblique hauls from surface to 10 m depth. Filtered volumes were estimated using a flowmeter mounted in the mouth of each net (the volume filtered averaged 100 m³) Scyphomedusae (*Aurelia aurita* and *Cyanea capillata*) were counted from the 500
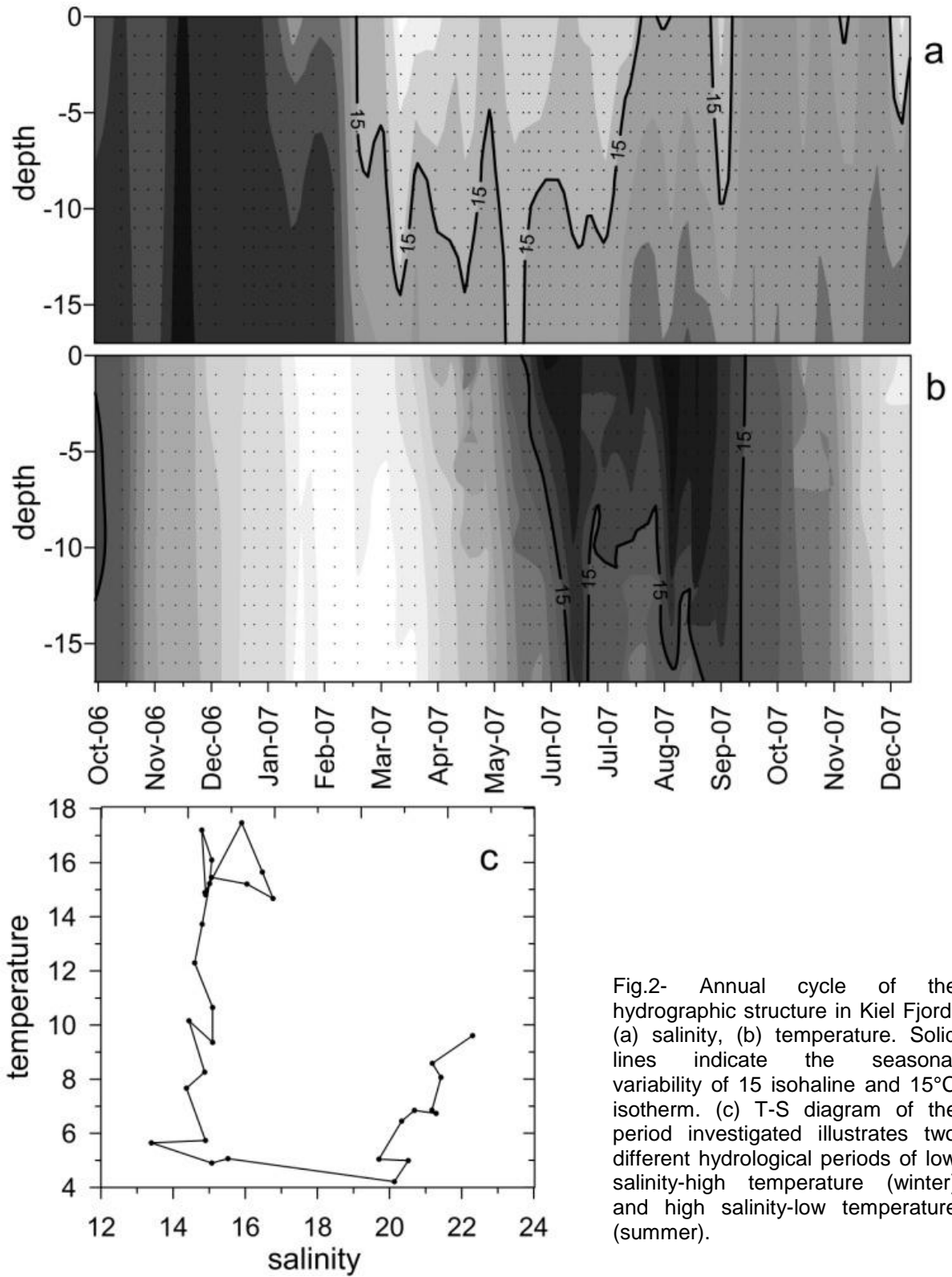
Fig.2- Annual cycle of the hydrographic structure in Kiel Fjord. (a) salinity, (b) temperature. Solid lines indicate the seasonal variability of 15 isohaline and 15°C isotherm. (c) T-S diagram of the period investigated illustrates two different hydrological periods of low salinity-high temperature (winter) and high salinity-low temperature (summer).

μm net on board and ichthyoplankton (fish larvae and eggs) of 500 μm net was preserved in a 4 % buffered formaldehyde-seawater mixture for later quantification.

Samples of *M. leidyi* were taken with a WP2 net (0.8 m net opening, 500μm mesh size) making four replicated vertical hauls from the bottom to the surface. From March 2007 onwards samples from 2 distinct depth strata (0-10 m and 10-18 m) were taken with a closing system matched to the WP2 net at the same station. Samples were concentrated on a 0.5 mm sieve and individuals counted and measured alive immediately after sampling, since *M. leidyi* has been found to disintegrate in all types of fixation solutions (Javidpour, personal observation). Total length was measured to the nearest 0.1 mm on individuals with closed lobes. Temperature and salinity were measured at the 1 meter interval of the whole water column at each sampling day.

Data Analysis - data were $\log_{10}$-transformed and then standardized at zero mean and unit variance. Environmental windows allowing high abundance of *M. leidyi* were identified by means of cumulative abundance distribution in the temperature and salinity ranges (Perry and Smith 1994; Paramo et al. 2003). Seasonal changes in the age structure were assessed by means of the ratio larval stages:adults. This allows identifying major periods of elevated reproductive activity of *M. leidyi* in the Kiel Fjord. In addition, the vertical distribution of *M. leidyi* was analyzed according to a vertical distribution parameter (VDP) (Huntley and Escritor 1991; Escribano and Hidalgo 2000).VDP was calculated as: VDP = $\log (n_1 / n^2)$, where n_1 is the mean abundance in the upper layer (10m) and n^2 is the mean abundance in the deeper layer (8m). The obtained time series was standardized at zero mean and unit variance (z-scores) and the chart of cumulative *z*-scores was used to identify the date of trend initiation in seasonal changes of vertical distribution of *M. leidyi*.

Results

Hydrgraphical features **-** The seasonal development of temperature and salinity is displayed in Figure 2. During the study period, high salinity of 20-22 PSU characterized autumn and winter periods. In spring, salinity dropped to a minimum value of < 11 PSU followed by a slight increase to 15 PSU (Fig. 2a). In turn, temperature varied from an average of 4.9°C in February-March to 17.2°C in mid-August. During most of the investigation period the water column was thermally weakly stratified except during a short

period from July to August, where a stronger thermocline was detected, as indicated by the isotherm of 15°C (Fig 2b). The main hydrographic changes are revealed by the T-S diagram which shows two main periods of vertical homogeneity related to cold and saltier waters during autumn and winter, and to warm and less saline waters during late spring – summer (Fig. 2c).

Plankton annual cycle **-** The spring bloom of phytoplankton started from May consisting mainly of the diatom *Skeletonema costatum* (up to 99% of total abundance), followed by *Thalassiosira* spp. which dominated the post-bloom period, from late June to middle July (Fig. 3a). The first peak of zooplankton dominated by copepodite stages of the complex *Para-Pseudocalanus* occurred in December 2006. Copepods were by far the most abundant taxon of the mesozooplankton community throughout the year accounting for more than 50% of the total abundance of mesozooplankton. Cirriped and polycheate larvae ranked second (22 %) and third (18 %) in relative abundance, respectively (Fig. 3b). Fish larvae and eggs were observed for the first time in the middle of January, although their peak occurred from mid-June to mid-July (Fig. 3c) which was dominated by Clupeidae (79.55%) and followed by Gobiidae (17.37%). Gelatinous carnivores peaked later and were mainly composed of *Aurelia aurita* and *Cyanea capillata*. Their abundance was however low (< 4 ind. $10m^{-3}$).

Seasonal changes of Mnemiopsis leidyi - During the study period, *M. leidyi* was always present. The population however showed marked fluctuations on short-time scales that ranged from 6 to 166 ind m^{-3} within one week. After the first record in Kiel Fjord in October 2006 at densities of ~30 ind m^{-3}, the population density of *M. leidyi* increased to a peak of ca. 100 ind m^{-3} which followed a sharp decreased to 1 ind. m^{-3} during the wintertime (Fig. 3d). Its abundances remained low until June 2008. From August 2007 onwards *M. leidyi* reached the highest densities being > 5-fold higher (505 ind m^{-3}) than the densities observed in the 2006 (Fig. 3d). During most of the sampling period approximately 85- 90% of the population consisted of small larvae and post larvae of < 10 mm. However, during its first occurrence and during late summer and autumn 2007 larger size classes were also common. The largest individual captured was one specimen with 60 mm total length, whereas the mean value of all adult specimens averaged 20 ±0.3 mm.

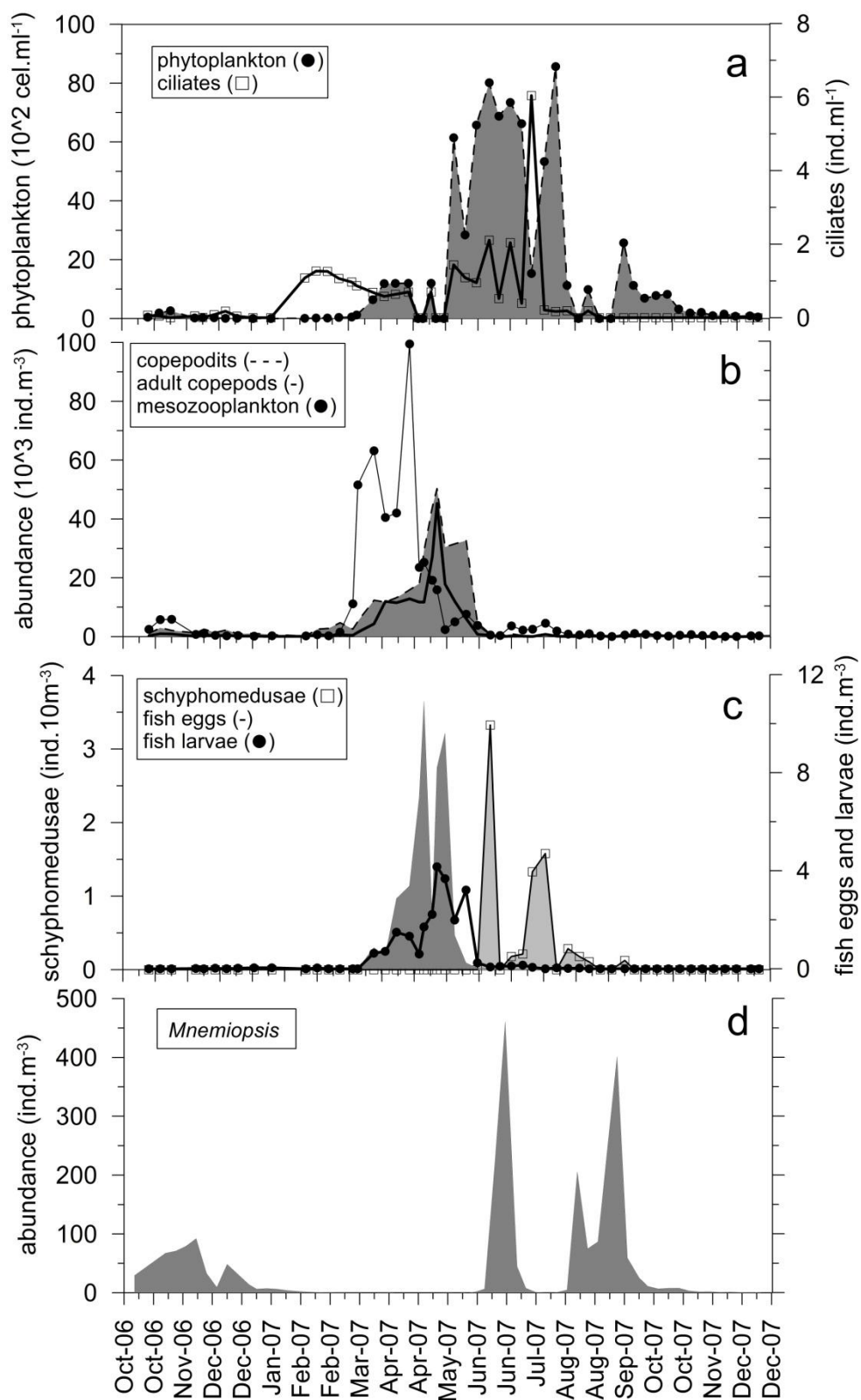Fig.3- Annual cycle of plankton communities' succession in Kiel Fjord. (a) microplankton (b) mesozooplankton (c) ichthyioplankton and matured schyphomedusae and (d) *Mnemiopsis leidyi.*
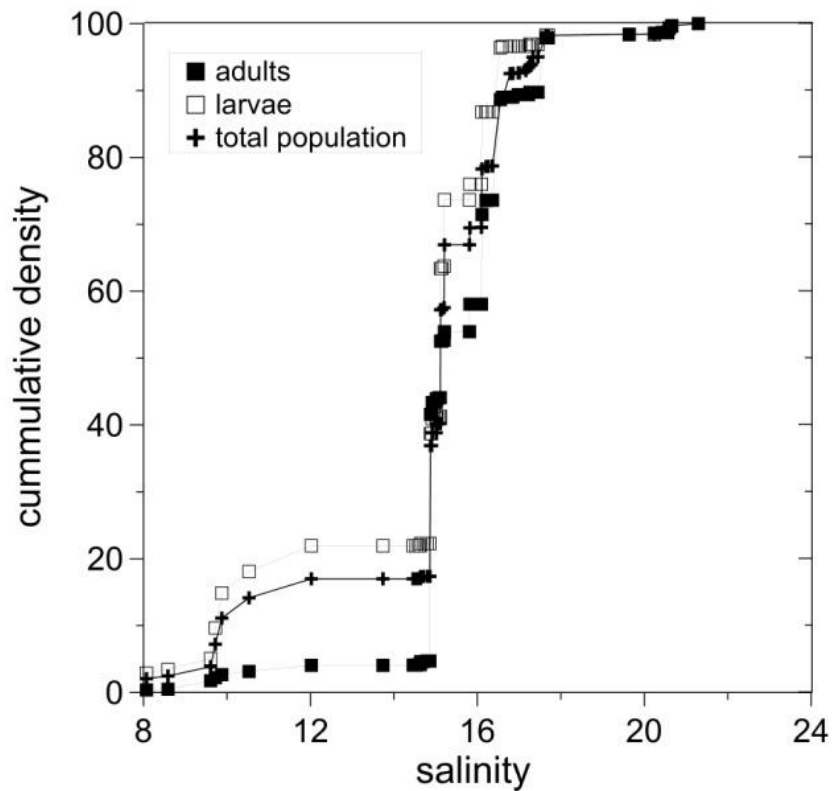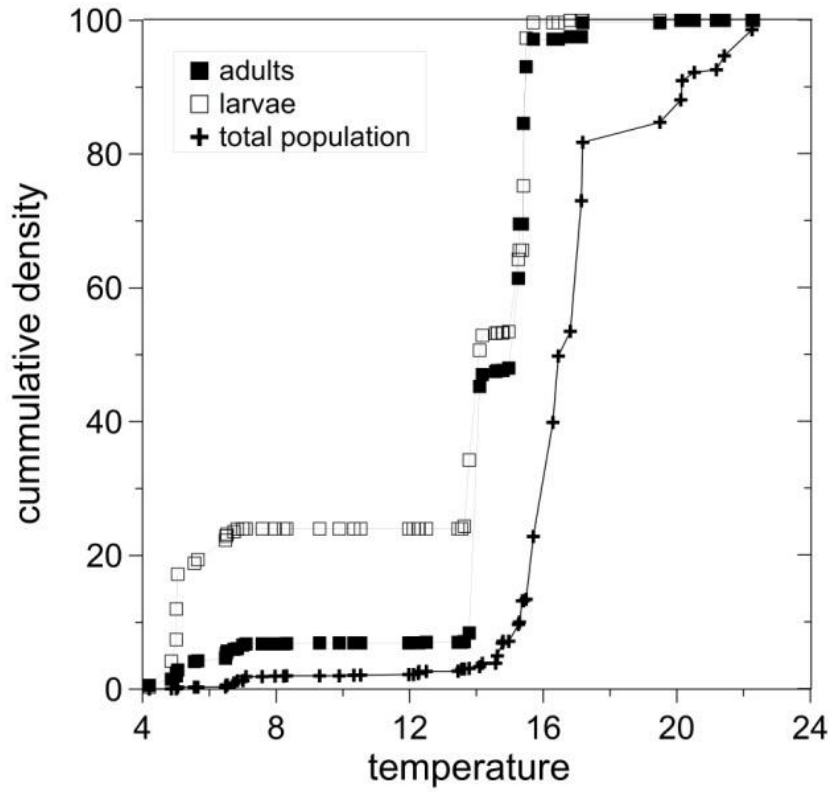
Fig.4- Cumulative density of *Mnemiopsis leidyi* responding to temperature (upper panel) and salinity (lower panel). Note that temperature of 15 °and salinity of 15‰ are triggered the population outburst of *M. leidyi*
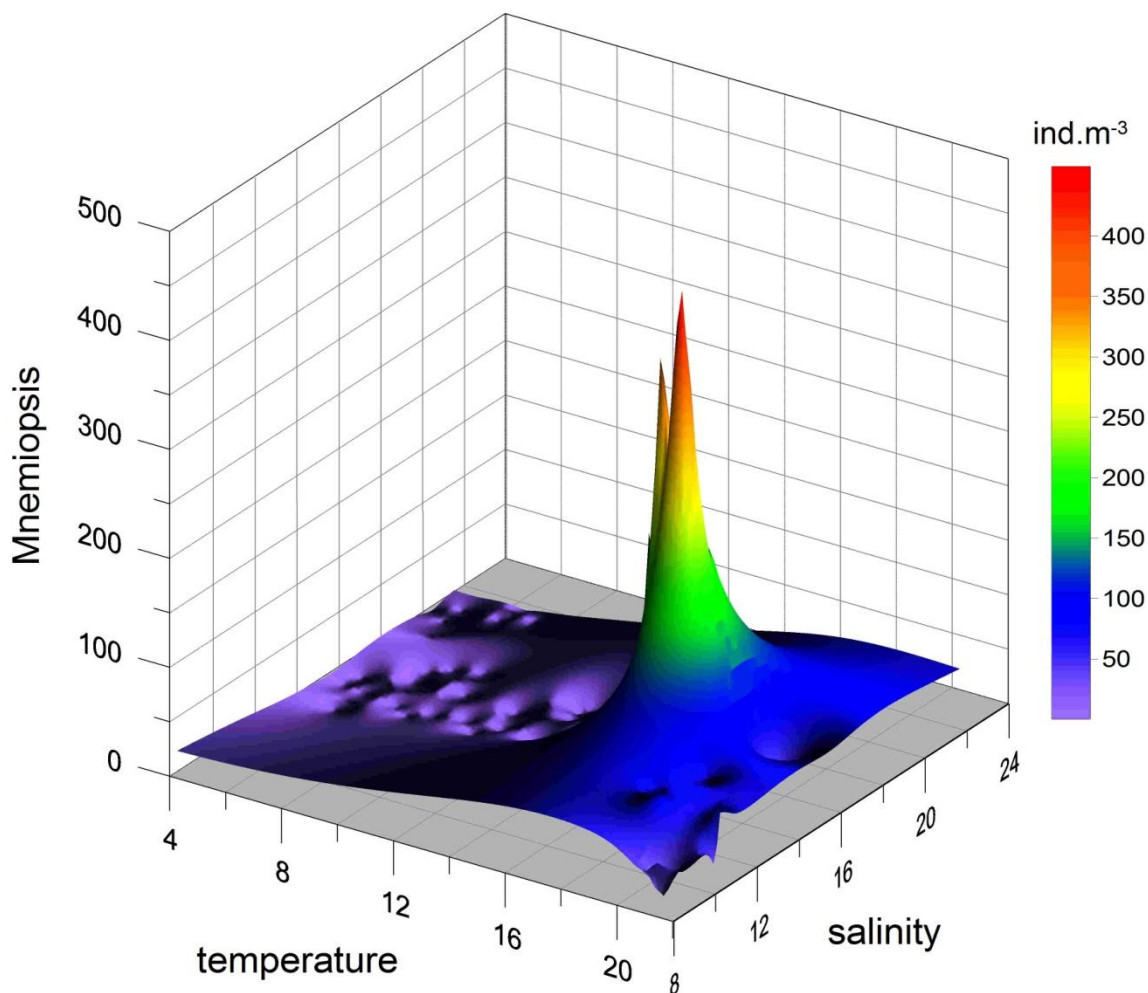
Fig.5- 3D graph of *Mnemiopsis leidyi* abundance-temperature-salinity. *M.leidyi* reaches its highest density in a narrow environmental space (between 14-17°C and salinity of 16-20) that mainly corresponds to summer season.

The cumulative abundances increased markedly toward high percentiles in narrow ranges of temperature (14 – 16°C) and salinity (15 – 16), which were related to the summer period (Fig. 4). The temperature – salinity – *M. leidyi* diagram (Fig. 5) displays the narrow environmental space where the species reached the highest densities and emphasize the magnitude of the outburst the species may reach in the Kiel Fjord in short time scales.

Age structure and seasonal changes in the vertical distribution of M.leidyi - The age structure showed a marked seasonal pattern characterized by an alternation of periods dominated by larval stages followed by an increase of the proportion of adults (Fig. 6) emphasizing the recruitment dynamics of *M. leidyi* in the Kiel Fjord. In accordance with the temporal trend of the age structure, the vertical distribution of the species followed the same trend (r = 0.6; p < 0.05) and exhibited marked seasonal changes. During winter and spring, when the species showed low densities and a high proportion of adults were present, the bulk of the population was concentrated in bottom waters. Afterwards, with the rising temperatures and the slight development of the vertical stratification, the population growth was dominated by a higher proportion of larval stages, and the bulk of the population shifted toward the upper layers (Fig. 6).

Discussion

We have shown the plankton annual cycle in Kiel Fjord after the first report of *M. leidyi* occurrence. The weekly monitoring of plankton communities allowed us to recognize the timing of the first observation of the invader *M. leidyi* in the south-west Baltic Sea. After one year of its first record in this area, it has become clear that *M. leidyi* can successfully reproduce in Kiel Fjord and possibly the entire Baltic Sea, as suggested by the seasonal changes in the ratio of larval stages:adults. *M. leidyi* is now established in the Baltic Sea as indicated in recent studies on the presence of the species in other sites of this area (Table 1). The potential predatory impact of this species in the pelagic ecosystem makes the recent range of expansion a matter of concern.

Hydrographic features in the water balance of the Kiel Fjord are mainly driven by the baroclinic forcing of Kiel Bight. The mean flushing time in the fjord has been calculated to be about 45 days but can be shorter during winter. Under strong wind conditions Kiel Fjord can completely be flushed within a few days (Fig 2a: Nov-Dec 06 and Feb-Mar 07, Lehmann, pers. comm.)

Table 1 Baltic Sea locations where *Mnemiopsis leidyi* has been recorded after the first apparition in the Kiel Fjord. The maximal abundances reported, size of individuals, plankton net used, as well as the hydrographic conditions are indicated. NA= not available

Location	Period of observation	Max.abundance (ind. m-3)	Size (cm)	mesh size (µm)	T °C	S ‰	Reference
Central Baltic Sea	Jan.-May 2007	<4	0.5	WP2, 400	3-14 °	8-11	Kube et al. 2007
Bornholm Basin	Aug. 2007	0.4	NA	Bongo, 335 and 500	4-8°	1-16	Haslob et al. 2007
Gulf of Gdansk	Oct.-Nov. 2007	3-20	.8-8	divers, NA	6-14°	NA	Janas 2007
Gulf of Finland	Aug. 2007	24	5	WP2, 500 and 100	4.5-5 °	5-9	Lehtiniemi et al. 2007
Limfjorden	Sep. 2007	629	5-15	plankton net, 2000	15°	7-28.5	Riisgard et al. 2007
Little Belt	Feb. & May-Sep. 2007	NA	12	divers, NA	NA	NA	Tendal et al. 2007

In this framework, the annual cycle of mesozooplankton in Kiel Fjord followed the recurrent pattern of temperate pelagic ecosystems. After a minor bloom of phytoplankton in March, the main spring bloom started in May 2007. The peak of fish larvae matched with the maximum abundances of mesozooplankton, suggesting a predator-prey interaction with fish larvae controlling the drop of mesozooplankton. Gelatinous carnivores peaked later and matched with the peaks of phytoplankton and ciliates. The general annual cycle of the pelagic system of the Kiel Bight is basically similar to the gained data of ours with the spring diatom bloom, the late spring copepod maximum and the summer stratification (Smetacek 1983).

It is worth noting that *M. leidyi* has been the only ctenophore observed from late summer 2006 onwards. Previous to its invasion, the ctenophore *Pleurobrachia pileus* was common during wintertime in the Kiel Bight. In recent decades Baltic Sea has faced hydrological changes which were driven by global warming (Lehmann and Hinrichsen 2000). As *P. pileus* population of the Baltic Sea shows a preference for cold water (Schneider, 1987) it is possible that the recent environmental changes reported in the hydrographic properties of the Baltic Sea (i.e. warm temperatures), have impaired the development of *P. pileus*. This should be however verified by getting longer data sets.

Population dynamics and vertical distribution - The one year data reported here allowed us tracking general features of the *M. leidyi* population dynamics in the Kiel Fjord. The annual abundance of *M. leidyi* is similar to the annual pattern of populations distributed in its northern native habitat and in the exotic habitat of the Black Sea and the Caspian Sea (Purcell et al. 2001; Finenko et al. 2006a; Finenko et al. 2006b) where the annual cycle is characterized by a main peak in late summer-early autumn. Moreover, the seasonal pattern of the population of *M. leidyi* show marked changes in the relative abundance of larval stages and adults, which were accompanied by changes in the dominant size classes. The pattern suggests two periods of high reproduction activity associated to warmer temperatures, i.e. early autumn 2006 and late summer 2007, and one main period of low reproductive activity associated to the lowest temperatures and the low population density (Fig. 6). It is worth noting that the maximum abundances of *M. leidyi* did not match with the peaks of mesozooplankton and fish larvae.
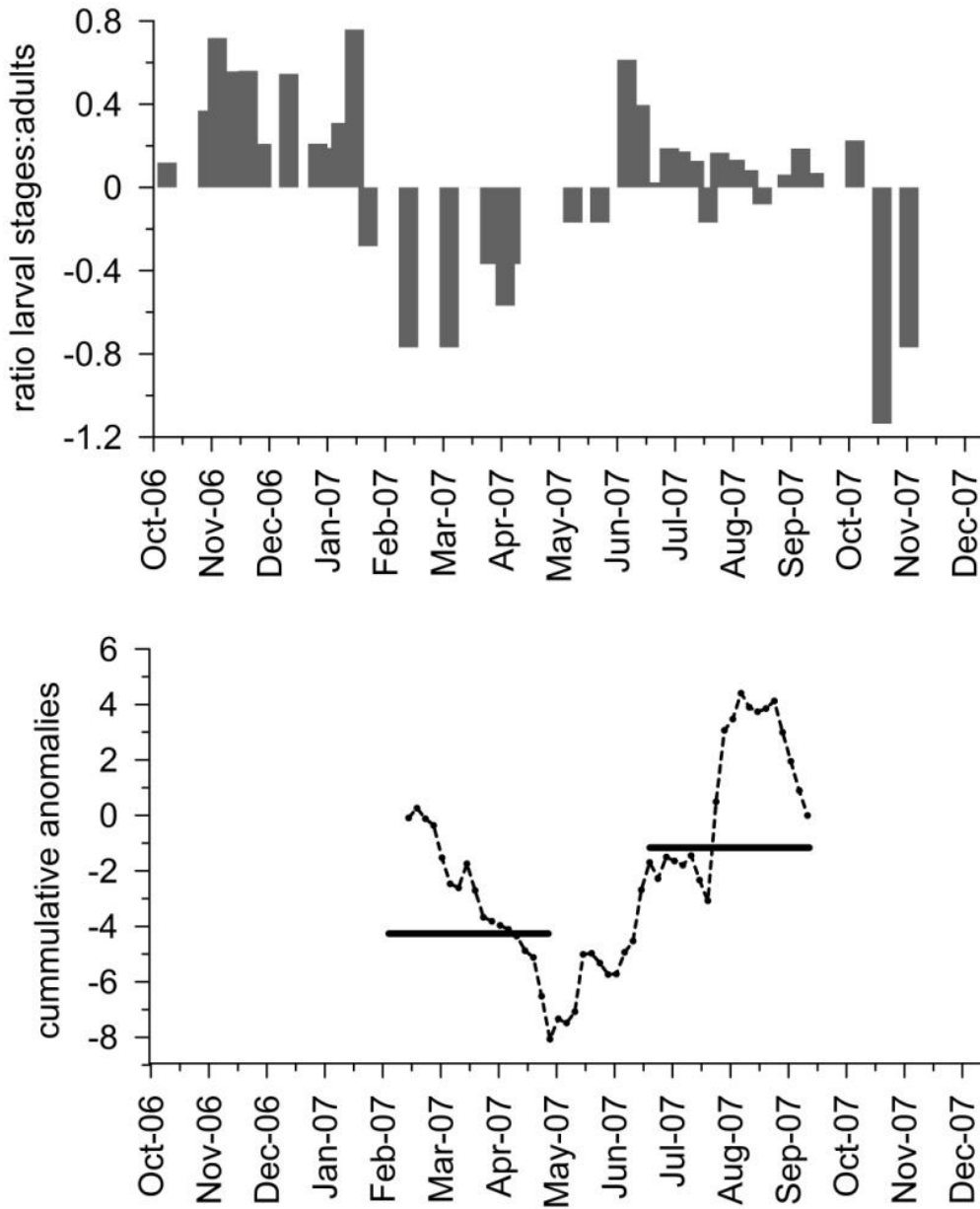
Fig.6- Temporal variation in ratio larvae:adults (upper panel) and cumulative anomalies of the vertical distribution of *Mnemiopsis leidyi* (bottom panel). Horizontal bars indicate the mean abundance during the two main periods related to the vertical distribution of the species. The downward trend indicates the predominance of the population located in bottom layers and the downward trend indicates the shift of the vertical distribution to upper layers starting in May.

Instead it appears coupled with the peak of microzooplankton, suggesting a primary predation on microzooplankton (i.e. ciliates) by the high density of larval stages. It is known that gelatinous carnivores are able to exploit microplankton communities, including the microbial food web and prey on ciliates, which have proven a nitrogen-rich food source (Gifford 1991). Although *M. leidyi* has been traditionally considered as strictly carnivore, empirical investigations have shown that all size classes of *M. leidyi* larvae and postlarvae consumed nano- and microplankton in excess of their minimum food requirement, which may represent a main nitrogen source for population growth (Sullivan and Gifford 2004). This can have important ecological implications since by exerting high predation pressures on ciliates a potential impact on the structure of microzooplankton assemblages may favour in some cases the formation of red tides, as shown by Pitt et al. (2007) in mesocosms experiments. Moreover, we cannot exclude cannibalism and predation on other gelatinous zooplankton, as suggested by the high concentrations of jellyfish planula larvae in the gut content of *M. leidyi* in summer (Javid Pour, personal observation).

The assessment of the vertical distribution during the period March – December 2007 allowed detecting two contrasting situations, low and high abundances, where the vertical population structure changed markedly. While during the low abundance period (March –June) the bulk of the population was concentrated in deep layers, during the outburst of the species (August-September) the vertical pattern shifted and the bulk of the population was located in the upper layers. Dense aggregation of the *M. leidyi* in deep layers are likely a population response to low temperatures, which have been found to constrain the reproductive potential and as an energy saving strategy of ctenophores (Esser et al. 2004). The shift in the vertical pattern from bottom to upper layers matched with the temperature increase in late spring, which enhances the reproduction capacities of the species and allows a fast expansion in the water column. The benefits of such strategy may provide a refuge to *M. leidyi* to avoid flushing in upper layers, and subsequently provide inocula for late-spring population growth. Support to this interpretation has been given by Costello et al. (2006) who showed that during winter months and low population densities *M. leidy*i concentrate in coastal areas that provide refuge and play an important role as population source for the summer population growth. As shown by these authors, such a pattern is common in the *M. leidyi* populations inhabiting temperate regions with cold winters (Costello et al. 2006).

The life history traits of *M. leidyi* allow the species to be highly responsive to environmental opportunities. As we have shown here, within favorable environmental conditions the species may double its population size within a few days. Owing to the potential impacts of this ctenophore on the pelagic food web, their abundance variations over the interannual scale may then constitute valuable ecosystem state indicators.

Consequences for the ecosystem function - Jellyfish are now recognized as critical indicators and drivers of ecosystem performance and change (Molinero et al. 2005, Hay 2006; Lynam et al. 2006). Jellyfish mass developments in several coastal areas may allow ecosystem shifts from fish dominance to dominance of gelatinous carnivores, which have been found generally irreversible, as jellyfish may control fish eggs and larvae and compete with fish for food (Lynam et al. 2006). Since these voracious predators may channel flows of energy and matter away from the economically important food chain algae–copepods–fish (Sommer et al. 2002; Stibor and Tokle 2003), the integration of jellyfish understanding and data becomes a critical component of an ecosystem approach to fishery management increasingly critical (Lynam et al. 2005). In the particular case of the Baltic Sea it is not yet clear whether *M. leidyi* can severely affect zooplankton and fish populations through its feeding on fish larvae and eggs or competition for food. However, owing to the expected increase in water temperatures in the next decade of the Baltic Sea and the remarkable ability of this invader to double its population size in short time periods, it is definitely a matter for current concern and a critical challenge in predicting future risks of the Baltic Sea ecosystem development. In addition, in the global warming framework, synergism between marine invaders, overfishing and climate change may have drastic consequences in the functioning of the Baltic Sea pelagic ecosystem. *M. leidyi* is now established in the Baltic Sea but the spread in the basin as well as the consequences in the food-web constitute a current challenge in the ecology of the Baltic Sea. Future research should deal with the identification of hot-spot areas which may potentially act as refuge during low population densities, as well as Allee effects and invasion risks in global warming scenarios. In fact, adequate risk analysis of biological invasion cannot neglect these considerations. Owing to the key role of *M. leidyi* in coastal ecosystems biological oceanographers and resource managers in the Baltic Sea cannot afford to ignore this invasive species. In this framework, the results here presented can be considered as baseline for future research on *M. leidyi* and its potential effects in the Baltic Sea.

Acknowledgments

Chapter III

Potential pathways of invasion and dispersal of Mnemiopsis leidyi in the Baltic Sea

Andreas Lehmann, Jamileh Javidpour

Abstract

The fast spread of *M. leidyi* across the entire Baltic Sea after its first observation gave rise to the question of its invasion pathway and the possible vector of its transport. We tested two possible transport routes of this invader for 2006/2007 by simulating drift routes using Lagrangian particle tracking model. Additionally we used the Kiel Baltic Sea Ice-Ocean Model *(BSIOM)* to investigate whether there has been a temperature shift during winter which favoured the outbreak of the invader. Based on the model we exclude advection from the Kattegat as the main source of *M. leidyi* transport through the Baltic Sea. Moreover, simulated pathways originating form harbours with high ship traffic is in good agreement with the distribution pattern of *M. leidyi*.

Key words: invasive species, range expansion, Mnemiopsis leidyi, Baltic Sea

Introduction

Invasions by alien species represent one of the major threats to the functioning of natural ecosystem (Brook et al. 2008; Sala et al. 2000; Wolters et al. 2000). The global increase of species invasions is thought to be driven mainly by two factors: floristic and faunistic homogenization due to intensified human transport vectors (e.g. ballast water of ship traffic) and weakening of invasion resistance of recipient ecosystems due to overexploitation, species removal and environmental changes (Carlton 1999; Jackson et al. 2001). For a successful a number of sequential stages is required, including initial introduction, establishment in the new habitat and range expansion. Dispersal is considered as a critical process for invasive species and their ecological impact it might have (Lockwood et al. 2007). With increasing the dispersal distances, the proportion of the population that moves further and might alter the function of the invaded habitat increases (Kot et al. 1996).

Aquatic invasion ecologists use new genetic techniques (Correa et al. 2007; Kinlan and Gaines 2003) as well as new statistical models (Kinlan et al. 2005) to improve the ability to determine the proportion of individuals that spread across new habitats (jumped dispersal).One of the best examples of such multidisciplinary work on the range expansion of an aquatic invader are the studies on the Zebra Mussel *Dreissena polymorpha.*By using different techniques from population genetic (Gosling et al. 2008) to application models of boater movement (Bossenbroek et al. 2007) invasion ecologists could detect the range and pattern of this invader in the exotic habitat.

Although the transport of pelagic individuals by ocean currents might lead to long-distance dispersal at a fairy constant rate (Grosholz 1996), accurate predictions of range expansion are unlikely, because by changing densities and environmental conditions and, therefore, population growth conditions might weaken our ability to predict (Clark et al. 1999).Approximately 120 aquatic invasive species have been recorded in brackish waters of the Baltic Sea, most of them being introduced during the last 100 years most likely with shipping (ballast water) as the most important individual vector (about 80 species; Gollasch and Leppaekoski 2007). It is likely that organisms once introduced into one Baltic port may subsequently spread and reach other Baltic areaseither by the natural circulations and drift or by internal ship traffic. In the Baltic Sea including Kattegat about 76 ports handle more than 1 million tones of cargo per year. The busiest port is St.

Petersburg with more than 14,500 ships visits per year. The number of ship operations (voyages, excluding ferry traffic) in the Baltic is estimated at 150,000 per year (Gollasch and Leppaekoski 2007), and it is assumed that the shipping activities will considerable increase in the future.

In the Baltic Sea, the invasion of *Mnemiopsis leidyi* caught the attention of scientists in 2006 and caused quite a stir. This species expanded its distribution through the whole Baltic Sea in less than 6 months (Javidpour et al. 2008). In 2005 *M. leidyi*'s presence in northern European waters has been reported in some Netherlands estuaries where it probably existed already since several years, and recent records indicate a progressive northward and eastward spread. It also has been observed in 2005 from Oslo fjord, Norway (Oliveira 2007), then later in the North Sea, off the western coast of the Netherlands (Fasse and Bayha 2006), and from the Swedish west coast, in the Kattegat region and the southwestern Baltic Sea in autumn 2006 (Javidpour et al. 2006). In 2006-2007 it was widely distributed in Danish waters (Tendal et al. 2007), and has further been observed in the Pommeranian Bay, Arkona and Bornholm Basins, the Bay of Gdansk as well as in the Åland Sea and Bothnian Sea (Kube et al, 2007, Haslob et al. 2007, Lehtiniemi et al. 2007, Janas and Zgrundo 2007). As the pattern of its abundance in different parts of the Baltic Sea seems to be very heterogeneous, it seems necessary to study its dispersal pathways.

So far the North Sea, Kattegat and Skagerak have been considered a potential source for the dispersal of other ctenophore species, such as *Pleurobrachia pileus* into the Baltic Sea via advection (Schneider 1987). By entering into a habitat with low salinity dispersal of ctenophores moves the population below the threshold of successful reproduction and leads to establishment of a sink population in the central Baltic.

Here we provide first estimations of potential pathways of *M. leidyi* invasion to the Baltic Sea. In the present work we have tested two hypotheses: Firstly, if *M. leidyi* was transported to the observation points by currents, where would be the origin point of advection? Secondly we have tested whether the drift pattern of released ballast water in big harbors fit to the distribution pattern of *M. leidyi*. We utilize a Langrangian tracking technique to simulate the dispersion of *M. leidyi* in the Baltic Sea. Although the biological features of *M. leidyi* are not considered by the model, the pattern obtained by the tracking method can be useful to evaluate potential routes of the invader expansion.

Material and methods

*Baltic Sea Ice-Ocean Model (BSIOM)-*The numerical model, used in this study, is a general three-dimensional coupled sea ice-ocean model of the Baltic Sea (BSIOM; Lehmann and Hinrichsen, 2000a, 2002). The model domain comprises the Baltic Sea, including Kattegat and Skagerrak. At the western boundary, a simplified North Sea basin is connected to the Skagerrak, to take up sea level elevations and to provide characteristic North Sea water masses due to different forcing conditions (Lehmann, 1995, Novotny et al., 2005).

The coupled sea ice-ocean model is forced by realistic atmospheric conditions taken from the Swedish Meteorological and Hydrological Institute (SMHI Norrköping, Sweden) meteorological database (Lars Meuller, pers. comm.) which covers the whole Baltic drainage basin on a regular grid of 1 x 1° with a temporal increment of 3 hours. The database, which for modelling purposes is further interpolated onto the model grid, includes surface pressure, precipitation, cloudiness, air temperature and water vapour mixing ratio at 2 m height and geostrophic wind. Additionally, runoff data are specified for 42 individual rivers distributed around the Baltic and the Kattegat.

In 2006 the first observation of *M. leidyi* was made in the Kattagat/Skagerrak and southwestern Baltic Sea. If this area is a source region for further spreading of *M.leidyi* it is interesting to analyze the temperature evolution during winter over recent years. We choose Kiel Bight as a representative area for the southwestern Baltic Sea. To classify different winters over the period 1970-2008 we calculated the seasonal winter temperature anomalies for the months DJFM at Kiel Lighthouse (54°30'N, 10°16.5'E).

Results

Recent temperature evolution of the western Baltic Sea-. Air temperature anomalies at Kiel Lighthouse (Fig.1) reveal that since 1998 the seasonal mean winter temperature (DJFM) was well below 4°C. The exceptions are the winters of 2006/2007 and 2007/2008. For the winter 2005/2006 the seasonal mean temperature was 1.06°C (minimum SST=0.1°C), for 2006/2007 DJFM=5.87°C (minimum SST=4.0°C) and for 2007/2008 DJFM=4.46°C (minimum SST=4.0°C). This data indicates that the last two winters were mild in the southwestern Baltic area. On the other hand, the maximum sea
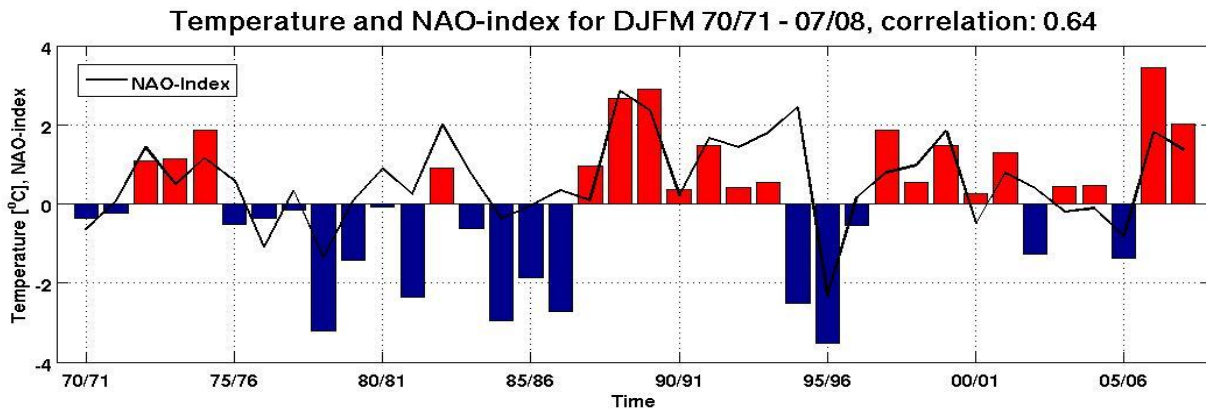
Fig.1. Winter air temperature anomaly (DJFM) at Kiel Lighthouse derived from SMHI-meteorological data base for the period 1970-2008 and winter NAO-index.

ice extent for 2006/2007 was 139,000 km² and for 2007/2008 a new low ice extent record occurred, the ice cover was only about 49,000 km², the smallest value since 1720 (www.fimr.fi/en/ajankohtaista/mtl_uutisarkisto/2008/en_GB/ice_winter_07). The positive and negative temperature anomalies are well correlated with the NAO winter-index (R=0.64) which relates the local temperature evolution to the large scale.

Tracking of potential pathways of invasion; diffusion via drifts-The years 2005 - 2007 were simulated by the Kiel Baltic Sea model (BSIOM), and the main drift routes of *M. Leidyi* calculated with a Lagrangian particle tracking model. The drift model allows a tracking as well as a back-tracking of individual drifters ('marked water particles'). To calculate starting and end positions of drift routes with respect to time, drifters released from the surface to the bottom along several sections through the main basins of the Baltic Sea (Fig. 2). Different areas were chosen to investigate main drift routes or possible pathways of invasion specific for the different areas of the Baltic Sea. Drifters were released in January 2005 (white circles, behind the colored lines), and end positions in December 2006 are marked with different colors. The end positions depend not only on the specific weather conditions and the starting points but also on the time when they were released. However, similar pictures obtained when launching drifters at different dates for the period January until March 2005. It can be seen that drifters which were launched in the Kattegat (yellow circles) reached Kiel Bight and Mecklenburg Bight during 2006. Principally an invasion of *M. leidyi* from the Kattegat to the western Baltic Sea could explain the detection records of it in autumn 2006 (Javidpour et al. 2006, Kube et al. 2007). However, drifters were not able to reach Mecklenburg Bight when released in early 2006. Drifters which were launched in the Arkona Basin (cyan circles) could be found in
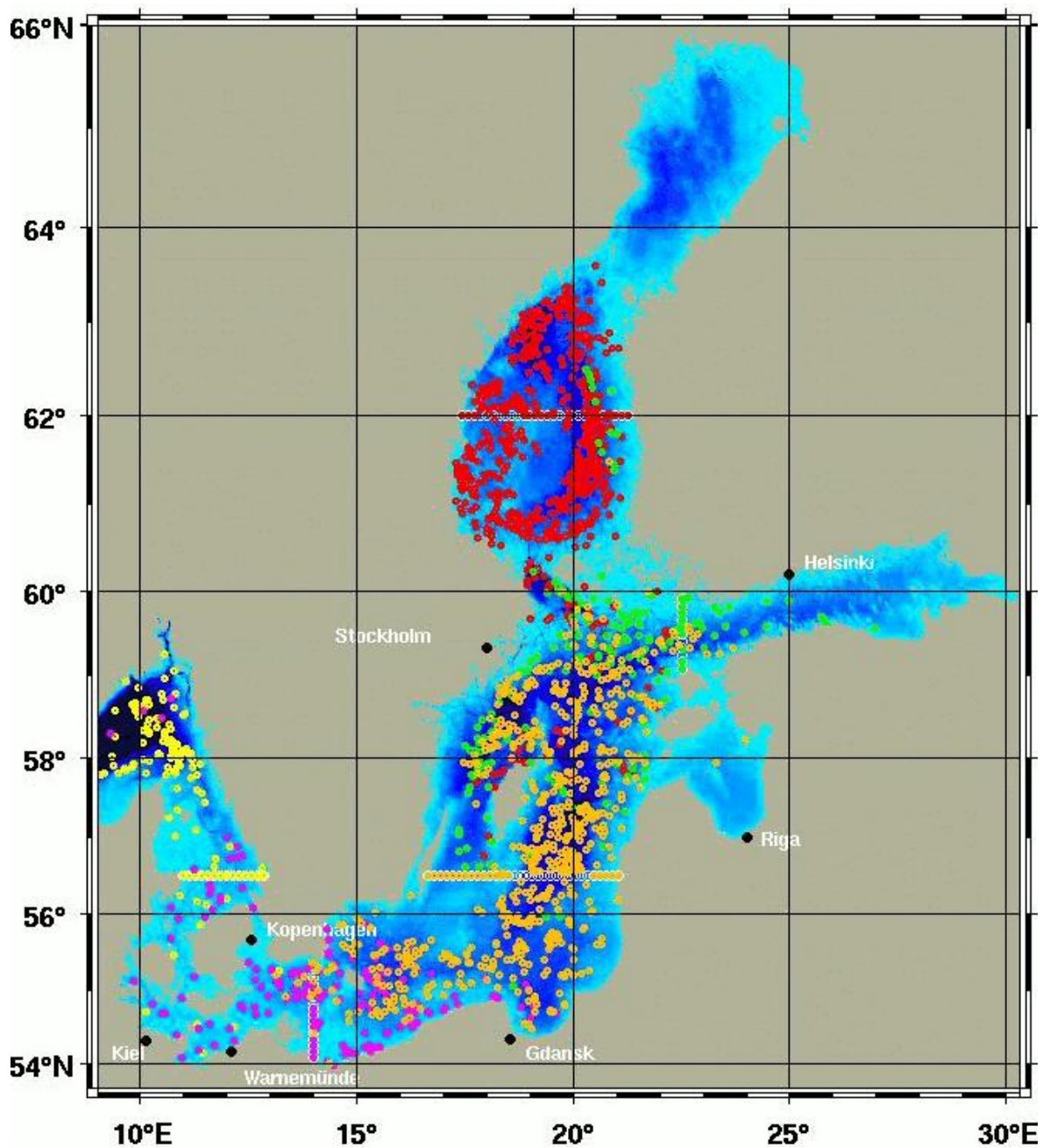
Fig.2. Start positions (white circles, behind the colored lines) of drifters released in January 2005 and end positions (colored circles; colors denote sub-basins of origin) in

the Belt Sea and along the southern coast of the Baltic Sea to the Bay of Gdansk. If we assume that *M. leidyi* has been introduced to the Arkona Basin already in 2005 all detection records in Mecklenburg and Kiel Bight as well as in the Danish waters could be explained. Drifters released in the Gotland basin (orange circles) were distributed over the Baltic Proper to the western Baltic Sea. Some of them reached the Gulf of Riga and the Bothnian Sea as well as the entrance of the Gulf of Finland. Drifters which were launched at the entrance of the Gulf of Finland (green circles) mainly reached the eastern Gotland Basin, the inner Gulf of Finland and the Bothnian Sea. Drifters which were launched in the Bothnian Sea (red circles) were strongly circulating in the Bothnian Sea or distributed further to the south in the eastern Gotland Basin, none of them reached the Bothnian Bay

Tracking of potential pathways of invasion; spread via ballast water- The rapid spreading of *M. leidyi* all over the Baltic Sea could also be possible through the release of ballast water at different harbors and sub-sequential distribution by the internal circulation. In a second experiment we tried to test the hypothesis that the main pathway of invasion happened through ballast water transport and release in the main harbors and subsequent dispersion by the internal circulation of the Baltic Sea. Drifters have been released at the surface close to the main harbors at different time stamps (every 1st and 15th day of each specific month) from July to December 2006. Drift routes have then been calculated until March 2008. Following the surface circulation caused by the wind, drifters distributed well over the sub-basins of the Baltic Sea. However, drifters could not reach deeper parts of the sub-basins because they were driven by the 3-D current field which excluded vertical convection and turbulent mixing. Thus, the deeper regions where *M. leidyi* has been observed could not be reached.

During the cold season *M. leidyi* has been observed only close or within the halocline, and in shallow areas close to the bottom (Kube et al. 2007). It seems that during winter *M. leidyi* moves to larger depth to avoid cold temperatures at the surface. Thus we specified for each drifter a sinking rate when the sea surface temperature dropped below 10°C. Again drifters were released at the main harbors form July to December and the drift tracking lasted until March 2008. When released during the warm season drifters followed the surface circulation, and with the surface cooling during autumn and winter, drifters slowly migrated downwards with a sinking rate of 1 m/day. The sinking rate was reset to zero when the environmental temperature reached 5.5°C which was the temperature of halocline waters observed in 2007. Thus, drifters were able to
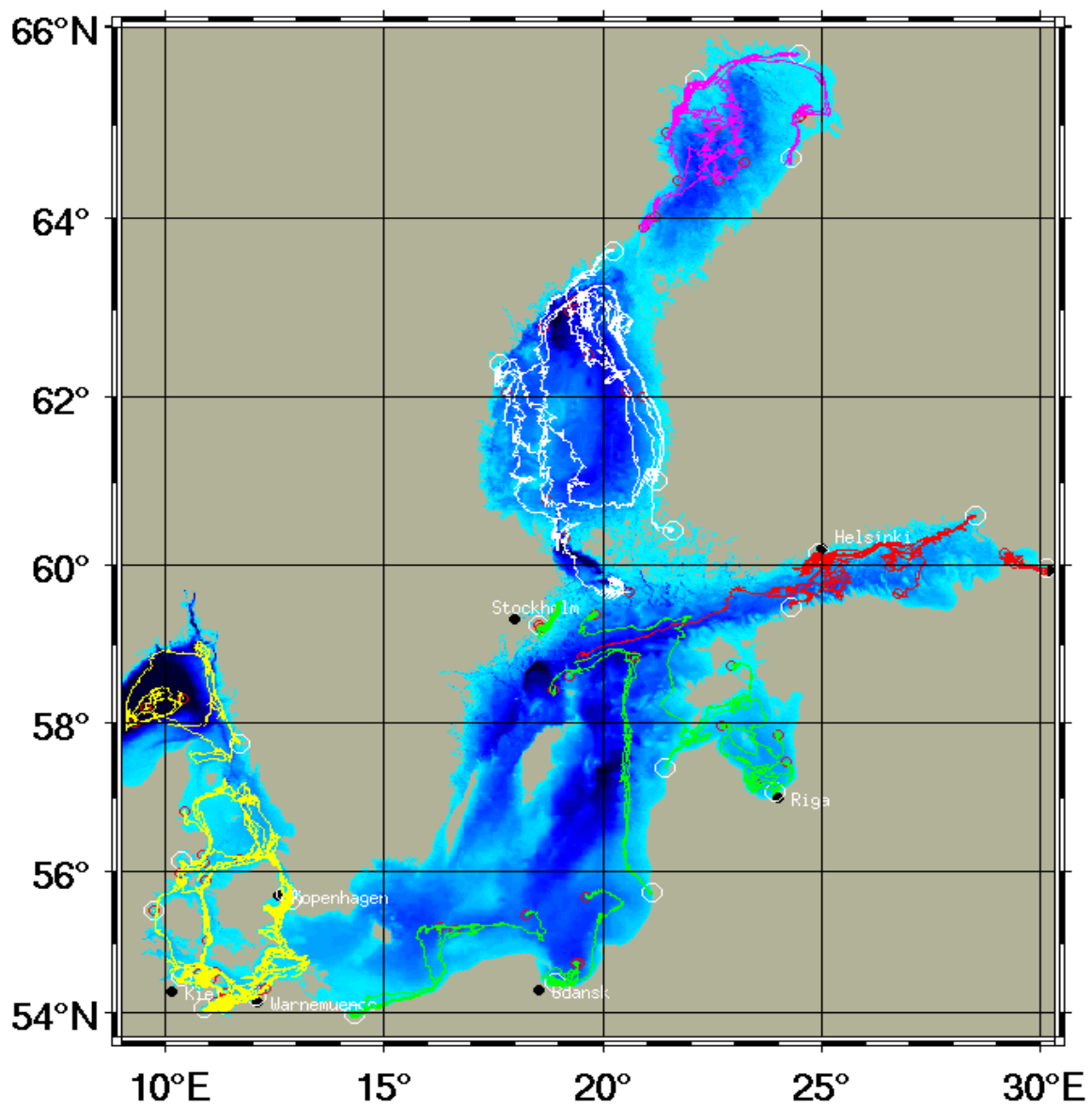
Fig.3- simulating drift pathways originated from important harbors in The Baltic Sea for the period of Oct. 2006 to Mar. 2008

move gently downwards and stop sinking when reaching halocline waters. Figure 3 shows the resulting drift tracks where drifters have been released close to the main harbors in October 2006. The experiment only proves that there is a certain probability that *M. leidyi* could be observed along the drift tracks. However, when comparing observations of *M. leidyi* in the Baltic Sea in 2007 most of these locations have been crossed by the drift tracks.

Discussion

The fast spread of *M. leidyi* across the entire Baltic Sea after its first observation gave rise to the question of its invasion pathway and the possible vector of its transport. There are many biological models for estimation of expansion rates of non- native species (for review see (Kinlan and Hasting 2005). Most of those models rely on assumptions about population parameters (growth rate, offspring size, demography, adaptation adaptation) and environmental conditions which limit those biological variables. The flexibility of the particle tracking model used here, and the fact that it is independent of the biological features of this species in the new habitat (which is still unknown), provided a general insight of patterns of spread of this invader in this area. Our model can be a helpful tool to understand the biogeography of the species in terms of large scale distribution and in mapping and explaining its static features, rather than precisely mimicking the dynamic process. *The role of temperature for the establishment of M. leidyi-* The sudden occurrence and subsequent establishment of the invasive species can be attributed to the already ongoing climate warming or related changes in environmental conditions. The mild winter conditions of 2006 to 2008 probably favor the establishment of this invasive species. As has been reported by Lehmann and Hinrichsen (2007) there is a warming trend for the Baltic Sea of 0.52°C/decade for the period 1985-2005.

However the successful establishment of introduced or post-spread population increases with the number of introductions and the number of individuals in each introduction (Foggo et al. 2007; Grigorovich et al. 2002), while the life history adjustment and physiological plasticity of the invader organism play the first step role for a successful establishment (Lockwood et al. 2007). *M. leidyi* tolerates a wide range of salinity (<2–38 psu) and temperature (2 to 32 °C) (Purcell et al. 2001). Therefore, that the abiotic conditions set no real limitation to the establishment in the brackish Baltic Sea. However, surface waters temperature can drop significantly below 4 °C during winter. If temperature

is a constraint for the development and distribution (Kremer 2001), *M. leidyi* would be limited in coastal and shallow areas with weak salinity stratification during severe winters. For the deep basins of the Baltic Sea where a permanent halocline exists winter water temperatures are normally not below 4°C. If *M. leidyi* has already established in the deep basins there is even in winter time no limitation or temperature threshold for successful persitence. It seems that *M. leidyi* can survive under low temperature and salinity conditions but for reproduction higher temperatures are necessary (> 12°C, Purcell et al. 2001). However, Lehtiniemi et al (2007) reported of eggs and larvae of *M. leidyi* in the Åland Sea in September from depths of 155 to 50 m where the temperature was between 4.5-5°C. It is likely that *M. leidyi* colonized different realms of the Baltic Sea but remain at such low population sizes that no one could detect them before 2006. It is also worth noting that previously little attention was focused on the ecological role of ctenophores in the Baltic Sea.

The pattern of distribution- Drift routes reveal potential pathways of *the M. leidyi* invasion. The more or less complete distribution of *M. leidyi* over the Baltic Sea in 2007 could partly be explained by the circulation within the Baltic Sea basins. However, it seems hardly possible that the only source of invasion was the Kattegat area. The rapid spreading of *Mnemiopsis* all over the Baltic Sea could also be possible through the release of ballast water at different harbors and sub-sequential distribution by the internal circulation. The output from the simulation particle tracking model strongly suggests that *M.leidyi* range expansion after its first observation is unlikely to be via passive dispersal of the western Baltic currents to the central or from the central Baltic to the northern parts. Instead introduction via ballast water would be the main possible way for spreading of *M. leidyi* through the Baltic Sea.

Ballast water vector- increase in ship traffic activity and its role for the homogenization of the world's aquatic fauna and flora is a key challenge for natural management (Leppaekoski and Olenin 2000; Gollasch and E.Leppaekoski 2007). Our model illustrated the pattern of spreading of *Mnemiopsis leidyi* after releasing of ballast water at different harbors. As shown by the model (Fig. 2) it is likely that organisms once introduced into one Baltic port may subsequently spread and reach other Baltic regions by the natural circulations and drift. This supports the recent reports of *M. leidyi* temporal distribution which indicates the concentration of individuals in deeper parts of the Baltic Proper and Northern Baltic (Haslob et al. 2007; Viitasalo et al. 2008).

Conclusion- Here we have provided the first preliminary model simulations to show the general pattern of dispersion via ocean circulation. The further synthesis of population spread rate should consider biological characters of different population sources of *M. leidyi*. Both life history and the spatio-temporal pattern of the environment are critical determinants of spread rate (Elton, 1958). The ability to reproduce at low densities, or secondary spread by offspring can be particularly important factor influencing spread rate. Because juveniles are frequently the stage most likely to disperse, reduces reproduction, even if it does not come with a strong reduction in population size or growth, can lead to slower rates of geographical range expansion (Lockwood et al. 2007).

By considering the modeled drift distribution and the fact that drifters provided some fragmented habitat, we suggest a meta-population of *M. leidyi* for the Baltic Sea which in some arias shows a sort of connectivity. Therefore further ecological-evolutionary works is needed to examine this theory.

In general, besides the global anthropogenic modification of marine systems due to high transport rates of invasive species by ballast water, the ecological niche of aquatic members can change due to accelerating climate change world wide (Dulvy et al. 2008). In fact a recent meta-analysis found that climate change has already been associated with an average 6.1 km per decade pole-ward shift in species' ranges (Parmesan and Yohe 2003). The current biogeography configuration of *M. leidyi* and the fact that it expanded far from its previous habitat to the North, may serve as another example of large scale geographic changes of an organism. A predictive understanding of future shifts, as well as previous shifts that have led to the current establishment of this species, will require detailed knowledge of the long term processes determining biogeographic pattern across the Baltic Sea as well as the adaptive divergence between populations along the salinity gradient within the Baltic Sea.

Acknowledgement

Chapter IV

Annual assessment of the predation of Mnemiopsis leidyi in a new invaded environment, the Kiel Fjord (Western Baltic Sea): a matter of concern?

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Abstract

The sudden occurrence of the comb jelly *Mnemiopsis leidyi* has been reported recently from all over the Baltic Sea and it is assumed that the species is established. Here we provide the first set of quantitative data of seasonal diet composition and life history traits of *M. leidyi* and its predatory role in the pelagic ecosystem of the Western Baltic Sea. The size structure of the species appeared dominated by small size classes and only a few adults were as large as those reported in the native region of the species and in other invaded sites. We show that the species has a high preference for small sized and slow swimming prey, mainly during the low temperature period of winter. Barnacle nauplii appeared as the main source of carbon for the over-wintering population of *M. leidyi*. A preference for copepods was only found during August when these prey contributed up to 20% of the gut composition. During the summer period, planula larvae of the jellyfish *Aurelia aurita*, were the most abundant prey in the gut content (feeding rate of 621 ind. ctenophore^{-1}day^{-1}). During the summer outbreak we found also strong cannibalism of *M. leidyi* on its own larvae, which were a major carbon source of reproducing adults. Overall these results are discussed in the context of trade-offs *M. leidyi* face in the new environment and adverse environmental conditions, which are likely forcing the species toward reduced sizes and consequently reducing its potential predatory impact in the freshly invaded environment.

Key words: *Mnemiopsis leidyi*, predation, diet composition, Baltic Sea, Biological invasion

Introduction

Increasing awareness of blooms of gelatinous predatory zooplankton has lead to an increased interest in their ecology because of their potentially serious impacts on the functioning of the marine systems (Arai 1988; Brodeur et al. 2008). For instance, owing to their high growth rate, the population size of gelatinous carnivore can have massive developments within short time-windows. This may significantly increase competition with and predation on fish larvae and on a wide range of zooplankton, ranging from microzooplankton to copepods (Purcell 2001). Subsequently gelatinous carnivore outbreaks can channel flows of energy and matter away from fish (Sommer et al. 2002; Hong et al. 2008) affecting fish densities and ecosystem production (Lynam et al. 2006; Doyle et al. 2008). Most of the gelatinous carnivores' impact on pelagic ecosystem structure occurs through the predation on both microplankton and higher trophic levels (i.e. copepods, fish larvae). The evaluation of such impacts has been mainly done through laboratory experiments. A serious difficulty of this method results from the effects of confining large and motile predators, e.g. ctenophores or scyphomedusa, to the small space of aquarium tanks (Hansson and Kiorboe, 2006), which artificially increase encounter rates and prey vulnerability (Larson 1987a), and may lead to overestimations of predation rates. Alternative approaches are therefore required to provide complementary insights to the experimental approach. Of these, gut content analysis has been widely used to assess the impact of predators in the natural field prey (Sullivan and Reeve 1982; Rapoza 2005). Potential sources of error of this approach, however, should also be considered to avoid biased assessments. For instance, when gelatinous carnivores are collected, they may either loose prey during capture or gain food by feeding in the augmented prey concentration of the cod end of the plankton net (Hansson 2006).

Recently, the comb jelly *Mnemiopsis leidyi* (*Mnemiopsis* hereafter) has been reported for the first time from different sites of the Baltic Sea, and is considered to be established in the entire region (Lehtiniemi et al. 2007; Javidpour et al. 2008). This species show a high plasticity due to its tolerance for wide ranges of temperature and salinity, hermaphroditic reproduction and regeneration ability (Henry and Martindale 2000; Purcell et al. 2001). *Mnemiopsis* is globally notorious for its invasion of several seas of the Mediterranean basin and the Caspian Sea (Purcell et al. 2001) where it has been associated with severe declines in fish stocks (Shiganova and Bulgakova 2000; Shiganova et al. 2003). Although its predation impact has been emphasized in different

ecosystems, few records exist on field observations of its diet composition (Larson 1987b; Mutlu and Bingel 1999). A thorough assessment of the predation impact of *Mnemiopsis* in its freshly invaded environment therefore requires the identification of quantity and type of food.

In this paper, we evaluate the predation impact of *Mnemiopsis* in the Kiel Fjord, southwestern Baltic Sea, during the first year after its arrival in the fjord. We aim at identifying possible seasonal changes in prey composition and to quantify the predation impact on zooplankton functional groups. We discuss the possible mechanisms leading *Mnemiopsis* to prey on particular food types and on the potential impact the species may have in its new environment.

Material and Methods

Study site – the sampling station is located in the inner Kiel Fjord (area ~ 14.1 km², mean depth ~13 m), which constitutes a small extension of Kiel Bight in the Belt Sea, the southwestern part of the Baltic Sea. The Belt Sea area is the transition zone where   higher saline water masses from the Kattegat originating from the North Sea and brackish waters from the central Baltic Sea meet in a frontal zone, the Belt Sea front. Mainly under the influence of the wind, this frontal zone moves back and forth. Salinity changes in Kiel Bight occur through the movement of this front and directly influence the salinity in Kiel Fjord by baroclinic exchange. Under strong wind conditions the water masses of Kiel Fjord can be completely exchanged within a few days.

Mnemiopsis data – weekly samples were taken by vertical hauls from the bottom to the surface at a central station in Kiel Fjord (54° 27' 55''N, 10° 14' 70''E) using a WP2 net (0.8 m net opening, 500µm mesh size). Additional samples (n~10) were taken for gut content analyzes. A sample of 100 individuals was taken to estimate the carbon and nitrogen content. To avoid the inclusion of prey carbon in the biomass measurements of individuals, the individuals were kept in ambient water (filtered through 0.2µm filter) for gut evacuation.

Mesozooplankton was sampled at the same station with a plankton net (0.6 m diameter opening, 200 mm mesh size) from integrated vertical tows of 18 m depth to the surface. Samples were preserved in 5% buffered formaldehyde-seawater mixture for later quantification. All mesozooplankton in the samples were identified to at least the genus

level under a dissecting microscope. Further details in sampling techniques have been reported in Javidpour et al. (2008).

Hydrographic records of temperature and salinity were taken at 1 m intervals for the whole water column on each sampling day.

As the estimation of predatory impacts depends on the predator size (Bamstedt 1998), we used adult stages of similar size (2±0.5 cm) to evaluate gut content analysis, and avoid as much as possible any bias in our analysis.

The differences in the winter and summer densities of *Mnemiopsis* forced us to treat them differently. In winter, water samples were taken until we reached a minimum of 36 *Mnemiopsis* to analyse gut contents (range of 36-77 ind). The animals were shock frozen by liquid nitrogen to stop digestion and, thereafter, stored in a deep freezer for later gut content analysis. In summer, high abundances of *Mnemiopsis* allowed us to make direct observations on stomach contents (n=30) on the day of collection using live animals. Very low density of adult *Mnemiopsis* in the period of May to August prevented us from evaluating gut content for those periods.

The minimum time difference between sampling and the last microscopic observation was less than 15 minutes. Feeding within the plankton net is assumed to be negligible because of usage of coarse mesh size (500µm) which resulted in very low densities of potential prey organisms.

Feeding rates – *In situ* feeding rates of mesozooplankton (F) from gut content analysis data were calculated according to the following equation:

$$F = N_{prey} / t_d \times 24 \text{ h}$$

where N_{prey} is the number of prey consumed by the *Mnemiopsis*, and t_d is the gut clearance time. Gut clearance time for copepods was determined at mean temperatures occurring during spring/autumn (10°C) and summer (17°C). We used 10 organisms of approximately the same size (~2.5 cm) and adult stages of *Acartia tonsa* as food. *Mnemiopsis* were placed individually into one liter jars to observe the copepods' ingestion. After the onset of ingestion, each ctenophore was transferred to a one liter container with filtered sea water and observed for complete gut evacuation. Evacuation was used as an indicator of gut clearance time. This was assessed through direct observations every 10

min for the first hour, afterwards we increased the frequency of observations until the last evacuation took place. The only study so far on *Mnemiopsis* (native populations) showed that the gut clearance time for adult calanoid copepods is roughly double the time for small preys, i.e. copepod nauplii, barnacle nauplii, *Oithona* sp. (Larson 1987a). Here we used the same size-based relationship for the prey categories found in our study, i.e. the gut clearance time for barnacle larvae and cladocerans was assumed to be half of the time for *A. tonsa*. For the soft body prey types, i.e. *Mnemiopsis* and planula larvae, and *Oikopleura*, we used a gut clearance time of 0.3 h (J. Javidpour personal observation). In addition, the impact of *Mnemiopsis* in terms of carbon fluxes was estimated to be the product of the number of prey in the gut by the prey carbon value using table 2.

Selectivity - seasonal variations in prey selection were assessed by using the selectivity index (D_i) used in Jacobs (1974):

$$D_i = (r_i - p_i) / (r_i + p_i - 2 r_i p_i)$$

where r_i= relative abundance of prey type i in the diet, and p_i= the relative abundance of prey type i in the environment.

Results

Community composition and physical environment- The seasonal cycle of the water column structure in the Kiel Fjord is characterized by high salinities and a vertically mixed water column during late autumn and winter and low salinities under vertically stratified conditions during spring and summer (Fig. 1a). Salinity changes are directly related with changes in the Kiel Bight by the moving Belt Sea front. Kiel Fjord is divided into an inner and outer fjord by narrows which restricts the water exchange with Kiel Bight. The seasonal cycle in temperature is typical for the southwestern Baltic Sea; the winter water temperatures are vertically homogenous. During spring and summer a seasonal thermocline can be observed. However, because of the low depth of the Kiel Fjord, strong wind events can lead to strong vertically mixing and an erosion of the thermocline even in summer (Fig. 1b). The particular seasonal evolution of temperature and salinity is determined by the prevailing atmospheric conditions over the western Baltic Sea area which shows high inter-annual variability.

Table 1- Seasonal variation of feeding rate (carbon consumed per day) of adult *Mnemiopsis leidyi* for the period of December 2006 until October 2007. Per capita Carbon content of prey items is given in the first row.

|	C µg ind-1	Feeding rate (µg C ctn^{-1} d^{-1})						reference
		Dec.06	Jan.07	Feb.07	Aug.07	Sep.07	Oct.07	
Barnacle nauplii	5.1	0.66	0.27	0.09	0.01	0.04	0.71	this study
Copepoda	3.5	0.03	0.02	0.00	0.13	0.12	0.88	this study
Cladocerans	2.1	0.00	0.00	0.00	0.00	0.01	0.01	Sommer 2003
Oikopleura sp	3.2	0.02	0.00	0.00	0.00	0.00	0.00	Sommer 2003
Planula larvae	0.36	0.00	0.00	0.00	0.00	0.06	0.43	Schneider 1985
Mn.larvae	301±35	0.00	0.00	0.00	36.45	21.31	10.77	this study
Mn.adult	521.4±377							this study
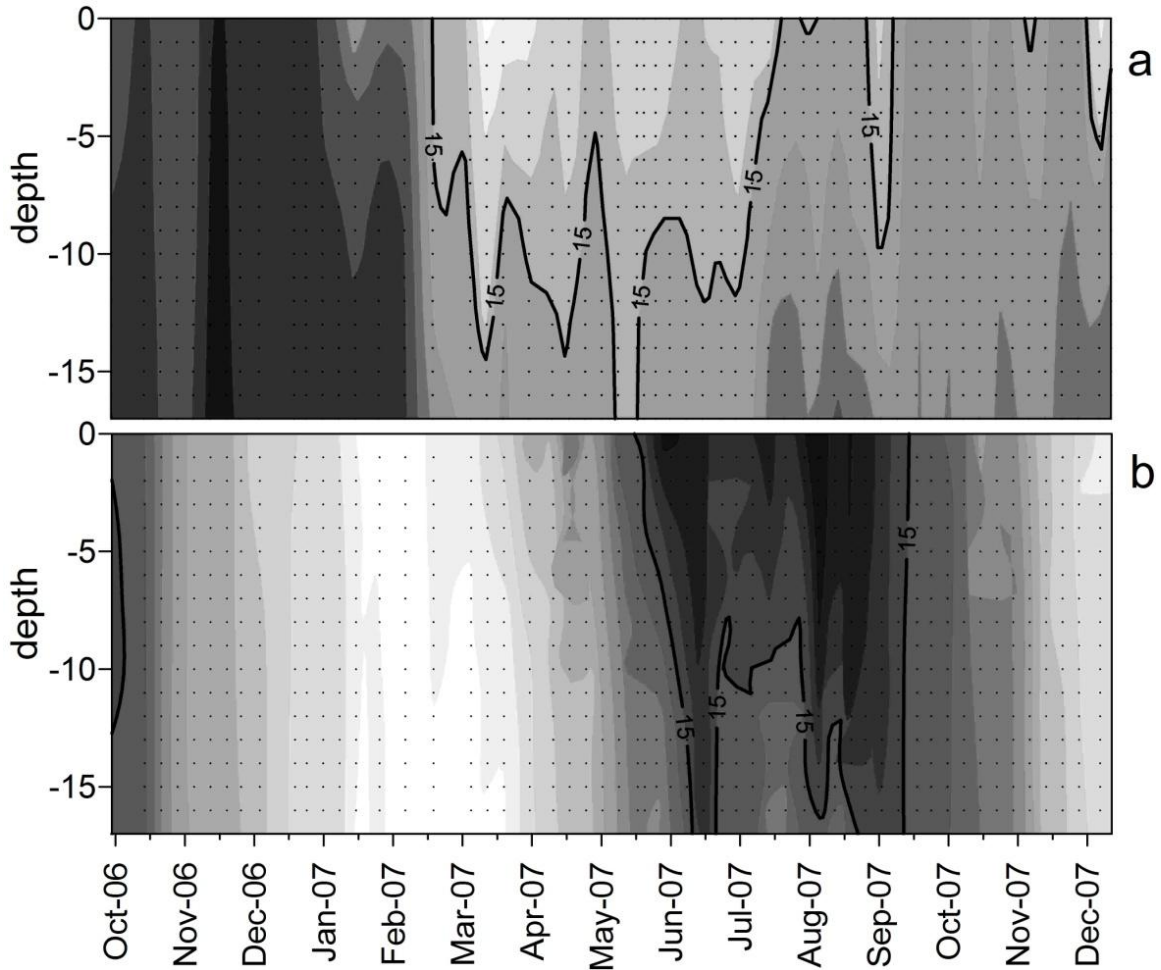
Fig.1- Hydrographic conditions in the Kiel Fjord from December 2006 to December 2007. Salinity (a) and temperature (b) diagram of Kiel Fjord water.

Mnemiopsis was recorded for the first time in the plankton samples of Kiel Fjord in October 2006 (Javidpour et al. 2006). From October 2006 to October 2007 larvae of < 5 mm were dominant, and only a few of the adult stages reached large sizes with reduced oral lobes (Max. 60 mm) (Fig. 2). Depressed abundances were found from February to May, although the species never disappeared. In June, for one sampling date (26th of July), an abrupt increase in the abundance of *Mnemiopsis*, mainly composed of small larvae and post larvae of less than 10 mm (Fig.2), was found. This increase was probably due to the water mass exchange with the Kiel Bight, as indicated by the increased salinity. From August to October, an increase of medium sized individuals (~20 mm), likely related to recruitment processes, was observed although small larvae were still dominant (Fig. 2).

The size structure of the population was dominated by small size classes and only few adults (> 4 cm) were as large as reported in the native region of the species (US east coasts) and in other invaded sites (i.e. Black Sea).

The seasonal dynamics of mesozooplankton prey was characterized by a spring maximum dominated by calanoid copepods (50% of total mesozooplankton) and while cladocerans reached only 22% of total (Fig. 3). The most abundant copepod throughout the different seasons was *Pseudocalanus* sp. with maximum densities in June when it reached 78% of total copepods. Among other mesozooplankton, polycheate larvae ranked second and reached a relative abundance of 38% of total the annual mesozooplankton. In August, however, polycheate and barnacle larvae dominated the mesozooplankton community of the Kiel Fjord (37 and 30% of total respectively). From September to October, when *Mnemiopsis* density reached the annual maximum, copepods and barnacle larvae were the most dominant species of total mesozooplankton communities, whereas cladocerans were almost absent from samples during the late summer-early fall period.

Seasonal diet composition and prey selection - Mean gut clearance times of adult *Mnemiopsis* at 10° and 17 °C for *A. tonsa* varied from 1.9±0.9 h to 1.5±0.4 h respectively. Figure 4 illustrates the seasonal composition of *Mnemiopsis* diet and the marked seasonality in prey fed during the investigated period. During wintertime, the diet of *Mnemiopsis* was mostly composed by slower swimming mesozooplankton like the larvae of the barnacle *Balanus* sp. (82% in average). The relative abundance of copepods in the *Mnemiopsis* diet reached only 6% of total prey on average. Cladocerans contributed to a small portion of the diet of *Mnemiopsis* (~1%).

In August, *Mnemiopsis* larvae bigger than 5 mm dominated the gut content and contributed up to 76% of the total prey items (Fig. 4a). Contrary to wintertime, copepods ranked second in prey captured by *Mnemiopsis* (23%). In late summer *Mnemiopsis* fed mostly on planula larvae of the scyphomedusa *Aurelia aurita* (57% in September and 72% in October). The relative abundance of copepods in the *Mnemiopsis* gut content was 13% in September and 15% in October.

Based on the gut clearance rate, we have calculated the daily feeding rate of *Mnemiopsis* on mesozooplankton prey (Fig. 4b). In the winter period, there was a sharp
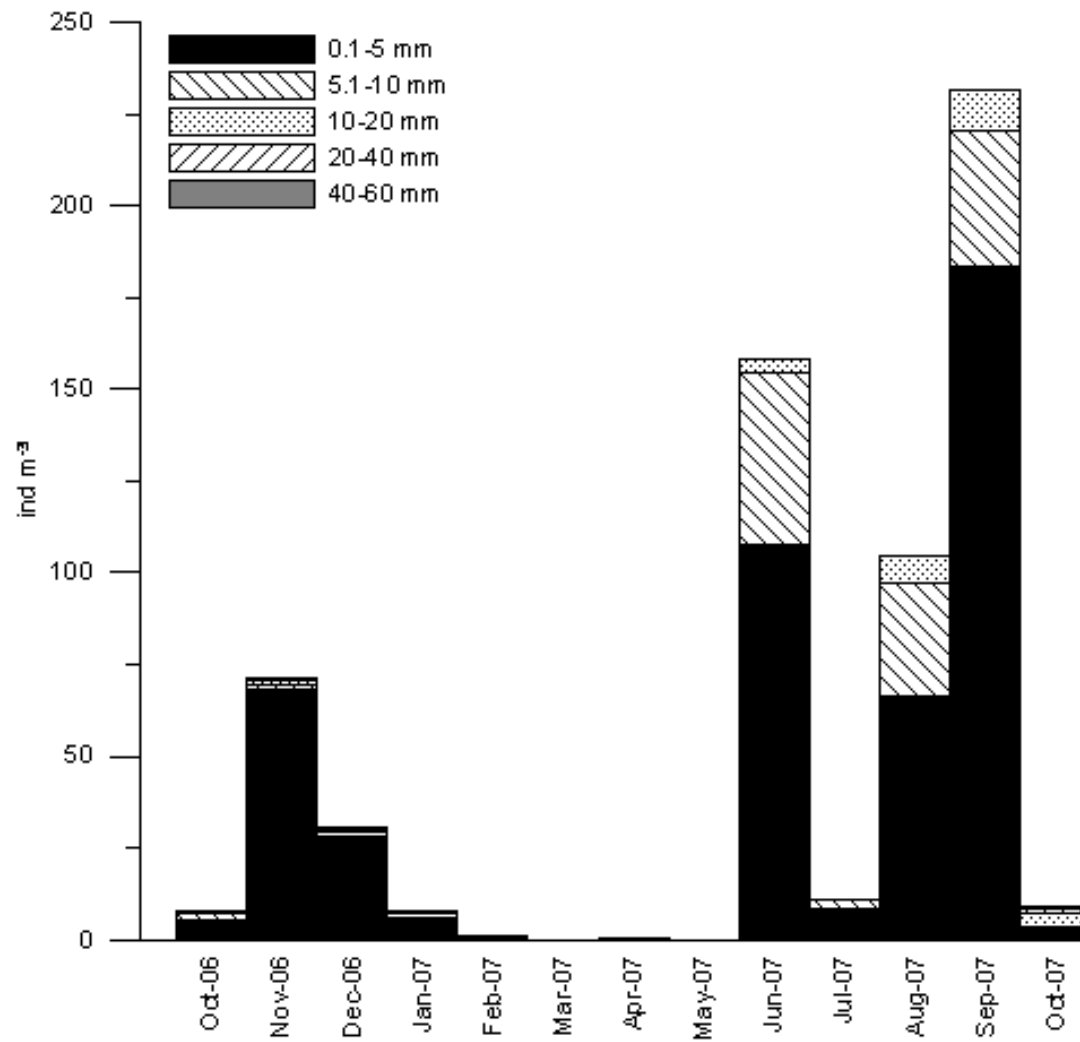
Fig.2- Size structure of *Mnemiopsis leidyi* population in the Kiel Fjord from November 2006 to November 2007.
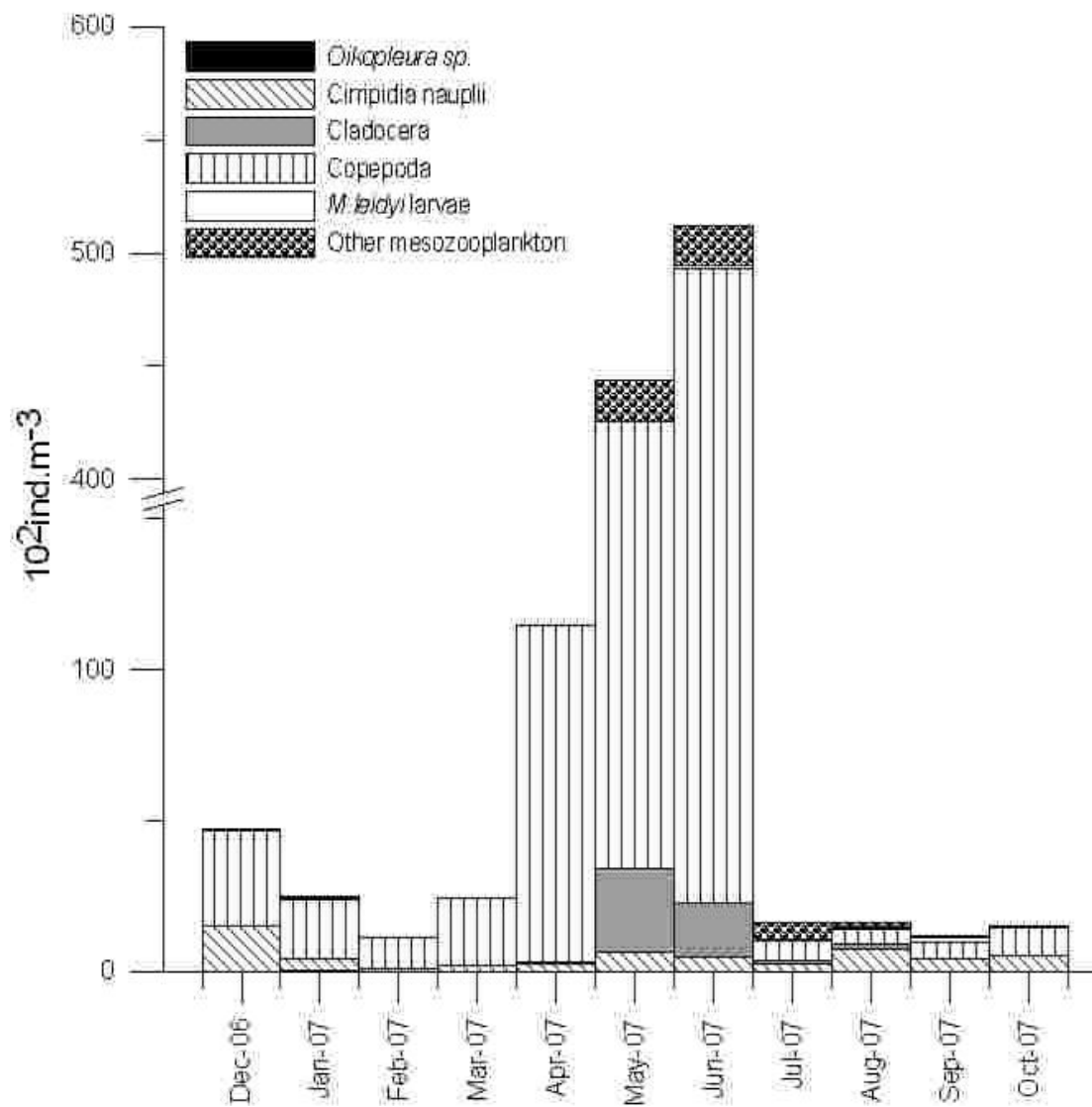
Fig.3- Mesozooplankton abundance and composition of the Kiel Fjord from December 2006 to December 2007.

decrease in the feeding rate, from December to February for all the prey items. The highest feeding rate was on barnacle larvae in December (max. of 66 N_p N_m^{-1} d^{-1}). With increasing water temperature a noticeable increase in the feeding rate was observed in late summer. Maximum feeding was on planula larvae of scyphomedusa (621 N_p N_m^{-1} d^{-1}). Unfortunately, we were not able to estimate the concentration of this type of food in the environment because of the mesh size of 200µm used. The feeding rates of *Mnemiopsis* showed significant differences between winter and summer (Student's *t*; $P<0.05$). Table 1 shows results of the feeding rate based on biomass of prey (µg C). Barnacle larvae contributed 91-97% of carbon consumed per day during the wintertime, whereas in summer *Mnemiopsis* larvae appeared as the main source of carbon among other prey (84-99%). Due to a low carbon biomass of other prey types like planula larvae which were the most dominant prey of the gut in late summer, contribution of this prey in terms of carbon biomass was very low.

In winter, *Mnemiopsis* showed a positive selection for slow swimming plankton like barnacle larvae and cladocerans. Negative selection was shown towards other species with bigger size (i.e. *Oikopleura* sp.) or higher escape abilities (i.e. calanoid copepods) (Fig. 5). This pattern changed in summer, as indicates by the pronounced positive selection for cladocerans and *Mnemiopsis* larvae, as well as for copepods in August. Also, in August and September negative selection of barnacle larvae was found, and it changed in October when the selection for barnacle larvae was again positive.

Discussion

We have investigated the impact of *Mnemiopsis* on plankton communities in the Kiel Fjord during the year following its first appearance. We focused on feeding selectivity because food competition with fish and predation on fish larvae or eggs are considered the most deleterious effects of *Mnemiopsis.* Previous investigations on the prey preference of *Mnemiopsis* have shown that prey items with low swimming velocity (e.g. barnacle larvae) appeared more vulnerable compared with the active and relatively large prey, like copepods whose escape ability is considerably greater (Larson 1987b). In agreement with this we found higher predation pressure of *Mnemiopsis* on low speed swimmers (e.g. *Evadne*) and small sized prey (i.e. barnacle nauplii), particularly during periods of low temperature (i.e. December to February) regardless the prey field
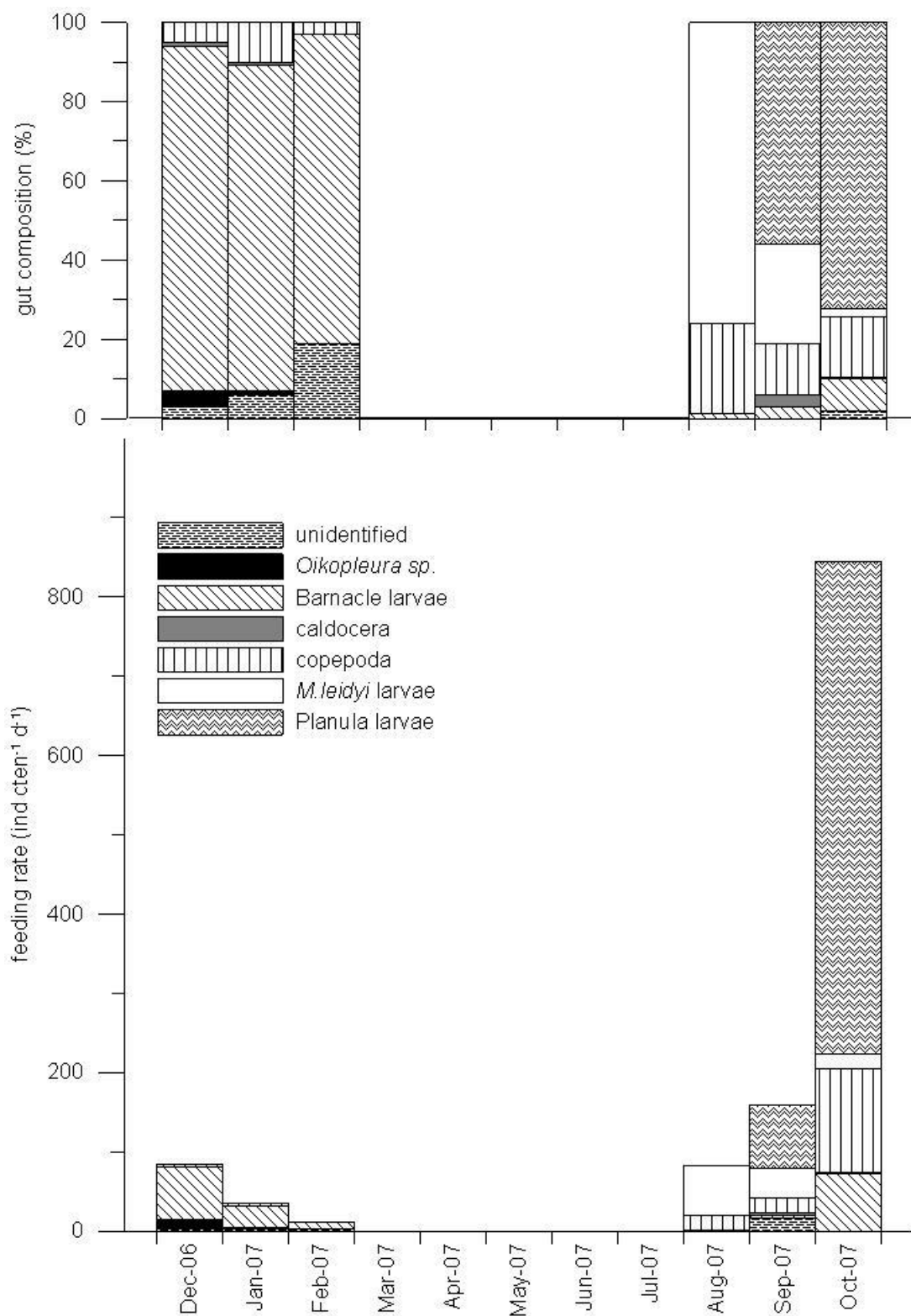
Fig.4- Gut content analysis of adult *Mnemiopsis leidyi* of Kiel Fjord for the investigated period. upper panel indicates temporal changes in the diet composition and lower panel shows feeding rate of *Mnemiopsis leidyi* based on empirical estimated of gut clearance time
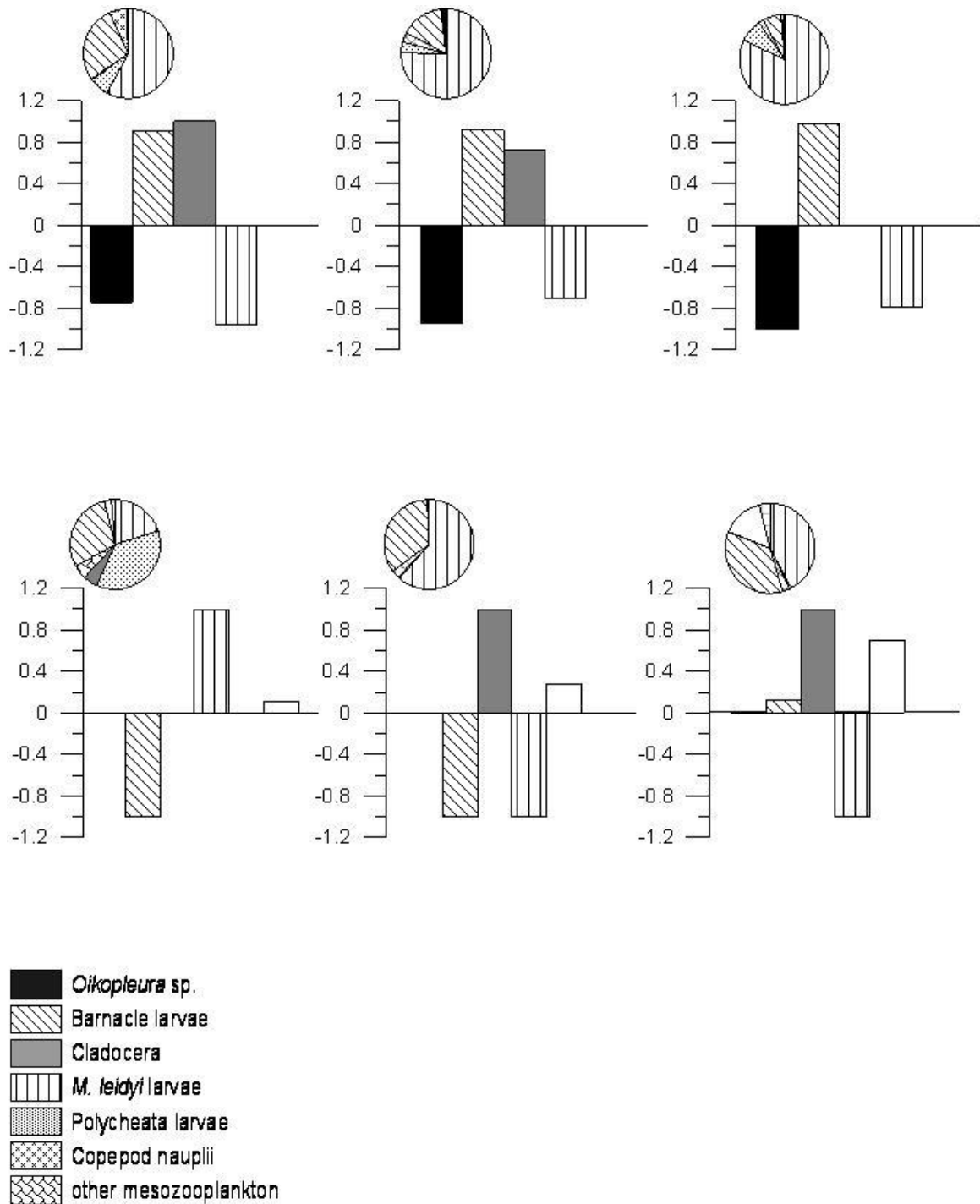
Fig.5- Prey selectivity index. Positive values indicate prey preference and negative relates to no preference. The upper pie chart illustrates the field-prey (relative abundance) for each periods of the time.

composition (Fig. 5). With high temperatures, feeding rates significantly increased and predation preference shifted to larger sized prey (i.e. *Mnemiopsis* larvae). These changes coincide with the period of high temperatures and the development of the thermocline. For instance, during winter (low temperature and homogenized water column) copepods dominated the bulk of mesozooplankton but the most important prey was barnacle nauplii (low speed swimmers). Conversely, in August when the conditions were warmer *Mnemiopsis* preyed on copepods (Fig. 5).

The positive selection for copepods in a short time scale of August may be related to the temperature effect on the active motion of predator which likely explores a larger volume of water under warmer conditions (qualitative obs. by the first author). The general low predatory impact on copepods might also be related to salinity effects on the morphologyy of the oral lobes (prey capture surface), the size of *Mnemiopsis* and the viscosity of the mucus on the surface of the lobes. For instance, in the areas with higher salinity (i.e. US coasts, Black Sea), the length of the oral lobes is larger (Shiganova personal communication, Javidpour pers. obs.), and the lobes' area, as well as the viscosity of mucus are tightly related to the efficiency of predation. Support to this has been given by Waggett and Costello (1999) which shows that up to 97% of encountered copepods captured by adult *Mnemiopsis* were carried by the surface of the oral lobes. Therefore the low salinities in September could act as a limiting factor affecting predatory efficiency of *Mnemiopsis* although the temperature was still high. These effects may explain the differences between the *Mnemiopsis* population of the Kiel Fjord with the northern native population of US coasts, where temperature and annual cycles of zooplankton (including *Mnemiopsis*) show a similar pattern, but copepods are the major prey for *Mnemiopsis* in the Narragansett Bay system (Purcell et al. 2001). This is likely related to the generally larger sizes the species can reach in its native habitat compared to the Baltic Sea (>4 cm, Kremer and Nixon 1976) which might cause a significant increase of predation.

A novel finding was the predator-prey relationship between *Aurelia aurita* and adult *Mnemiopsis*. Previous investigations have reported an indirect interaction between *Mnemiopsis* and *A. aurita* through competition for zooplankton prey. For instance, in the Black Sea it has been hypothesized that *Mnemiopsis* out-competed *A. aurita* from the mixed layer (Shiganova 1998; Kideys and Romanova 2001; Purcell et al. 2001). To our knowledge no predatory impact of *Mnemiopsis* on *A. aurita* has been reported so far,

probably because of overlooking of small soft body larvae in the gut content of *Mnemiopsis* which can be digested in short times compared to other type of preys. In turn *A. aurita* may also have a considerable predatory impact on the *Mnemiopsis* (Purcell 1991 and own observations). In addition, the relationship may be more complex when considering the dietary overlap of *A. aurita* adults and *Mnemiopsis* in the Kiel Fjord. *In situ* estimations of diet composition of *A. aurita* in the Kiel Bight indicated a broad food spectrum of different sizes of zooplankton for this predator (Schneider and Behrends 1994) which suggests a strong competitive interaction during the period of co- occurrence. On the other hand, it is ecologically plausible that changes in the timing of maximum abundance for these gelatinous carnivores may alter their interaction resulting in an advantage for the first arriving adult population. In this case, the different life histories of the two mentioned species and their ability to cope with environmental perturbations should be considered. For instance, compared to the scyphomedusa *A. aurita*, with three different life phases and a complex bentho-pelagic life cycle (Lucas 2001), *Mnemiopsis* has a holoplanktonic life history with a shorter life cycle of a few weeks. It is therefore possible that *Mnemiopsis* abundance responds faster to windows of opportunity.

An additional novel result in this study suggests that cannibalism may play a regulatory role in the population dynamics of *Mnemiopsis*. In addition predation on its own larvae provides the main carbon source during the period of high reproduction (Javidpour 2008). The strong predation of *Mnemiopsis* on its larvae points towards a possible density dependent control of its population growth, which has been elusive so far. In the Black Sea, previous it has been hypothesized that food limitation may act as the most important controlling factor of the biomass of *Mnemiopsis* until 1997, before appearance of its main predator *Beroe ovata* (Kideys and Romanova 2001). Although the potential predation control of *A. aurita* in the Kiel Fjord is not excluded, *Mnemiopsis* population is probably density-dependent as its predation on its own larvae increased during the peaks of maximum abundance.

The present results indicate that *Mnemiopsis* mainly preys on a wide range of plankton organisms, ranging from < 100μm (planula larvae), to up to 5 mm (*Mnemiopsis* larvae), thereby competing for food with many other predators of Kiel Fjord like fish larvae and Scyphomedusa. Interestingly, our results suggested a predator – prey link with *A. aurita* in which either *Mnemiopsis* or *A. aurita* can be preyed on by the adults of the other group. However there is still a need to extend our knowledge about demographic rates

incurred by each predator. The sizes found in the observation period (most of them small, compared to other sites where salinity is much higher, i.e. US eastern coasts, Black Sea), opens the question of environmental forcing on the *Mnemiopsis* development, and how it deals with non-optimal conditions (i.e. salinity). The implications of this work concern not only the role gelatinous carnivores may have on the general overexploited Baltic fish stocks (i.e. cods), but also on the success of biological invasions. While *Mnemiopsis* has generally been regarded as on of the most destructive invasive species, the indirect effects of relatively adverse environmental conditions might reduce its impact on the food web components relevant for fisheries. However, even here strong predation on copepods is possibly under certain environmental conditions.

Acknowledgments

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Conclusion and outlook

A systematic monitoring on gelatinous carnivores in the western Baltic Sea allowed detecting of the first time the presence of *Mnemiopsis leidyi*. The puzzle of mass occurrence of cold water ctenophore Bolinopsis infundibulum in the late summer coastal waters of the Netherlands was solved after providing the morphological characters which distinguished *M. leidyi* from *B. infundibulum* (chapter I). This highlights the importance of taxonomical background of any researcher working on field collection samples.

In the Baltic Sea, the pelagic ecosystem is characterized by low diversity and subsequently any substantial change in its structure may have drastic impacts (Casini et al. 2008) given the vast ecological and economic impacts the *M. leidyi* invasion had in its previously invaded habitats, the appearance of this ctenophore in the Baltic became a topic of major concern. Additionally it provided a unique "natural experiment" by following an invasive species immediately after the first observation (Sax et al. 2005).

This work highlights some ecological aspects of *Mnemiopsis* invasion in the Baltic. In chapter II, we have provided data on general features of population dynamics and seasonal variation of *M. leidyi*. These data improved our understanding of successful establishment of this invader in new habitat. The importance of late summer outbreak of *M. leidyi* and its implication on the structure of microzooplankton community needs to be improved further.

In chapter III we exclude advection from the Kattegat as the only source of *M. leidyi* transport and emphasized the importance of ballast water for rapid distribution of this invader through the Baltic Sea. Although the ballast water is in use for more than 100 years, invasion rate via ballast water increased recently. The 'window of introduction' hypothesis suggest how environmental changes in recipient habitat can provide a successful invasion. The recent increase of water temperature in the Baltic Sea (Chapter III) as well as other anthropogenic disturbances like eutrophication, overfishing and pollution (Alheit 2005) may facilitate the establishment of the comb jelly in the Baltic Sea. Recently there are increasing attempts to prevent biological invasion via ballast water exchange programs (http://massbay.mit.edu/resources/pdf/ballast-treat.pdf) and particular ballast water management for the Baltic (Gollasch and E.Leppaekoski 2007).

While release of ballast water may lead to the introduction of new species in a local port, the diffusion of this species to other areas is a key factor for the estimation of its potential range of expansion. With the help of our model we showed the main covered area by transporting the released ballast water and trajectories of comb jelly invader in the Baltic Sea. The approach we have used for estimation of *M. leidyi* spread might be used for a broad range of other plankton organisms, for instance those that do not show significant vertical migration.

The fact that there was no seasonal overlap between *M. leidyi* and fish eggs and larvae in the Western Baltic Sea, leads to estimate a low potential direct impact on the fish eggs and larvae. In the previously invaded ecosystems it still remains uncertain whether *M. leidyi* can consume big amount of fish eggs and larvae to cause a sharp decline in the fish stocks. The only report that exist shows a extremely low proportion (1%) of eggs and larvae of fish in the gut content of nearly 10.000 examined individuals (Mutlu 1999). Even if *M. leidyi* co-occurs with fish eggs in the Baltic Sea, for example in the central Baltic Sea (Haslob et al. 2007), it would not lead to a direct predation on fish stock, as the results of chapter IV suggest. In chapter IV we also discussed the role of environmental conditions in influencing the feeding selectivity of *M. leidyi*. We have shown a reduction in predatory impact of *M. leidyi* during low temperature and low salinity conditions and a preference for small sized or slow swimmer prey. *M. leidyi* had a positive selection for small sized prey particularly during the low temperature-salinity period which is common hydrological conditions in the Bornholm Basin. Additionally, in direct selectivity experiments Hamer (2008) observed a strong negative selectivity against fish eggs, as well as a stable isotope signal that makes it very unlikely that *M. leidyi* consumes fish eggs. The prevailing environmental conditions seems to acts negatively on the body size of *M. leidyi* and consequently on its predation efficiency (chapter IV). In fact the maximum size *M. leidyi* reached in the Baltic Sea is smaller than in other systems which it invaded before (chapter I): in the Northern Baltic Sea it was less than 10 mm (Viitasalo et al. 2008). It is also argued that *M. leidyi* is the most efficient consumer of mesozooplankton in its native and other previous invaded habitat (Purcell et al. 2001; Roohi et al. 2008). In the case of the Baltic Sea our findings on the diet composition and prey selectivity of *M. leidyi* highlight a low contribution of copepods, as key prey item, to the diet. A particularly interesting result was found on the cannibalism of the species that provided the main carbon source for the adults.
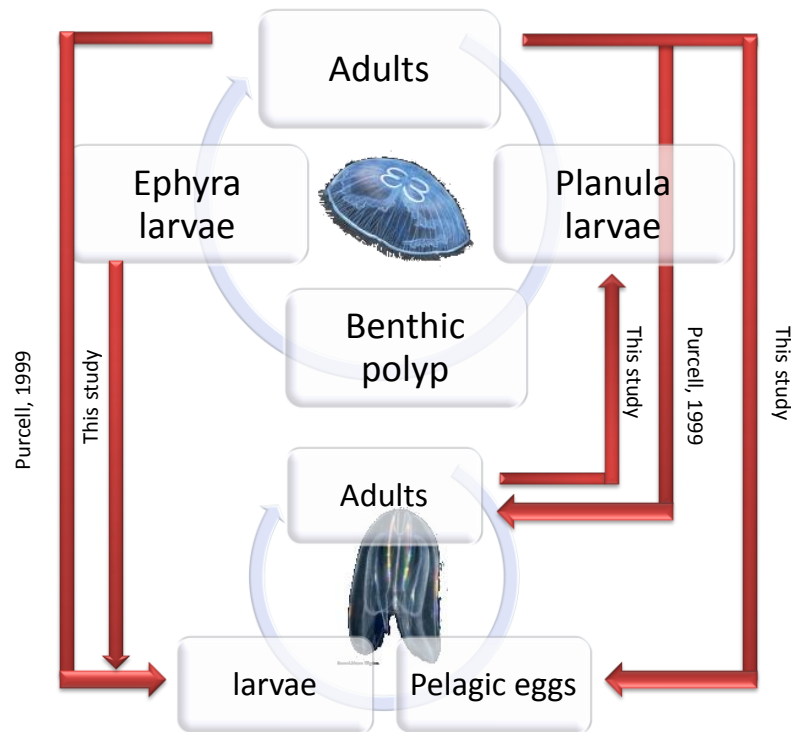
Fig.1- Schematic illustration of some interrelationships between *Mnemiopsis leidyi* and *Aurelia aurita*. The dashed arrows are those interactions which have been indicated in literatures.

Mortality is a major principle of population dynamics. We have indicated the role of some environmental as well as hydrographical conditions for establishment of *M. leidyi* in the Western Baltic Sea. It was also discussed in which extent such environmental conditions may influence the timing and seasonality of this species. The potential density-dependent population control and its consequence for the successful establishment of *M. leidyi* might be considered as a major point for further research and a stimulus to reassess the population dynamics of this species in other ecosystems. Probably there are other sorts of population control in the Baltic Sea which need more investigation: Greve (1972) indicated some adult fishes of the German Bight as the potential predators of ctenophores, although he did not indicate in which extent ctenophore mortality occurs by fish predation.

Among the results of the Chapter IV, the predatory role of *M. leidyi* on *Aurelia* larvae is a particularly important aspect of the invasion impact of *M. leidyi* (Fig.1). A relevant question to ask, given that *Aurelia* causes a top-down trophic cascades in the local habitat of the Western Baltic Sea (Schneider and Behrends 1998), is whether the observed changes via direct predation on *Aurelia* larvae by *M. leidyi* can be considered as "invasion benefit "of *M. leidyi* or not. Therefore, the complexity underlying food web dynamics of the invasion of *Mnemiopsis leidyi* in the Baltic Sea and how it affects the biodiversity at the local and regional level needs to be addressed on both spatial and temporal scales.

This work provided new insights to the understanding of some of the processes involved in the invasion dynamics of *Mnemiopsis leidyi* into the Baltic. More efforts are needed to provide a clearer picture of its ecological role under recent and future change.

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Other relevant experiences

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Jan.2007-Jan 2008   Collaborator of the project: Die Invasion der räuberischen Rippenqualle *Mnemiopsis leidyi* in der Ostsee, funded by „Landesamt für Natur und Umwelt des Landes Schleswig Holstein",Germany

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                                 Temperature effect on the reproductive potential of *Mnemiopsis leidyi* in the Kiel Fjord (by:D.Sarpe)

                                Temperature and salinity effects on Respiration rates of *Mnemiopsis leidyi* (by:T.Grosskopf)

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Grants

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Publications

A.Lehmann**, J.Javidpour,** (**2008**), Pattern of Geographical expansion of an invader in the Baltic Sea: *Mnemiopsis leidyi*. in prep.

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Statement

Herewith I explain that the present thesis, apart from the consultation of my supervisor and the contribution of my co-worker in the third chapter, was made independently by me and that it is my own work after form and contents. It was presented to no other place within the scope of an examination procedure. This is my only and doctorate procedure first up to now. The doctorate should occur in the field Biological oceanography. Furthermore I explain that I admit listener with the Disputation.