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**Inter-annual variation in abundance of three species of jellyfish in the
Bornholm Basin**

Master Thesis, March 2016



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DTU - Technical University of Denmark, Kgs. Lyngby – 2016

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Project period: August 2015- March 2016

ECTS: 35

Education: MSc

Field: Aquatic Sciences

Class: Public

Remarks: This report is submitted as partial fulfilment of the requirements for graduation in the above education at the Technical University of Denmark.

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Abstract:

Jellyfish have been receiving increasing attention ever since the 1950's, as humans started to consider them as a potential threat. This concern is especially relevant in the Central Baltic (Bornholm Basin) since it is a significant spawning ground for commercially important species such as Atlantic cod (*Gadus morhua*) and sprat (*Sprattus sprattus*). To address this problem, during this project I created the most extensive jellyfish database in the Southern Central Baltic Sea, covering a time period of 10 years and using a standard 45 station grid sampling area throughout the Bornholm Basin. This database allowed to analyse inter-annual variations in jellyfish biomass and abundance during spring (March) and autumn (November), finding that jellyfish biomass during the 2000's has been up to one order of magnitude higher than that of the 1970's. Additionally, the analysis of correlations with changing hydrographic factors such as salinity and temperature revealed that summer temperature has a significant effect on jellyfish populations during autumn.

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1. Introduction:

Jellyfish possess a simple but highly effective body structure that has allowed them to survive for millions of years (Boero 2013). Their fossil records date back to the Cambrian period, where both medusoid and polypoid stages have been discovered (Fig. 1; Scrutton 1979). These gelatinous marine invertebrates have been receiving increasing attention ever since the 1950's as humans started to consider them as a potential threat (Purcell 2012). For instance, they began to interfere with activities such as, tourism (Fenner et al. 2010), fishing (Nagata et al. 2009, Dong et al. 2010), and aquaculture (Doyle et al. 2008, Delannoy et al. 2011), as well as have been clogging water intake screens on power production and desalination plants (Daryanabard & Dawson 2008). Additionally, the ecological impact of jellyfish is now getting attention, as their biomass and abundance appears to be increasing (Hay 2006, Condon et al. 2012).

This project focuses on the Central Baltic Sea, particularly on the Bornholm Basin covering the period from 2002-2003 and 2008-2015. The Baltic Sea, especially the Bornholm Basin is considered a significant spawning ground for commercially important species such as Atlantic cod (*Gadus morhua*) and sprat (*Sprattus sprattus*). Therefore, patterns of jellyfish abundance and occurrence and factors regulating them are of special interest (Barz et al. 2006). Brackish waters, as found within the Bornholm Basin, are characterised by a low number of indigenous species (Paavola et al. 2005). As such, there is a limited number of jellyfish species detected in this region of the Baltic. For this reason, we focused on two species which regularly occur in this area: Scyphomedusae *Aurelia aurita* and *Cyanea capillata* (Margónski & Horbowa 1994) as well as an additional species, the invasive ctenophore *Mnemiopsis leidyi* for comparison purposes.

Studies suggest that mass occurrence of *A. aurita* is limited to the seasonal periods of August to November, whereas *C. capillata* is found from time to time (Margónski & Horbowa 1994). However, it is unclear if *C. capillata* and *A. aurita* complete their whole life cycle in the Bornholm Basin, as the absence of ephyrae for both species suggests that strobilation takes place in a different location (Barz et al. 2006).

During the last three decades, research shows an extreme patchiness on jellyfish distribution as well as varied inter-annual abundance pattern (Margónski & Horbowa 1994). The perception that jellyfish blooms are increasing in numbers (Condon et al. 2012) has led to this project. Here, my objectives are to analyse seasonal and inter-annual abundance and biomass, as well as delineate factors that may be promoting blooms. Also the creation of a jellyfish database which will include abundances and biomass for the species of interest. To accomplish my objectives data were collected over 10 years spanning a total of 1023 sampling stations in the Bornholm Basin.

Taken together, I have included 17,101 jellyfish samples: 7831 *A. aurita*, 4144 *C. capillata* and 5126 *M. leidy*. Additionally, temperature and salinity for years 2002-2003 and 2008-2013 were used to provide the framework to allow a comparative study of the Bornholm Basin ecosystem under different hydrological conditions.

Currently, the causes and consequences of this apparent increase in jellyfish abundance are under investigation (Helmholz 2010). Nevertheless, it has become clear that issues regarding jellyfish require further attention (Purcell et al. 2007), especially with regard to the spatial and temporal occurrence of jellyfish (Condon et al. 2012). Therefore, this project aims to investigate jellyfish abundance and distribution pattern in one of the most important spawning ground for commercially important fish species in the Baltic Sea. It is important to continue investigating such processes as jellyfish can have a major impact on the ecosystems, especially during years of high abundance (Barz et al. 2006).

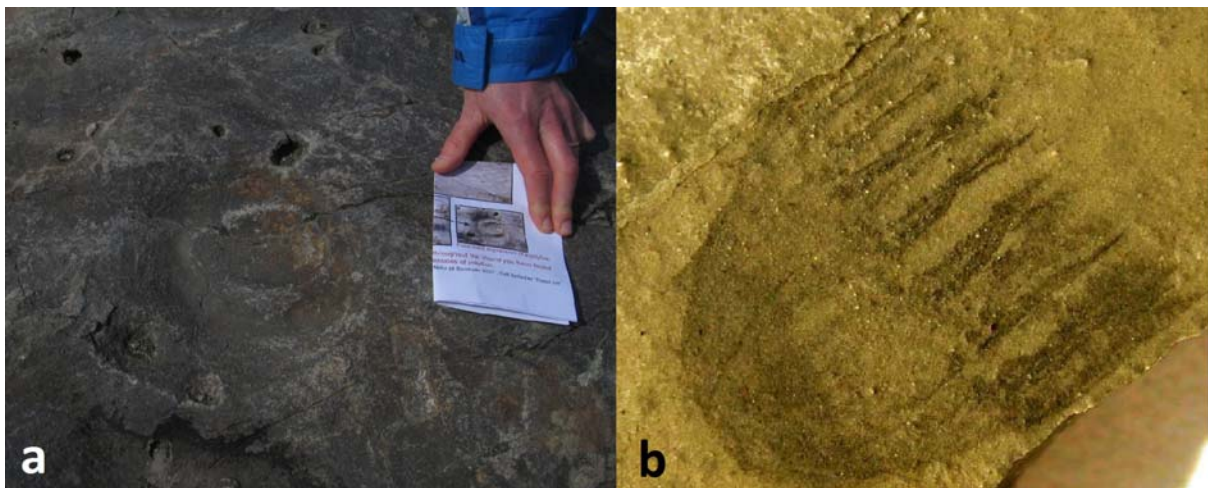


Fig.1 (a) Jellyfish fossil found on the island Bornholm, central Baltic Sea Photo: Brian MacKenzie. (b) Jellyfish fossil (ca. 500 mio. years old) found in Utha, USA by Richard D. Jarrad and Susan Halgedhal (Image source: Joe Bauman 2007).

2. Background

The following chapter will introduce important topics related to Scyphomedusae, starting with basic information about their taxonomy, physiology, ecology in different ecosystems, and possible factors controlling their abundances, as well as their impact on ecosystems they inhabit.

2.1 Classification:

Jellyfish is a popular term used to define gelatinous macrozooplankton, that have a high content of water in their body tissues (Boero 2013). Jellyfish include both Ctenophora and Cnidarians, even though, only Cnidarians can be regarded as “true” jellyfish.

Cnidarians are primarily composed of two tissue layers, the endoderm and ectoderm (Fig. 2; Edwards & Breazeale 2012). Between these two cell layers is the mesoglea, which is usually the biggest part of the body in Scyphozoa (Fig. 2; Hale 1999). Members of the phylum Cnidaria share a unique characteristic, as they possess specialized cells called cnidocytes (also known as Nematocyst; Fig. 2), which contain a complex mixture of diverse toxins and give Cnidarians their name. When a prey item gets close, the cnidocyst capsules are discharged as a response to physical or chemical stimuli. Then the toxin may induce different effects on the prey, such as paralysis (Helmholz 2010).

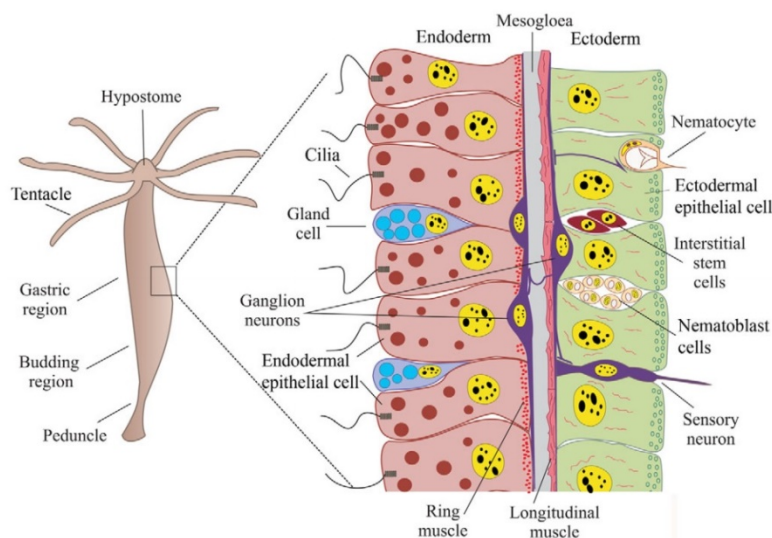


Fig.2 Bi-layered cellular organization of a hydra polyp (from Technau & Steele 2011)

2.2 Jellyfish physiology:

Scyphozoans have a very wide size distribution, ranging from millimeters to more than 2 m in diameter (Hale 1999). Despite their development to such enormous sizes, Scyphozoans have no skeleton, have no special organs for respiration or excretion, and they lack a heart (Arai 1997).

These invertebrates are quite primitive. Their simple body structure is radially symmetrical, meaning that their parts are arranged symmetrically around a central axis (Cadet 2015). The body encompasses a single sac like body space, the coelenteron, which resembles the shape of a bell; this cavity serves for gas exchange and digestion (Hale 1999). Medusae (or adult jellyfish) are equipped with tentacles hanging from the margin of their body (Fig 3). They also possess microscopic stinging capsules, the nematocysts, which help while capturing prey (Hale 1999) and is the defining characteristic of this phylum (Hessinger & Lenhoff 1988). The tentacles surround a single body opening, the mouth (Fig. 3), which is located at the end on the manubrium, a tube-like structure that hangs from the centre of the bell and connects the mouth to the coelenteron and its surroundings (Cadet 2015).

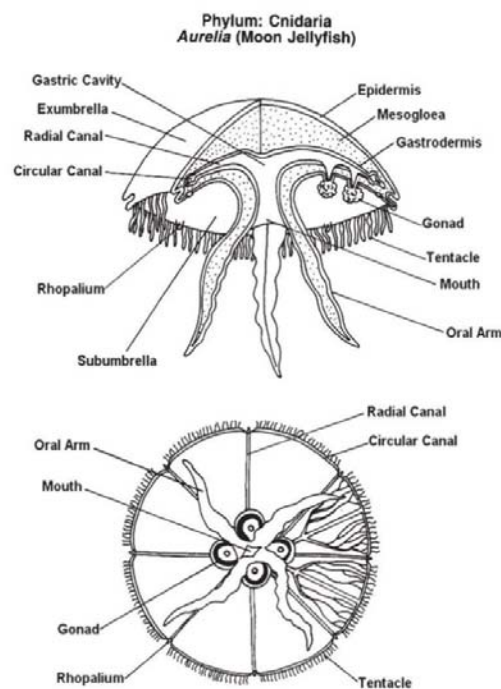


Fig.3 *Aurelia aurita* anatomy (retrieved from: <http://cronodon.com/BioTech/Jellyfish.html>. Retrieved: 01/10/2015

Jellyfish do not have a single centralized brain, instead they possess a relatively simple and radially distributed nervous system (Katsuki & Greenspan 2013) which consists of very efficient sensory receptors capable of detecting light, odour, and different kinds of chemical and hydrodynamic stimuli (Hammer 1995). There are major neuronal components that are known to be physiologically and histologically distinct in the Scyphozoan nervous system (Katsuki & Greenspan 2013):

- The rhopalium is located at the bell margin (Fig. 3; Hale 1999) and contains three main sensory structures: (i) the ocelli, which are pigmented photosensitive structures; (ii) gravity receptors called statocysts, which are located between the tentacles or near the tentacle base and are responsible for gravity perception, and (iii) pacemaker neurons that set the basic swim rhythm. Most scyphozoans have eight rhopalia around the bell margin.
- Motor nerve net covers the entire sub umbrella muscle sheet and it is the network of neurons that activates muscle contractions in response to signals from the pacemaker.
- Diffuse nerve net consists of a neuronal group that induces marginal tentacle contraction. It provides modulatory input to the musculature and affects the pacemaker.

Together, this system provides a mechanism through which jellyfishes become informed about their orientation and surroundings, as a response they will alter their posture by stronger contractions on one side of the bell (Arai 1997).

2.3 Locomotion:

Jellyfish are believed to be weak swimmers, as they are usually carried long distances by currents, making them the largest planktonic organisms (Richardson et al. 2009). When necessary they might show escape responses where higher velocities are attained. This happens when the circular muscles contract and squeeze the sub umbrella, forcing out the water in their body cavity (Cadet 2015). Jellyfish have the most energy efficient transport motion of any animal using critical pauses between contractions and expansions of the body helping them to travel 30% faster with each stroke cycle, thus reducing the metabolic energy demand (Gemmell et al. 2014).

2.4 Life cycle:

The typical life span of a jellyfish ranges from 4-8 months and normally does not exceed a year (Barz et al. 2006). Jellyfish are small in size during winter to early spring when there is limited light and

nutrients, but exponentially grow once zooplankton and phytoplankton blooms occur during spring and animals grow up until summer. After this period, the medusa (jellyfish) will usually start sexual reproduction and subsequently start shrinking (Franco 2009). Members of Scyphozoa present a characteristic alteration in generations where there is a sexual planktonic generation and an asexual benthic generation (Miyake et al. 1997). This planktonic generation is what we commonly refer to as medusa, while the benthic generation, known as the polyp, represents their sessile life stage (Edwards & Breazeale 2012).

During the reproduction process adult medusae reproduce sexually, where gametes are either shed into the sea to be fertilized, or kept internally to “protect” the larvae during early development in the oral arms of some Scyphozoa species (Cadet 2015). Each fertilization event leads to the formation of a larva, the planula, which after a motile period will attach to hard substrate and settle to eventually develop into a polyp. Polyps will typically form colonies and remain physically attached to one another (Cadet 2015) on hard surfaces and in shaded places (Barz et al. 2006). In some colonies, polyps share a common coelenteron through which food captured by any member is distributed to others. Examples, of colonies are anthozoan or soft corals and most reef-forming hard corals (Cadet 2015). Polyps will start an asexual process known as strobilation where the next life stage, the ephyrae, is produced. Strobilation is triggered by seasonal progression or a combination of environmental changes such as sea temperature, salinity, food, and light (Barz et al. 2016). Ephyra will eventually grow into the medusae stage, become sexual mature and repeat the life cycle (Boero 2013). During their medusa phase cnidarian species are capable of sexual reproduction, however asexually reproduction may occur in both phases. Among known species, some hermaphrodites, defined as individuals with both sexes, are found although each sex is commonly separate (Cadet 2015).

In the central Baltic Sea polyp populations are rarely known (see Barz et al. 2006 for discussion). The closest *A. aurita* polyp population is reported in the Kiel Bight (western Baltic) and Kerteminde Fjord (Belt Sea), followed by an *A. aurita* and *C. capillata* population in the Gullmar Fjord (as reviewed in Barz et al. 2006). As mentioned above, there are no large polyp populations reported in the central Baltic, which includes the Bornholm Basin. This area is characterised by the absence of ephyrae and a late appearance of young medusa (Barz et al. 2006). Together, this reinforces the believe that medusas found in this area are being drifted from other regions, either from the west (as reviewed in Barz et al. 2006) or from the east (Wikström 1932).

2.5 Feeding:

Jellyfish have a single opening, the mouth, which also functions as the anus. Close to the mouth are 4 to 8 oral arms which are used to transport food items that have been captured by the tentacles. All cnidarians are carnivorous and possess stinging organs (cnidocysts or nematocysts) on the tentacles, which are extremely useful for capturing prey (Hale 1999). Most cnidarians are passive hunters, meaning that prey contacting the tentacles elucidates the nematocysts to fire which leads to paralyzing the prey which will then be ingested (Edwards & Breazeale 2012). There are also other species that are known to absorb nutrients directly from seawater (Edwards & Breazeale 2012). The development and distribution of certain types of cnidocysts and the injection of bioactive compounds is a crucial factor for prey capture and digestion by cnidarians (Kintner et al. 2005; Regula et al. 2009). In an earlier study, Fraser (1969) concluded that most jellyfish mainly feed on small crustaceans, such as copepods (Purcell 1993).

2.6 Ecological interactions:

The functioning of marine ecosystems is based on blooms, like the spring bloom of phytoplankton, which is then followed by a zooplankton bloom that takes advantage of the phytoplankton. The zooplankton peak sustains the rest of the food web, being predated upon by carnivorous plankters, such as fish larvae, which will eventually become representatives of the nekton (Boero 2013). This pathway represents the back bone of marine production and every part of this system works in union. Thus, if everything is in balance the ecosystem will produce fish which can be harvested for human consumption (Boero 2013).

As mentioned, blooms are the key to a healthy and sustainable ecosystem. This, as could be expected there are also jellyfish blooms, which are a normal phenomenon. Jellyfishes reproduce rapidly and in great quantities, giving them the ability to expand in population size (Richardson et al. 2009). Every now and then, if these blooms are produced under the right conditions, it will allow them form bloom abundances. Jellyfish compete with fish larvae, juveniles and planktivore fish species for the same resources. Additionally, jellyfish blooms will also have a direct impact on the fish population, since jellyfish also predate on fish eggs and larvae (Möller 1984). However, jellyfish have predators as well, as they are known to be preyed upon by sea turtles (which are not found in some of the areas where big blooms occur), fish, and other invertebrates (as reviewed in Richardson et al. 2009). Since jellyfish do not represent a good nutritious source they are not preyed upon as much as other marine organisms (Edwards & Breazeale 2012). There are also other factors that might reduce bloom occurrences of jellyfish, which have been associated with the parasites such as

Hyperia galba parasitizing *A. aurita* in the Mediterranean and recently in the North Sea (Fig. 4). This parasite causes a reduction in bell diameter as well as a reduction in population size (Mills 1993). There are several theories trying to explain the increase in jellyfish presence, such as environmental changes due to global warming (as reviewed in Richardson et al. 2006), as well as the high pressure put on their predators due to over fishing (Pauly et al. 2009).

Even though jellyfish blooms are a natural part of any marine ecosystem, there is a growing concern regarding the negative effects that a high abundance of gelatinous macrozooplankton might have on fish recruitment (Richardson et al. 2006). This is why, in the last decades, some of the predicted effects have been described in some publications (Båmstedt 1990; Båmstedt et al. 1994; Omori et al. 1995; Behrends & Schneider 1995; Lynam et al. 2005a; Lynam et al. 2006; Malej et al. 2007; Barz & Hirche 2007; Møller & Riisgaard 2007; Titelman et al. 2007).

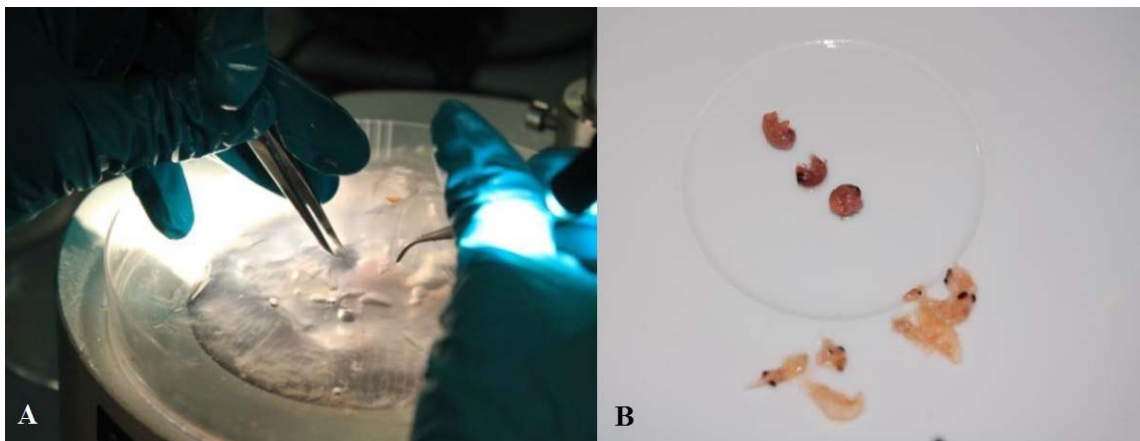


Fig.4. A) Dissection and removing of parasites on *Aurelia aurita*, B) Parasite *Hyperia galba* found attached to several specimens collected in the Kattegat, the Skagerrak and the North Sea, during a research cruise with R/V Dana from 25/6 to 8/7 2014 (Photo by: Anna K. Mienser)

2.7 Causes of blooms:

After the 1950's jellyfish populations have shown an increasing trend in abundances in most marine ecosystems (Brotz et al. 2012). This global regime shift is changing marine ecosystems, that once were mainly populated by fish, to be heavily populated by jellyfish (Mills 2001; Condon et al. 2012). There are several theories behind the causes of this phenomenon (Purcell et al. 2007), however this emergence of blooms seems far from being understood (Rupp 2013). One fact is clear and that is that coastal waters around the world have been progressively degraded by humans (Purcell 2012) and jellies have benefited from these changes, such as global warming, eutrophication, overfishing, coastal construction, and species introductions (Purcell et al. 1999, 2001, 2007; Arai 2001; Mills 2001; Pauly & Palomares 2001; Purcell 2005; Graham & Bayha 2007; Richardson et al. 2009; Dong et al. 2010; Uye 2010). Worst of all is that these changes are occurring simultaneously around the world for many different ecosystems (Purcell 2012)

Historical records document that fishing pressure on ecosystems was moderated and remained constant between the 1950's to 1970's. After this, due to market demand fishing activities increased exponentially (Swartz et al. 2010) as a result the effects of this activity were greatest during 1977–1988 when the zooplanktivorous fish populations were considerably reduced. Coincidentally, these dates coincide with big jellyfish blooms that occurred during the 80's, when an increase in species such as *A. aurita* (1977-1980) and *M. leidyi* (1989-1994) occurred. Scientists believe that this increase was triggered by overfishing which caused system-wide trophic cascades (Kideys 2002; Purcell 2012). In addition, overfishing is removing top predators either intentionally or accidentally. When there is a large fish population, the offspring of fish will overcome the presence of gelatinous zooplankton and competition for food will not represent a problem. However, if there is a small population of fish, jellyfish will have no competitor (Boero 2013).

Global warming is helping to increase the abundances of some jellyfish species, but is not necessarily the same trend for all species. For instance, it favours tropical species by widening the windows for sexual reproduction as well as creating conditions for successful establishment, allowing further population increases (Boero 2013). In the North Sea abundances of *A. aurita* and *C. capillata* appear to be linked to large-scale inter-annual climatic change (Lynam 2005b). In this area populations are probably also affected by local variability in the environment manifested in inter-annual changes in temperature, salinity, current strength/direction and prey abundance (Lynam 2005b).

When conditions are favourable, the biomass of jellyfish may bloom to unexpectedly high levels. As mentioned above, *A. aurita* appears to be linked to climate changes. An example of this is a historical bloom that occurred in the Black Sea during the late 1980's, where the size of the population

reached an estimated of 300–500 million tons (Mills 2001) or for *C. capillata* where by catch increased from < 1% of the total catch in 1993 to 85% in the Yangtze river (Xian et al. 2005).

Other cause related to an apparent increase in jellyfish abundance is the transportation of non-indigenous species (Richardson et al. 2006). One particular case is that of the Black Sea, which became severely affected by the introduction of *M. leidyi* (Kideys 2002).

Alien species such as *M. leidyi* are introduced by humans in different ways, i.e via ballast water or by their introduction for ornamental or recreational purposes which might end up with an accidental spread, eventually leading to population outbreaks (Bolton & Graham 2006).

Some theories support eutrophication as a cause for blooms (Richardson et al. 2006). For instance, due to the use of fertilizers, deforestation, and agriculture, humans have increased the nutrient composition of coastal waters, since the majority of the waste water produced by these activities is being released into the ocean. Increases in eutrophication has been linked to increases in human populations, which overall is becoming a major global pollution problem (Howarth 2008). Some of the consequences of eutrophication are altered nutrient ratios and increased turbidity. With an increase in nutrients there is also an increase in biomass at all trophic levels. For jellyfishes this means that more food for polyps and medusae will be available and thus will increase their growth and reproductive output (Purcell 2012).

Due to their short generation times, jellyfish populations appear to be tightly linked to climatic regimes (Lynam et al. 2005b). Patterns of abundance and occurrence of *A. aurita* and *C. capillata* in the Central Baltic Sea have been related to inflow events, which are induced by climate variations and meteorological events (Barz et al. 2006).

2.8 Impact of jellyfish blooms:

High abundances of jellyfish are hindering human activities as they represent a nuisance for fishing activities during years of high abundance as they clog fishing nets and eventually damage trawls (Arai 1997; Brierley et al. 2001; Mills 2001; Xian et al. 2005). Jellyfish also interfere with tourism, as their stinging capacity is an ongoing concern, particularly in tropical and subtropical regions where lethal species can be found (Helmholz 2010). When a human is stung the victim may experience skin rashes, muscle cramp, or even death (Hale 1999). Whereas, *A. aurita* is harmless for humans, *C. capillata* can cause severe dermal irritations and pain by accidental contact (Helmholz 2010). Jellyfishes are carnivorous and *A. aurita* has been shown to intensively prey on copepod copulations in the Kiel Bight (Kerstan 1997). In this area zooplankton abundances remained low during June, July,

and early August and peaked again during autumn. This decline in biomass during summer has been attributed to *A. aurita* grazing impact. Populations develop during May and reach highest abundances during June and early July in Kiel Bight (Möller 1980; Schneider 1989). This reduction in zooplankton communities may lead to changes in lower trophic levels and thus *A. aurita*, as a top predator, might be regulating the whole plankton system (Behrends 1995). In the North Sea, the distribution of jellyfish and herring overlap spatially and temporally. Thus, there is a possibility that they are causing an impact upon herring (*Clupea harengus*) recruitment since they consume the same prey as herring larvae impacting larval survival (Lynam et al. 2005a). This is specially an issue since *A. aurita* has previously been reported to drastically impact Atlantic herring larvae in the Baltic Sea (Möller 1984). This competition for resources along with known predation rates on larvae and fish eggs could potentially harm commercial fish stocks. The Bornholm Basin, is the most important spawning ground for cod and sprat (Köster et al. 2005). Inter-annual variation in jellyfish abundance will likely cause year-to-year variation in fish population dynamics.

2.9 Area and species of Interest:

The Baltic Sea covers 415,266 km², with a huge and highly populated catchment area of 1.7 million km² which is four times as large as the Sea itself. The Baltic Sea is only connected to the world's oceans via the Danish Straits (i.e. Great Belt, Little Belt, Øresund) and due to its special geographical and oceanographic characteristics, this area is very sensitive to environmental impacts and human activities (Eero 2008). The Baltic Sea is a semi-enclosed water body and has one of the largest brackish areas in the world. It is characterised by strong salinity gradients having 20 PSU in areas such as the Kattegatt and 1-2 PSU in Northern areas. Salinity is controlled by inflows from the North Sea and by freshwater from rivers (Schinke and Matthäus 1998).

The central Baltic is permanently vertically stratified since a strong salinity gradient in the deepest areas prevents the vertical mixing of waters, however the water column is not very saline (6-8 PSU) in the areas closest to the surface, but salinity increases as it deepens. During spring a temperature gradient develops at 25-30 m. This thermocline establishes due to solar radiation and restricts water circulation and persists until autumn; it separates the warm surface layer from the intermediate winter-water and forms three water masses or layers with different thermal and haline conditions. The only way in which water is renewed, is by inflows of saline oxygenated water coming from the North Sea (Schinke and Matthäus 1998).

Contemporary investigators suggest that oceanographic and meteorological conditions are necessary for the occurrence of inflows (Matthäus and Franck 1992; Matthäus and Schinke 1994) however their occurrence is difficult to predict. Before the 1970's the largest periods without inflows lasted 3-4 years and thus, salinity was reduced. There were specially low inflow periods during the 1920's to early 1930's and in the 1950's (Fonselius et al. 1984). The longest period without a major inflow event lasted 10 years (1983-1993). The decreasing frequency of inflows since the 1980's has been responsible for observed shifts in the ecosystem structure due to changes in the hydrographic regime (Ojaveer et al.1998; Möllmann et al. 2000; Möllmann et al. 2002; Matthäus and Nausch 2003).

Salinity and temperature are extremely important since they influence horizontal and vertical distributions of zooplankton species (Ackefors 1969; Hernroth & Ackefors 1979; Hansen et al. 2004). This seasonal variation in species distribution will also affect population dynamics, thus zooplankton variations might be affected by important inflow events from other areas (Viitasalo et al. 1995a, Viitasalo et al. 1995b; Vuorinen et al.1998; Ojaveer et al. 1998; Dippner et al. 2000; Möllmann et al. 2000).

Sampling for this MSc project was conducted in the Baltic Sea (Fig.5), covering areas such as Bornholm Basin (BB), the Arkona Basin (AB), and the Gotland Basin (GB). The Bornholm Basin (Fig. 8) represents the area where most of the sampling took place and it also has a standard sampling grid consisting of 45 stations which has been sampled repeatedly over many years. As mentioned above, this area is an essential spawning ground for Baltic cod (Köster et al. 2005) which is why it is of great importance and special interest. Jellyfish species such as *A. aurita* and *C. capillata* are regularly found in the Bornholm Basin, though they are not found all year round (Janas & Witek 1993; Barz & Hirche 2005).

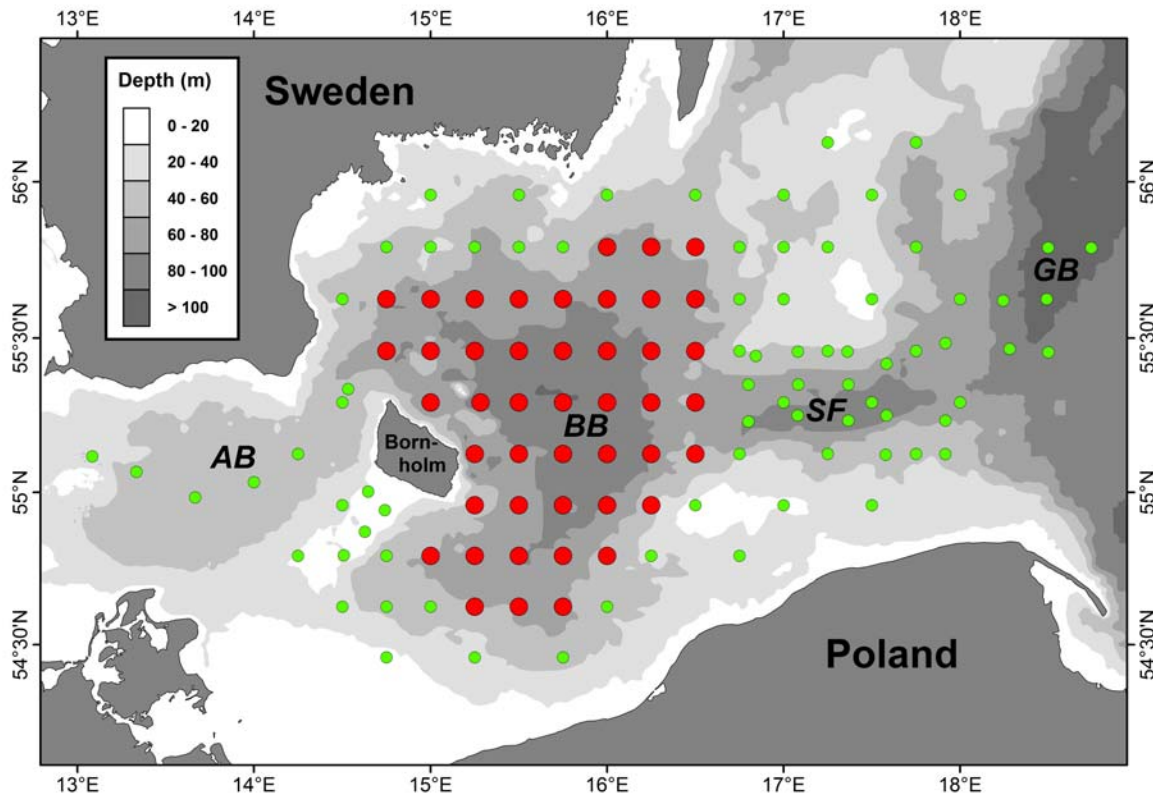


Fig.5: Overview of the study area and sampling stations. Red dots represent the 45 station standard grid in the Bornholm Basin (BB) which has been sampled on all cruises from 2002/2003 and 2008-2015 during March and November. Other locations which have occasionally been sampled (green dots) are AB = Arkona Basin; GB = Gotland Basin and SF = Slupsk Furrow.

A. aurita

A. aurita are cnidarians belonging to the class Scyphozoa, which are commonly known as true jellyfish. *A. aurita* is one of the two naturally occurring species in the Baltic Sea. This species is commonly referred to as a “moon jelly” due to its shape and colour. It has 4 horseshoe shaped rings. The gonads are placed just below these pouches and are quite visible, especially on females where they appear as pink or purple clumps (Franco 2009).

A. aurita captures their prey by stinging them with nematocysts located on the tentacles and moves the prey to the mouth by cilia movement (Richardson et al. 2009). This species reproduces asexually during its polyp stage and sexually during its medusa stage in the summer (Möller 1980). Their life span typically lasts between 4 to 8 months, but in a few cases populations have lived as long as 2 years in Japanese waters (Franco 2009). The species shows seasonal changes in size, where they

gradually increase in size from winter until summer. They will then reach sexual maturity, and then after this peak they will usually shrink and die (Franco 2009).

Large medusa blooms occur during summer (Hammer & Dawson 2009), but it appears that such blooms occur with higher frequency in temperate regions compared to tropical regions. This process, however varies globally depending on different factors, such as nutrient and light availability as well as salinity and physical factors (Franco 2009).

A. aurita is mainly found in surface waters (0-40 m) of the central Baltic (Möller 1980; Lischka 1999; Barz & Hirche 2005), however there is no record of polyp populations for the central Baltic (Bornholm Basin). Polyps are confirmed for other regions such as the Danish Straits (Olesen et al. 1994), South West Finland (Wikström 1932) and the Skagerrak (Grøndahl 1988). Together, this suggests that adults present in the central Baltic Sea may be drifted into the area from two different polyp populations originating from the Skagerrak and the Southwest Finnish coastline.

C. capillata

C. capillata has sensory organs such as light receptors, balance organs, and odour pits. Their bell colour ranges from reddish gold to brownish violet. This species is widely distributed, and can often be found in the cooler regions of the Atlantic Sea, the Pacific, North Sea, and Baltic Sea. It catches its prey by slowly sinking with spread tentacles and stinging the prey with venom to paralyze it (Naylor 2000).

3. Objectives:

During the last decades, research has shown an extreme patchiness on jellyfish distribution as well as varied internal abundance (Margónski & Horbowa 1994). Overall, there has been little emphasis put on spatial and temporal occurrence of jellyfishes during ichthyoplankton surveys. Additionally there is a perception that jellyfishes blooms are increasing in number, which has led to the aim of this project. Here, I aim to learn more about jellyfish occurrences by using a long-term data base to achieve a better understanding of the species dynamics. In order to achieve this goal I have:

- Collected and organized handwritten datasheets of Baltic Sea Surveys
- Created and compiled a digital database based on handwritten datasheets
- Standardized the digital database
- Analysed inter-annual seasonal variation in abundances of the most common jellyfishes species occurring in the Central Baltic (*A. aurita* and *C. capillata*)
- Analysed inter-annual seasonal variation in biomass of the most common jellyfishes species occurring in the Central Baltic (*A. aurita* and *C. capillata*)
- Analysed possible mechanisms influencing jellyfish abundances and biomass variations in the Central Baltic, such as salinity and temperature.
- Analysed clearance rates of *A. aurita* and *M. leidyi*.

4. Materials and methods:

Sample collection:

Samples were obtained during yearly survey cruises with the Danish research vessel DANA as part of the IBTS cruises in March and November (2008 to 2015). Additionally, data for 2002 and 2003 were added from GLOBEC cruises for March and November. Every year, surveys took place during early spring in the first weeks of March (with exception of 2008 and 2014), while autumn samplings have been conducted during the first weeks of November. Jellyfish samples were attained from a standard station grid covering the Bornholm Basin, Central Baltic Sea (Fig. 5 for details). These 45 standard stations have been covered during all cruises and therefore been used for statistical analyses. Additional sampling was conducted in the Arkona Basin, Stolpe Furrow and occasionally in the Gotland Basin (Fig. 5). These occasional stations have been included in mapping temporal jellyfish distribution pattern only. The investigation covered an area from approximately 13.00° E to 18.45° E and 54.30° N to 56.15° N located in the southern central area of the Baltic Sea.

To assess abundances and biomass of the native jellyfish species *A. aurita*, and *C. capillata* hauls with a Bongo net (60 cm diameter) were taken on a total of 1023 stations. The invasive comb jelly *M. leidyi*, which had been recorded in the Bornholm Basin for the first time during 2007, is disregarded in this study but included in total gelatinous macrozooplankton biomass and clearance rate comparisons.

Samples were attained by use of a bongo net which was equipped with two nets of different mesh sizes (335 μm and 500 μm). Each net was equipped with a flowmeter to estimate the filtered water volume. The bongo net was towed in a double oblique haul integrating the entire water column, from 5 m above the bottom to the surface, at a towing speed of ca. 3 knots. Upon retrieval, *C. capillata* and *A. aurita* specimens were immediately sorted from the samples, counted and the diameter measured to the nearest cm using a calliper (1 ± 0.5 cm) (Fig. 6). In the case of *M. leidyi* the body without lobes, hence the oral-aboral length of each individual had been measured to the nearest mm using a calliper (1 ± 0.5 mm). All samples were analysed within 30 min after capture. For further analyses the numbers of specimens found from the two nets were averaged.

Jellyfish count data have been standardised to abundances m^{-3} taking the filtered water volume of each net from the flow meter readings into account. Abundances per m^{-2} have been attained by multiplying abundances m^{-3} with the sampling depth at the respective station. During the 10 year sampling period a total of 7831 specimens of *A. aurita*, 4144 specimens of *C. capillata* and 5126 *M. leidyi* were caught using the Bongo nets.

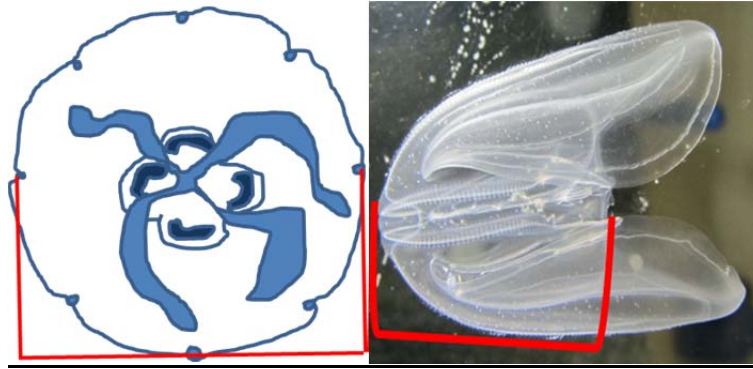


Fig.6. Size measurements used for *A. aurita* (left, inter-rhopalia umbrella diameter) and *M. leidyi* (right, oral-aboral length) indicated by red brackets Pictures: C. Jaspers.

Database:

A total of 17,101 individual jellyfish were compiled for the years 2002-2003 and 2008 to 2015. Data for 2002-2003 is based on published abundance data and have been substituted with unpublished size measurements to allow for extrapolation of data to biomass and clearance rates (data source from Kristina Barz, TI, Germany).

For 2008 to 2015, data were collected from 2123 pages of hand written datasheets and manually typed into an excel database. This excel database contained year and season of the analysed cruises, as well as all gear information, sampled stations, jellyfish species, counts, and length.

Additionally, a second database was created which contained flow data information of 1023 stations with their corresponding coordinates, sampling depth, and flow meter readings for each mesh (335 μm and 500 μm). From the delta flowmeter readings, the filtered water volume has been calculated. Sums of jellyfish abundance and biomass per station were merged to this database in order to calculate the number of jellyfishes and biomass m^{-3} and m^{-2} .

Data treatment:

To visualize spatial and temporal distribution pattern of *A. aurita* and *C. capillata*, maps covering all stations have been produced using ArcGIS (version 10.1). All sampled cruises (spring and autumn), as well as the number of stations in which jellyfishes were found are included in Table.1. For March, no data were available for 2008 and 2014. During March, *A. aurita* abundances were very low and a total of 21 individuals have been caught during the 8 cruises. This is why size and biomass distribution for March have not been included in statistical analyses. Size distribution of *A. aurita* (November only) and *C. capillata* (November and March) have been plotted to visually investigate the change in size distribution between year and season.

Measured sizes have been used to calculate biomass as well as clearance rates (see below). In <20% of the cases no size measurements were available (stations with very high jellyfish abundances). For those cases, average sizes from that station have been used for calculating biomass and clearance rates.

Cruise name	Nr. stations
AvH44/03/01	50
AvH440208	59
Dana 02/10	66
Dana 02/11	76
Dana 03/09	76
Dana 04/12	52
Dana 04/13	44
Dana 04/15	45
Dana 07/10	59
Dana 08/08	40
Dana 08/09	63
Dana 08/11	57
Dana 10/13	47
Dana 10/14	71
Dana 11/15	77
Dana 13/12	46
He181	51
HE201	44

Table 1: Cruise name and number of stations where jellyfish have been quantified for the period 2002/2003 and 2008 to 2015.

Conversion factors:

For extrapolations, measured lengths were used to calculate wet weights as a proxy for biomass, and clearance rates as a proxy for grazing impact using literature regressions (see below).

The recently observed invasive comb jelly *M. leidyi* has only been considered for total gelatinous macrozooplankton biomass estimations and for comparing clearance rates of *A. aurita* and *M. leidyi* since it remains questionable if the captured *C. capillata* are actively feeding as diet investigations from the Baltic Sea are lacking.

For *Aurelia aurita* bell diameter (D , mm) of freshly caught animals have been converted to wet weights (WW,g) using the published regression from Schneider (1988):

$$WW(g) = 1.565 \times 10^{-4} \times D (mm)^{2.75} \quad (1)$$

This regression is based on a size range covering animals from 10 to 280mm and animals have been caught at a salinity of 15 as summarized in Hirst and Lucas (1998).

For *C. capillata*, the only available diameter (D) to wet weight (W) conversion available has been used which is based on animals originating from Bergen, Norway (Båmstedt *et al.*, 1994).

$$WW(g) = 0.185 \times D (cm)^{2.774} \quad (2)$$

For *M. leidyi*, wet weights have been estimated by converting measured oral-aboral lengths (L_{oa} , mm) to displacement volume (V , mL) following Jaspers *et al.* (2015):

$$V (mL) = 0.0009 \times L_{oa} (mm)^{2.84} \quad (3)$$

Displacement volume has then been converted to wet weight (g) assuming a specific weight ratio of $1.0g\ cm^{-3}$, following earlier assumptions for *A. aurita* (Schneider, 1988; Weisse and Gomoiu 2000).

Clearance rates (F) for *A. aurita* have been calculated using published regressions for copepod prey conducted at 15°C (Møller and Riisgård 2007):

$$F(L\ Ind.^{-1}\ d^{-1}) = 0.0073 \times D (mm)^{2.1} \quad (4)$$

Published clearance rates of *C. capillata* show a high prey diversity including other gelatinous macrozooplankton. Direct feeding estimates for the low saline Baltic Sea are not available. Due to this uncertainty, clearance rates have not been calculated for *C. capillata*.

For comparison, clearance rates (F , $L\ ind^{-1}\ h^{-1}$) for *M. leidyi* have been included in the analyses and calculated using published regressions between oral-aboral length (L_{oa} , mm) to clearance rates for a

representative prey species (*Acartia tonsa*). This regression has been derived from gut content analyses of field collected animals in the Skagerrak at 20°C and a salinity of 32 (Granhag et al. 2011)

$$F(L \text{ Ind.}^{-1} h^{-1}) = 0.0022 \times L_{oa} (mm)^{2.33} \quad (5)$$

All rates have been temperature corrected to 15°C using a Q_{10} of 2.8, which has been estimated for different functional groups covering a large size range (Hansen et al. 1997).

Abiotic conditions:

Temperature and salinity CTD data for the Bornholm Basin, averaged over the upper 30m of the water column and the entire Bornholm Basin (see 45 station standard grid, Fig. 5), for the years 2002-2003 and 2008-2013 were provided by Burkhard von Dewitz (Helmholtz Centre for Ocean Research, Kiel – GEOMAR). For 2014 and 2015, data were not available yet. To visualize yearly variation in abundance, biomass, and size within each season all statistical test were plotted using Sigma Plot v12.5 (Systat Software).

Statistical analyses:

A series of repeated measures ANOVA models (SAS PROC MIXED; SAS Institute Inc., Cary, NC, USA) were used to determine whether differences existed in jellyfish abundance, biomass, or size over the sampling period. The models included the Year main effect, Season main effect (spring and autumn), as well as the Year x Season interaction. If a significant Year x Season interaction was detected the model was decomposed into a series of one-way ANOVA models to examine the effect of Year for each Season. Alpha was set at $P < 0.05$. Tukey's range test was used to test for differences between the treatments. Residuals were tested for normality (Shapiro-Wilk test; PROC UNIVARIATE; SAS Institute 2003) and homogeneity of variance (PROC GPLOT; SAS Institute 2003). In case data violated the assumption of normality data were transformed to meet the assumptions and homoscedasticity when necessary.

To decipher a possible mechanism for changes in *A. aurita* and *C. capillata* abundance, biomass, and size over the sampling period a series of correlations were generated (SAS PROC CORR; SAS Institute Inc., Cary, NC, USA). The correlation matrixes included the following variables: *A. aurita* biomass, *C. capillata* biomass, Total jellyfish biomass, spring temperature, summer temperature, autumn temperature, spring salinity, summer salinity, autumn salinity, *A. aurita* abundance, *A. aurita* size, *C. capillata* abundance, *C. capillata* size. If a significant correlation ($P < 0.05$) was detected, simple linear regression models (SAS PROC REG; SAS Institute Inc., Cary, NC, USA) were then run to assess relationships between the predictors (i.e. temperature or salinity) and abundance, biomass, and/or size.

5. Results

Database:

A database with all gelatinous macrozooplankton counts from the Bornholm Basin area has been created with a total of 17,101 count data. This database was created from scratch using 2123 pages of handwritten datasheets and was supplemented by jellyfish counts and sizes for the years 2002 and 2003 from Kristina Barz (Thünen Institute, Germany). The database contains jellyfish observations in the Bornholm Basin area for the years 2002/2003 and 2008 to 2015 and includes information such as years of catch, seasons of catch, sampled stations, used gear, mesh sizes of gear, sampled species, count and size information of jellyfish. The analysed dataset sampled a total of 1023 stations from which 7831 individuals corresponded to *A. aurita*, 4144 to *C. capillata*, and 5126 to *M. leidyi*.

Temporal and spatial distribution pattern:

Temporal and spatial distribution data showed that *A. aurita* is basically absent from the Bornholm Basin during spring (Fig. 7), while they were abundant during autumn (Fig. 8). During the 8 sampling years, a total of 21 *A. aurita* were caught during spring, whereas in 2002, 2003, 2008, 2012 and 2014 no *A. aurita* were captured (Fig. 7). For autumn, jellyfish were present every year (Fig. 8). *A. aurita* showed a large spatial distribution and were typically captured in all stations in the extended Bornholm Basin (Fig. 8). No pattern in spatial distribution was evident and jellyfish were distributed independent of e.g. bottom depth (Fig. 8). Highest abundances of *A. aurita* were observed during 2002 (Fig. 8k), 2009 (Fig. 8n) and 2013 (Fig. 8r) with a station maximum of ca. 10 ind m⁻². Overall largest *A. aurita* abundances were observed during 2009 (Fig. 8n) and 2013 (Fig. 8r) with an average density of 2 ind. m⁻². Lowest abundances were found in 2011 with an average of 0.4 ± 0.35 ind m⁻² (Figs. 8p).

C. capillata was present in the Bornholm Basin during spring and autumn, apart from the years 2002 and 2003, where animals were only caught at one station during November 2002 (Fig. 9ab, Fig. 10kl). The spatial distribution pattern showed that *C. capillata* was absent from the Arkona Basin with only one record during autumn 2010 (Fig. 10o). Also during autumn 2011 and 2014, the distribution was shifted towards the east with highest abundances attained outside the central Bornholm Basin in the Stolpe Furrow and the southern Gotland Basin (Fig. 10ps).

In contrast to *A. aurita*, *C. capillata* showed higher abundances during spring (Fig. 9) compared to autumn (Fig. 10). For spring 2009 (Fig. 9d) a maximum of 5.3 *C. capillata* m⁻² were observed, while in 2010 a maximum of 3 *C. capillata* m⁻² were observed (Fig. 9e). Maximum abundances during autumn

were 1.9 and 1.8 ind m⁻² for the years 2009 (Fig. 10n) and 2013 (Fig. 10r), respectively. Average abundances per spring cruises ranged between 0.06 to 1.78 *C. capillata* m⁻² for the years 2009 to 2015 (no data were collected in 2014), while no jellyfish were present in spring 2002 and 2003 (Fig. 9). For autumn, average abundances per cruise ranged between 0.003 and 0.7 *C. capillata* m⁻² for the years 2002 (Fig. 10k) and 2008 to 2015 (Fig. 10m-t), while no *C. capillata* have been caught during November 2003 (Fig. 10l).

Size distribution:

The average diameter of *A. aurita* during spring was 70 mm (n = 21). In contrast, *C. capillata* showed an average size range of 5 to 48 mm (Table.2). The *C. capillata* abundance peak observed during spring 2009 (Fig. 9d) was driven by very small sized animals with an average diameter of 5 mm (Table.2).

For autumn, average sizes range between 96 to 131 mm for *A. aurita* (Table 2, Fig. 11), while *C. capillata* were much smaller with an average size range between 33 to 48 mm (Table 2, Fig. 12).

Size distribution data for *A. aurita* showed that for the years 2002, 2010, 2011, 2012, average observed sizes during autumn were higher compared to the overall average (Fig. 11). In contrast, during 2003 and 2014, observed sizes were smaller compared to the overall average (Fig. 11). For *C. capillata*, jellyfish were largest during spring 2011 and 2012, compared to other years (i.e. 2010, 2013, 2015), while the community was primarily composed of small ephyra during 2009 and 2010 (Fig. 12). For autumn, the largest jellyfish were observed during 2008, 2012 and 2013, while they were smaller during 2009, 2014 and 2015 (Fig. 12). Together, this change in size frequency distribution can inform us about population dynamics and age structure, which will be discussed later on.

Spatial *A. aurita* biomass distribution in the Bornholm Basin (Fig. 13,14) followed observed abundance distribution pattern (Fig. 7,8). Maximum biomass, expressed as wet weight, at a particular station was reached during autumn 2002 and 2013 with 0.9 and 0.8 kg m⁻², respectively (Fig. 14kr, Table 3). Overall, average *A. aurita* biomass was significantly higher during autumn 2009, 2012 and 2013 (Figs. 14nqr, 18d). Biomass of *C. capillata* was 1 to 2 orders of magnitude lower compared to *A. aurita* (Figs. 14l16). Spatial observations showed that *C. capillata* were more patchily distributed compared to *A. aurita*. During autumn 2014, a more eastward biomass distribution of *C. capillata* compared to the other years was evident (Fig. 10s, 16s). For *C. capillata*, peak abundance during spring 2009 (Fig. 9) was not represented in the biomass distribution (Fig. 15). Largest spatial

extend of *C. capillata*, along with highest overall biomass in the investigation area was observed during spring 2012 (Fig. 15) as well as autumn 2012 and 2013 (Fig. 16). During these periods, maximum biomass per station ranged between 20 to 30 g WW m⁻² which corresponded to an average biomass in the investigation area of max. 5 g WW m⁻² during spring 2012 and 9-11 g WW m⁻² for autumn 2012 and 2013 (Table 3).

For *A. aurita* and *M. leidy*, abundance and size data were used to calculate community clearance rates for estimating grazing impact and thereby impact on the food web. The *A. aurita* community (m⁻³) had a maximum clearance rate of 21 and 15 L for maximum abundance stations during 2002 and 2013, respectively (Table 3). This corresponds to a filtration of 2% for 2002 and 1.5% for 2013 of the water column per day (Table 3). The average temperature corrected community clearance for autumn ranges between ~1 to 2.5 L d⁻¹ which relates to a clearance of 0.1 to 0.2% of the water column per day (Fig. 17a). In comparison, *M. leidy* had 1 to 2 orders of magnitude lower maximum biomass and their maximum community clearance rate ranged between 0.1 to 0.5% of the water column per day (Table 3). The average community clearance rate was even lower with 0.01 to 0.15% of the water column being filtered by the *M. leidy* community during autumn d⁻¹ (Fig. 17b).

For the repeated measures ANOVA models abundance, size and biomass of *A. aurita* showed a significant Year x Season interaction for all parameters ($p < 0.0001$). Therefore, the models were decomposed into a series of one-way ANOVAs to examine the effect of year for spring and autumn. For spring, *A. aurita* showed no significant year effect for abundance ($F_{7,304}=1.67$, $p = 0.117$; Fig. 18a), biomass ($F_{7,304}=1.59$, $p = 0.137$; Fig 18c) or size ($F_{4,3}=0.78$, $p = 0.606$; Fig. 18e). It is important to emphasize that during the spring sampling period, there were few *A. aurita* captured, so statistical analyses were only performed on 21 individuals. On the other hand, all parameters analysed in autumn were significant (Fig. 18bdf); i.e. abundance ($F_{9,307}=6.09$, $p < 0.001$), biomass ($F_{9,305}=4.61$, $p < 0.001$) and size ($F_{9,276}=17.79$, $p < 0.001$). More specifically, abundance for *A. aurita* was highest in 2009 and lowest in 2011 (Fig. 18b), while biomass was relatively high in all sampling years with a peak biomass in 2013 (Fig 18d). Interestingly, *A. aurita* peaked in size during 2011 (Fig. 18f).

For *C. capillata* the repeated measures ANOVA models showed a significant Year x Season interaction for abundance ($F_{7,638}=27.39$, $p < 0.001$), biomass ($F_{7,643}=28.94$, $p < 0.001$) and size ($F_{5,638}=29.86$, $p < 0.001$) (Fig. 19). Therefore, models were decomposed into a series of one-way ANOVA models to look at the effect of Year for each Season. For spring, a significant Year effect for abundance ($F_{7,302}=42.52$, $p < 0.001$; Fig. 19a), biomass ($F_{7,303}=23.52$, $p < 0.001$; Fig. 19c) and size ($F_{5,148}=88.77$, $p < 0.001$; Fig. 19e) was evident from the data. Here, *C. capillata* abundances was highest in 2009 (Fig.19a), biomass was highest in 2012 (Fig. 19c), and largest animals were observed

in 2011 and 2012 since there was not a significant variation between these years (Fig. 19e). The autumn one-way ANOVA models showed a significant abundance year effect ($F_{9,306}=40.82$, $p < 0001$), biomass ($F_{9,308}=37.90$, $p < 0001$) and size ($F_{8,176}=6.49$, $p < 0001$), for this season abundance was highest during 2013 (Fig 19b), biomass was also highest during 2013 and lowest during 2002 and 2003 (Fig. 19d). Surprisingly, although 2002 had low abundance and biomass, jellyfish were relatively large, being 2002 the year with largest jellyfish (Fig. 19f).

To decipher a possible mechanism for these observed changes in abundance, biomass and size over the sampling period, these data were then linked (using correlation and regression approaches) to temperature and salinity profiles in the Bornholm Basin. For these analyses two additional variables were added: total jellyfish abundance and total jellyfish biomass. These new variables consider all jellyfishes, including *A. aurita*, *C. capillata* and *M. leidyi*, in order to gain a better understating on how hydrographic conditions impact total gelatinous macrozooplankton biomass.

For results, a significant relationship was detected between spring salinity and spring *C. capillata* biomass ($p = 0.040$, $r^2 = 0.60$, Fig. 20a) as well as spring salinity and total jellyfish biomass ($p = 0.029$, $r^2 = 0.65$, Fig. 20b). Significant negative relationships were detected between autumn temperature and spring *C. capillata* abundance ($p = 0.003$, $r^2 = 0.65$, Fig. 21a) as well as autumn temperature and spring total jellyfish biomass ($p = 0.037$, $r^2 = 0.62$, Fig. 21b).

Positive relationships were detected between summer temperature and autumn *A. aurita* abundance ($p = 0.005$, $r^2 = 0.75$, Fig. 22a), summer temperature and autumn *A. aurita* biomass ($p = 0.043$, $r^2 = 0.52$, Fig. 22b), summer temperature and autumn *C. capillata* abundance ($p = 0.043$, $r^2 = 0.51$, Fig. 22c), as well as summer temperature and autumn *total jellyfish* biomass ($p = 0.035$, $r^2 = 0.55$, Fig. 22d). For each significant relationship the equation of the line is reported in Fig. 20 to 22.

Fig. 7 *Aurelia aurita* abundance (ind. m⁻²) and distribution pattern in the Bornholm Basin, central Baltic Sea during spring (March), covering the time period 2002/2003 and 2008 to 2015 (a-j). In spring 2008 and 2014 no data were available (na). Sampled stations without *A. aurita* (+) and total number of sampled animals (n) are indicated.

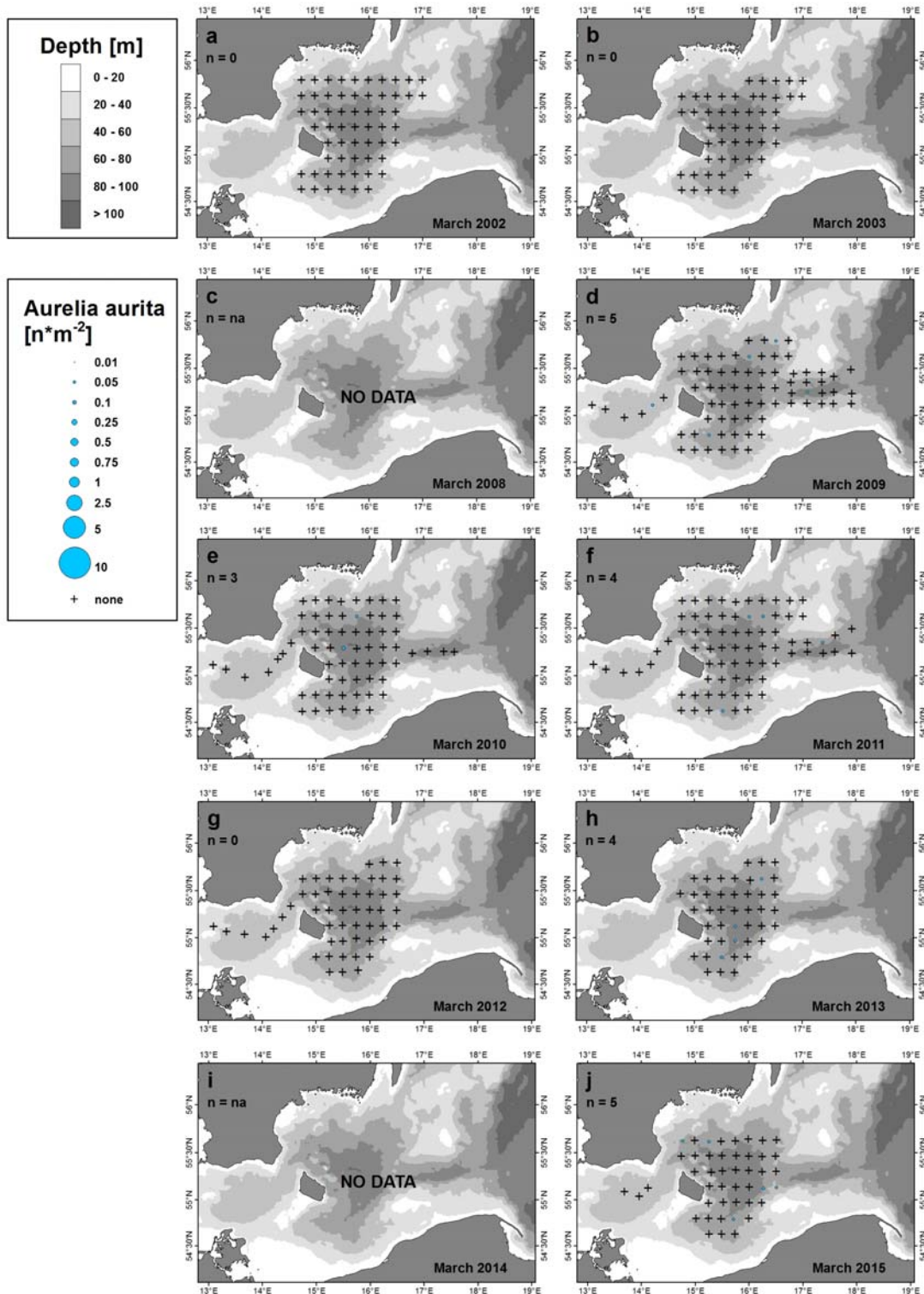


Fig. 8 *Aurelia aurita* abundance (ind. m⁻²) and distribution pattern in the Bornholm Basin, central Baltic Sea during autumn (November), covering the time period 2002/2003 and 2008 to 2015 (k-t). In autumn 2008 and 2014 no data were available (na). Sampled stations without *A. aurita* (+) and total number of sampled animals (n) are indicated.

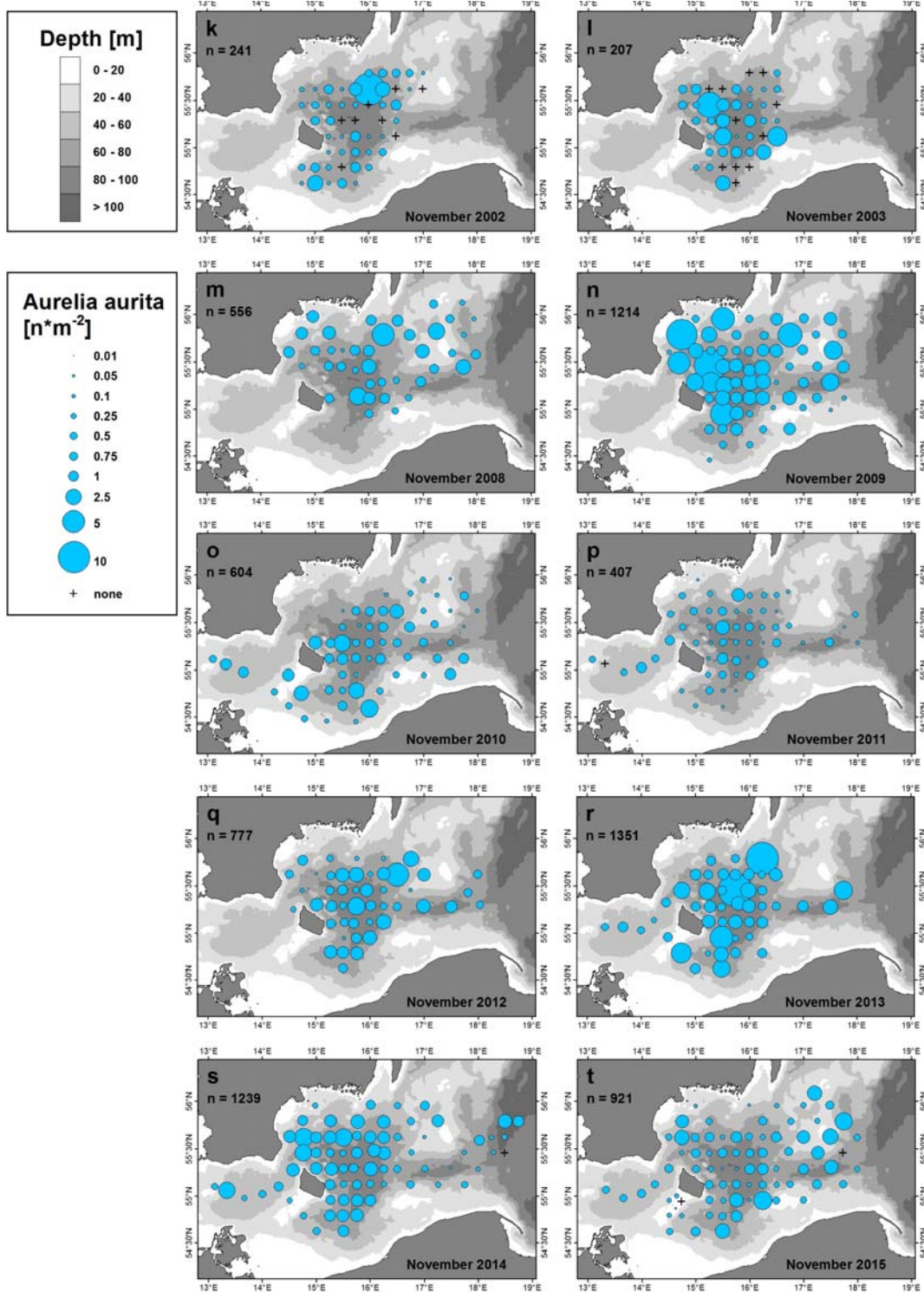


Fig. 9 *Cyanea capillata* abundance (ind. m⁻²) and distribution pattern in the Bornholm Basin, central Baltic Sea during spring (March), covering the time period 2002/2003 and 2008 to 2015 (a-j). In spring 2008 and 2014 no data were available (na). Sampled stations without *A. aurita* (+) and total number of sampled animals (n) are indicated.

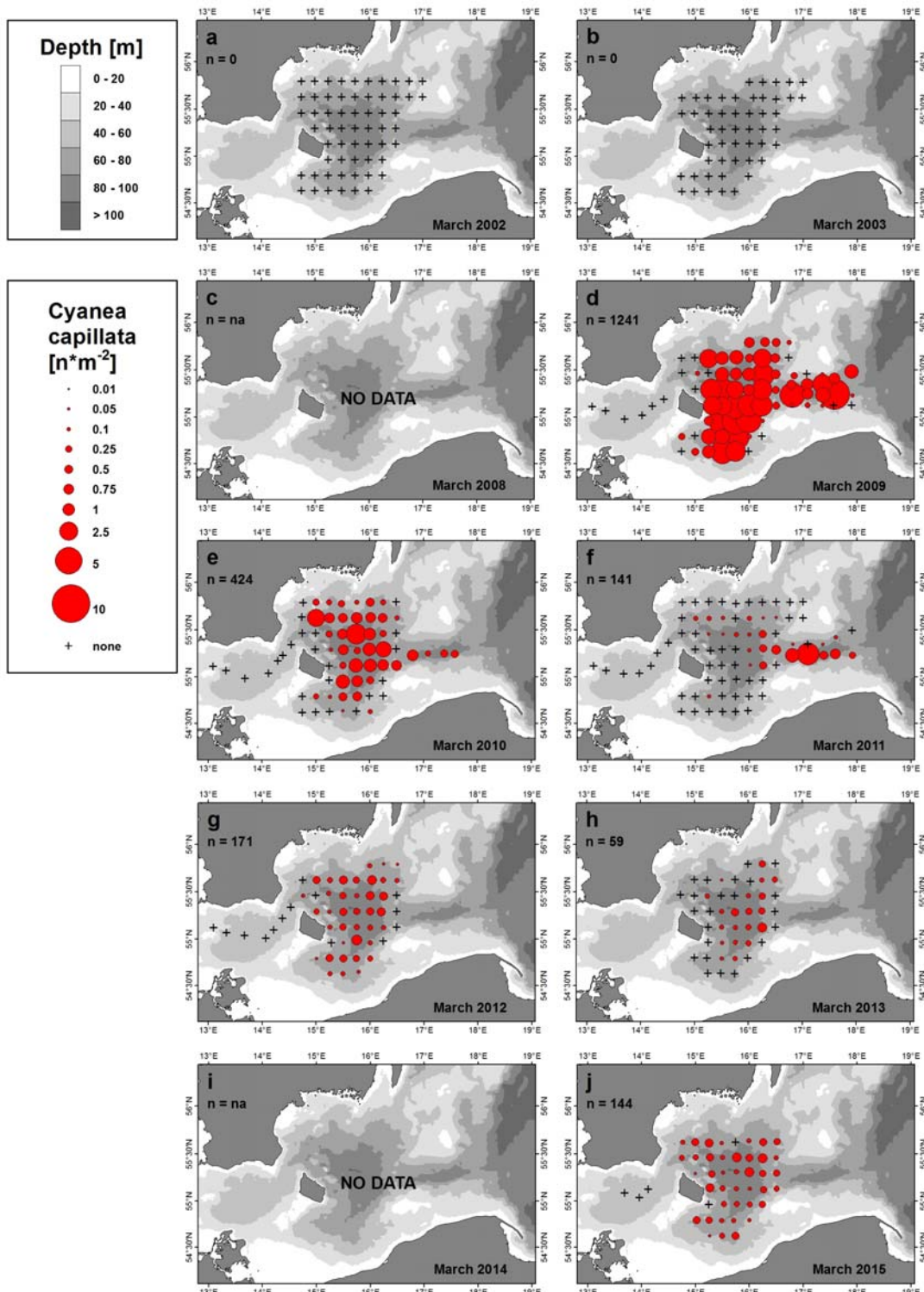


Fig. 10 *Cyanea capillata* abundance (ind. m⁻²) and distribution pattern in the Bornholm Basin, central Baltic Sea during autumn (March), covering the time period 2002/2003 and 2008 to 2015 (k-t). In autumn 2008 and 2014 no data were available (na). Sampled stations without *A. aurita* (+) and total number of sampled animals (n) are indicated.

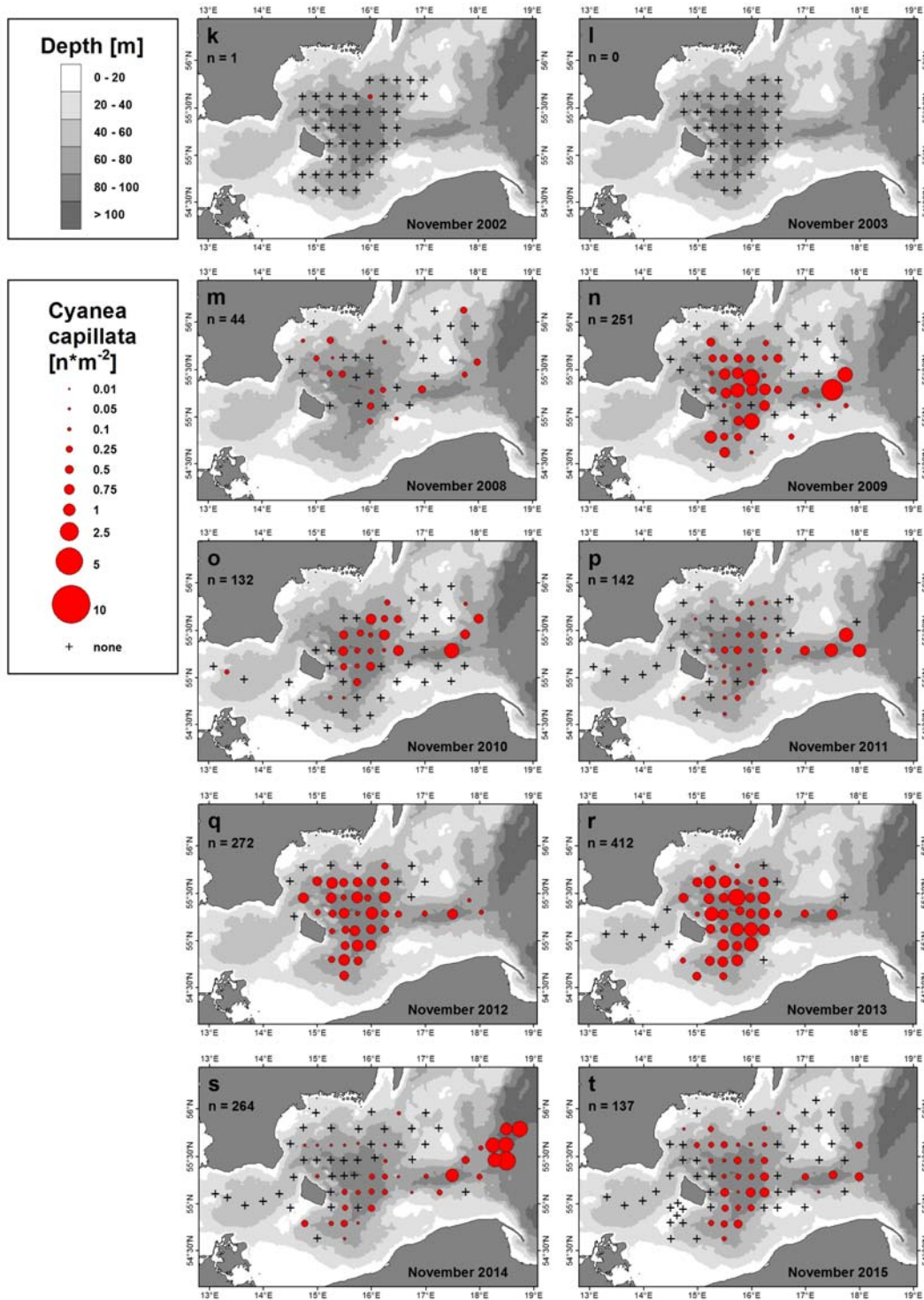


Fig. 11 Size distribution of *Aurelia aurita* as fraction of counts within each 1 cm size bin compared to sum of all sizes per cruise. The average size per cruise (dashed red line) and overall average from all autumn or spring cruises (solid green line) are indicated. Data for spring (March), are not presented due to low sample size (n=21).

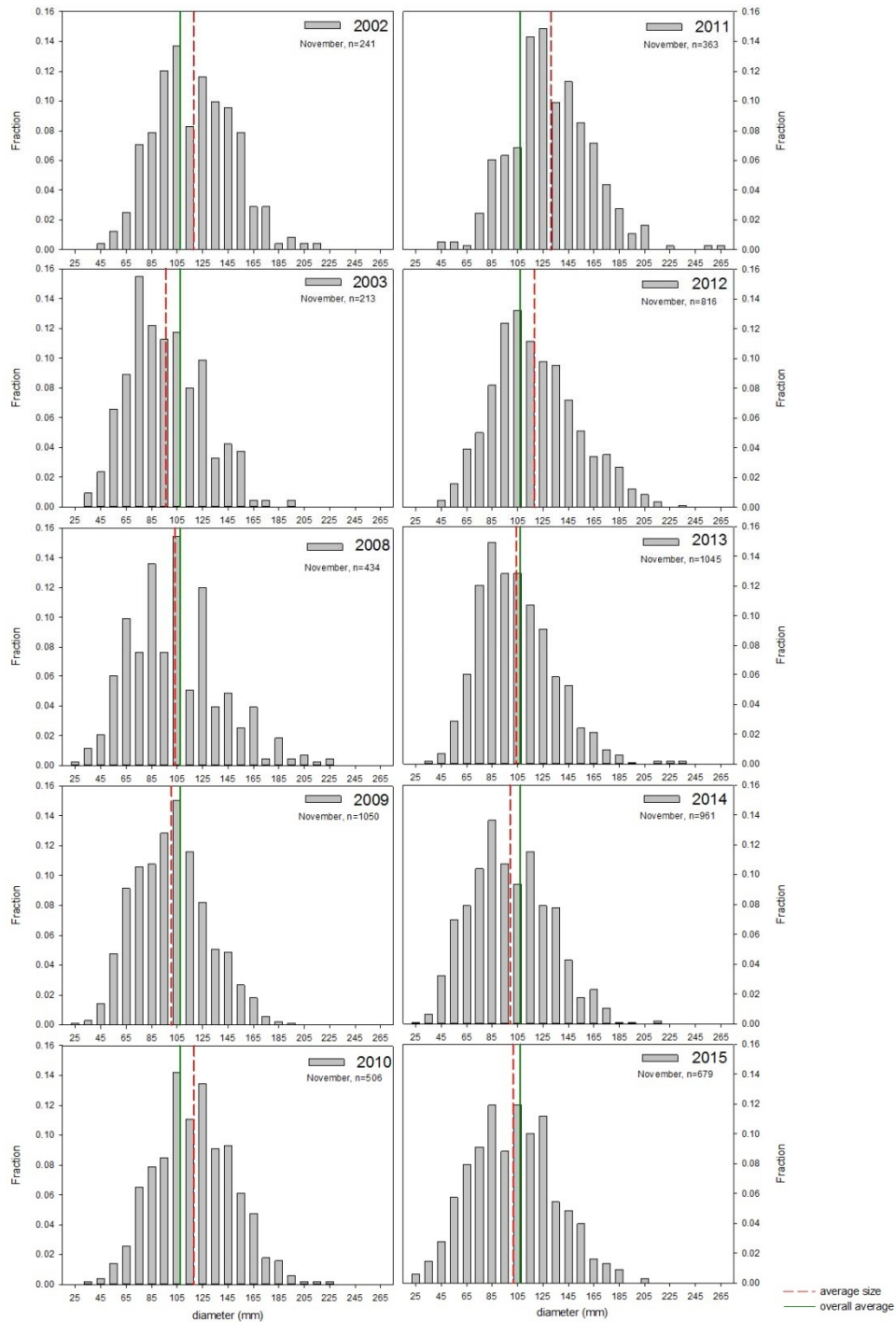


Fig. 12 Size distribution for *Cyanea capillata* as fraction of counts within each 1cm size bin compared to sum of all sizes per cruise. The average size per cruise (dashed red line) and overall average from all autumn or spring cruises (solid green line) are indicated.

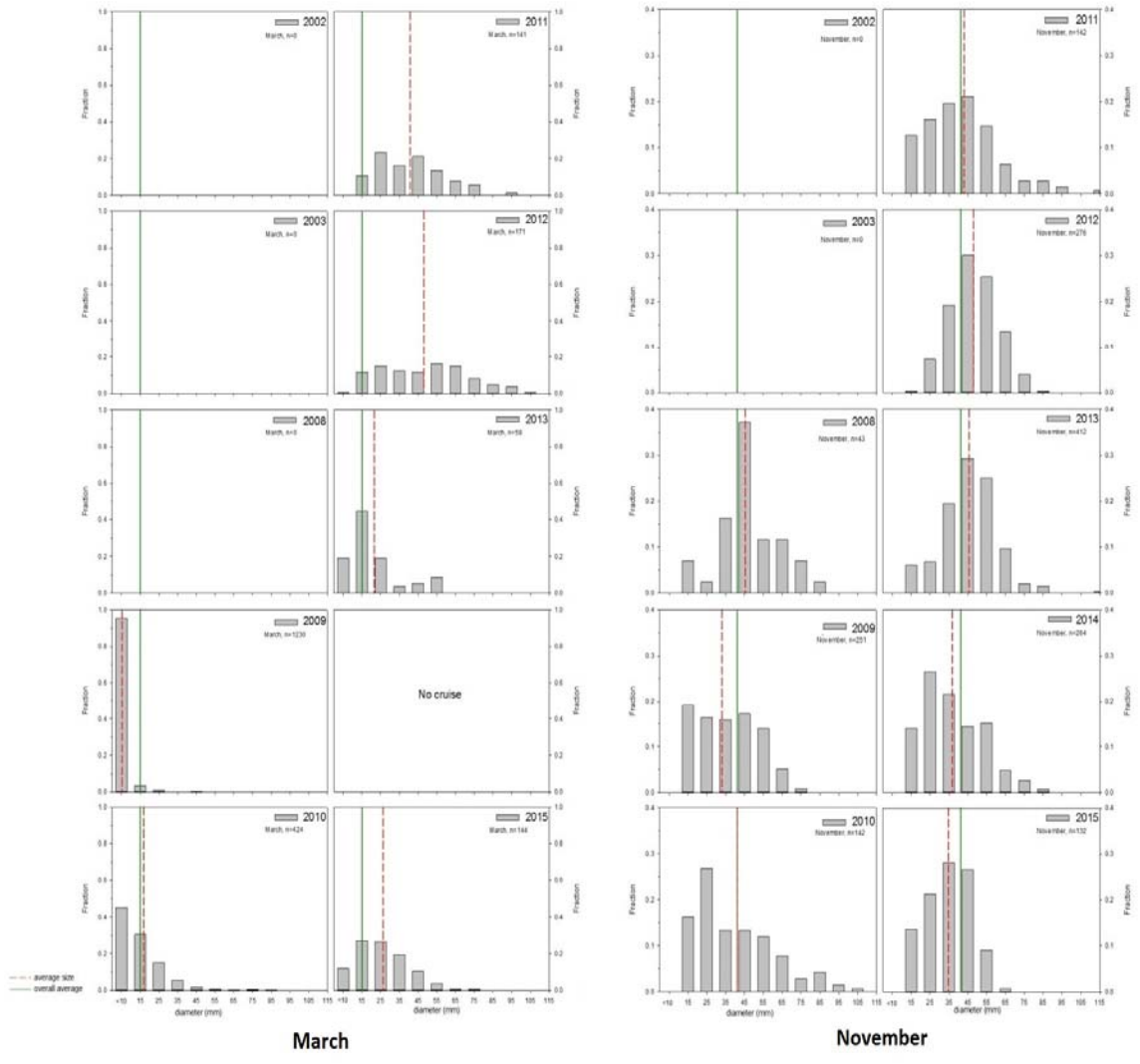


Fig. 13 *A. aurita* biomass (wet weight, $g\ m^{-2}$) distribution in the Bornholm Basin, central Baltic Sea for spring (March) (a-j) covering the time period 2002/2003 and 2008 to 2015. Spring 2008 and 2014 no data available (na), sampled stations without *A. aurita* (+) and total number of sampled animals (n) are indicated.

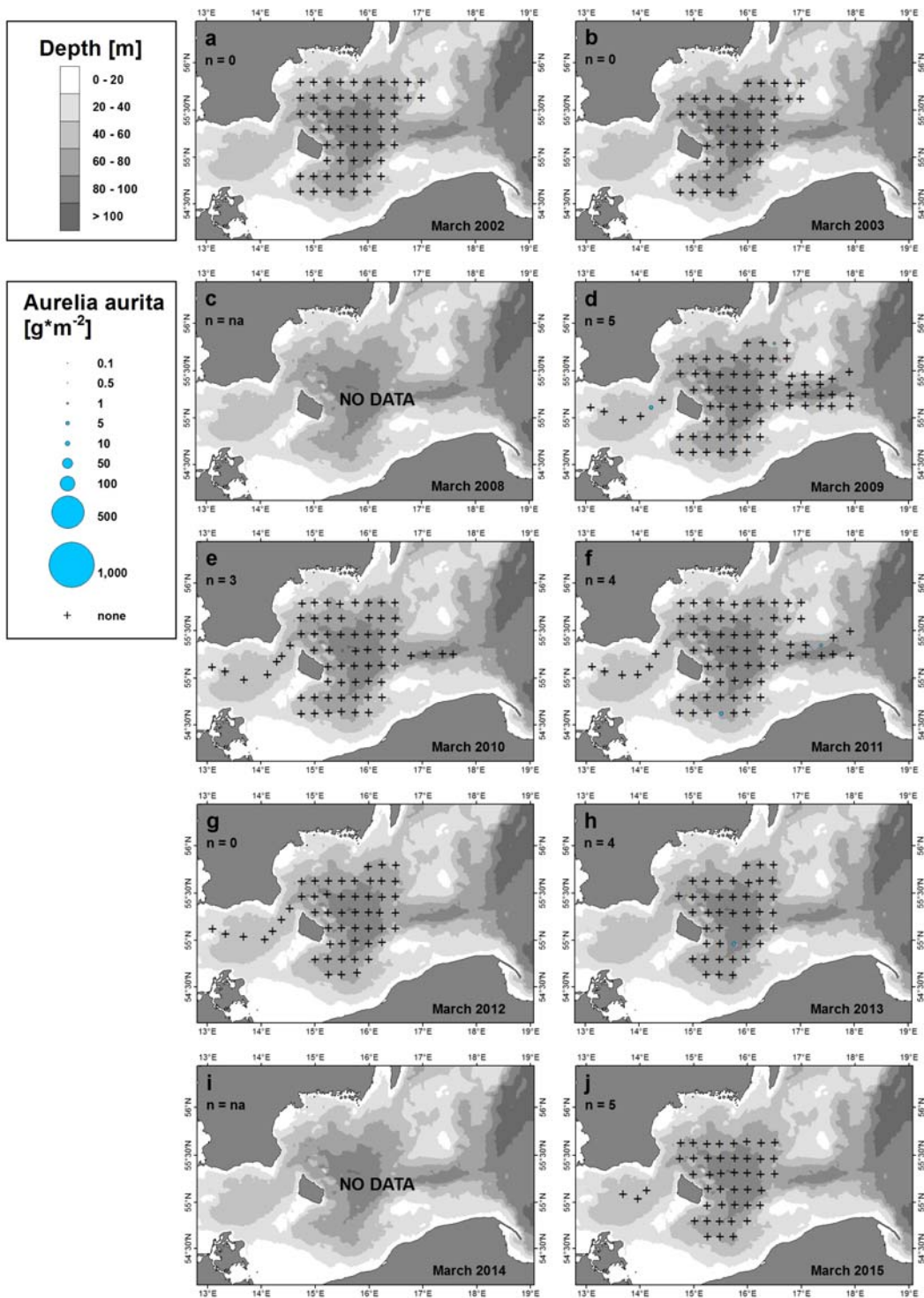


Fig. 14 *A. aurita* biomass (wet weight, $g\ m^{-2}$) distribution in the Bornholm Basin, central Baltic Sea for autumn, November (k-t) covering the time period 2002/2003 and 2008 to 2015. Sampled stations without *A. aurita* (+) and total number of sampled animals (n) are indicated.

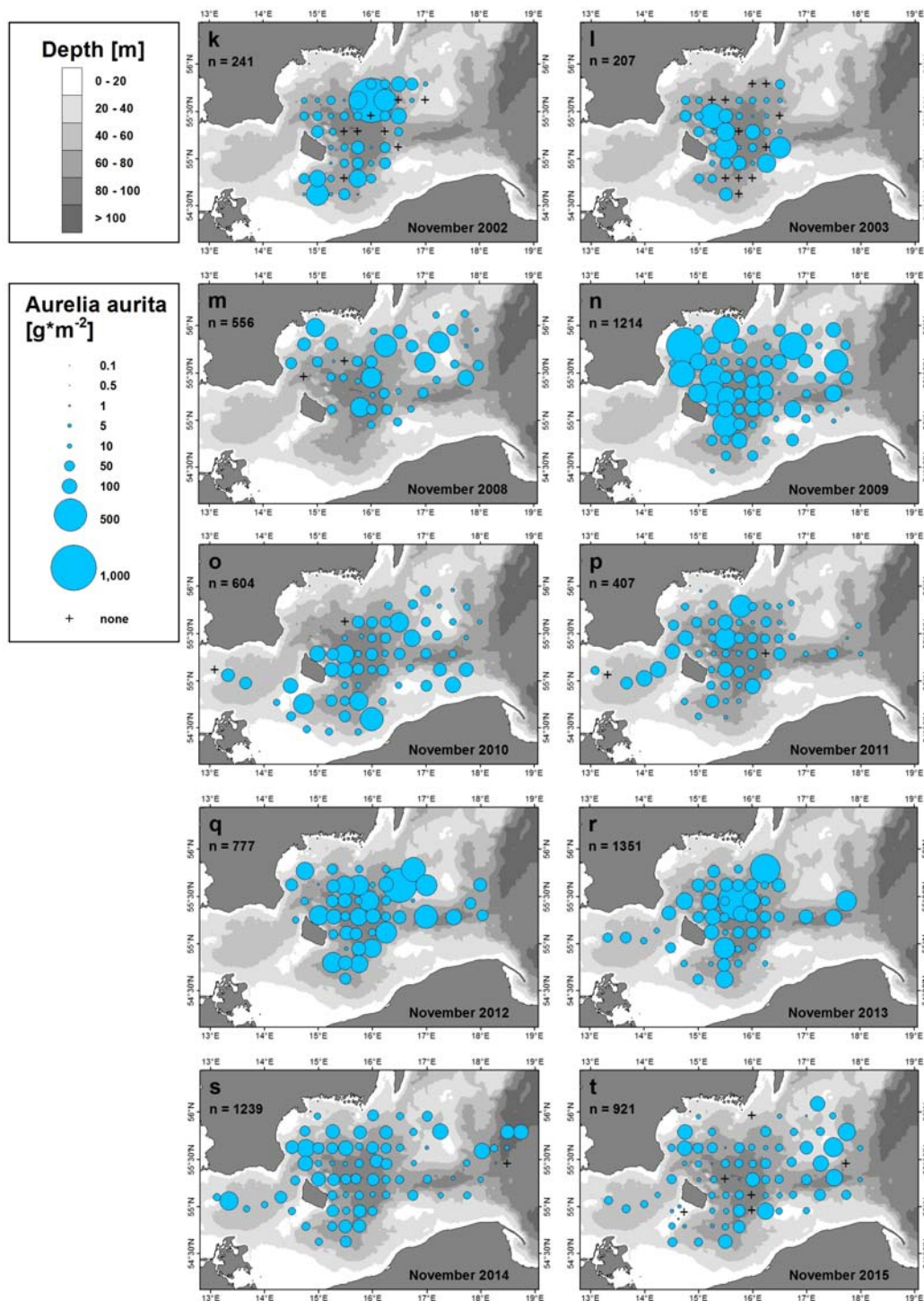


Fig. 15 *C. capillata* biomass (wet weight, g m^{-2}) distribution in the Bornholm Basin, central Baltic Sea for spring, March (a-j) and autumn, November (k-t) covering the time period 2002/2003 and 2008 to 2015. March 2008 and 2014 no data available (na), sampled stations without *C. capillata* (+) and total number of sampled animals (n) are indicated. Note: different scale.

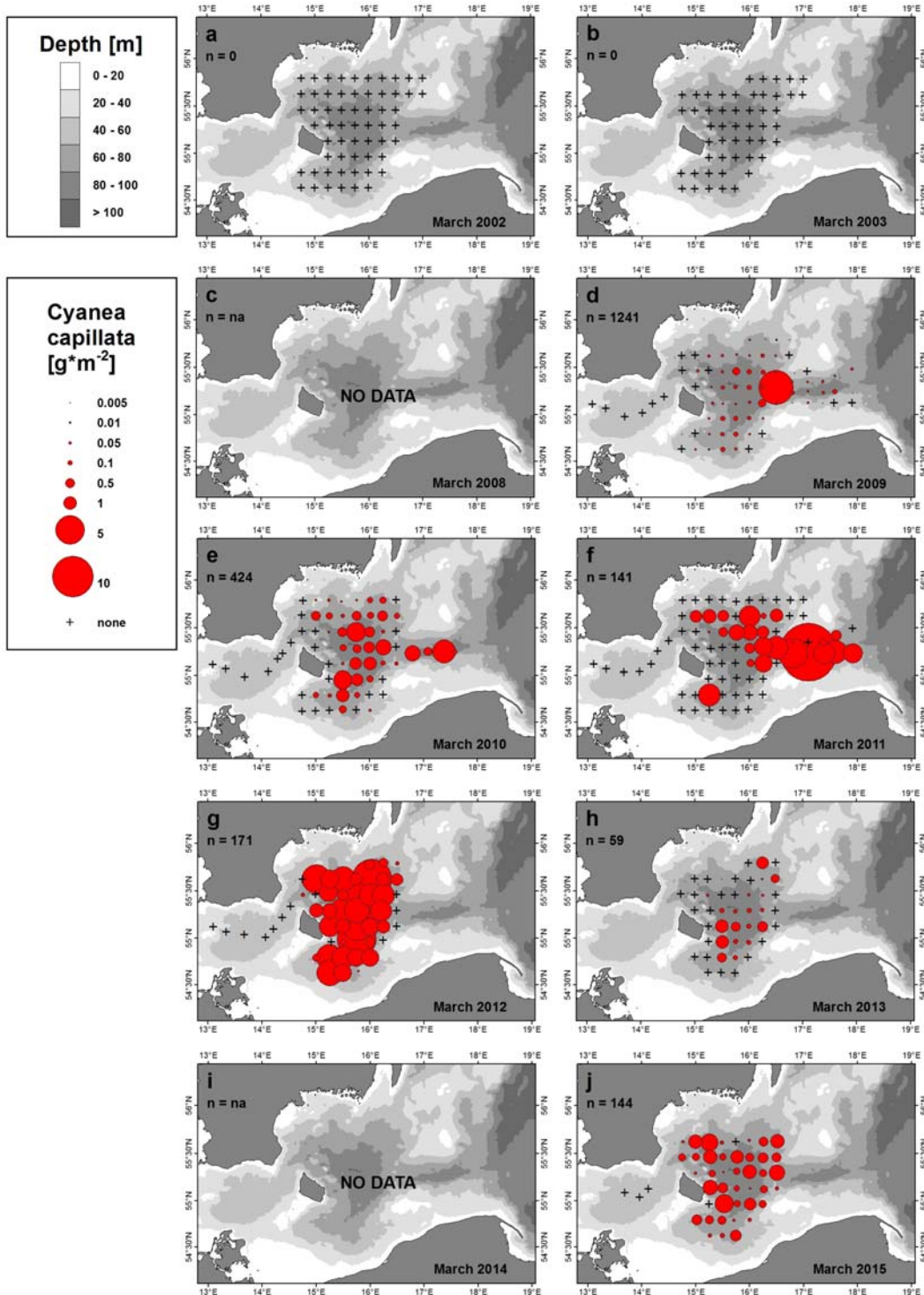


Fig. 16 *C. capillata* biomass (wet weight, g m^{-2}) distribution in the Bornholm Basin, central Baltic Sea for spring, March (a-j) and autumn, November (k-t) covering the time period 2002/2003 and 2008 to 2015. March 2008 and 2014 no data available (na), sampled stations without *C. capillata* (+) and total number of sampled animals (n) are indicated. Note: different scale.

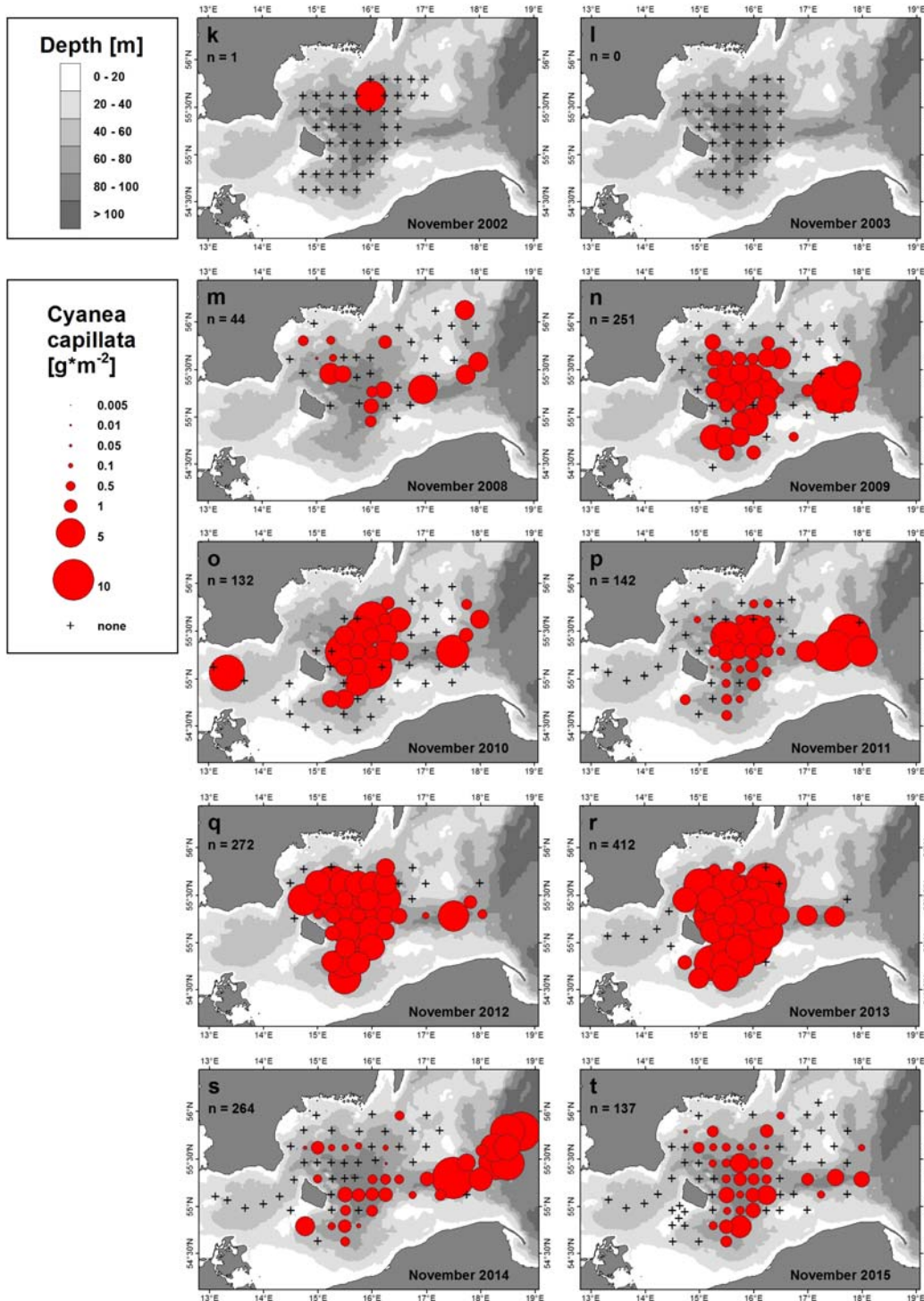


Fig. 17 Average community clearance rates ($L m^{-3} d^{-1}$) of (a) *A. aurita* and (b) *M. leidy* (grey bar \pm SD) during November along with average November temperatures (dots.)

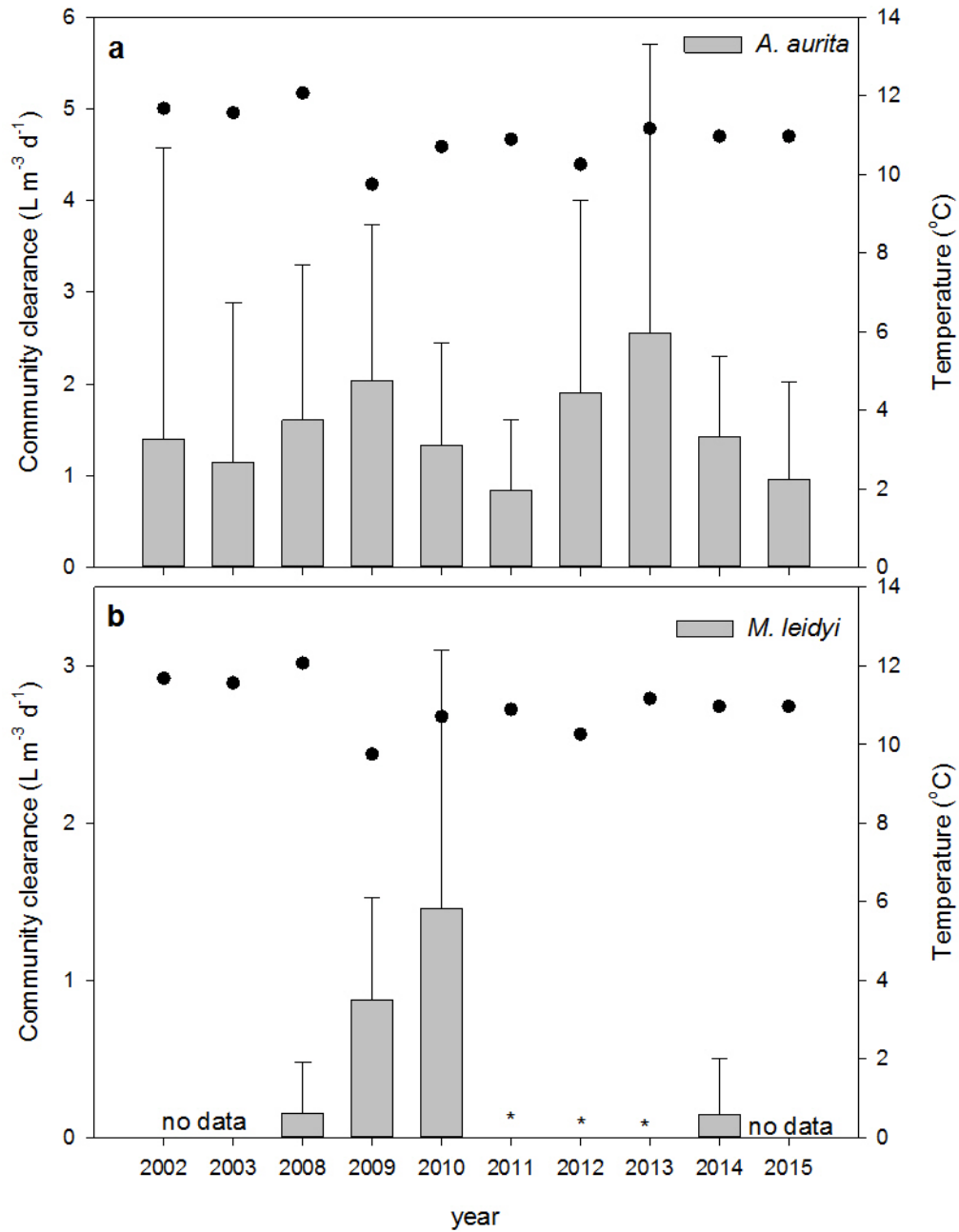


Fig. 18 The effect of Year on abundance (ab), biomass (cd) and size (ef) of *Aurelia aurita* in 45 stations in the Bornholm Basin. First, a series of repeated measures ANOVA models (SAS PROC MIXED; SAS Institute Inc., Cary, NC, USA) were used to determine whether differences existed over the sampling period. If a significant Year x Season interaction was detected the models were decomposed into a series of one-way ANOVA models to examine the effect of Year for each Season. Tukey's range test was used to test for differences between the treatments. Letters indicate significant difference ($\alpha = 0.05$) among groups. Error bars are standard errors.

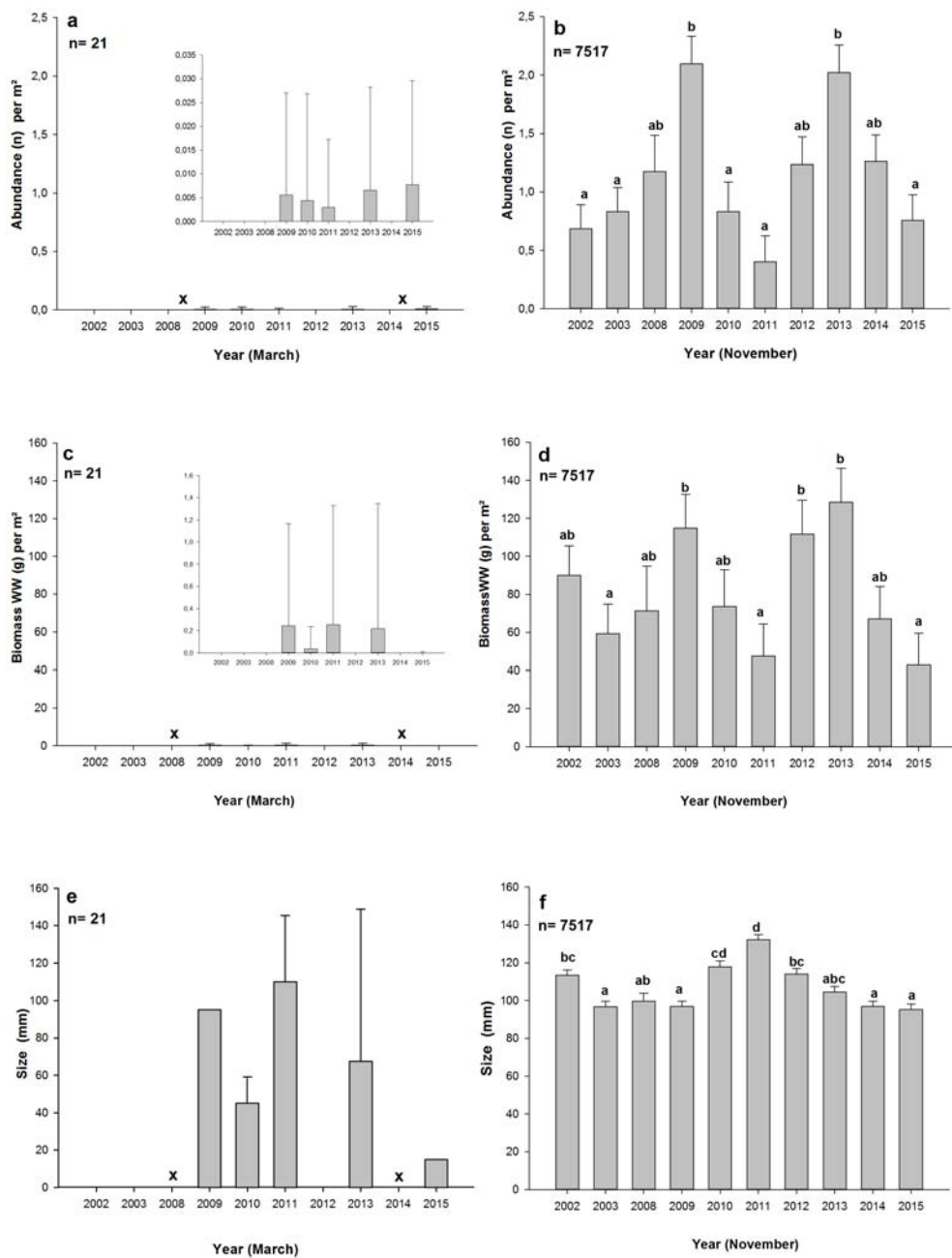


Fig. 19 The effect of Year on abundance (ab), biomass (cd) and size (ef) of *Cyanea capillata* in 45 stations in the Bornholm Basin. First, a series of repeated measures ANOVA models (SAS PROC MIXED; SAS Institute Inc., Cary, NC, USA) were used to determine whether differences existed over the sampling period. If a significant Year x Season interaction was detected the models were decomposed into a series of one-way ANOVA models to examine the effect of Year for each Season. Tukey's range test was used to test for differences between the treatments. Letters indicate significant difference (alpha = 0.05) among groups. Error bars are standard errors.

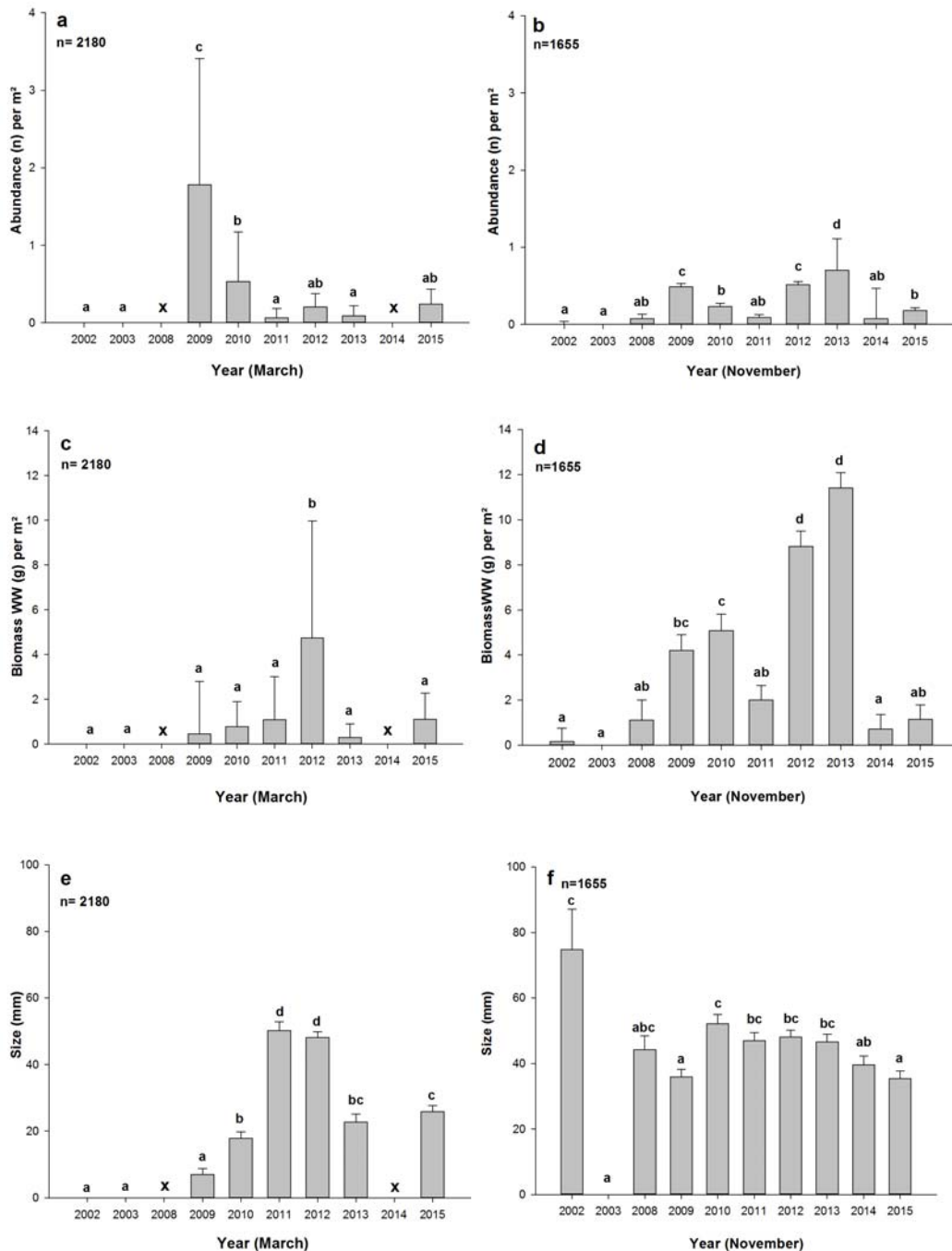


Fig. 20 Relationship between Spring salinity and March *C. capillata* abundance (left) and March total jellyfish biomass (right). Solid lines show significant linear relationship.

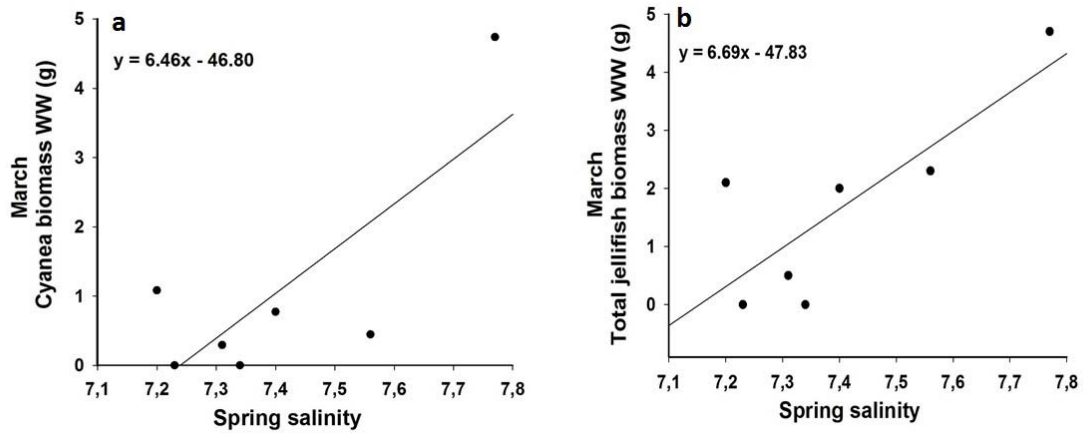


Fig. 21 Relationship between November temperature and March *C. capillata* abundance (left) and March total jellyfish biomass (right). Solid lines show significant linear relationship.

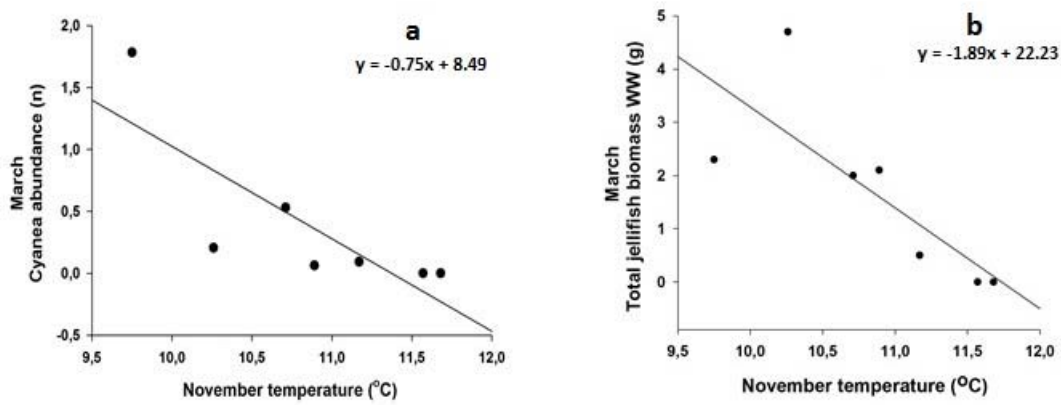


Fig. 22 Relationship between Summer temperature and November abundance (upper panel left) and biomass (upper panel right) of *A. aurita*, *C. capillata* abundance (lower panel left) and total jellyfish biomass (lower panel right). Solid lines show significant linear relationships.

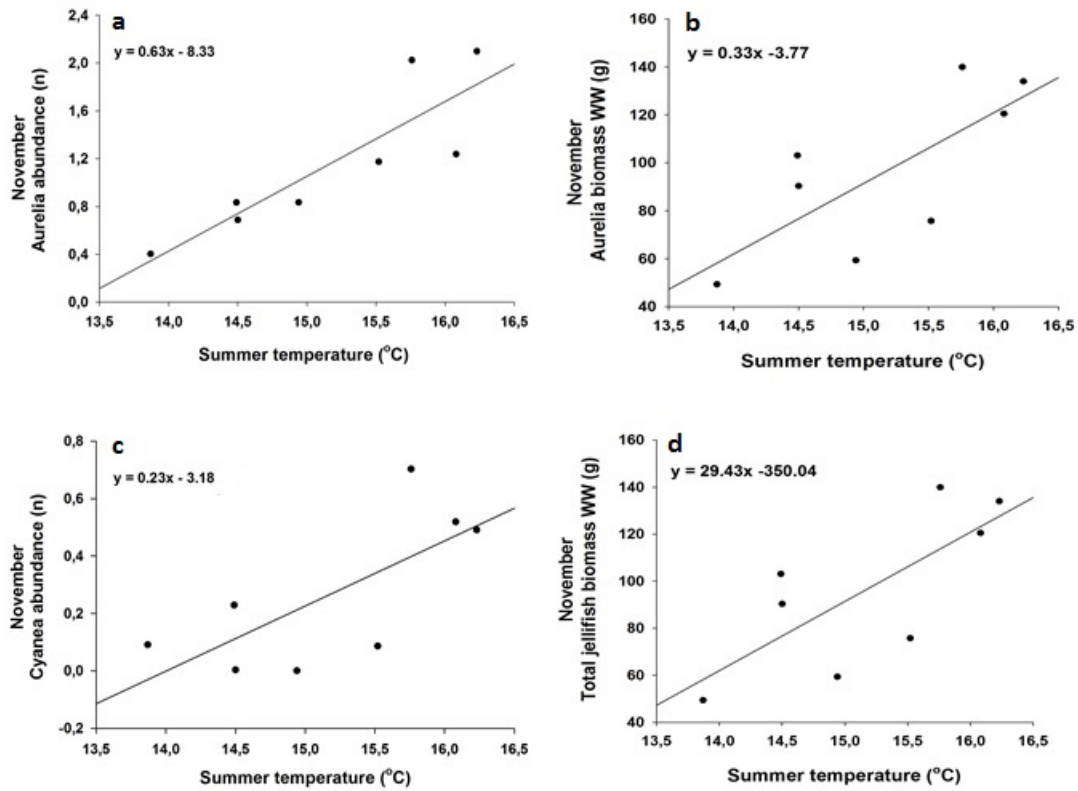


Table 2 Average diameter (\pm SD) of the two scyphozoan species present in the Bornholm Basin during spring (March) and autumn (November) for consecutive years – no data for *A. aurita* during March.

	Year	Diameter	SD
November		mm	mm
<i>A. aurita</i>	2002	118	31
	2003	96	30
	2008	103	36
	2009	101	29
	2010	118	31
	2011	131	32
	2012	119	34
	2013	104	30
	2014	99	31
	2015	102	33
	average:	107	33
<i>C. capillata</i>	2002	no jellies	
	2003	no jellies	
	2008	46	18
	2009	33	17
	2010	41	24
	2011	43	22
	2012	48	13
	2013	46	15
	2014	37	16
	2015	35	12
	average:	41	17
March			
<i>C. capillata</i>	2002	no jellies	
	2003	no jellies	
	2008	no jellies	
	2009	5	5
	2010	17	11
	2011	41	18
	2012	48	23
	2013	22	14
	2015	26	13
		average:	15

Table 3 Summary table for ranges (maximum, minimum) of biomass (wet weight, WW, g) and community clearance rate estimates ($L m^{-3} d^{-1}$) from a 45 station standard grid in the Bornholm Basin, central Baltic Sea, covering the years 2002/2003 and 2008 to 2015 for two scyphozoan species (*Aurelia aurita*, *Cyanea capillata*) and the invasive American comb jelly *Mnemiopsis leidyi*. *M. leidyi* has been included in this table for comparison to community clearance rates of *A. aurita*. Since clearance estimates for *C. capillata* have a large uncertainty, due to a broad diet including other gelatinous organisms, no community clearance have been calculated. March 2014 no cruise.

Month	Year	<i>Aurelia aurita</i>				<i>Cyanea capillata</i>		<i>Mnemiopsis leidyi</i>			
		WW $g m^{-2}$		Community clearance $L m^{-3} d^{-1}$		WW $g m^{-2}$		WW $g m^{-2}$		Community clearance $L m^{-3} d^{-1}$	
		max	min	Max	min	max	min	max	min	Max	min
November	2002	941.1	0	20.8	0	6.9	0	no data			
	2003	288.4	0	7.5	0	0.0	0	no data			
	2008	253.2	7.3	7.3	0.20	5.8	0	6.3	0	1.1	0
	2009	372.3	4.1	7.05	0.12	17.5	0	19.9	0	2.3	0
	2010	217.1	5.6	4.2	0.12	23.2	0	13.8	0	5.3	0
	2011	276.7	4.7	4	0.09	23.5	0				
	2012	563.0	1.6	11.3	0.04	19.4	0				
	2013	784.2	10.1	14.6	0.27	32.7	0				
	2014	178.6	14.0	3.9	0.30	2.9	0	3.05	0	1.5	0
	2015	171.3	1.9	5.7	0.05	6.4	0	no data			
March	2002	0	0	0	0	0	0	0	0	0	0
	2003	0	0	0	0	0	0	0	0	0	0
	2009	3.8	0	0.05	0	15.8	0	7.5	0	0.36	0
	2010	1.4	0	0.01	0	4.7	0	3.6	0	0.28	0
	2011	6.1	0	0.05	0	7.1	0	2.6	0	0.11	0
	2012	0	0	0	0	22.0	0	0	0	0	0
2013	7.4	0	0.05	0	2.3	0	0	0	0	0	
2015	0.02	0	0.001	0	4.5	0	0	0	0	0	

6. Discussion:

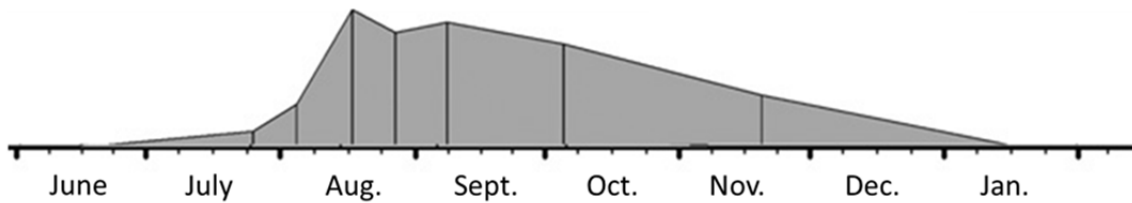
Gelatinous zooplankton blooms are episodic and seasonal, they exhibit high inter-annual variability (Mills.2001). These irregular patterns of occurrence and abundance are part of the reason for a long standing discussion whether jellyfish are on a rise at a global scale or if observed jellyfish blooms are a matter of increased public awareness, since there is a lack of continuity in the data collection, such that the public perception is shaped in the absence of a historical baseline (Fig.24) (Condon et al.2012). A major problem in answering this question has been the in-availability of long term data. Here, the longest data series on abundance and biomass data for two scyphozoan species (*A. aurita* and *C. capillata*), present in the central Baltic Sea, has been compiled. The same sampling gear and 45 station standard grid has consistently been used since 2002. Jelly population sizes typically show dramatic inter-annual fluctuations. However, determination of true fluctuations or increases and the causes have been hampered by the short duration (<10 years) of most available data sets. Henson et al. (2010) concluded that time series of ~40 years are necessary to distinguish trends due to global warming from natural inter-annual and decadal variability. Therefore, few jelly data sets are sufficiently long to evaluate if population sizes have increased over time (Lynam.2005b). This dataset is a first attempt to investigate jellyfish population dynamics in the central Baltic Sea covering a time period of 10 years. We show that *A. aurita* is the most prominent gelatinous macrozooplankton species with maximum biomass of up ca. 1 kg wet weight m⁻² as observed during autumn 2002 and 2013. However, *C. capillata* is known to have a much lower biomass contribution to the jellyfish community being 1 to 2 orders of magnitude lower (Janas & Witek.1993; Lischka.1999; Barz & Hirche.2005). While *A. aurita* is seldom present in the Bornholm Basin during spring, *C. capillata* is present in spring and autumn during most years.

A. aurita has been shown to strobilate from October to April along the Swedish Kattegat coast, while *C. capillata* strobilates later in the season, during March to May (Gröndahl.1988). It has been shown that both species can be drifted into the Bornholm Basin (Barz et al.2006). Especially *C. capillata* seems to recruit to the central Baltic via drift recruitment, since animals are exclusively found in deep waters of the Bornholm Basin (Lischka.1999; Barz & Hirche.2005), i.e. in the depth layers where inflowing water from the western Baltic is usually deposited due to its higher salinity and density. Furthermore, no strobilation sites further into the Baltic Sea than the Swedish Kattegat coast have been identified (Gröndahl & Hernroth.1987; Gröndahl.1988). In agreement with this, *C. capillata* abundance as well as total jellyfish biomass during March were positively correlated with salinity. Increasing salinities in the central areas are a proxy for higher saline waters stemming from more westerly areas. In our analyses, we use average salinities of the upper 30m of the water

column in the Bornholm Basin. This does not allow extrapolation to deep water inflow events, which most likely carry *C. capillata* into the central Baltic Sea as suggested by Barz et al. (2006). On the other hand, *A. aurita* is mostly restricted to the upper 30m of the water column in the Bornholm and Gotland basins (Lischka 1999; Barz & Hirche 2005; Barz et al. 2006). Hence, higher salinities can directly be linked to water inflow from more westerly Baltic Sea areas with known strobilation sites for *A. aurita* (Janas & Witek 1993; Holst & Jarms 2010). Active strobilation for *A. aurita* has also been described for low saline areas of the North East Baltic Sea (Wikström.1932). It has been suggested that both sub-populations have a slightly different timing in their reproduction biology. However, the degree of mixing between both sub-populations as well as their geographic extend within the Baltic Sea is unknown.

In the South West Baltic Sea, *A. aurita* has been described to show an abundance increase during spring/early summer with a subsequent drastic decrease during early autumn (Möller 1979; Schneider 1989). However, in this study we show that animals are numerous during autumn in the Bornholm Basin, and few adults are still around during March. Published seasonal population development studies of *A. aurita* in the Bornholm Basin show that peak abundances are attained during August (Barz & Hirche 2005; Schulz et al. 2012). During November, abundances can be less than half compared to peak abundances attained during August and animals have been shown to disappear from the system during winter (Schulz et al. 2012). Comparison of two consecutive spring samplings in the Bornholm Basin revealed that *A. aurita* appeared during April in 2003, while animals were first observed 2 months later during 2002 (Schulz et al. 2012). The earlier presence of animals during 2003 has been suggested to be related to successive inflow events observed during January 2003 (Schulz et al. 2012). Similarly, drift recruitment of scyphozoan species in the Bornholm Basin has been suggested and corroborated by drift model analyses (Barz et al. 2006). Drift from westerly adjacent areas could be a possible explanation why extraordinary high abundance along with small size classes of *C. capillata* have been observed during March 2009. No major inflow event, as observed during 2003, could be seen during the 2008/2009 winter. However, consecutive small inflow events of high saline water from the Kattegat are common during winter and could be a possible explanation, since no recruitment of *C. capillata* is expected for the low saline Southern Baltic Sea (Barz et al. 2006; Holst and Jarms 2010). Further drift studies are necessary to enlighten the connectivity between the higher saline Kattegat and the lower saline central Baltic Sea.

Fig. 23: Seasonal abundance development of *A. aurita* from the Bornholm Basin during the period July 2002 to mid February 2003 – modified from Schulz et al. 2012. Note, March and November data have been included in the current analyses.



If animals observed in the central Basins of the Baltic Sea stem from the north-east, low saline population, as has been suggested by earlier studies (Thiel 1962; Möller 1980a; Möller 1980b) or belong to the SW Baltic Sea population which are drifted into the Bornholm Basin, remains to be elucidated e.g. via molecular markers.

Average maximum abundance in July in the larger Kiel Bight areas has been reported to be 0.14 ind. m⁻³, which was extrapolated to a total standing stock of 7x10⁹ for the entire Kiel Bight area (Möller 1979). Peak abundances during their yearly investigation were reached during July (Möller 1979). Similarly, Schulz et al. (2012) observe that maximum *A. aurita* abundances are reached during August in the Bornholm Basin (Fig. 23). During November Möller (1979) quantified average abundances of 0.04 *A. aurita* 100m⁻³ in Kiel Bight. In comparison, we find average abundances between 0.6 to 3 ind. 100 m⁻³ for the Bornholm Basin during November. Average wet weights (WW) in this study are much higher than previously published for the Bornholm Basin. In this study, average wet weights range between 40 to 110 g m⁻² during November. In comparison, Hernroth and Ackefors (1979) find an average wet weight of 13-28g m⁻² in 7 sub-divisions of the Baltic Proper during September/October (as cited in Möller 1980b). Möller (1980b) find a higher wet weight in the Kiel Bight and southern Baltic inshore waters of av. 36g m⁻² during September 1978. Even though we sample 1 to 2 months later compared to these studies, when biomass of *A. aurita* is expected to be lower (Fig. 23), we still find abundances being up to 1 order of magnitude higher.

Our data show that higher summer temperatures lead to a higher abundance and biomass of *A. aurita* and *C. capillata* in the Bornholm Basin, whereas spring temperatures do not have an impact on the jellyfish community investigated during November. Our data indicate that summer temperatures are crucial for the population development of gelatinous macrozooplankton in the southern central Baltic Sea. This is especially pronounced when including the invasive comb jelly *M. leidyi* into the analyses, since total autumn gelatinous macrozooplankton biomass shows the highest summer temperature dependency among all cases tested. Though the temperature analyses only

includes a shorter time period due to unavailability of averaged temperature and salinity data for 2014 and 2015, the significant effect of summer temperature on jellyfish community biomass is interesting. It is likely that under future climate change, which is expected to lead to increased summer temperatures of the Baltic Sea, jellyfish blooms might be favoured.

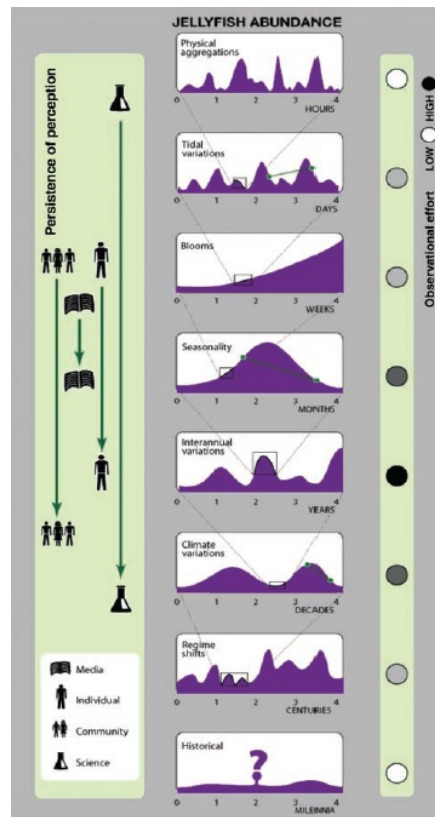
Additionally, we find a significant negative relationship between November temperatures and total jellyfish biomass during March. Lower biomass might be due to increased respiration rates with higher temperatures (Lilley et al. 2014), hence a higher metabolic demand and therefore higher shrinkage. Investigated jellyfish species in this study have a 1 year life cycle, hence it is expected that they reach the end of their life span during winter. There is growing evidence which suggests that climate alters the phenology of jellyfish, causing temporal shifts in bloom formation and trophic mismatches in the food web (Condon et al. 2012).

C. capillata has been shown to feed on mesozooplankton and fish eggs/larvae, similar to *A. aurita* (Båmstedt et al. 1994). However, *C. capillata* can exert a high grazing pressure on *A. aurita* populations (Båmstedt et al. 1994). This has been shown to lead to a population control in high saline areas (Båmstedt et al. 1994). Since *C. capillata* is primarily found in deep waters with low spatial overlap of the *A. aurita* population which is primarily present in surface waters (Barz & Hirche 2005; Barz et al. 2006), direct predation control is expected to be negligible. It is important to elucidate the physiological state of captured *C. capillata* from deep waters to evaluate the predatory impact of *C. capillata* in the Baltic Sea. To do so, direct gut content analyses should be conducted to elucidate if captured animals are still actively feeding or dying due to salinity stress and low temperature regimes.

7. Conclusions:

First of all, during the process of this project, a new database has been developed to allow the analysis of seasonal and inter-annual variations in jellyfish abundances and biomass in the Baltic Sea. So far, our dataset covers the most extensive period sampled in the southern-central Baltic Sea using a standard 45 station grid throughout the Bornholm Basin covering a time period of 10 years from 2002/2003 and 2008 to 2015.

Figure 24. Scales of variability in jellyfish abundance related to the scales of perception by humans. (Condon et al. 2012)



Our analyses indicate that summer temperatures have a significant effect on jellyfish population sizes during autumn. Additionally, biomasses in the Bornholm Basin observed during the 2000's in this study are up to one order of magnitude higher than observations for the same area from the 1970's. However, due to the limited amount of available jellyfish data from the 1970's, the observed rise in jellyfish biomass in the central Baltic Sea needs further investigation. Our results highlight that such investigations are important background information to elucidate the long standing question if gelatinous zooplankton organisms are on a rise as consequence of anthropogenic impact via degradation of natural ecosystems, increased hard substrate (e.g. due to underwater constructions such as bridge pillars, piers, dams etc.) and overfishing. It also highlights the need for standardized monitoring efforts. The scarcity of long term data on gelatinous macrozooplankton blooms results in a continuous sliding frame of references. Thus, the creation of standardized datasets such as the one resulting from this project is an important contribution to future research.

8. Acknowledgements:

First of all I would like to thank all my supervisors: Cornelia Jaspers, Ian Butts, Bastian Huwer and Brian MacKenzie for all their guidance. I know it has been a long way, which sometimes was quite frustrating, thank you all so much for your incredible help and patience. To Marja Koski, for all her help while organizing and helping to choose my classes. I would also like to thank Burkhard von Dewitz for providing salinity and temperature data for the Bornholm Basin, the R/V Dana crew and students for gathering jellyfish information and Kristina Barz for providing raw data for jellyfish and size measurements for March and November 2002 and 2003. To my friend Anna Miesner, who invited me to my first cruise and introduced me to the jellyfish world. My love and gratefulness to all my family members who have always supported me from far away, especially to my parents who taught me to keep going even during hard times; thank you to four great women for believing in me: Lucia, Palina , Alejandra and Lupe, who is no longer with us. And last but not least to Moises Pacheco who encourages me to keep going when I am tired and helps me to grow up, you are my strength.

This work is part of the BONUS project BIO-C3, funded jointly by the EU, the BMBF (Grant No. 03F0682A) and the Innovation Fund Denmark.

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