Thesis for the degree of Doctor of Philosophy

# Environmental drivers of gelatinous zooplankton distribution

*Mnemiopsis* in the Baltic

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# Abstract

Factors governing zooplankton distributions and dispersal have since long interested pelagic ecologists. This thesis presents studies of how the interaction between gelatinous zooplankton and the environment can shape their distributions, either by biophysical drivers (papers I-III), or through interactions with predators (paper III & IV) or competing species (paper V).

In papers I & II we followed the newly invaded ctenophore *Mnemiopsis leidyi* population in Kattegat, Skagerrak and Baltic Proper during a year, and showed strong environmental restrictions on the sampled population. Salinity and temperature clearly influenced the presence of adult *M. leidyi* (paper I), and low transitional-to-adult ratios in the low saline Baltic Proper indicated a failed reproduction (paper II). Advection from the higher saline Skagerrak and Kattegat area to the Baltic Proper seem to sustain the sporadic population in the Baltic Proper. One way in which plankton organisms can alter their spatial distribution is trough their vertical positioning. In paper III we investigated the fine scale vertical distribution in field by the use of video methods. We show how some life stages (e.g. size) of *M. leidyi* performs diel vertical migration, suggestively in response to light. The presence of *M. leidyi* was also tightly coupled to higher salinities, where lower salinities in combination with strong stratification seemed to prevent the vertical migration.

In paper IV, we experimentally investigate the potential predation control of *M. leidyi* by *Beroe gracilis*. Applying the determined clearance rates to *in situ* distributions (from paper I) showed that *B. gracilis* has limited ability to control the *M. leidyi* population in the field, partly due to a predatory size refuge. Finally in paper V we used a theoretical approach to investigate the competitive relationship between gelatinous plankton and zooplanktivorous fish, depending on eutrophication and water clarity. Tactile predation by jellyfish makes them less dependent on water clarity than are visually foraging fish. The model predicted a two sized effect of eutrophication for organisms utilizing vision (fish) with an optimal degree

of eutrophication and water clarity. Above this threshold, tactile predators like jellyfish would be favored over visual predators like fish.

The results from this thesis contribute to the understanding of how the environment acts to shape gelatinous zooplankton populations, and may on a larger perspective help to understand future potential invasions.

# Populärvetenskaplig sammanfattning

Faktorer som styr utbredning och spridning av djurplankton har sedan länge intresserat ekologer som jobbar med pelagialen. I den här avhandlingen presenterar jag arbeten med gelatinösa plankton (här definierat som maneter och kammaneter) och hur deras utbredning påverkas av miljöfaktorer (artiklarna I-III), predatorer (artiklarna III & IV), eller konkurrerande arter (artikel IV).

I artikel I & II följde vi den nyligen introducerade kammaneten *Mnemiopsis leidyi* under ett år i Kattegat, Skagerrak och Östersjön. Vi fann att utbredningen av *Mnemiopsis* styrdes kraftigt av den omgivande miljön, där salthalt och temperatur hade störst betydelse. Förhållandet mellan de yngre och äldre livsstadierna visade även att reproduktionen av *Mnemiopsis* var begränsad i Östersjön där salthalten är låg. Populationen i Östersjön var därför beroende av att nya djur rekryterades via transport med strömmar.

Kammaneternas djupfördelning påverkade också den horisontella utbredning. I artikel III bestämde vi den vertikala utbredningen med hjälp av videofilmning. Vi kunde visa att vissa livsstadier hos *Mnemiopsis* vandrar vertikalt under dygnet. Det är vanligt hos många andra djurplankton; de uppsöker djupare och mörkare vatten under dagen för att undvika att bli uppätna av fiskar som söker föda med hjälp av synen. Den vertikala utbredningen var även starkt beroende av salthalten, och i områden där vattnet var starkt skiktat såg man ingen vertikal migration hos *Mnemiopsis*.

Utbredningen av kammaneterna påverkas också av predation. I artikel IV undersökte vi relationen mellan *Mnemiopsis* och dess predator *Beroe gracilis* (även den en kammanet) experimentellt. Resultat från experimenten visade dock att *Beroe* saknade betydelse som predator på *Mnemiopsis* populationen. Detta berodde bland annat på att *Beroe* bara kunde äta byten som var lika stora eller mindre än deras egna storlek, och därmed undgick *Mnemiopsis* predation eftersom de generellt var större än *Beroe*.

Slutligen använde vi oss i artikel V av en teoretisk modell och data från Östersjön för att undersöka hur konkurrensen mellan fisk och gelatinösa plankton påverkas av eutrofiering och grumligheten i vattnet. Gelatinösa plankton använder sin känsel för att hitta föda (taktila predatorer), jämfört med fisk som använder sig av synen (visuella predatorer). Detta gör gelatinösa plankton mindre känsliga för förändringar i vattnets grumlighet. Modellen visade att till en början gynnas fisken av den ökade produktivitet som eutrofiering orsakar, men då grumligheten blir så stor att dom får svårt att hitta föda gynnas istället gelatinösa plankton. När vi jämförde modellens resultat med nuvarande eutrofiering i Östersjön såg vi att Östersjön närmar sig ett system som kan gynna gelatinösa plankton.

Resultaten från min avhandling bidrar till vår förståelse om hur miljöfaktorer styr utbredningen av gelatinösa plankton. I ett större perspektiv kan det hjälpa oss att förstå möjliga framtida invasioner av främmande arter.

## Contents

## List of papers

**I.** **Haraldsson M**, Jaspers C, Tiselius P, Aksnes DL, Andersen T, Titelman J (2013) Environmental constraints of the invasive *Mnemiopsis leidyi* in Scandinavian waters. *Limnology and Oceanography* 58: 37-48
Erratum *Limnology and Oceanography* 58: 563

**II.** Jaspers C, **Haraldsson M**, Lombard F, Bolte S, Kiørboe T (2013) Seasonal dynamics of early life stages of invasive and native ctenophores give clues to invasion and bloom potential in the Baltic Sea. *Journal of Plankton Research* 35: 582-594

**III.** **Haraldsson M**, Båmstedt U, Tiselius T, Titelman J, Aksnes DL (*Submitted*) Evidence of diel vertical migration in *Mnemiopsis leidyi*.

**IV.** Hosia A, Titelman J, Hansson LJ, **Haraldsson M** (2011) Interactions between native and alien ctenophores: *Beroe gracilis* and *Mnemiopsis leidyi* in Gullmarsfjorden. *Marine Ecology Progress Series* 422: 129-138

**V.** **Haraldsson M**, Tönnesson K, Tiselius P, Thingstad TF, Aksnes DL (2012) Relationship between fish and jellyfish as a function of eutrophication and water clarity. *Marine Ecology Progress Series* 471: 73-85

The papers are reprinted in this thesis with the kind permission from Association for the Sciences of Limnology and Oceanography, Inc. (**paper I**), Oxford University Press (**paper II**) and Inter-Research (**papers IV** and **V**). In the following text the papers are referred to by their roman numerals.

## Related papers not included in thesis

Jaspers C, Titelman J, Hansson LJ, **Haraldsson M**, Ditlefsen CR (2011) The invasive ctenophore *Mnemiopsis leidyi* poses no direct threat to Baltic cod eggs and larvae. *Limnology and Oceanography* 56: 431-439

Jaspers C, **Haraldsson H**, Bolte S, Reusch TBH, Thygesen U, Kiørboe T (2012) Ctenophore population recruits entirely through larval reproduction in the central Baltic Sea. *Biology Letters* 8: 809-812

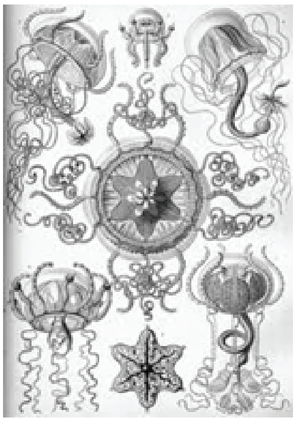
Dinasquet J, Titelman J, Friis Møller L, Selätä O, Granhag L, Andersen T, Båmstedt U, **Haraldsson M**, Hosia A, Katajisto T, Kragh T, Kuparinen J, Scrøter ML, Søndergaard M, Tiselius P, Riemann L (2012) Cascading effects of the ctenophore *Mnemiopsis leidyi* on the planktonic food web in a nutrient-limited estuarine system. *Marine Ecology Progress Series* 460: 49-61

# Synthesis

## Introduction

Jellyfish INFOBOX-1 are a huge evolutionary success! Being among the oldest complex-bodied organisms still existing, jellyfish have survived through history since over 500 million years ago (Hagadorn et al. 2002), from the Cambrian explosion to modern human time. They are found in all types of marine habitats, from the tropics to the Polar Regions, in shallow bays and estuaries to the deep oceans. Jellyfish populations are common and important parts of most pelagic ecosystems.

### INFO BOX 1 : Gelatinous zooplankton



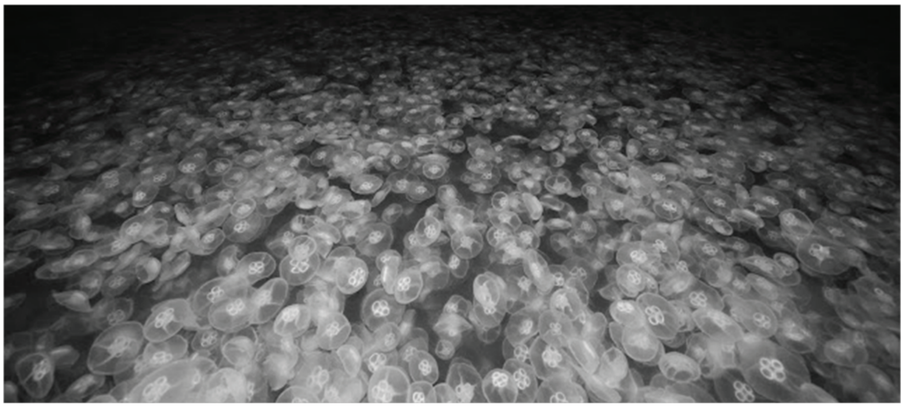
▲ Medusae by Ernst Haeckel

In this thesis I am using the term gelatinous zooplankton or jellyfish to refer to ctenophores and pelagic cnidarians. Although they belong to different phyla, they have certain life-history characteristics in common, which are relevant to their ecology.

Gelatinous zooplankton have **large gelatinous bodies** consisting mostly of water. Their large size and diluted tissue is believed to make them less attractive to some predators, and their **transparency** makes them difficult to see. Their large bodies also increase the encounter rate with their prey, making them **efficient feeders**. They are all **predators** and many species are **opportunistic** and feed on a wide array of prey. Although their feeding mechanisms differ, they are generally **tactile** predators and do not rely on vision to detect prey. Also their reproductive strategies differ (with complex life histories in the pelagic cnidarians), but both groups have a **high reproduction potential** being able to rapidly produce offspring during environmentally favorable conditions.

Note: Because there are many different species of gelatinous zooplankton all do not fall within the generalized characteristics pointed out below.

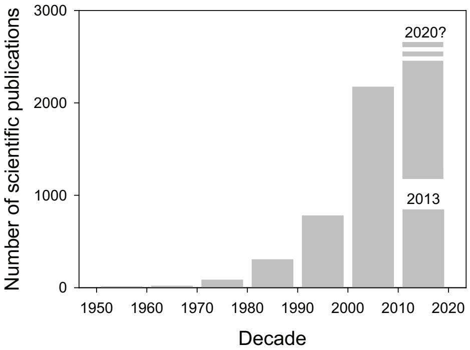
Their life-history characteristics bring them to bloom during favorable conditions (Figure 1), a common feature among them (Hamner & Dawson 2009). During such events their predatory potential on zooplankton can be extremely high and they may quickly transfer energy away from the lower part of the food web, thus shaping and altering the pelagic food web (Roohi et al. 2010, Riisgård et al. 2012).



▲Figure 1. A bloom of the jellyfish *Aurelia aurita* in Denmark. Photo by Casper Tybjerg

Despite their ecological importance and ancient history, jellyfish were traditionally neglected in ecological surveys and hence our general knowledge about this group of organism is surprisingly small. Maybe the lack of research interest was because of their uncharismatic nature or the lack of direct economical interest for humans (although big blooms may have huge economical consequences). Most likely were the difficulties in working with jellyfish contributing, as their fragile bodies make them difficult to sample and preserve. However, since the 1990's the scientific and public attention has rapidly increased INFOBOX-2. Repeated studies report on increased abundances, more frequent blooms, wider distributions and invasions of new species (e.g. Mills 2001, Richardson et al. 2009, Purcell et al. 2012).

## INFO BOX 2 : A jellyfish trend?



▲ Abstract painting of jellyfish by Sheddot.
▶ Inspiration from jellyfish on the catwalk.

▲ A quick search on Web of Knowledge (the major online database for scientific research) using the keywords "jellyfish" or "gelatinous zooplankton" reveals an exponential increase in the number of scientific articles published since the 1950's. The public attention is also increasing. Today jellyfish are often depicted in art, fashion and design.

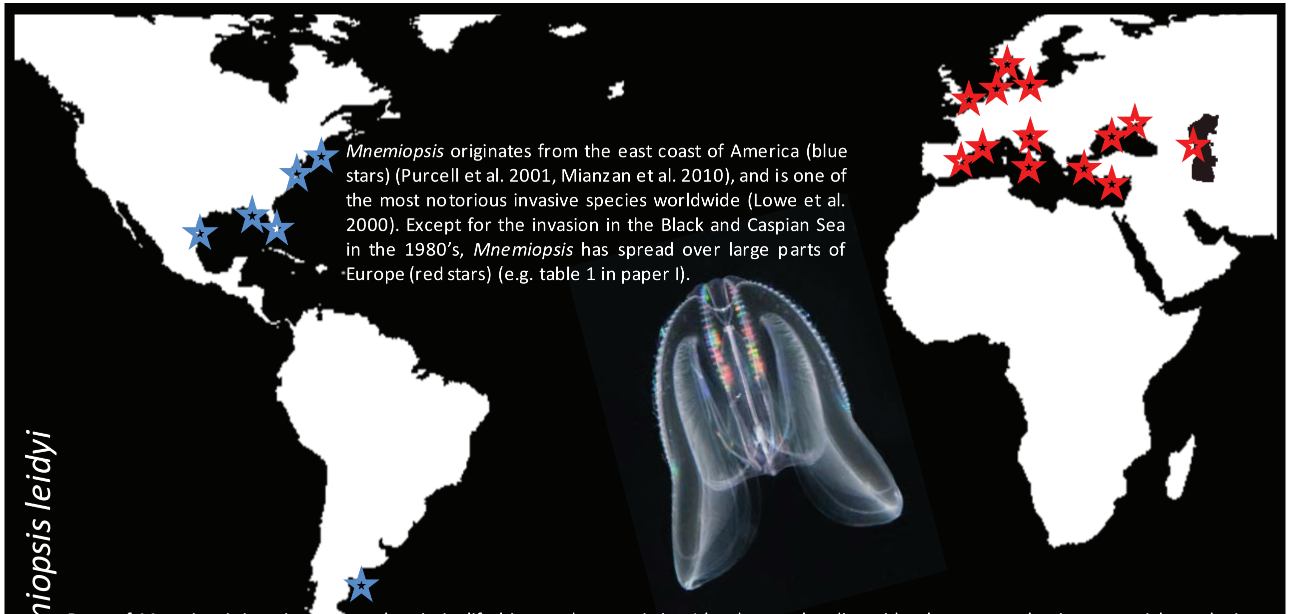
Anthropogenic changes have been hypothesized to favor this group of organisms generally. Such changes include eutrophication (Parsons & Lalli 2002, Purcell et al. 2007) and hypoxia (Decker et al. 2004, Thuesen et al. 2005), overfishing (Brodeur et al. 2002, Lynam et al. 2006), temperature increase (Purcell et al. 2007, Lynam et al. 2011), and degradation of the light environment (Aksnes 2007, Sørnes et al. 2007). Although local populations may have increased (e.g. Brodeur et al. 2002, Lynam et al. 2006), this perception of a global increase is hampered by the fact that very few longer time series actually exist, and also a global increase is hard to separate from normal fluctuations (Condon et al. 2012). Nevertheless, jellyfish deserve research attention. We need to increase our understanding of their general ecology and of factors driving their occurrence and distributions.

## Jellyfish of Scandinavia

In Scandinavian waters a range of native gelatinous plankton exist. Some are found frequently, while others only temporarily visit when being drifted in from the North Sea. Among the true jellyfishes, the scyphozoan medusa, *Aurelia aurita* (moon jellyfish) and *Cyanea capillata* (Lion's mane jellyfish) are common components of the summer plankton community (Schneider & Behrends 1994, Behreds & Schneider 1995). Also *C. lamarckii*, the Bluefire jellyfish, is regularly seen, while *Chrysaora hysoscella* (Compass jellyfish) and *Rhizostoma pulmo* (Barrel jellyfish) are rarer. Within in the ctenophore phyla the northerly lobate *Bolinopsis infundibulum* (common Northern Comb jelly), the cydippid *Pleurobrachia pileus* (Sea Gooseberry) and *Beroe cucumis* and *B. gracilis* are common during parts of the year (Greve 1975). Since 2011, also the cydippid ctenophore *Euplokamis dunlapae* has been occasionally observed in Skagerrak and Gullmar fjord (Granhag et al. 2012). A wide number of species within the smaller sized hydromedusae are also often present (Allwein 1968). Most of these species are common and reproduce in Skagerrak and Kattegat, while they are only occasionally found in the Baltic Sea.

In 2005 the invasive ctenophore *Mnemiopsis leidyi* $^{\text{INFOBOX-3}}$ was first observed in Scandinavian waters (Oliveira 2007), and a year later it was reported from the North Sea (Faasse & Bayha 2006, Boersma et al. 2007), Skagerrak (Hansson 2006), Kattegat (Tendal et al. 2007), and the southern (Javidpour et al. 2006) and central Baltic Sea (Kube et al. 2007). Its introduction caused immense attention, and many feared for its potential ecological effects on the already sensitive Baltic Sea system (Javidpour et al. 2006, Haslob et al. 2007, Huwer et al. 2008). The fear was based on *M. leidyi*'s previous accidental introduction in the Black and Caspian Sea during the 1980's, were it quickly established itself with severe ecological and economical consequences (Knowler 2005). With its huge abundances and high predation on zooplankton prey, fish eggs and larvae, it was blamed for the collapse of the important Sardine fishery (Kideys 2002).

## INFO BOX 3 *Mnemiopsis leidyi*



*Mnemiopsis* originates from the east coast of America (blue stars) (Purcell et al. 2001, Mianzan et al. 2010), and is one of the most notorious invasive species worldwide (Lowe et al. 2000). Except for the invasion in the Black and Caspian Sea in the 1980's, *Mnemiopsis* has spread over large parts of Europe (red stars) (e.g. table 1 in paper I).

Parts of *Mnemiopsis* invasive success lays in its life history characteristics. It's a hermaphrodite with a huge reproductive potential, producing 12-14 000 eggs $y^{-1}$ (Kremer 1976, Zaika & Revkov 1994). Already at a larval stage is *Mnemiopsis* capable to reproduce, however continuous reproduction starts first at the adult stage (Martindale 1987). Reproducing individuals realizes the eggs strait into the water column, and within 24 hours the eggs hatch into a tentaculate larvae (Pang & Martindale 2008).

*Mnemiopsis* has three distinct life-history stages; tentaculate larvae (~ < 5 mm); transitional (~ 5-6 mm); adult lobate stage (> 6 mm), characterized by their feeding mode (Sullivan & Gifford 2004). As a tentaculate larva they catch their prey with their two tentacles. At this stage their diet is omnivorous including nano-, micro- and mesoplankton (Stoecker et al. 1987, Sullivan & Gifford 2004, Waggett & Sullivan 2006). Gradually are their two lobes developing while they still carry the tentacles, which they use in a combination to capture prey (Sullivan & Gifford 2004). In the final adult stage are the feeding lobes well developed, and with their cilia they produce a feeding current which efficiently brings prey to their mouth (Colin et al. 2010). At this stage are meso- and ichtyoplankton important parts of their diet (Purcell et al. 2001).

However, overfishing (Daskalov 2002, Daskalov & Mamedov 2007, Llobe et al. 2011) and habitat destruction (Aksnes 2007) most likely had as an important part of the resulting regime shift. A few years later, the reduced fishery allowed the ecosystem to slowly recover (Bilio & Niermann 2004), which was also facilitated by a second introduction by *Beroe ovata*, a natural predator of *M. leidyi* (Finenko et al. 2003).

In the three first years (2006-2009) following the first observations of *M. leidyi*'s in the Baltic, it was repeatedly observed from the North Sea (van Ginderdeuren et al. 2012) to the central (Janas & Zgrundo 2007, Haslob et al. 2007, Javidpour et al. 2009, Schaber et al. 2011) and northern Baltic (Viitasalo et al. 2008), with a reported year-round population in Kiel Bight, Oct. 2006 - Sep. 2007 (Javidpour et al. 2009). However, the mapping of the new invasion was complicated by the discovery of a second ctenophore, *Mertensia ovum*, in the central and northern parts of the Baltic (Gorokhova et al. 2009). In the brackish Baltic Sea, *M. ovum* does not reach adult sizes, and the small larval ctenophores are easily miss-indentified with other cydippid ctenophores, e.g. larval *M. leidyi* or *P. pileus* (Gorokhova et al. 2009, Jaspers et al. 2012). *M. ovum* is most likely an Arctic relic species, which prior to *M. leidyi*'s introduction had been miss-identified as *P. pileus*. Intense field sampling in the region (**paper I**) showed that *M. leidyi* and *M. ovum* have different but overlapping distributions in Swedish waters, where *M. ovum* seem to prefer the lower saline water in the central and northern Baltic Sea (**paper II**).

The introduction of *M. leidyi* in the Baltic gave an excellent opportunity to study the dynamics between jellyfish distributions and the environment.

## Aim of thesis

This thesis presents studies of the interaction between the environment and gelatinous zooplankton. Distributions may be shaped by biophysical drivers (**papers I, II & III**), or through interactions with predators (**paper III & IV**) or competing species (**paper V**). Specifically **papers I-V** aim at:

| | |
|---|---|
| **Papers I-II.** | Describing the spatial and temporal dynamics of *M. leidyi* along the salinity gradient in the Baltic Sea, including Skagerrak and Kattegat, and identifying the major environmental factors governing the distribution of adults (**paper I**), eggs and larvae (**paper II**). |
| **Paper III.** | Describing the fine scale vertical distribution of *M. leidyi* in Kattegat and central Baltic Sea in relation to environmental factors, and testing if *M. leidyi* performs diel vertical migrations. |
| **Paper IV.** | Experimentally quantifying predation rates of the native ctenophore *B. gracilis* on *M. leidyi*. |
| **Paper V.** | Theoretically analyzing the competitive relationship between zooplanktivorous jellyfish and fish, which utilize the same resource, as a function of eutrophication and water clarity. |

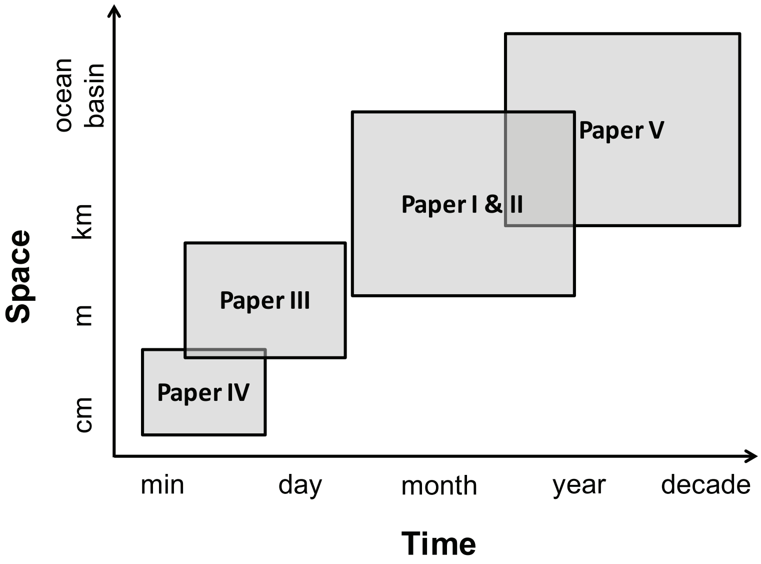
In the rest of this synthesis I focus the discussion on how the biophysical environment have the potential to shape distributions of gelatinous zooplankton generally, and *M. leidyi* specifically, while I highlight the more general results from **papers I-IV**.

Detailed information on methodology, equations and specific results or discussions can be found in respective paper and is not included. For clarity I have, however, included a brief overview of the range of methods used.

## General methods

In the papers in this thesis I have used a range of methods covering different scales in space and time (Figure 2). For the large-scale and long-term perspective in **papers I & II**, we followed the newly invaded *M. leidyi* population in Skagerrak, Kattegat and Baltic Sea during one year. Multinet sampling was used, allowing for stratified sampling. The morphological species identification was also confirmed with molecular methods. The research questions in **papers I & II** were addressed with statistical modeling (Generalized Additive Models in **paper I**, and General Linear Models in **paper II**).

**Paper II** focused on a smaller spatial and temporal scale relevant for individual jellyfish. Here, we used video-profiling that allow for a higher resolution of the vertical distribution. This study was conducted in the same region as **paper I**.



▲Figure 2. Visualization of the different scales targeted in **papers I-V**

The predator-prey interactions in **paper III** were studied using incubation experiments. The resulting clearance rates from **paper III** were applied to parts of the field data in **paper I**, to estimate the potential predation pressure on *M. leidyi*.

Finally in **paper IV**, we used a theoretical approach to explore a larger ecosystem question relevant to the Baltic Sea. A generic model were used ("Killing the Winner", Thingstad et al. 2010) with observations from literature and **paper I**.

My PhD work was part of the BONUS EU project BAZOOCA (Baltic ZOOplankton Cascades), a Nordic cooperation aiming to understand the impact and potential cascading effects of *M. leidyi* in the Baltic Sea food web. While the papers included in my thesis are focused mainly on adult life stages, the larval perspective is covered in detail in an earlier thesis (Jaspers 2012) including related papers.

# Results and discussion

## The biophysical environment

The ocean is a highly dynamic and variable place, with distinct water masses with different environmental characteristics. Environmental gradients vary on vertical, horizontal and temporal scales and are characteristic to the pelagic habitat. Vertical gradients are especially important for planktonic organisms. With their limited mobility plankton cannot perceive the large scale horizontal patterns (on a kilometer scale) of the ocean, however, the vertical gradients (µm-m) are easily accessible for most plankton. The distribution of a plankton organism will thus depend on the characteristics and movement of the water, in interaction with its behavior (e.g. in response to the environment or other organisms).

## The shaping effects of salinity and temperature

Salinity and temperature have fundamental physiological impacts on all aquatic organisms, and will largely determine the large-scale distribution patterns (**papers I & II**, Angiletta et al. 2009, Holst & Jarms 2010, Albert 2012). Temperature regulates a broad range of physiological processes related to population growth, such as egg production in ctenophores (Costello et al. 2006) or strobilisation in scypozoans (Liu et al. 2009), as well as feeding (Friis Möller & Riisgård 2007) and somatic growth (Hansson 1997). Thus, temperature can partly control gelatinous zooplankton populations (e.g. Ruiz et al. 2012), which is generally reflected in their seasonality (e.g. **papers I & II**, Costello et al. 2006, Zang et al. 2012).

Salinity is a major constraining factor for many organisms in the brackish water of the Baltic Sea (Renabe & Schlieper 1958). With the exception of a few hydromedusae (Jankowski 2001) jellyfishes are marine osmoconformers and thus regulate their osmolarity to the surrounding water (Arai 1997, Foshtomi et al. 2007).

*M. leidyi* is observed in a wide range of salinities and temperatures in both its native and exotic habitats (see figure 1 and table 2 in **paper I**, references therein), with established populations in high saline (Mianzan et al. 2010) as well as in brackish habitats (Kremer 1994). Strong salinity constrains were found on both the adult and larval *M. leidyi* in the Baltic Sea (**papers I & II**), limiting the establishment of permanent populations of *M. leidyi*. A tenfold decrease in adult abundances was found when going from higher saline water in Skagerrak and Kattegat, to the brackish water in the Baltic Proper (Figure 4 in **paper I**). The low numbers of larvae and transitional-to-adult stage ration further indicated a failed reproduction in the low saline water of the Baltic Proper (**paper II**), which agrees with a salinity constrained egg production (Jaspers et al. 2011, Lehtiniemi et al. 2012).

The preference for high salinities in *M. leidyi* (**papers I & II**) was also driving the vertical distribution, which differed along the salinity gradient from Skagerrak into the Baltic Proper. Lower salinities in surface layers generally resulted in a deeper occurrence of adult *M. leidyi* (**paper I**). This may partly be due to the habitat structuring effects of salinity and temperature as they are directly related to the water density. In the Baltic and surrounding Seas, which exhibit large salinity differences, salinity contributes most to the density (**paper I**). Vertical migration in *M. leidyi* seemed to have been prohibited by strong salinity stratification (figure 8, **paper III**). Jellyfish aggregations are commonly found associated to density discontinuities (Graham et al. 2001). This pattern may be due to the passive aggregation due to the osmolarity differences between the surrounding water and the jellyfish, or due to behavioral or physiological responses to the sudden salinity stress (Graham et al. 2001).

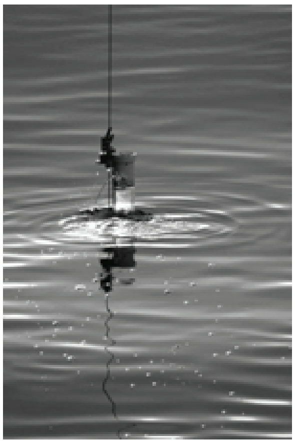
*M. leidyi* and *M. ovum* showed opposite responses to salinity. *M. ovum* was found in highest abundances in the low salinities in the central Baltic Proper (**paper II**). Also, the abundance of *M. ovum* was negatively correlated with temperatures, which accords with its distribution in the Arctic (Siferd & Conover 1992, Raskoff et al. 2005).

## Light as an ecological driver

Light drives life and productivity, and is therefore the major structuring factor in the pelagic. It fuels the primary production in the euphotic zone (given the presence of nutrients), which is further channeled to secondary producers and predators. In addition to such bottom-up effect, light also has important top-down implications as many fish and some invertebrates use vision to locate prey (Guthrie 1986, Torgersen 2001).

Visual encounter with prey is dependent on attributes of the prey (e.g. size, contrast, movement, and coloring) and the predator's visual system in combination with the light irradiance levels (Aksnes & Utne 1997, Utne 1997). The light irradiance in turn, depends on the depth and the optical properties INFOBOX-4 of the water (Aksnes & Utne 1997). Thus, light can affect both growth and survival (Fiksen et al. 2002) through controlling the efficiency at which visual predators feed (Aksnes et al. 2004).

### INFO BOX 4 : Water optics



When light passes through water it will be scattered and/or absorbed. This decrease of light with depth is described by an exponential function (Kirk 1994). The water molecules themselves, as well as other components in the water like colored dissolved organic matter (CDOM), phytoplankton and other particles play major roles in the absorption and scattering of light (Wozniak & Dera 2007). The sum of the absorbance and scatter is called the beam attenuation (the decrease of light), and is a characteristic of the nature of the medium. These parameters are inherent optical properties, and are independent of the amount of irradiance (Kirk 1994, Wozniak & Dear 2007).

◄ sampling of water for optical measurements

In contrast to visual foragers jellyfish are independent of vision, but rather use tactile senses, and their feeding rates are thus independent of light

(Francett & Jenkins 1988, Sørnes & Aksnes 2004, Titelman & Hansson 2006). The optical habitat can therefore affect the balance between predators using either of these two feeding modes, with consequences for the ecosystem structure (**paper V**).

Another light dependent behavior that is common among many zooplankton and fish is diel vertical migration (DVM), where organisms typically avoid risky illuminated waters during daytime and migrates deeper, while returning to feed in the surface when protected by the nightly darkness (Ringelberg 1995, Hays 2003, Pearre 2003). Many gelatinous zooplanktons also vertically migrate on a daily basis (**paper III**, Graham et al. 2001). It is more common in the pelagic cnidarians phyla (e.g. Schuyler & Sullivan 1997, Kaartvedt et al. 2011) than in the ctenophore phyla (Graham et al. 2001). We observed DVM in *M. leidyi*, and a seeming avoidance of high irradiance levels (**paper III**). The DVM however depended on life stage (e.g. size), and only occurred at locations where other environmental drivers (i.e. salinity) were less prominent (**paper III**). The resulting vertical distribution, however, may have important consequences on the dispersal and spread (Albert 2007). Vertical migration in response to light (**paper III**, Wang et al. 1995, Sørnes et al. 2007, Dupont & Aksnes 2010), or tidal turbulence (Kopacz 1994), is important for some jellyfish populations to retain in their coastal habitat.

### Effect of oxygen

Oxygen usually varies with depth, from the oxygenated surface layers down to the bottom, that in extreme but not uncommon cases can be oxygen depleted. Because the tolerance level to hypoxia is highly species dependent, a reduction in oxygen will typically alter the species composition, rather than increasing the distribution of a specific species (Ekau et al. 2010). Many gelatinous plankton do well in poor oxygen conditions when compared to co-occurring zooplankton and fish (Grove & Breitsburg 2005, Ekau et al. 2010). Their jelly tissue seems to function as a buffer allowing them to survive for hours without oxygen (Thuesen et al. 2005a, Thuesen et al. 2005b). Thus, observations of gelatinous plankton in poorly oxygenated waters are common (e.g. Purcell et al. 2001, Moriarty et al. 2012), and may in some cases increase the feeding rates on prey, whose mobility and escape abilities are hampered by low oxygen levels (Shoji et al. 2005, Decker et al. 2004). Also, poorly oxygenated water can function as a predator refuge (Purcell et al. 2001).

In the Baltic and adjacent Seas we found no relation between *M. leidyi* and the oxygen concentration (**papers I-III**), which is in agreement with a high tolerance to varying oxygen levels.

### A note about turbulence

Water motion on different scales is essential for life in the plankton. While turbulence is not covered in my papers, it can modify the vertical distribution of gelatinous plankton by mixing as well as affect behavior and sensory functions directly (Visser et al. 2009). While small scale turbulence may increase encounter rates between plankton organisms (Kiørboe & Saiz 1995), larger scale turbulence can be directly damaging for the fragile bodies of gelatinous plankton (Acuña et al. 1994) and may disturb their feeding activities (Costello et al. 2012). Gelatinous plankton may therefore directly respond to turbulence by altering their motility or behavior (Shank & Graham 1987, Rakow & Graham 2006, Albert 2011) and their preferred vertical distribution (Miller 1974, Albert 2007), which has also been indicated for *M. leidyi* (Mianzan et al. 2010).

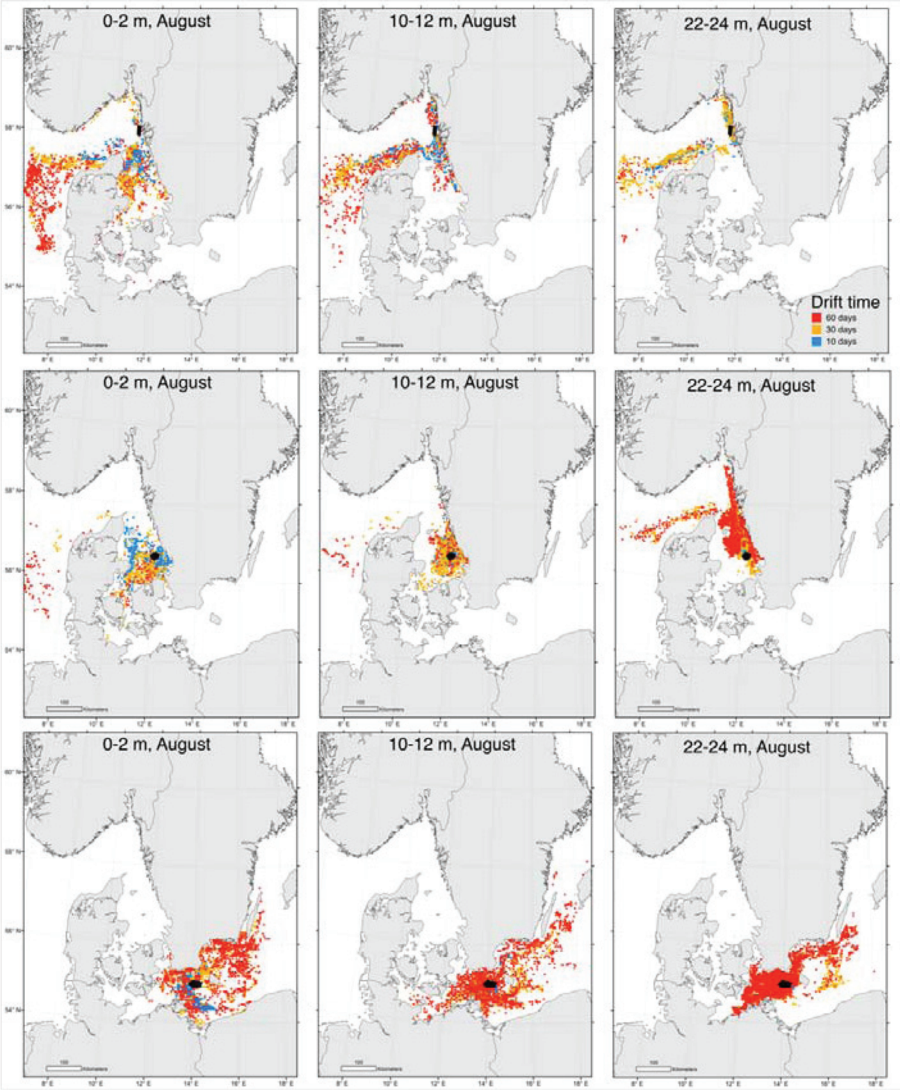
## Drift and distribution of *Mnemiopsis* in Swedish waters

Although the swimming potential of some jellyfish is large (Moriarty et al. 2012), jellyfish as other plankton drift with tides and currents (Graham et al. 2001). Tides or local current systems can have diluting or aggregating effects depending on jellyfish's vertical distribution and migration behavior (Graham et al. 2001).

The vertical depth preference of *M. leidyi* is critical for the dispersal in the Baltic Sea system, where the counter-current system can potentially have huge implications for spreading (Barz et al, 2006, Corell et al. 2012). *M. leidyi*'s vertical distribution seemed to be highly dependent on salinity (**papers I & III**) and the degree of stratification (**paper III**), and at some locations to the daily variation in light (**paper III**).

The Baltic Sea is seemingly acting as a sink for the *M. leidyi* population (**papers I & II**). During high abundance seasons the Baltic Proper was most likely reseeded from the high-saline areas in Skagerrak and Kattegat (**paper I**), when reproduction was at peak (**paper II**). However, whether *M. leidyi* overwinters in the region or not, is still uncertain. Overwintering of *M. leidyi* in the region was initially reported from the Kiel Bight during the first years after the introduction (Javidpour et al. 2009), but has not been reported since. In some native and exotic habitats *M. leidyi* cannot survive the low winter temperatures and are instead dependent on reseeding from other source populations (Costello et al. 2006, Shiganova et al. 2001).

Drift from the North Sea, where the closest reported year round population exists (van Ginderdeuren et al. 2012), may also reseed the *M. leidyi* to Skagerrak, Kattegat and the Baltic proper from year to year (**papers I & II**). Examples of preliminary outputs from drift modeling (Figure 3), indicates that the first individuals that appeared in Skagerrak in August (paper I) originated with a large probability from the North Sea (Figure 3, top panel), and further into the Kattegat (Figure 3). The drift model showed also a large variability in dispersal pattern depending on depth.



▲Figure 3. Back-tracking drift of *M. leidyi*, starting from the location of the monitoring stations (black cells) starting in August, approximately the time of the year when *M. leidyi* first appeared in the samples during 2009 (**paper I**). The colored cells shows the most probable source locations given the start location and a drift time of 10 (blue), 30 (yellow) or 60 (red) days. Haraldsson, Jaspers, Moksnes & Jonsson (*in prep*). For location and name of stations see **paper I**.

While the biophysical environment and ocean currents will set the stage and limitations of plankton distributions, interactions with prey, predators and competitors have the potential to further alter behavior and thus also distributions. For example, in laboratory experiments *M. leidyi* responds to the scent of a gelatinous predator by altering its vertical distribution (Titelman et al. 2012).

### Food web interactions

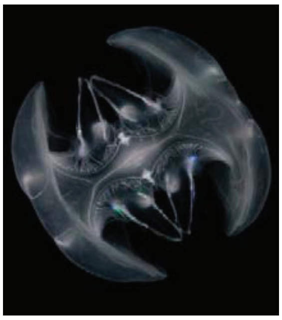
As most animals, gelatinous plankton at large, as well as *M. leidyi*, are both a prey and a predator simultaneously. Gelatinous plankton have often been considered as trophic dead ends, contributing to a less diverse ecosystem (Sommer et al. 2002). However, predation on gelatinous plankton is widespread over many groups of organisms, although quantitative data is generally scarce (Arai 2005). The different life stages are exposed to variable predation risks. Benthic species may be able to control scyphozoan populations by predating on the benthic polyp stages (Hernroth & Gröndahl 1985), while some animals like the Leatherback turtle are pure jellyfish specialists (Heaslip et al. 2012). Many fish also feed on jellyfish (reviewed in Ates 1988, Purcell & Arai 2001, Arai 2005, Cordona et al. 2012) and the predation pressure may vary temporarily depending on the accessibility of gelatinous plankton or other prey (Mianzan et al. 1996). In addition, pelagic microbes refuel energy and nutrients from gelatinous plankton into the pelagic food web (Hansson & Norrman 1995, Titelman et al. 2006, Riemann et al. 2006, Condon et al. 2011).

Predation by other gelatinous plankton is also common (**paper IV**, Arai 2005, Purcell 1991) and in some cases these predators may control the jellyfish populations (e.g. Purcell & Cowan 1995, Finenko et al. 2003). For example, *Cyanea capillata* is an important predator on *Aurelia aurita* in Scandinavian waters (Båmstedt et al. 1994, Hansson 1997, Titelman et al. 2007).

In its native habitat populations of *M. leidyi* may be controlled by the Atlantic Sea Nettle (*Chrysaora quinquecirrha*), while the ctenophore *Beroe ovata* controls populations in the Black Sea (Finenko et al. 2003). One common reason for the success of alien species is the lack of natural predators (Wolfe 2002). This was clearly illustrated in the case of *M. leidyi* in the Black Sea, which reached extreme abundances prior to the second introduction of *B. ovata* (Kideys 2002).

Potential predators in the Skagerrak to Baltic include *C. capillata* (Hosia & Titelman 2011) and several *Beroe* species. *B. gracilis* fed well and reproduced on a *M. leidyi* diet (**paper IV**), despite that *B. gracilis* is described throughout the literature as a specialist on *Pleurobrachia* sp. (Greve 1970, Greve & Reiners 1988). Applying the field data from **paper I** to rates in **paper IV** revealed an overall potential mortality rate of only $8.8\times10^{-4}$ day$^{-1}$, which is not enough to reduce the *M. leidyi* population. The low predation mortality was in part due to the large size of *M. leidyi*, which protected them from being fully ingested. During the rest of the year, the temporal and spatial overlap was larger between *Beroe spp*. and *P. pileus*, than between *Beroe spp* and *M. leidyi* (Haraldsson & Hansson 2011), and further indicating *Beroe*'s limited ability to control and shape the distribution of *M. leidyi*'s in the Baltic region.

## INFO BOX 5 : The predatory jellyfish



▲the view of the prey as *Mnemiopsis* approaches
Photo by LJ Hansson

Gelatinous plankton plankton depend on their tactile senses (Colin et al. 2010, Sørnes & Aksnes 2005), and some also use chemical cues (Arai 1991, Tamburri et al. 2000) to detect their prey. Despite their comparably simple feeding strategy (when compared to e.g. visually feeding fish), their large body volume increases the encounter rate, and compensates for their limited mobility and often passive prey capture mechanisms (Acuña et al. 2011). Their killing rates increases proportionally with prey density (e.g. Båmstedt et al. 1994, ref) often up to extreme prey densities were many other zooplanktivours predators would experience satiation or handling limitations Sørnes & Aksnes 2005). This is in part facilitated by their large gut volume (Hansson & Kiørboe 2006) and quick digestion time (Martinusen & Båmstedt 1999), and allows them to utilize patchy or temporary food resources (Hansson & Kiørboe 2006).

*M. leidyi* is an efficient feeder (Colin et al 2010) on both mesozooplankton (Riisgård et al. 2007, Finenko et al. 2006, Granhag et al. 2011) and ichthyoplankton (Cowan & Houde 1993, Purcell & Arai 2001). Because of the moderate abundances of *M. leidyi* in Scandinavian waters since 2009-2010 predation mortality on zooplankton in general is minute. Despite being 30-50 times higher in Skagerrak and Kattegat compared to the Baltic Proper, potential mortality never exceeded 4 % $d^{-1}$ in 2009-2010 (Haraldsson & Hansson 2011). This is too low to control zooplankton populations (Finenko et al. 2006). In the Skagerrak-Baltic *M. leidyi* is thus at present not a strong competitor with commercially important zooplanktivorous fishes (Tiselius et al. 2011, Haraldsson & Hansson 2011). Also, their predation pressure on cod eggs and larvae is ignorable (Jaspers et al. 2011).

## Changing environmental drivers and ecosystem effects

Degradation of marine ecosystems due to anthropogenic activities is today evident on a global scale (Halpern et al. 2008). Shifts in ecosystem structure and function have been reported from around the world (e.g. Hare & Mantua 2000, Cury & Shannon 2004, Rodionov & Overland 2005, Alheit et al. 2005, Daskalov et al. 2007). Such regime shifts are typically trigged by changes in climatic or environmental drivers or by unsustainable resource utilization (Sheffer et al. 2001, Collie et al. 2004). In some cases this has been shown to favor gelatinous plankton, and the system has turned from a fish to a jellyfish dominated system (Brodeur et al. 2002, Lynam et al. 2006, Daskalov et al. 2007). Increases in gelatinous zooplankton abundances have been linked to a range of factors, although few have investigated the actual mechanisms behind.

One factor that has the potential to change the competitive relationship between visually feeding fish and tactile feeding jellyfish is the light environment. During illuminated conditions fish are more efficient predators of zooplankton than are jellyfish (Sørnes & Aksnes 2004). However, as the water clarity is directly related to the size of the feeding habitat for visual feeders, a reduction in water clarity may open up a competitive space for the jellyfish. Some evidence exist of a general darkening of oceans (Aksnes et al. 2009, Aksnes & Ohman 2009), which has in some instances been linked to the reduced biomasses of zooplanktivorous fish (Aksnes et al. 2004, Sørnes & Aksnes 2006, Aksnes 2007).

The Baltic Sea is a heavily exposed ecosystem experiencing extensive environmental changes (see table 1 **paper V**). One of the major problems in the Baltic is eutrophication (Struck et al. 2000, Andersen et al. 2011) with reduced water clarity as a consequence (Sanden & Håkansson 1996, Fleming-Lehtinen & Laamanen 2012). In **paper V** we used data from the Baltic Sea system to parameterize a theoretical model investigating the competitive relationship between zooplanktivorous fish (sprat and herring) and gelatinous zooplankton (the dominant gelatinous plankton at present, *Aurelia aurita* and *Cyanea capillata*). Despite the simplicity of the model, it gave general insight of a jellyfish system when going from an oligotrophic to eutrophic state (**paper V**).

Initially, the increased eutrophication and productivity is channeled to the common resource (zooplankton) and the zooplanktivorous fish (sprat and herring). This is in line with historically estimated fish biomasses, which increased during the 1950's in accordance with increased eutrophication (Thurow et al. 1997). At a later stage the productivity is channeled to the top predator (cod) and finally to the jellyfish. For the visual feeder, eutrophication had a two-sided effect with an optimal degree of eutrophication (Figure 4 and 5 in **paper V**) where fish biomass is maximum. After this threshold the feeding habitat of the visual feeder decreases, as does their ability to utilize the resource, and the zooplankton are instead utilized by the gelatinous plankton. Comparison with the present state of eutrophication indicates that the Baltic Sea is gradually approaching the potential tipping point, at which gelatinous plankton may be favored (Figure 5 in **paper V**).

In summary, this thesis shows a range of factors with differing significance, that effects the distribution of the newly invaded *M. leidyi* in Scandinavian waters. Salinity is the major driving factor in this habitat, which in combination with drift and dispersal shapes *M. leidyi*’s distribution horizontally, vertically and temporally. Even migration behavior seems to be prohibited by strong salinity stratification, and the potential controlling effect of the predator *B. gracilis*, is overshadowed by the forcing factors of salinity. However, with the gradual decreasing light environment in the Baltic Proper the environment may slowly turn to a place more favorable to jellyfish.

## Conclusions and perspectives

The main findings of this thesis can be summarized by:

- *Mnemiopsis leidyi* has not established a year round population in the Baltic Sea, Skagerrak or Kattegat, but seem to be transported in by advection, most likely from the North Sea (**papers I & II**).
- Salinity constrains *M. leidyi* on both small (**paper III**) and large (**papers I & II**) spatial scales. It hinders vertical movement (**paper III**), which may affect the advection of the populations. It also constrains the establishment of a year round population in the Baltic Proper (**papers I & II**).
- Some life stages (size) of *M. leidyi* perform diel vertical migrations. The migration behavior was most likely in response to light, which may reflect avoidance of predators (**paper III**). This is the first study indicating a light sensitivity in *M. leidyi*.
- *M. leidyi* have a predator in the native ctenophore *Beroe gracilis*, in addition to previously known beroid predators, which feeds and reproduces on a *M. leidyi* diet. However, *M. leidyi* is protected by a size refuge as *B. gracilis* cannot ingest *M. leidyi* larger than themselves (**paper III**). *B. gracilis* could not control the *M. leidyi* populations (**paper III**).
- A theoretical model shows that eutrophication has a two-sided effect on visually feeding organisms (fish), opposed to tactile predators (jellyfish). The increased productivity in association with eutrophication will at first increase the biomass of the visual feeding fish. However, after a given threshold, the water clarity gets reduced as does the ability of visual feeders to utilize the resource (**paper V**), and the mass of the system is shifted to the jellyfish.
- The model suggests that the light environment is important for the competition between visual (fish) and tactile feeders (jellyfish), and that the current high cod fishery in the Baltic Proper contributes to a suppression of the Baltic Sea jellyfish biomass (**paper V**).

# References

Acuña, J. L., Deibel, D., & Sooley, S. (1994). A simple device to transfer large and delicate planktonic organisms. *Limnology and Oceanography, 39*(8), 2001-2003.

Acuña, J. L., López-Urrutia, A., & Colin, S. (2011). Faking Giants: The evolution of high prey clearance rates in jellyfishes. *Science, 333*(6049), 1627-1629.

Aksnes, D. L. (2007). Evidence for visual constraints in large marine fish stocks. *Limnology and Oceanography, 52*(1), 198-203.

Aksnes, D. L., Dupont, N., Staby, A., Fiksen, O., Kaartvedt, S., & Aure, J. (2009). Coastal water darkening and implications for mesopelagic regime shifts in Norwegian fjords. *Marine Ecology-Progress Series, 387*, 39-49.

Aksnes, D. L., Nejstgaard, J., Soedberg, E., & Sørnes, T. (2004). Optical control of fish and zooplankton populations. *Limnology and Oceanography, 49*(1), 233-238.

Aksnes, D. L., & Ohman, M. D. (2009). Multi-decadal shoaling of the euphotic zone in the southern sector of the California Current System. *Limnology and Oceanography, 54*(4), 1272-1281.

Aksnes, D. L., & Utne, A. C. W. (1997). A revised model of visual range in fish. *Sarsia, 82*(2), 137-147.

Albert, D. J. (2007). *Aurelia labiata* medusae (Scyphozoa) in Roscoe Bay avoid tidal dispersion by vertical migration. *Journal of Sea Research, 57*(4), 281-287.

Albert, D. J. (2011). What's on the mind of a jellyfish? A review of behavioural observations on *Aurelia sp* jellyfish. *Neuroscience and Biobehavioral Reviews, 35*(3), 474-482.

Albert, D. J. (2012). Controlled activation of species typical behaviour to low salinity, seawater movement and seawater depth in *Aurelia labiata* (Scyphozoa) Jellyfish in Roscoe Bay, Canada. *Hydrobiologia, 680*(1), 179-186.

Alheit, J., Möllmann, C., Dutz, J., Kornilovs, G., Loewe, P., Mohrholz, V., & Wasmund, N. (2005). Synchronous ecological regime shifts in the central Baltic and the North Sea in the late 1980s. *Ices Journal of Marine Science, 62*(7), 1205-1215.

Allwein, J. (1968). Seasonal occurence of hydromedusae at Helsingör, Denmark, 1966-67. *Ophelia, 5*, 207-214.

Andersen, J. H., Axe, P., Backer, H., Carstensen, J., Claussen, U., Fleming-Lehtinen, V., . . . Villnas, A. (2011). Getting the measure of eutrophication in the Baltic Sea: towards improved assessment principles and methods. *Biogeochemistry, 106*(2), 137-156.

Angiletta, M. J., Jr. (2009). *Thermal adaptation: a theoretical and empiricial synthesis*.

Arai, M. N. (1991). Attraction of *Aurelia* and *Aequorea* to prey. *Hydrobiologia, 216*, 363-366.

Arai, M. N. (1997). A functional biology of Scyphozoa. *Chapman & Hall, New York, 316 pp.*

Arai, M. N. (2005). Predation on pelagic coelenterates: a review. *Journal of the Marine Biological Association of the United Kingdom, 85*(3), 523-536.

Ates, R. M. L. (1988). Medusivorous fishes, a review. *Zoologische Mededelingen (Leiden), 62*(1-4), 29-42.

Båmstedt, U., Martinussen, M. B., & Matsakis, S. (1994). Tryophodynamics of the 2 scyphozoan jellyfish, *Aurelia aurita* and *Cyanea capillata*, in western Norway. *Ices Journal of Marine Science, 51*(4), 369-382.

Barz, K., Hinrichsen, H. H., & Hirche, H. J. (2006). Scyphozoa in the Bornholm basin (central Baltic Sea) - The role of advection. *Journal of Marine Systems, 60*(1-2), 167-176.

Behrends, G., & Schneider, G. (1995). Impact of *Aurelia aurita* medusae (cnidaria, scyphozoa) on the standing stock and community composition of mesozooplankton in the Kiel Bight (western Baltic Sea). *Marine Ecology-Progress Series, 127*(1-3), 39-45.

Bilio, M., & Niermann, U. (2004). Is the comb jelly really to blame for it all? *Mnemiopsis leidyi* and the ecological concerns about the Caspian Sea. *Marine Ecology Progress Series, 269*, 173-183.

Boersma, M., Malzahn, A. M., Greve, W., & Javidpour, J. (2007). The first occurrence of the ctenophore *Mnemiopsis leidyi* in the North Sea. *Helgoland Marine Research, 61*(2), 153-155.

Brodeur, R. D., Sugisaki, H., & Hunt, G. L. (2002). Increases in jellyfish biomass in the Bering Sea: implications for the ecosystem. *Marine Ecology-Progress Series, 233*, 89-103.

Cardona, L., Alvarez de Quevedo, I., Borrell, A., & Aguilar, A. (2012). Massive Consumption of Gelatinous Plankton by Mediterranean Apex Predators. *Plos One, 7*(3).

Colin, S. P., Costello, J. H., Hansson, L. J., Titelman, J., & Dabiri, J. O. (2010). Stealth predation and the predatory success of the invasive ctenophore *Mnemiopsis leidyi*. *Proceedings of the National Academy of Sciences of the United States of America, 107*(40), 17223-17227.

Collie, J. S., Richardson, K., & Steele, J. H. (2004). Regime shifts: can ecological theory illuminate the mechanisms? *Progress in Oceanography, 60*(2-4), 281-302.

Condon, R. H., Graham, W. M., Duarte, C. M., Pitt, K. A., Lucas, C. H., Haddock, S. H. D., . . . Madin, L. P. (2012). Questioning the Rise of Gelatinous Zooplankton in the World's Oceans. *Bioscience, 62*(2), 160-169.

Condon, R. H., Steinberg, D. K., del Giorgio, P. A., Bouvier, T. C., Bronk, D. A., Graham, W. M., & Ducklow, H. W. (2011). Jellyfish blooms result in a major microbial respiratory sink of carbon in marine systems. *Proceedings of the National Academy of Sciences of the United States of America, 108*(25), 10225-10230.

Corell, H., Moksnes, P. O., Engqvist, A., Doos, K., & Jonsson, P. R. (2012). Depth distribution of larvae critically affects their dispersal and the efficiency of marine protected areas. *Marine Ecology Progress Series, 467*, 29-+.

Costello, J. H., Bayha, K. M., Mianzan, H. W., Shiganova, T. A., & Purcell, J. E. (2012). Transitions of *Mnemiopsis leidyi* (Ctenophora: Lobata) from a native to an exotic species: a review. *Hydrobiologia, 690*(1), 21-46.

Costello, J. H., Sullivan, B. K., Gifford, D. J., Van Keuren, D., & Sullivan, L. J. (2006). Seasonal refugia, shoreward thermal amplification, and metapopulation dynamics of the ctenophore *Mnemiopsis leidyi* in Narragansett Bay, Rhode Island. *Limnology and Oceanography, 51*(4), 1819-1831.

Cowan, J. H., & Houde, E. D. (1993). Relative predation potentials of scyphomedusae, ctenophores and planktivorous fish on ichthyoplankton in Chesapeake Bay. *Marine Ecology Progress Series, 95*(1-2), 55-65.

Cury, P., & Shannon, L. (2004). Regime shifts in upwelling ecosystems: observed changes and possible mechanisms in the northern and southern Benguela. *Progress in Oceanography, 60*(2-4), 223-243.

Daskalov, G. M. (2002). Overfishing drives atrophic cascade in the Black Sea. *Marine Ecology Progress Series, 225*, 53-63.

Daskalov, G. M., Grishin, A. N., Rodionov, S., & Mihneva, V. (2007). Trophic cascades triggered by overfishing reveal possible mechanisms of ecosystem regime shifts. *Proceedings of the National Academy of Sciences of the United States of America, 104*(25), 10518-10523.

Daskalov, G. M., & Mamedov, E. V. (2007). Integrated fisheries assessment and possible causes for the collapse of anchovy kilka in the Caspian Sea. *Ices Journal of Marine Science, 64*(3), 503-511.

Decker, M. B., Breitburg, D. L., & Purcell, J. E. (2004). Effects of low dissolved oxygen on zooplankton predation by the ctenophore *Mnemiopsis leidyi*. *Marine Ecology-Progress Series, 280*, 163-172.

Dinasquet, J., Titelman, J., Møller, L. F., Setala, O., Granhag, L., Andersen, T., . . . Riemann, L. (2012). Cascading effects of the ctenophore *Mnemiopsis leidyi* on the planktonic food web in a nutrient-limited estuarine system. *Marine Ecology Progress Series, 460*, 49-61.

Dupont, N., & Aksnes, D. L. (2010). Simulation of optically conditioned retention and mass occurrences of Periphylla periphylla. *Journal of Plankton Research, 32*(6), 773-783.

Faasse, M. A., & Bayha, K. M. (2006). The ctenophore *Mnemiopsis leidyi* A. Agassiz 1865 in coastal waters of the Netherlands: an unrecognized invasion? *Aquatic Invasions, 1*(4), 270-277.

Fiksen, O., Aksnes, D. L., Flyum, M. H., & Giske, J. (2002). The influence of turbidity on growth and survival of fish larvae: a numerical analysis. *Hydrobiologia, 484*(1-3), 49-59.

Finenko, G. A., Kideys, A. E., Anninsky, B. E., Shiganova, T. A., Roohi, A., Tabari, M. R., . . . Bagheri, S. (2006). Invasive ctenophore *Mnemiopsis leidyi* in the Caspian Sea: feeding, respiration, reproduction and predatory impact on the zooplankton community. *Marine Ecology Progress Series, 314*, 171-185.

Finenko, G. A., Romanova, Z. A., Abolmasova, G. I., Anninsky, B. E., Svetlichny, L. S., Hubareva, E. S., . . . Kideys, A. E. (2003). Population dynamics, ingestion, growth and reproduction rates of the invader Beroe ovata and its impact on plankton community in Sevastopol Bay, the Black Sea. *Journal of Plankton Research, 25*(5), 539-549.

Fleming-Lehtinen, V. L., M. (2012). Long-term changes in Secchi depth and the role of phytoplankton in explaining light attenuation in the Baltic Sea. *Estuarine, Coastal and Shelf Science, 102-103*, 1-10.

Foshtomi, M. Y., Abtahi, B., Sari, A. E., & Taheri, M. (2007). Ion composition and osmolarity of Caspian Sea ctenophore, *Mnemiopsis leidyi*, in different salinities. *Journal of Experimental Marine Biology and Ecology, 352*(1), 28-34.

Francett, M. S., & Jenkins, G. P. (1988). Predatory impact of scyphomedusae on ichthyoplankton and other zooplankton in Port Phillip Bay. *Journal of Experimental Marine Biology and Ecology, 116*, 63-77.

Gorokhova, E., Lehtiniemi, M., Viitasalo-Frosen, S., & Haddock, S. H. D. (2009). Molecular evidence for the occurrence of ctenophore *Mertensia ovum* in the northern Baltic Sea and implications for the status of the *Mnemiopsis leidyi* invasion. *Limnology and Oceanography, 54*(6), 2025-2033.

Graham, W. M. (2001). Numerical increases and distributional shifts of *Chrysaora quinquecirrha* (Desor) and *Aurelia aurita* (Linne) (Cnidaria : Scyphozoa) in the northern Gulf of Mexico. *Hydrobiologia, 451*(1-3), 97-111.

Granhag, L., Majaneva, S., & Møller, L. F. (2012). First recordings of the ctenophore *Euplokamis sp* (Ctenophora, Cydippida) in Swedish coastal waters and molecular identification of this genus. *Aquatic Invasions, 7*(4), 455-463.

Granhag, L., Moller, L. F., & Hansson, L. J. (2011). Size-specific clearance rates of the ctenophore *Mnemiopsis leidyi* based on in situ gut content analyses. *Journal of Plankton Research, 33*(7), 1043-1052.

Greve, W. (1970). Cultivation experiments on North Sea ctenophores. *Helgolander Wissenschaftliche Meeresuntersuchungen, 20*(1-4), 304-549.

Greve, W. (1995). Die Rippenquallen der sudlichen Nordsee und ihre interspezifischen relationen. *Wissenschaftlicher Film*, Begleitpublikation C 1182. Institut für den Wissenschaftlichen Film, Göttingen, p 2-14

Greve, W., & Reiners, F. (1988). Plankton dynaimcs in German Bight – a systems approach. *Oecologia, 77*(4), 487-496.

Grove, M., & Breitburg, D. L. (2005). Growth and reproduction of gelatinous zooplankton exposed to low dissolved oxygen. *Marine Ecology Progress Series, 301*, 185-198.

Guthrie, D. M. (1986). Role of vision in fish behavior. *In the behavior of Teleost fishes, Ed. Pitcher TJ. London: Croom Helm*, pp 75-113.

Hagadorn, J. W., Dott, R. H., & Damrow, D. (2002). Stranded on a Late Cambrian shoreline: Medusae from central Wisconsin. *Geology, 30*(2), 147-150.

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., . . . Watson, R. (2008). A global map of human impact on marine ecosystems. *Science, 319*(5865), 948-952.

Hamner, W. M., & Dawson, M. N. (2009). A review and synthesis on the systematics and evolution of jellyfish blooms: advantageous aggregations and adaptive assemblages. *Hydrobiologia, 616*, 161-191.

Hansson, H. (2006). Ctenophores of the Baltic and adjacent Seas – the invader *Mnemiopsis* is here! *Aquatic Invasions, 1*(4), 295-298.

Hansson, L. J. (1997). Effect of temperature on growth rate of *Aurelia aurita* (Cnidaria, Scyphozoa) from Gullmarsfjorden, Sweden. *Marine Ecology Progress Series, 161*, 145-153.

Hansson, L. J., & Kiørboe, T. (2006). Effects of large gut volume in gelatinous zooplankton: ingestion rate, bolus production and food patch utilization by the jellyfish *Sarsia tubulosa*. *Journal of Plankton Research, 28*(10), 937-942.

Hansson, L. J., & Norrman, B. (1995). Release of dissolved organic carbon (DOG) by the scyphozoan jellyfish *Aurelia aurita* and its potential influence on the productivity of planktonic bacteria. *Marine Biology, 121*(3), 527-532.

Haraldsson, M., & Hansson, L. (2011). New knowledge about the spatial and temporal changes of gelatinous zooplankton in the Baltic. *Scientific report for bazooca (report 2 / wp 1).*

Haraldsson, M., & Hansson, L. J. (2011). Predation effects of different size-classes of Mnemiopsis across the Baltic salinity gradient. *Scientific report for bazooca (report 4 / wp 1).*

Hare, S. R., & Mantua, N. J. (2000). Empirical evidence for North Pacific regime shifts in 1977 and 1989. *Progress in Oceanography, 47*(2-4), 103-145.

Haslob, H., Clemmesen, C., Schaber, M., Hinrichsen, H. H., Schmidt, J. O., Voss, R., . . . Koster, F. W. (2007). Invading *Mnemiopsis leidyi* as a potential threat to Baltic fish. *Marine Ecology Progress Series, 349*, 303-306.

Hays, G. C. (2003). A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia, 503*(1-3), 163-170.

Heaslip, S. G., Iverson, S. J., Bowen, W. D., & James, M. C. (2012). Jellyfish support high energy intake of Leatherback Sea Turtles (*Dermochelys coriacea*): Video evidence from animal-borne cameras.. *Plos One, 7*(3).

Hernroth, L., & Gröndahl, F. (1985). On the biology of *Aurelia aurita* (L). 2. Major factors regulating the occurrence of ephyrae and young medusae in the Gullmar fjord, western Sweden. *Bulletin of Marine Science, 37*(2), 567-576.

Holst, S., & Jarms, G. (2010). Effects of low salinity on settlement and strobilation of scyphozoa (Cnidaria): Is the lion's mane *Cyanea capillata* (L.) able to reproduce in the brackish Baltic Sea? *Hydrobiologia, 645*(1), 53-68.

Hosia, A., & Titelman, J. (2011). Intraguild predation between the native North Sea jellyfish *Cyanea capillata* and the invasive ctenophore *Mnemiopsis leidyi*. *Journal of Plankton Research, 33*(3), 535-540.

Huwer, B., Storr-Paulsen, M., Riisgård, H. U., & Haslob, H. (2008). Abundance, horizontal and vertical distribution of the invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea, November 2007. *Aquatic Invasions, 3*(2), 113-124.

Ivanov, V. P., Kamakin, A. M., Ushivtsev, V. B., Shiganova, T. A., Zhukova, O. P., Aladin, N., . . . Dumont, H. J. (2000). Invasion of the Caspian Sea by the comb jellyfish *Mnemiopsis leidyi* (Ctenophora). *Biological Invasions, 2*, 255-258.

Janas, U., & Zgrundo, A. (2007). First record of *Mnemiopsis leidyi* A. Agassiz, 1865 in the Gulf of Gdańsk (southern Baltic Sea). *Aquatic Invasions, 2*(4), 450-454.

Jankowski, T. (2001). The freshwater medusae of the world - a taxonomic and systematic literature study with some remarks on other inland water jellyfish. *Hydrobiologia, 462*, 91-113.

Jaspers, C. (2012). Ecology of gelatinous plankton. With emphasis on feeding interactions, distribution pattern and reproduction biology of *Mnemiopsis leidyi* in the Baltic Sea. *PhD thesis, Copenhagen*.

Jaspers, C., Haraldsson, M., Bolte, S., Reusch, T. B. H., Thygesen, U. H., & Kiørboe, T. (2012). Ctenophore population recruits entirely through larval reproduction in the central Baltic Sea. *Biology Letters, 8*(5), 809-812.

Jaspers, C., Titelman, J., Hansson, L. J., Haraldsson, M., & Ditlefsen, C. R. (2011). The invasive ctenophore *Mnemiopsis leidyi* poses no direct threat to Baltic cod eggs and larvae. *Limnology and Oceanography, 56*(2), 431-439.

Jaspers, C. H., Matilda, Lombard, F., Bolte, S., & Kiørboe, T. (2013). Seasonal dynamics of early life stages of invasive and native ctenophores give clues to invasion and bloom potential in the Baltic Sea. *Journal of Plankton Research*, 1-18.

Javidpour, J., Molinero, J. C., Peschutter, J., & Sommer, U. (2009). Seasonal changes and population dynamics of the ctenophore *Mnemiopsis leidyi* after its first year of invasion in the Kiel Fjord, Western Baltic Sea. *Biological Invasions, 11*(4), 873-882.

Kaartvedt, S., Titelman, J., Rostad, A., & Klevjer, T. A. (2011). Beyond the average: Diverse individual migration patterns in a population of mesopelagic jellyfish. *Limnology and Oceanography, 56*(6), 2189-2199.

Kideys, A. E. (2002). Fall and rise of the Black Sea ecosystem. *Science, 297*(5586), 1482-1484.

Kirk JTO (1994) Light and photosynthesis in aquatic ecosystems. Cambridge University Press, London-New York

Kiørboe, T., & Saiz, E. (1995). Planktivorous feeding in calm and turbulent environments, with emphasis on copepods. *Marine Ecology Progress Series, 122*(1-3), 135-145.

Knowler, D. (2005). Reassessing the costs of biological invasion: *Mnemiopsis leidyi* in the Black sea. *Ecological Economics, 52*, 187-199.

Kopacz, U. (1994). Evidence for titally induced vertical migration of some gelatinous zooplankton in the Wadden Sea area near sylt. *Helgolander Meeresuntersuchungen, 48*(2-3), 333-342.

Kremer, P. (1976). Population dynamics and ecological energetics of a pulsed zooplankton predator, the ctenophore *Mnemiopsis leidyi*. *In Wiley, M. (ed), Estuarine Processes; Uses, stresses and adaptations to the estuary. Academic Press, New York*, pp. 197-215.

Kremer, P. (1994). Pattern of abundance for *Mnemiopsis* in US coastal waters – a comparative overview. *Ices Journal of Marine Science, 51*(4), 347-354.

Kube, S., Postel, L., Honnef, C., & Augustin, C. (2007). *Mnemiopsis leidyi* in the Baltic Sea – distribution and overwintering between autumn 2006 and spring 2007. *Aquatic Invasions, 2*(2), 137-145.

Lehtiniemi, M., Lehmann, A., Javidpour, J., & Myrberg, K. (2012). Spreading and physico-biological reproduction limitations of the invasive American comb jelly *Mnemiopsis leidyi* in the Baltic Sea. *Biological Invasions, 14*(2), 341-354.

Liu, W. C., Lo, W. T., Purcell, J. E., & Chang, H. H. (2009). Effects of temperature and light intensity on asexual reproduction of the scyphozoan, *Aurelia aurita* (L.) in Taiwan. *Hydrobiologia, 616*, 247-258.

Llope, M., Daskalov, G. M., Rouyer, T. A., Mihneva, V., Chan, K. S., Grishin, A. N., & Stenseth, N. C. (2011). Overfishing of top predators eroded the resilience of the Black Sea system regardless of the climate and anthropogenic conditions. *Global Change Biology, 17*(3), 1251-1265.

Lowe, S., Browne, M., Boudjelas, S., & De Poorter, M. (2000). 100 of the World's worst invasive alien species. A selection from the global invasive species database. *Published by the Invasive Species Specialist Group (ISSG) a Specialist Group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN)*.

Lynam, C. P., Gibbons, M. J., Axelsen, B. E., Sparks, C. A. J., Coetzee, J., Heywood, B. G., & Brierley, A. S. (2006). Jellyfish overtake fish in a heavily fished ecosystem (vol 16, pg 492, 2006). *Current Biology, 16*(19), 1976-1976.

Lynam, C. P., Lilley, M. K. S., Bastian, T., Doyle, T. K., Beggs, S. E., & Hays, G. C. (2011). Have jellyfish in the Irish Sea benefited from climate change and overfishing? *Global Change Biology, 17*(2), 767-782.

Martindale, M. Q. (1987). Larval reproduction in the ctenophore *Mnemiopsis mccradyi* (order lobata). *Marine Biology, 94*(3), 409-414.

Martinussen, M. B., & Båmstedt, U. (1999). Nutritional ecology of gelatinous planktonic predators. Digestion rate in relation to type and amount of prey. *Journal of Experimental Marine Biology and Ecology, 232*, 61-85.

Mianzan, H. W., Mari, N., Prenski, B., & Sanchez, F. (1996). Fish predation on neritic ctenophores from the Argentine continental shelf: A neglected food resource? *Fisheries Research, 27*(1-3), 69-79.

Mianzan, H. W., Martos, P., Costello, J. H., & Guerrero, R. A. (2010). Avoidance of hydrodynamically mixed environments by *Mnemiopsis leidyi* (Ctenophora: Lobata) in open-sea populations from Patagonia, Argentina. *Hydrobiologia, 645*(1), 113-124.

Miller, R. J. (1974). Distribution and biomass of an estuarine ctenophore population, *Mnemiopsis leidyi* (A. Agassiz). *Chesapeake Science, 15*(1), 1-8.

Mills, C. E. (2001). Jellyfish blooms: are populations increasing globally in response to changing ocean conditions? *Hydrobiologia, 451*(1-3), 55-68.

Møller, L. F., & Riisgård, H. U. (2007). Respiration in the scyphozoan jellyfish *Aurelia aurita* and two hydromedusae (*Sarsia tubulosa* and *Aequorea vitrina*): effect of size, temperature and growth. *Marine Ecology Progress Series, 330*, 149-154.

Moriarty, P. E., Andrews, K. S., Harvey, C. J., & Kawase, M. (2012). Vertical and horizontal movement patterns of scyphozoan jellyfish in a fjord-like estuary. *Marine Ecology Progress Series, 455*, 1-12. Oliveira, O. (2007). The presence of the ctenophore *Mnemiopsis leidyi* in the Oslofjorden and considerations on the initial invasion pathways to the North and Baltic Seas. *Aquatic Invasions, 2*(3), 185-189.

Pang, K., & Martindale, M. Q. (2008). *Mnemiopsis leidyi* spawning and embryo collection. *Cold Spring Harbor Protocols*.

Parsons, T. R., & Lalli, C. M. (2002). Jellyfish population explosions: revisiting a hypothesis of possible causes. *Mer (Tokyo), 40*(3), 111-121.

Pearre, S. (2003). Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biological Reviews, 78*(1), 1-79.

Purcell, J. E. (1991). A review of cnidarians and ctenophores feeding on competitors in the plankton. *Hydrobiologia, 216*, 335-342.

Purcell, J. E. (2012). Jellyfish and ctenophore blooms coincide with human proliferations and perturbations. *Annual Review of Marine Science, 4*, 209-235.

Purcell, J. E., & Arai, M. N. (2001). Interactions of pelagic cnidarians and ctenophores with fish: a review. *Hydrobiologia, 451*(1-3), 27-44.

Purcell, J. E., Breitburg, D. L., Decker, M. B., Graham, W. M., Youngbluth, M. J., & Raskoff, K. A. (2001). Pelagic cnidarians and ctenophores in low dissolved oxygen environments: A review. In N. N. Rabalais (Ed.), *Coastal and Estuarine Sciences, Vol 58: Coastal Hypoxia: Consequences for Living Resources and Ecosystems* (Vol. 58, pp. 77-100).

Purcell, J. E., & Cowan, J. H. (1995). Predation by the scyphomedusan *Chrysaora quinquecirrha* on *Mnemiopsis leidyi* ctenophores. *Marine Ecology Progress Series, 129*(1-3), 63-70.

Purcell, J. E., Uye, S., & Lo, W. T. (2007). Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology-Progress Series, 350*, 153-174.

Rakow, K. C., & Graham, W. M. (2006). Orientation and swimming mechanics by the scyphomedusa *Aurelia sp* in shear flow. *Limnology and Oceanography, 51*(2), 1097-1106.

Raskoff, K. A., Purcell, J. E., & Hopcroft, R. R. (2005). Gelatinous zooplankton of the Arctic Ocean: in situ observations under the ice. *Polar Biology, 28*(3), 207-217.

Remane, A., & Schlieper, K. (1958). Die biologie des Brackwassers. *Die Binnegawasser. Bd 22. Stuttgard "E. Schweizerbart"*, 348.

Richardson, A. J., Bakun, A., Hays, G. C., & Gibbons, M. J. (2009). The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. *Trends in Ecology & Evolution, 24*(6), 312-322.

Riemann, L., Titelman, J., & Båmstedt, U. (2006). Links between jellyfish and microbes in a jellyfish dominated fjord. *Marine Ecology Progress Series, 325*, 29-42.

Riisgård, H. U., Andersen, P., & Hoffmann, E. (2012). From fish to jellyfish in the eutrophicated Limfjorden (Denmark). *Estuaries and Coasts, 35*(3), 701-713.

Riisgard, H. U., Bottiger, L., Madsen, C. V., & Purcell, J. E. (2007). Invasive ctenophore *Mnemiopsis leidyi* in Limfjorden (Denmark) in late summer 2007 - assessment of abundance and predation effects. *Aquatic Invasions, 2*(4), 395-401.

Ringelberg, J. (1995). Changes in light intensity and diel vertical migration – a comparison of marine and freshwater environments. *Journal of the Marine Biological Association of the United Kingdom, 75*(1), 15-25.

Rodionov, S., & Overland, J. E. (2005). Application of a sequential regime shift detection method to the Bering Sea ecosystem. *Ices Journal of Marine Science, 62*(3), 328-332.

Roohi, A., Kideys, A. E., Sajjadi, A., Hashemian, A., Pourgholam, R., Fazli, H., . . . Eker-Develi, E. (2010). Changes in biodiversity of phytoplankton, zooplankton, fishes and macrobenthos in the Southern Caspian Sea after the invasion of the ctenophore *Mnemiopsis Leidyi*. *Biological Invasions, 12*(7), 2343-2361.

Ruiz, J., Prieto, L., & Astorga, D. (2012). A model for temperature control of jellyfish (Cotylorhiza tuberculata) outbreaks: A causal analysis in a Mediterranean coastal lagoon. *Ecological Modelling, 233*, 59-69.

Sanden, P., & Håkansson, B. (1996). Long-term trends in Secchi depth in the Baltic Sea. *Limnology and Oceanography, 41*(2), 346-351.

Schaber, M., Haslob, H., Huwer, B., Harjes, A., Hinrichsen, H. H., Koster, F. W., . . . Voss, R. (2011). The invasive ctenophore *Mnemiopsis leidyi* in the central Baltic Sea: seasonal phenology and hydrographic influence on spatio-temporal distribution patterns. *Journal of Plankton Research, 33*(7), 1053-1065.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature, 413*(6856), 591-596.

Schneider, G., & Behrends, G. (1994). Population dynamics and the trophic role of *Aurelia aurita* medusae in the Kiel Bight and western Baltic. *Ices Journal of Marine Science, 51*(4), 359-367.

Schuyler, Q., & Sullivan, B. K. (1997). Light responses and diel migration of the scyphomedusa *Chrysaora quinquecirrha* in mesocosms. *Journal of Plankton Research, 19*(10), 1417-1428.

Shanks, A. L., & Graham, W. M. (1987). Orientated swimmin in the jellyfish *Stomolopus meleagris* L-Agassiz (Scyphozoan, Rhizostomida). *Journal of Experimental Marine Biology and Ecology, 108*(2), 159-169.

Shiganova, T., & Malej, A. (2009). Native and non-native ctenophores in the Gulf of Trieste, Northern Adriatic Sea. *Journal of Plankton Research, 31*(1), 61-71.

Shiganova, T. A., Mirzoyan, Z. A., Studenikina, E. A., Volovik, S. P., Siokou-Frangou, I., Zervoudaki, S., . . . Dumont, H. J. (2001). Population development of the invader ctenophore *Mnemiopsis leidyi*, in the Black Sea and in other seas of the Mediterranean basin. *Marine Biology, 139*(3), 431-445.

Shoji, J., Masuda, R., Yamashita, Y., & Tanaka, M. (2005). Predation on fish larvae by moon jellyfish *Aurelia aurita* under low dissolved oxygen concentrations. *Fisheries Science, 71*(4), 748-753.

Siferd, T. D., & Conover, R. J. (1992). Natural history of ctenophores in the resolute passage area of the canadian high Arctic with special references to *Mertensia ovum*. *Marine Ecology Progress Series, 86*(2), 133-144.

Sommer, U., Stibor, H., Katechakis, A., Sommer, F., & Hansen, T. (2002). Pelagic food web configurations at different levels of nutrient richness and their implications for the ratio fish production: primary production. *Hydrobiologia, 484*(1-3), 11-20.

Sørnes, T. A., & Aksnes, D. L. (2004). Predation efficiency in visual and tactile zooplanktivores. *Limnology and Oceanography, 49*(1), 69-75.

Sørnes, T. A., & Aksnes, D. L. (2006). Concurrent temporal patterns in light absorbance and fish abundance. *Marine Ecology Progress Series, 325*, 181-186.

Sørnes, T. A., Aksnes, D. L., Båmstedt, U., & Youngbluth, M. J. (2007). Causes for mass occurrences of the jellyfish *Periphylla periphylla*: a hypothesis that involves optically conditioned retention. *Journal of Plankton Research, 29*(2), 157-167.

Struck, U., Emeis, K. C., Voss, M., Christiansen, C., & Kunzendorf, H. (2000). Records of southern and central Baltic Sea eutrophication in delta C-13 and delta N-15 of sedimentary organic matter. *Marine Geology, 164*(3-4), 157-171.

Sullivan, L. J., & Gifford, D. J. (2004). Diet of the larval ctenophore *Mnemiopsis leidyi* A. Agassiz (Ctenophora, Lobata). *Journal of Plankton Research, 26*(4), 417-431.

Tamburri, M. N. (2000). Chemically regulated feeding by a midwater medusa. *Limnology and Oceanography, 45*(7), 1661-1666.

Tendal, O. S., Jensen, K. R., & Riisgård, H. U. (2007). Invasive ctenophore *Mnemiopsis leidyi* widely distributed in Danish waters. *Aquatic Invasions, 2*(4), 455-460.

Thingstad, T. F., Strand, E., & Larsen, A. (2010). Stepwise building of plankton functional type (PFT) models: A feasible route to complex models? *Progress in Oceanography, 84*(1-2), 6-15.

Thuesen, E. V., Rutherford, L. D., Brommer, P. L., Garrison, K., Gutowska, M. A., & Towanda, T. (2005). Intragel oxygen promotes hypoxia tolerance of scyphomedusae. *Journal of Experimental Biology, 208*(13), 2475-2482.

Thuesen, E. V., Rutherford, L. D., & Brornmer, P. L. (2005). The role of aerobic metabolism and intragel oxygen in hypoxia tolerance of three ctenophores: *Pleurobrachia bachel*, *Bolinopsis infundibulum* and *Mnemiopsis leidyi*. *Journal of the Marine Biological Association of the United Kingdom, 85*(3), 627-633.

Thurow, F. (1997). Estimation of the total fish biomass in the Baltic Sea during the 20th century. *Ices Journal of Marine Science, 54*(3), 444-461.

Tiselius, P., Tönnesson, K., Aksnes, D. L., & Haraldsson, M. (2011). Explaining the functioning of the Baltic pelagic food web in the presence of gelatinous top predators, improving ability to predict changes and succession in pelagic ecosystems, in the Baltic and globally. *Scientific report for bazooca (report 1 / wp 6)*.

Titelman, J., Gandon, L., Goarant, A., & Nilsen, T. (2007). Intraguild predatory interactions between the jellyfish *Cyanea capillata* and *Aurelia aurita*. *Marine Biology, 152*(4), 745-756.

Titelman, J., & Hansson, L. J. (2006). Feeding rates of the jellyfish *Aurelia aurita* on fish larvae. *Marine Biology, 149*(2), 297-306.

Titelman, J., Hansson, L. J., Nilsen, T., Colin, S. P., & Costello, J. H. (2012). Predator-induced vertical behavior of a ctenophore. *Hydrobiologia, 690*(1), 181-187.

Titelman, J., Riemann, L., Sørnes, T. A., Nilsen, T., Griekspoor, P., & Båmstedt, U. (2006). Turnover of dead jellyfish: stimulation and retardation of microbial activity. *Marine Ecology Progress Series, 325*, 43-58.

Torgersen, T. (2001). Visual predation by the euphausiid *Meganyctiphanes norvegica*. *Marine Ecology Progress Series, 209*, 295-299.

Utne, A. C. W. (1997). The effect of turbidity and illumination on the reaction distance and search time of the marine planktivore *Gobiusculus flavescens*. *Journal of Fish Biology, 50*(5), 926-938.

van Ginderdeuren, K., Hostens, K., Hoffmann, S., Vansteenbrugge, L., Soenen, K., De Blauwe, H., . . . Vincx, M. (2012). Distribution of the invasive ctenophore *Mnemiopsis leidyi* in the Belgian part of the North Sea. *Aquatic Invasions, 7*(2), 163-169.

Viitasalo, S., Lehtiniemi, M., & Katajisto, T. (2008). The invasive ctenophore *Mnemiopsis leidyi* overwinters in high abundances in the subarctic Baltic Sea. *Journal of Plankton Research, 30*(12), 1431-1436.

Visser, A. W., Mariani, P., & Pigolotti, S. (2009). Swimming in turbulence: zooplankton fitness in terms of foraging efficiency and predation risk. *Journal of Plankton Research, 31*(2), 121-133.

Wang, Z., Thiebaut, E., & Dauvin, J. C. (1995). Spring abundance and distribution of the ctenophore *Pleurobrachia pileus* in the Seine estuary: Advective transport and diel vertical migration. *Marine Biology, 124*(2), 313-324.

Wozniak B, Dera J (2007) Light absorption in sea water. Springer Science

Wolfe, L. M. (2002). Why alien invaders succeed: Support for the escape-from-enemy hypothesis. *American Naturalist, 160*(6), 705-711.

Zhang, F., Sun, S., Jin, X., & Li, C. (2012). Associations of large jellyfish distributions with temperature and salinity in the Yellow Sea and East China Sea. *Hydrobiologia, 690*(1), 81-96.

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