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Review

Diversity and Physiological Tolerance of Native and Invasive Jellyfish/Ctenophores along the Extreme Salinity Gradient of the Baltic Sea

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Abstract: Global change has led to manifold changes of marine ecosystems and biodiversity worldwide. While it has been shown that certain jellyfish and comb jelly species have increased regionally, it remains to be investigated if this is a general trend or localized phenomenon. Especially for the economically important Baltic Sea, which is characterized by an extreme physical environmental gradient, this question has not been addressed to date. Here we present a detailed account of the gelatinous macro-zooplankton community including their physiological tolerance towards abiotic conditions and resulting distribution ranges in the Baltic. We show that the arrival and establishment of non-indigenous species has led to a rising importance of jellyfish and comb jellies in the Baltic. This accounts for the comb jelly *Mnemiopsis leidyi*, which was first observed in Northern Europe in 2005, as well as for the hydromedusae *Blackfordia virginica*, first sighted in 2014. Both species have been shown to attain high population densities with pronounced grazing impact in other invasive regions. Given the current and anticipated changes of the physical environment of the Baltic Sea, especially ongoing warming, amplification of their impact can be expected.

Keywords: *Aurelia aurita*; *Blackfordia virginica*; brackish water environment; invasive species; jellyfish blooms; *Mnemiopsis leidyi*; *Cyanea capillata*

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1. Introduction

1.1. The Baltic Sea and Its General Gelatinous Macro-Zooplankton Community

The Baltic Sea is a large body of brackish water in northwestern Europe, which can be regarded as the most extreme salinity gradient of any inland Sea in the world. The salinity gradient exhibits salinity levels that range from almost freshwater conditions (0–2) at the northeastern edge of the Baltic Sea to full strength saline water (>30) at the transition to the North Sea (Figure 1). Though the Baltic hosts >6065 multicellular species, it can be regarded as a relatively species-poor habitat with only simple food web interactions [1]. For gelatinous macro-zooplankton, only a few scyphozoan jellyfish (Phylum: Cnidaria) and comb jelly (Phylum: Ctenophora) can be found in the Baltic Sea. The most common species of scyphozoan jellyfish is the Moon jelly, *Aurelia aurita* (Linnaeus, 1758). *Aurelia aurita* contributes up to 99.8% of the total native gelatinous macro-zooplankton biomass in the SW Baltic Sea [2] and 100% in the NE [3]. *A. aurita* is harmless to swimmers/bathers but can be problematic for fishing gear or cooling water intake of power plants, if occurring at high densities [4]. The second scyphozoan jellyfish species present in the Baltic Sea is the Lion's mane jellyfish, *Cyanea capillata* (Linnaeus, 1758). Large individuals (>15 cm diameter) can be found regularly in higher saline areas of the Kattegat (Skagerrak) and occasionally in the SW Baltic Sea during unusual weather and wind conditions [5]. Additionally, small

C. capillata (average 4 cm, >95% being <10 cm [6] can be found in high saline bottom waters throughout the Baltic Sea [6–8]. *Cyanea capillata* does not reach high densities in the Baltic Sea; however, the occasional occurrence of larger individuals in the SW Baltic Sea attracts considerable public attention due to its stinging potential for bathers.

Apart from scyphozoan jellyfish, two comb jellyfish (Phylum: Ctenophora) species are present in the Baltic Sea. First, the arctic relict species *Mertensia ovum* (Fabricius, 1780), which is a common member of arctic food webs [9]. This cyddipid ctenophore has long been misidentified as *Pleurobrachia pileus* (Müller, 1776), especially in the central and northern Baltic Sea [10]. However, recent molecular identification tools have documented that *M. ovum* is common and occurs throughout the Baltic Sea [11–13]. The second ctenophore species is *Mnemiopsis leidyi* (A. Agassiz, 1865), which is non-indigenous to the Baltic Sea and was first observed in September 2006 along the eastern German coast [14]. Additionally, the non-indigenous hydromedusae *Blackfordia virginica* (Mayer, 1910) has been detected in the Kiel Canal since summer 2014 [15].

The higher saline Kattegat, which is the transition zone between the Baltic Sea and the North Sea, is known to harbor a more diverse zooplankton community. Other less common species of jellyfish sighted in the southern Kattegat and SW Baltic Sea include the hydrozoan jellyfish species *Sarsia tubulosa*, *Rathkea octopunctata* and *Obelia geniculata* and the ctenophores *Bolinopsis infundibulum*, *Pleurobrachia pileus* (as reviewed in [2]) as well as occasional sightings of different *Beroe* species in the Danish Straits [16].

1.2. Physical Environment of the Baltic Sea

The Baltic Sea is a marginal Sea of the Atlantic Ocean and is connected to the North Sea via the Skagerrak/Kattegat and the Danish Straits. The Danish Straits (Great Belt, Little Belt, and Øresund—the Sound) are the major obstacle for water exchange between the North Sea and the Baltic Sea [17], due to their narrow and shallow nature. Irrespectively, net precipitation and river run-off in the northeast of the Baltic Sea causes a freshwater surplus, which forces a general outflow of lower saline, brackish water at the surface [18]. In general, this brackish water leaves the Baltic Sea along the Swedish coast through the Øresund (the Sound, Figure 1), where it meets higher saline Kattegat waters and is gradually mixed while flowing out along the Swedish west coast. In the Kattegat/Skagerrak, three water masses meet: Baltic Sea water mainly coming through the Sound in the south, North Sea water carried with the Jutland Current along the Danish west coast, and sub-surface Atlantic Water branching off the Atlantic Current north of Scotland and flowing south along the coast of Norway. The Jutland and Baltic currents converge outside the northern tip of Denmark (Skagen), forming the Kattegat–Skagerrak Front [19]. This converged flow continues as Norwegian Coastal Current and transports relatively low saline water masses along the Norwegian coast.

The positive water balance of the Baltic Sea (due to net precipitation) is the primary driver leading to the extended surface salinity gradient of the Baltic Sea (Figure 1). Besides developing a seasonal thermocline in spring, the central Baltic Sea has a permanent halocline, which separates surface waters from the higher saline deep water. High-saline deep water originates from the North Sea and is renewed due to occasional inflow events of high saline, oxygen-rich water at depth, passing over shallow sills, and gradually flowing into the Baltic Sea basins. These events are essential for oxygen replenishment of the deep basin bottom waters in central areas of the Baltic Sea [20]. Major inflow events are caused by strong westerly winds over the eastern North Atlantic and northern Europe [21] and push Kattegat/North Sea water into the SW Baltic Sea. A major part of the high saline water enters the Baltic Sea through the Great Belt. This leads to an overall salinity zonation of the Baltic Sea on a horizontal and vertical scale. Irrespectively, the long-term mean of inflow and outflow is zero [18].

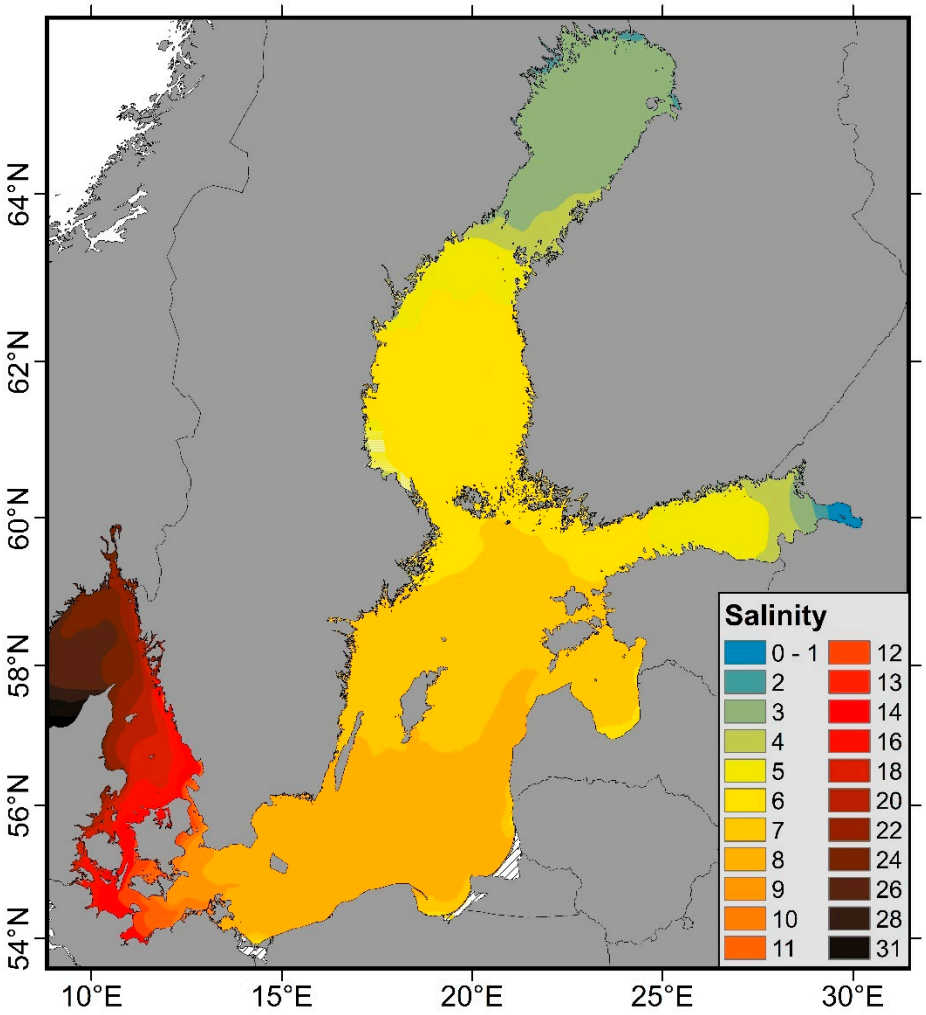


Figure 1. Five-year average (2015–2019) of the sea surface salinity (1.5 m) indicating the extended salinity gradient of the Baltic Sea, obtained from hydrodynamic modelling (data from Lehmann et al. [18]).

In general, the central Baltic Sea's topographic structure is characterized by a series of deep sub-basins separated by shallow sills. Lehmann et al. [18] showed that despite the ephemeral nature of the atmospheric conditions over the Baltic Sea, persistent cyclonic circulation patterns exist, which mostly comprise the sub-basins of the Baltic Sea with less transport between them. Typically, the vertical circulation is characterized by wind-induced up- and down-welling along the coasts, which can lead to episodic upwelling of oxygen poor waters in coastal areas, such as regularly experienced in Eckernförde- and Kiel Bay during autumn [22,23].

Owing to the irregularity of inflows of highly saline and oxygen-rich water masses, stagnation periods can prevail for several years such as experienced during 1983 to 1992 and 1994 to 2003 [20]. The Baltic Sea's deep basins are important spawning grounds of commercially important fish species [24]. However, a change in the oxygen profiles will directly and negatively impact their recruitment via reduced survival of their eggs and larvae [24]. It has actually been suggested that the only active spawning area left in the Baltic Sea is the Bornholm Basin, due to oxygen deficiency [25]. While fish such as Eastern Baltic cod are rather sensitive to low oxygen conditions [26], jellyfish and comb jellies can forage and survive for longer periods under low oxygen levels [27]. Hence, a competitive trade-off is expected.

The Baltic Sea's mean salinity decreased during the early 20th century, and again during the 1980s and 1990s; the latter is coupled with a complete lack of Major Baltic

Inflows during 1983–1992 [28,29]. Future climate projections expect that net precipitation is increasing, which will decrease the salinity of the Baltic Sea even further. Thus, it is expected that species distributions will change according to changes in the surface salinity gradient of the Baltic Sea [30]. Additionally, the Baltic Sea is expected to get warmer. During the most recent decades, the hydrographic conditions in the Baltic Sea were influenced by large-scale climate conditions. It has been confirmed by a model exercise [31] that this has resulted in above-average temperature (0.035 °C year^{-1}) throughout the water column, as well as a declining trend of salinity for deeper water depths (−0.03 year^{-1}). Changes in temperature conditions impact the oxygen saturation of water, and it has been shown that deep water layers of the Baltic Sea are not only frequently subjected to pronounced hypoxic and anoxic conditions, but that the extent of oxygen deficiency substantially increased during the past decades [32]. Hence, changes in inflow events to replenish oxygen in deep water layers as well as climate change act synergistically and pose a high pressure on current and expected future ecosystem functioning of the Baltic Sea.

1.3. Global Change and Jellyfish Blooms Potential Consequences for the Baltic Sea

Jellyfish blooms are irregularly observed in different areas around the world [33]. While some evidence suggests that jellyfish populations are increasing as a consequence of global change [34,35], other investigations do not show a conclusive picture of a general increase (e.g., [36,37]). However, conclusive results are hampered by the general lack of consistent long-term monitoring initiatives that systematically include jellyfish and comb jelly abundance data [37]. Irrespectively, factors such as global warming, eutrophication, overfishing, aquaculture, invasion of non-native species by marine traffic, and maritime constructions have been linked as likely explanatory variables to jellyfish blooms [38]. Blooms are reported to impact e.g., nutrient cycling [39], oxygen conditions [40], and fish stocks [38]. A prominent example for the latter is the northern Benguela upwelling current, where overfishing has induced a change in steady state from an ecosystem dominated by pelagic fish to jellyfish [34,35]. Recent studies have shown that marine constructions have the potential to increase problematic mass occurrence of jellyfish as a consequence of increased settling opportunity for their polyp offspring [41]. True jellyfish generally depend on the succession of a pelagic medusa population, which is then seeding the benthic, asexually reproducing polyp generation. However, especially for the benthic polyp generation of jellyfish, hard substrate might be the limiting factor controlling jellyfish outbursts in many ecosystems around the world [38,42]. Therefore, an increase of artificial hard substrate by maritime constructions is expected to provide new habitats, especially for the settlement and reproduction of benthic stages of scyphozoan jellyfish such as the moon jelly *A. aurita* and the lion's mane jellyfish *C. capillata*, present in the Baltic Sea. Results obtained by an interdisciplinary study performed by Janßen et al. [42] suggest that offshore wind farms have the potential to significantly increase the settlement probability of jellyfish polyps, which possibly could lead to an increase in abundance as well as increased spatial extent of jellyfish medusa populations in the Baltic Sea.

While it has been shown that certain jellyfish and comb jellyfish species have increased in certain areas of the world [36], it remains to be investigated if they are on the rise in the Baltic Sea. Irrespective of native species, it can be noted that non-indigenous gelatinous macro-zooplankton species are on the rise, especially in the Baltic Sea. This accounts for the invasive comb jelly *M. leidyi*, which was first observed in Northern Europe in 2005 and sighted in the Baltic Sea in 2006 (as reviewed in [43]), as well as for the hydromedusae *B. virginica*, which was first sighted in Kiel Canal in 2014 [15]. Both species have been documented to form blooms with high densities in certain regions of the Baltic Sea with documented food web cascades (e.g., [43,44]). Therefore, it is expected that non-indigenous jellyfish and comb jellyfish species can be regarded as important, novel predators imposing a significant grazing impact on zooplankton in the Baltic Sea ecosystem. Their specific characteristics are outlined in more detail below.

2. Jellyfish (Cnidaria)

2.1. The Moon Jelly Aurelia aurita (Linnaeus, 1758)

2.1.1. Importance in the Baltic Sea

The moon jelly *Aurelia aurita* (Figure 2) is one of the two naturally occurring scyphozoan jellyfish species in the Baltic Sea (for morphological characteristic see Section 2.4). Scyphozoans are characterized by their unique morphology and complex metagenic life cycle, where the benthic polyp stage reproduces asexually and gives rise to pelagic medusa, which sexually reproduce [45]. Once medusae get sexually mature, females take up sperm, which males release into the water column. Larvae are then raised in specialized brood pouches within the oral arms, from which planula larvae are released, which swim towards suitable hard substrate and settle to form the sessile polyp stage. Polyps (scyphistoma) reproduce asexually and release small pelagic ephyra during the strobilation process. These ephyra grow and eventually become the next sexually reproducing medusae stage. Additionally, polyps can produce sister colonies via budding as well as form cysts, so called podocysts, which help them to survive unfavorable conditions and have been shown to remain viable for 3.2 years [46]. Due to the potential to form dense blooms and their passive accumulation into high abundance patches via ocean currents, *A. aurita* medusa can have a substantial impact on food web dynamics [47,48]. *A. aurita* has been shown to be a direct predator of fish eggs and larvae [49] as well as being a competitor with pelagic fish for the same prey, removing up to two-thirds of the daily secondary production in the western Baltic Sea during bloom years [50]. It remains to be investigated if *A. aurita* abundances in the Baltic Sea are on the rise, as has been shown for other marine ecosystems [33,36].

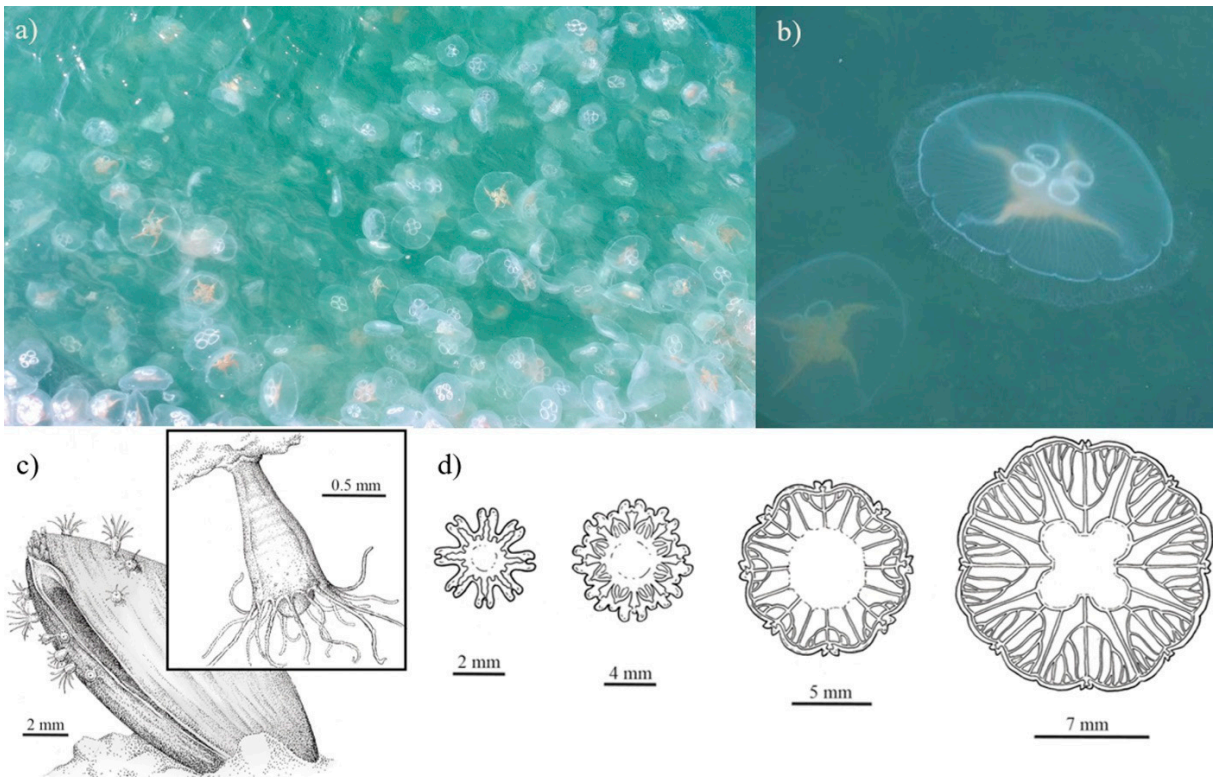


Figure 2. The moon jelly *Aurelia aurita* (**a**) in a high abundance patch in Eckernförde, SW Baltic Sea, June 2020, (**b**) a sexually mature female in Kiel Bight, August 2014, (**c**) polyp colony with close up of an individual polyp (inlet) and (**d**) development sequence of ephyra. Image credit (**a**,**b**): C. Jaspers, (**c**,**d**): N. Bezio.

2.1.2. Distribution in the Baltic

Although *A. aurita* is common in the entire Baltic Sea [3,6,7,51–53], they are primarily present in coastal waters or in the surface waters of the central basins (0–40m), with few animals being found at depths >50 m [3,6,8]. Max abundance of 300 ind. m^{-3} has been observed in Kertinge Nor, an embayment in the Great Belt during June 2009 [54].

Polyp populations have been confirmed along the Swedish Skagerrak coast [51], the Danish Straits [55], the SW Baltic [56], and SW Finland [53]. No substantial recruitment is suggested to take place along the southern Baltic coastline [7,8,57], due to the lack of hard substrate [57]. So far, no published records of *A. aurita* polyp populations from the Swedish east coast are available. Therefore, *A. aurita* present in the Baltic Sea are suggested to be seeded from two different polyp sub-populations [57], one situated in the high-saline southwestern Baltic/Skagerrak [55,56] and the other situated along the southwestern Finish coastline [53]. These sub-populations have been discussed to differ in their phenology as well as their physiological tolerance/preference.

2.1.3. Environmental Tolerances and Preferences

Previous work has shown high tolerance of planula, ephyra, and medusa to various low salinities [53,58]. For example, it has been shown that planula larvae produced from adults caught at a salinity of 7 PSU from the Greifswalder Bodden, eastern German coastline, develop into polyps at salinities >4 PSU and that larvae first disintegrated at salinities <2 PSU [58]. Overall, a general optimum salinity range was determined between 5–15 PSU, while salinities >18 PSU were lethal for *A. aurita* polyp populations from the southern central Baltic Sea [58]. On the other hand, active polyp populations are known from higher saline areas of the Baltic Sea, such as the Kiel Bight, Danish Straits, the Kattegat, and Skagerrak [51,55,56,59,60]. For example, active strobilation has been documented at salinities of ca. 15–20 in Kiel Bight [56].

This shows that *A. aurita* is not restricted to high saline recruitment areas [7] but that an active recruiting low saline sub-population might exist in southwestern Finland [53]. Both sub-populations show different salinity tolerances [58]. However, Thill [58] concluded that *A. aurita* present in the Baltic Sea is an ecological modification of the *A. aurita* present in the Danish Straits. He argued that observed differences are due to environmental factors and will not persist if F1 generations are raised under higher saline conditions. Due to the lack of comparative experiments, it therefore remains unknown if observed differences are based on phenotypic plasticity or local adaptation. Molecular analyses and common garden experiments [61] are necessary to enlighten this.

It has been shown experimentally that the lower temperature threshold for strobilation in *A. aurita* polyps is 0–1 °C, and adults have been observed in a temperature range from 0.2 to 18 °C [56]. Surprisingly, partly frozen animals continued to beat after they were transferred to warmer water [56]. This large temperature range supports that *A. aurita* is well adapted to life in the entire Baltic Sea, including northern, sub-arctic areas. The lowest oxygen level at which animals died was 0.14 mg O_2 L^{-1}, and reduced activity had been observed at oxygen concentrations below 1.4 mg O_2 L^{-1} [58].

2.2. Lion's Mane Jellyfish Cyanea capillata (Linnaeus, 1758)

2.2.1. Importance for the Baltic Sea

The Lion's mane jellyfish *Cyanea capillata* is the second of the two naturally occurring scyphozoan jellyfish species in the Baltic Sea, being characterized by a metagenic life cycle (see *A. aurita* for detail, Figure 2 and Section 2.4. for morphological details). Similar to *Aurelia aurita*, it is a potential predator of fish recruits and, in the Bornholm Basin, predation on cod and sprat eggs can be important [6]. Further, *C. capillata* has a large stinging capacity, thereby negatively impacting tourism and fishing activities, especially in higher saline areas of the Kattegat and the SW Baltic Sea after persistent westerly winds pushing higher saline waters into the area (see [5]). It remains unknown if *C. capillata* abundances have increased during recent decades in the Baltic Sea. However, *C. capillata* is known to be

dependent on gelatinous prey, especially ctenophores, for ephyra growth [62]. Therefore, the recent invasion of the ctenophore *M. leidyi*, as well as the presence of the arctic relict species *M. ovum*, might facilitate *C. capillata* growth and lead to increased abundance and distribution pattern in the Baltic Sea. Since *C. capillata* causes painful stings and is a known predator of cod and sprat eggs [6], with high temporal and spatial overlap [6–8], increasing population densities are expected to have negative economic impacts.

2.2.2. Distribution in the Baltic

Large *Cyanea capillata* (>15–20 cm diameter) are regularly observed in higher saline waters of the Kattegat and Skagerrak [3,7,8,63–66], and occasionally in the SW Baltic Sea during special weather and wind conditions [5]. However, small *C. capillata* (average 4 cm, >95% being <10 cm [6] can be found in high saline bottom waters throughout the Baltic Sea [6–8] as well as in the SW Baltic Sea. In previous studies, it has been suggested that those small-sized animals are seeded from the Gullmar Fjord via inflow of higher saline waters into the Baltic Sea [8]. However, drift studies did not support that Gullmar fjord can lead to *C. capillata* abundances observed in the Bornholm Basin [7].

Animals show primarily an offshore distribution and are found in the central Baltic at depths around and below the halocline [3]. In the Bornholm Basin, *C. capillata* was only found at depth (>45 m) [3,6–8], which has been related to drift recruitment from higher saline areas [7]. Occasionally, *C. capillata* specimens have been sighted in the northern Baltic Proper as far north as the Gulf of Finland and the Åland Sea [3,63,64,66]. In the Polish fisheries zone of the southern Baltic Sea, *C. capillata* was only sporadically present in the samples [57].

For the Baltic Sea, polyp populations of *C. capillata* have so far not been confirmed. The closest reproduction site is located in the Skagerrak, namely in Gullmar Fjord [51,63]. However, sexually mature animals with developed planula larvae in their brood pouches have been observed in the southwestern Baltic Sea [65]. This indicates that polyp colonies might exist in higher saline areas of the Baltic Sea [65].

2.2.3. Environmental Tolerances and Preferences

Very little is known about environmental tolerances and preferences of *C. capillata* in the Baltic Sea. Based on field observations, it has been shown that animals do not occur at oxygen concentrations <2.8 mg O_2 L^{-1} [8]. However, lethal oxygen concentrations are unknown. In addition, the upper and lower temperature thresholds in the Baltic Sea are not known, and it remains unsolved why animals are primarily present in deeper, colder water masses [3,6–8]. This can either be due to active accumulation and preference of *C. capillata* for colder water masses or, as has so far been widely suggested, due to passive processes since animals originate from higher saline areas via drift and are therefore found in deeper water layers of the Baltic Sea [3,7].

Intensive investigations in the Skagerrak showed that the western coast of Sweden is the geographical border for active recruitment of *C. capillata* [63]. Gröndahl and Hernroth [63] concluded that the *C. capillata* population observed in the Baltic Sea area originate from the North Sea and are likely poorly adapted to brackish Baltic Sea conditions. However, Holst and Jarms [65] showed that planula larvae, which were released from *C. capillata* medusa in Kiel Bight, developed into polyps at a salinity of 15, whereas *C. capillata* from the North Sea never settled when salinities were reduced below 20. Whether this apparent difference is due to maternal effects or local adaptation needs to be further investigated and confirmed by molecular methods.

2.3. Hydromedusa Blackfordia virginica (Mayer, 1910)

2.3.1. Importance for the Baltic Sea

The Black Sea jellyfish *Blackfordia virginica* is a non-native member of the jellyfish community. This hydromedusa has a metagenic life cycle with asexually reproducing polyp and sexually reproducing medusae generations, similar to the scyphozoan jellyfish

A. aurita and *C. capillata* - as discussed above (see Figure 2 for details and Section 2.4. for morphological characteristics). Due to the large environmental tolerance of *B. virginica* with a salinity range from 2 to 36 [67,68], and preference for low salinities of 5.6 to 10.3 [69], large areas of the Baltic Sea are at risk for potential colonization. Additionally, their diet covers a wide range of zooplankton organisms, including fish eggs and larvae [70]. This makes *B. virginica* a potential threat as a food competitor and direct predator of local fish populations in areas where they reach high population densities, as observed in other invaded areas of Europe [71]. In this context, coastal areas of the Baltic Sea are especially vulnerable, as those regions are known to support important spawning and recruitment sites of commercially important fish species e.g., Herring [72]. It is expected that very high abundances observed in the Kiel Canal [15], which is connecting the North Sea with the Baltic Sea, seed animals into the SW Baltic Sea, from where they can potentially colonize the entire Baltic Sea. Intensified monitoring activities are necessary to closely follow this non-native jellyfish species and their impacts on local fish stocks of the Baltic Sea.

2.3.2. Distribution in the Baltic Sea

Blackfordia virginica was first sporadically sighted in Kiel Canal in 2014 and 2015 and in the SW Baltic Sea since 2017. After 2016, *B. virginica* has developed persistent populations in the Kiel Canal [15], with confirmed presence up to 2020 (C. Jaspers personal observation, August 2020). Until 2020, no records outside the SW Baltic Sea have been recorded, irrespectively of continued intensive sampling effort (as outlined in [15]). First described by Mayer [73] from the US east coast, Virginia, during fall 1904, molecular analyses indicated low genetic diversity of the US east-coast population and suggested population origin in other areas of the world [74]. In 1935, Thiel [75] showed that *B. virginica* constituted a common member of the Black Sea hydromedusae community. In conclusion, Thiel [75] suggested that *B. virginica* was endemic to the Black Sea. Subsequently, *B. virginica* was confirmed from brackish water bodies around the world such as India [76,77], North America [69,78,79], South America [67,80], South Africa [81], and China (as reviewed in [80]). For Europe, *B. virginica* was first recorded in 1971 in the Loire estuary, France [82], the Mira estuary, Portugal in 1984 [68], and more recently in the harbor of Amsterdam, Netherlands [83] as well as the Gironde estuary, France [84], with the most recent record in northwestern Europe in 2014 from Kiel Canal [15]. In other areas of Europe, high abundances of *B. virginica* of 650 to 1700 ind. m^{-3} have been documented [71,84]. Similarly, high densities have been observed in Bombay Harbour-Thana and Bassein Creek in India, where up to 420 medusae m^{-3} have been found [85].

2.3.3. Environmental Tolerances and Preferences

Seasonal sampling confirmed that *B. virginica* shows the highest abundances during warm temperature months such as August to September in Gironde estuary, France [84], June throughout October in Kiel Canal, Germany [15], and May throughout October in lower Nappa River San Francisco Estuary CA, USA [70].

Even though a preference for lower salinities has been shown in San Francisco Estuary, CA, USA ranging from 5.6–10.3 [69], animals are known to have a large salinity tolerance covering a salinity range from 2 to 36 [67,68], while in the Kiel Canal, a salinity range from 7 to 13 had been documented [15]. Temperature ranges are known to range from 16.5–23 °C in CA, USA [70], and 8 to 20 °C in Kiel Canal, while temperatures >14 are associated with high population densities in north-western Europe [15]. Similarly, in the Mira estuary in Portugal, *B. virginica* was present at temperatures of 12 to 23.6 °C with dissolved oxygen conditions ranging from 1.83–8.25 mg O_2 L^{-1} [86]. Similar oxygen conditions had been recorded from CA, USA, with 3.8–6.9 mg O_2 L^{-1} [70], indicating an overall moderate tolerance towards low oxygen conditions.

Blackfordia virginica is a truly euryhaline species, documented by the successful establishment in a multitude of estuaries and brackish-water systems around the world (for

review, see [84]). Hence, it is suggested that the species has a high potential to colonize most of the Baltic Sea.

2.4. Morphological Characteristics of Polyps, Ephyrae and Medusa

2.4.1. *Aurelia aurita*

Polyps are solitary and found growing on hard surfaces such as the shells of bivalves, stones, and underneath wooden maritime harbor constructions. Polyps reach around 1.5 cm in height are typically conical in shape with a pronounced manubrium tipped with a single mouth (Figure 2). The mouth is surrounded by 14–20 filiform tentacles that have alternating nematocyst clusters [45,63].

Ephyra are small "snowflake" shaped typically reaction a diameter of >2 mm and are typically transparent or opaque in color with a large central disc (Figures 2 and 3). Margin of ephyra is separated into eight uniform marginal lappets tipped with a rhopalia, the length of each marginal lappet is separated into a lappet stem (two-thirds length) and a pair of rounded rhopalial lappets (one-third length). Rhopalial canals extent down entire length of lappet stem until the rhopalia, while the velar canal is roughly one-quarter to one-third the total length of the velar canal. Manubrium is present and square in shape. Developing tentacles may or may not be present. During development, the velar lappets (areas between the marginal lappets) begin to expand and fuse with the marginal lappets (Figure 2). Both the rhopalial and velar canals expand and fuse together near the developing bell margin, while the velar canal remains straight, the rhopalial canal develops into a serious of dichotomous branches (number vary to individual). Gonads begin to develop around individuals 12–15 mm in diameter as small protrusions around the central disk. These protrusions develop into a smooth genital ring around the manubrium, eventually separating and developing into the standard horseshoe shape (Figure 3) found in adults [87].

Medusae are large (<40 cm) and have a plate shaped flat to hemispherical bell with a thick mesoglea, which is typically colorless or opaque in color (color can vary depending on individual; pink, blue, white, or yellow). Adult medusae contain numerous (>100) thin tentacles that branch down from the bell margin. The bell margin is separated into eight slightly rounded lappets (giving off the illusion of a smooth edge), separated by eight rhopalia surrounded by two small rhopalial lappets, which are used for gravity sensing. In the center of the bell, four ribbon like oral arms, around 2 times the bell height, surround the mouth. Within the oral arms, specialized brood pouches are used by females to brood the fertilized eggs until they release the planula larvae. Adult medusae contain four gonads in the shape of a "four-leaf clover "or "horseshoe "shape. Gonads are typically either colorless (early development), brown/gold (adult females), or pink (males). Running between the gonads and the bell margin are a series of thin dichotomous branching radial canals used to transfer nutrients and waste from the gastric cavity to the rest of the body [63,88].

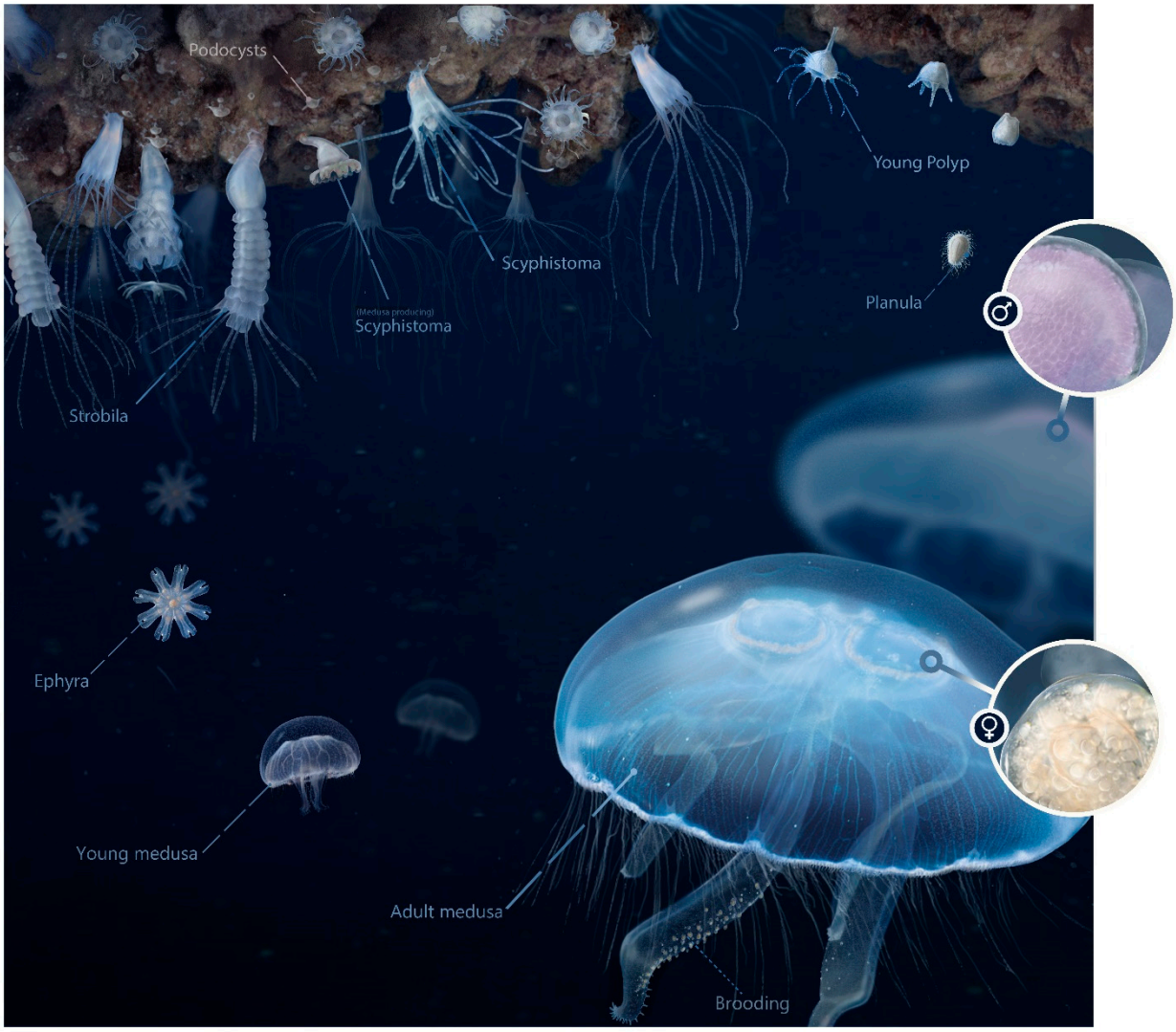


Figure 3. Metagenic life cycle of a scyphozoan jellyfish illustrated for the moon jelly *Aurelia aurita*. Planula larvae (upper right corner) are released from brood pouches of adult females (lower right corner) and settle on hard substrate, metamorphose into asexually reproducing polyps (scyphistoma), which release several small ephyrae via budding (upper left corner), but polyps can also form podocysts under unfavourable conditions. Ephyrae (left side) represent the new sexually reproducing pelagic life-stage with female and male medusae showing characteristic horseshoe gonad (four) structures, with female oocytes (opaque to brown/orange) and male spermatophores (pink). Note: Under special conditions, one scyphistoma can shortly after settlement metamorphose directly into one ephyra (direct development). Image credit: N. Bezio.

2.4.2. *Cyanea capillata*

Polyps are solitary and found growing on hard surfaces such as rocks and piers (Figure 4). Polyps reach around 2.5 mm in height are typically goblet in shape with a pronounced manubrium tipped with a single mouth. The mouth is surrounded by 16–18 filiform tentacles that have alternating nematocyst clusters [45,89].

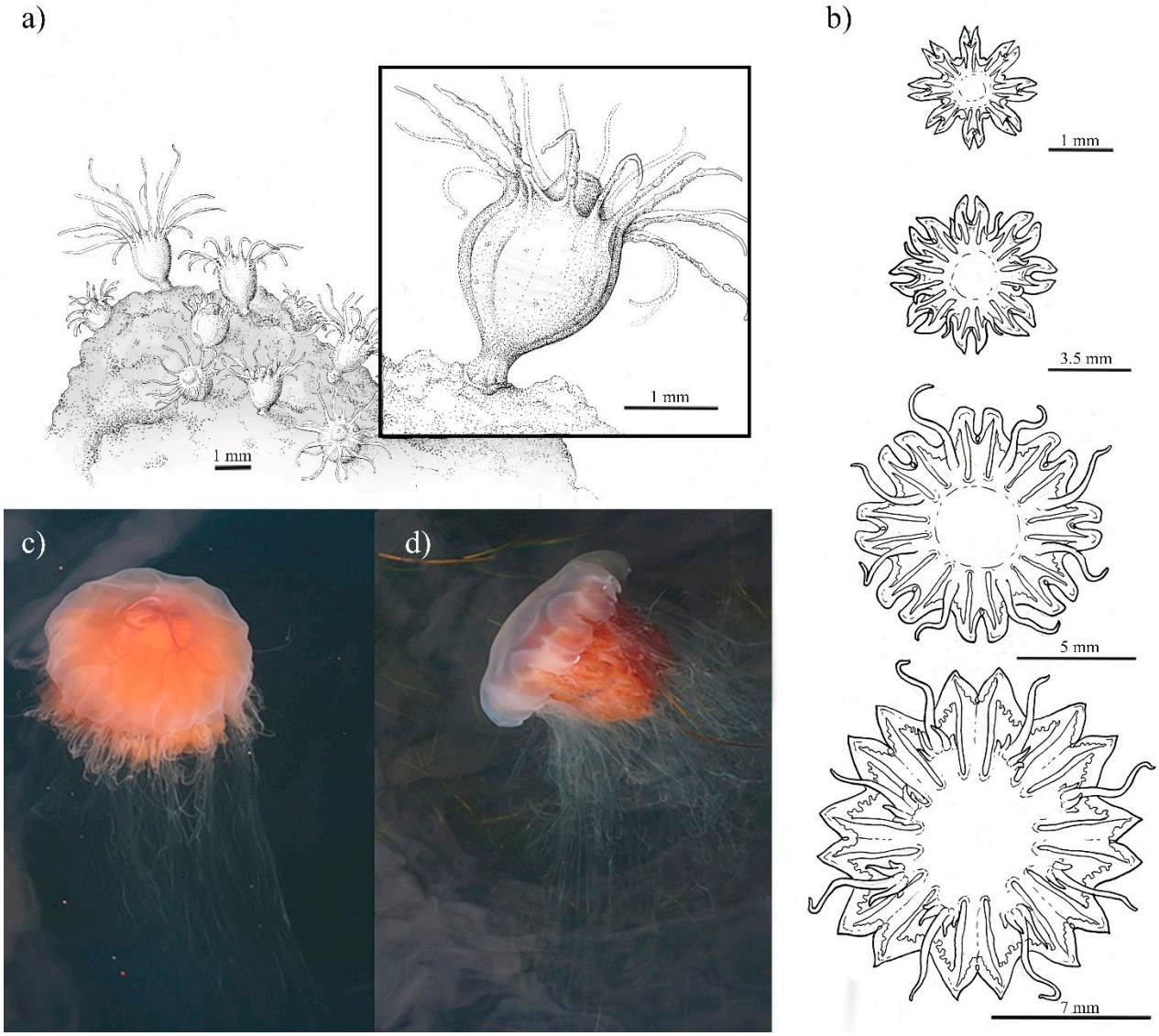


Figure 4. The Lion's mane jellyfish *Cyanea capillata* (**a**) with polyp colony and close up of an individual polyp (inlet), (**b**) development sequence of ephyra, (**c**,**d**) medusae (ca. 35 cm) in Kiel Fjord, Sept. 2014. Image credit (**a**,**b**): N. Bezio, (**c**,**d**): C. Jaspers.

Ephyra are small "snowflake" shaped typically reaction a diameter of >1.7 mm and are transparent, opaque or light yellow shaded in color with a large central disc (Figures 4 and 5). Margin of ephyra is separated into eight uniform marginal lappets tipped with a rhopalia, the length of each marginal lappet is separated into a lappet stem (one-half length) and a pair of pointed rhopalial la ppets (one-half length). Rhopalial canals extent down entire length of lappet stem branching into a "v" shape that continues down the length of the rhopalial lappets. While the velar canal is roughly one-half the total length of the velar canal and also branches into a "v" shape down with adjacent marginal lappets. The manubrium is present, large, and square in shape. Developing tentacles may or may not be present, but tentacle bulbs may be present on the margin of the ephyra in between the marginal lappets (Figure 4). During development, the velar lappets (areas between the marginal lappets) begin to expand and remain separated during development causing highly developed rhopalial lappets. The velar canal begins to heavily branch towards the velar lappet, while the rhopalial canal remains "v" shaped with minor branching towards the rhopalia [45,73,87].

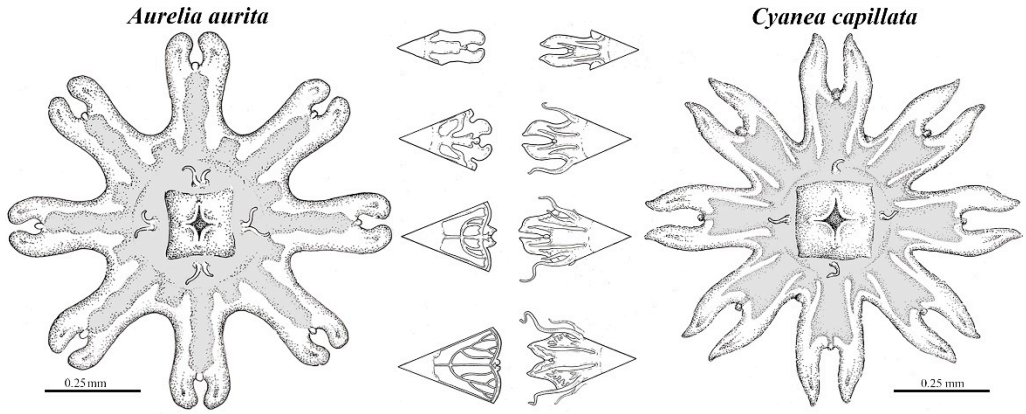


Figure 5. Morphological characteristics of Scyphozoan ephyra *A. aurita* (left) and *C. capillata* (right) with gradual change in lappet morphology during growth. Image credit: N. Bezio.

Medusae have a large plate shaped, flat bell with a thin mesoglea and are typically orange/bronze in color (mostly <50 cm). Bell Margin is defined by large developed rhopalial lappets (rough one-half to one-third of bell diameter). Gonads are typically pale in coloration and are hidden inside the opaque bell of the medusae (Figure 4). The bell margin is separated into eight lappets that are tipped by eight rhopalia surrounded by a pair of rhopalial lappets, which are used for gravity sensing. The medusae contain numerous thick filiform tentacles several times the height of the bell scalloped into eight distinct lobes, each lobe containing 70 to 150 tentacles arranged in four distinct rows. Adult medusae contain 13–15 coronal muscle folds between the radial septa. The center of the bell contains four ornate/folding oral arms roughly 3 times the height of the bell (normally yellowish to orange in color), which also include specialized brood pouches for their larvae. Canals are heavily branched with no clear uniform pattern [45,73].

2.4.3. *Blackfordia virginica*

Polyps and gonophores (reproductive structure in Hydrozoa that produces a single medusa) arise directly from creeping stolons and can contain numerous polyps. Individual polyps reach around 0.5 cm in height and are typically conical in shape (Figure 6). The mouth is surrounded by 20 filiform tentacles that have alternating nematocyst clusters. Tentacles contain notable webbing between other neighboring tentacles, which can be difficult to see without putting scyphistoma on microscope slides [78,79] (see Figure 6).

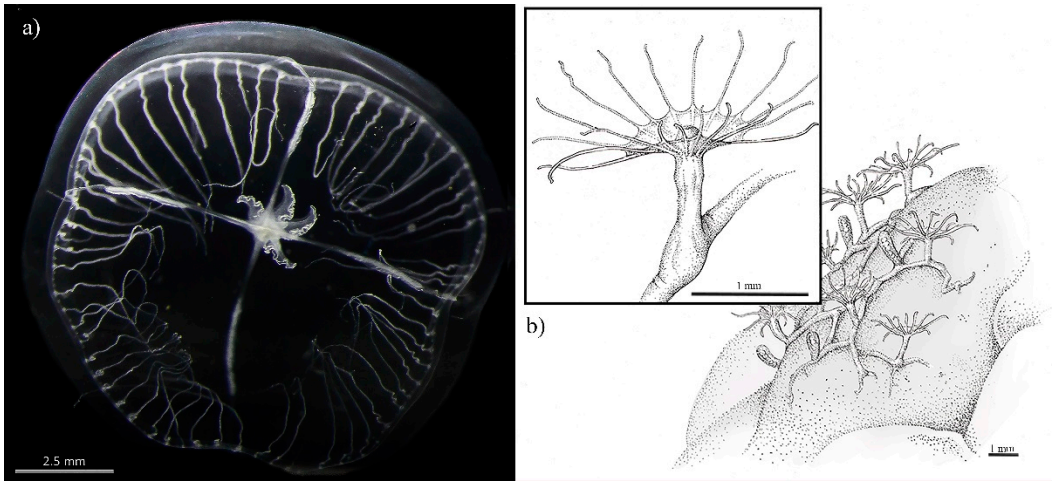


Figure 6. Non-indigenous hydromedusae *Blackfordia virginica* medusae (**a**), with polyp colony and detailed scyphistoma morphology (inlet). Image credit a: C. Jaspers, (**b**): N. Bezio.

Young medusae arise directly from gonophores on the stolon of the main polyp. When initially released the bell of young medusa are spherical in shape with a uniformly thin mesoglea, bell is 0.8 mm in height. Young medusae have a small manubrium roughly one-quarter of the height of the bell without pronounced marginal lips. On the bell margin, four perradial round marginal tentacle bulbs bearing a single simple tentacle and four developing interradial tentacle bulbs. Thin radial canals bearing no gonads can be found along the intramantle bell cavity. During development, the bell of the medusae begin to flatten to a more hemispherical shape. The manubrium lengthens to two-thirds the height of the bell and develops four curled, non-crenulated lips. Perradial tentacle bulbs begin to develop a more rounded/conical appearance with a single rhopalia in between tentacle bulbs. Gonads begin to develop as single protrusions halfway up the radial canals [73,78,80].

Medusae have a hemispherical bell with max 22 mm in diameter with a thick mesoglea and are typically colorless—apart from the whitish gonads, which are visible as crosses over the four radial canals (Figure 6). Gonads are thin and extend two-thirds the length of the radial canals Medusa contains a thin vellum with a maximum opening roughly three-quarters the diameter of bell margin. The number of tentacles varies and is dependent on development stage, but margin contains roughly 50–142 filiform tentacles. Specific diagnostic characteristics include endodermal cores of tentacles, which can project into the bell with a simple finger-shaped projection that points into the mesoglea. Additionally, between adjacent tentacles, closed lithocysts with 1–3 concretions with grey pigmentation at their base can be seen, even though this characteristic is not diagnostic for all *B. virginica* sub-populations (can best be observed in white field light mode of stereomicroscope inspection of life material [15]). Manubrium is large and round to square in shape while in cross section, typically two-thirds the height of the bell, opaque white in color, and tipped with four crenulated curved lips [15,73,78,80].

3. Comb Jellies (Ctenophora)

3.1. Sea Walnut Mnemiopsis leidyi (Agassiz, 1860)

3.1.1. Importance for the Baltic Sea

The comb jelly *Mnemiopsis leidyi* (Figure 7), native to the east coast of Americas, has been present in Northern Europe since 2005 (for summary see [43]). This simultaneous hermaphrodite is characterized by extraordinary high reproduction rates of >10,000 eggs ind.$^{-1}$ d^{-1} [90], high feeding rates [91,92], and bloom abundances of up to 1 ind. L^{-1} as observed in the extended Baltic Sea area (e.g., Limfjorden, [93]). These attributes make *M. leidyi* not only a potential competitor with pelagic fish species but also an important food web component, especially in higher saline regions of the Baltic Sea [94]. Due to its non-native origin, this species can be regarded as novel graze in the SW Baltic Sea with high abundances since first sightings in 2006 [14], as reviewed in [43].

3.1.2. Distribution in the Baltic

Mnemiopsis leidyi is one of the two ctenophore species present in the Baltic Sea [11,13], though its native distribution range belongs to the east coast of the Americas [95]. Its first record in the Baltic Sea dates back to September 2006 along the Mecklenburg coast of Germany, namely Nienhagen, Stolteraa, Hiddensee Island [14].

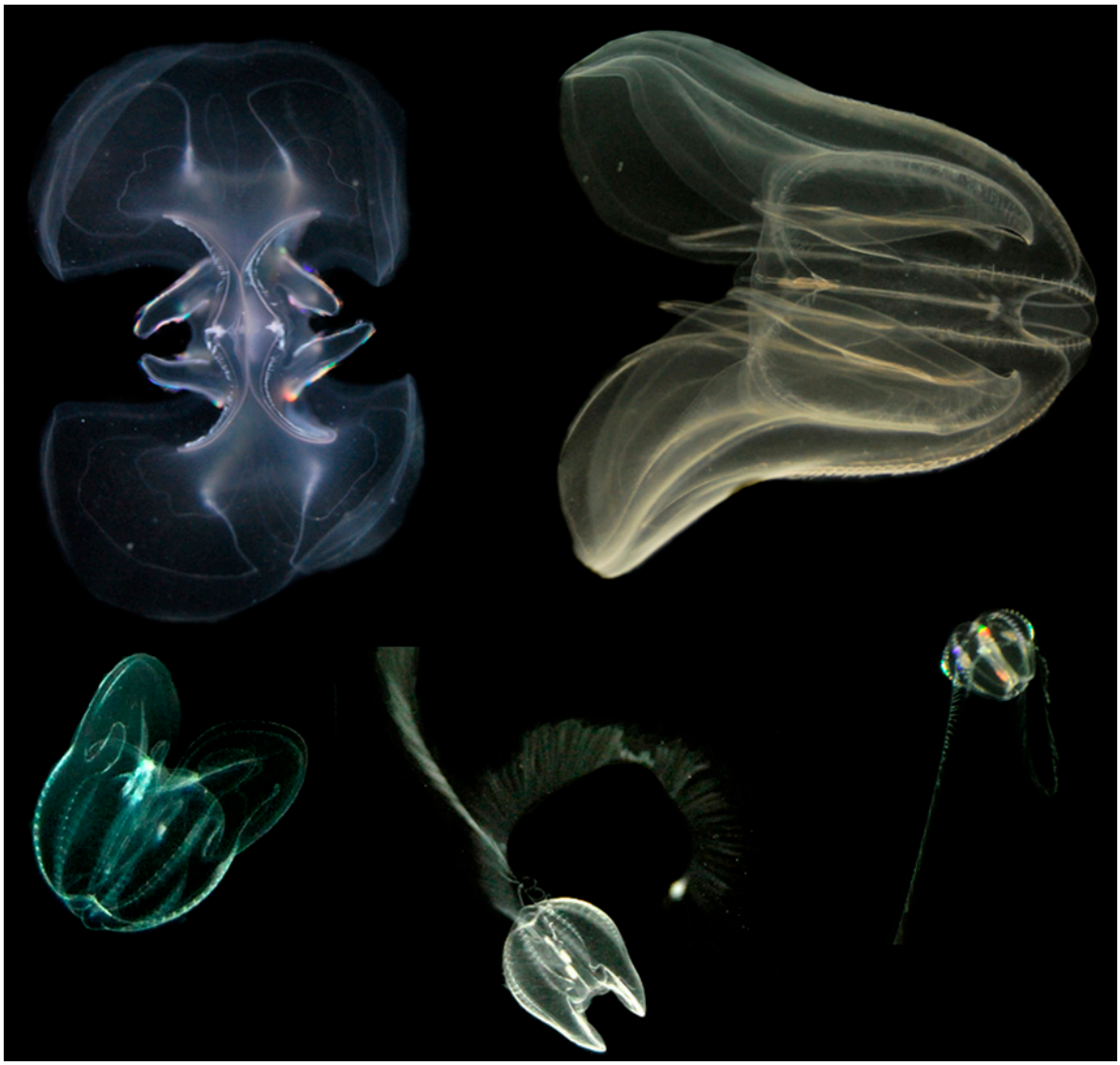


Figure 7. Non-indigenous comb jelly *Mnemiopsis leidyi* with holoplanktonic development sequence. Newly hatched larvae (0.5–1 mm, bottom right), larvae with developing lobes (2.5 mm, centre), transitional stage with reduced tentacles (5–6 mm, left) and adults with oral (left) and vertical (right) view, ca. 20 mm oral-aboral length. Image credit: C. Jaspers.

Mnemiopsis leidyi extends its range into the Baltic Sea as far as the Bornholm Basin and the south-western area of the Eastern Gotland Basin [13,94,96]. Animals are primarily located above the halocline in high saline areas of the Kattegat/Skagerrak and mainly below the halocline in lower saline regions [14,96–99], though they occasionally occur in upper water layers during peak abundance season (September and October) [94]. It has been shown that <27 mm sized *M. leidyi* can show diel vertical migration of up to 10 m during 12 h; however, strong haloclines seem to inhibit this pattern [100]. Similarly, change in depth distribution has been described for *M. leidyi* in its native range as a response to increased turbulence levels [101]. Wind-induced sheer and turbulence in surface waters show an exponential decrease with depth. Hence, avoidance of turbulent surface waters by *M. leidyi*, as observed, e.g., in South America [102], circumvents the degradation of their fragile feeding current [91,103] and allows them to sustain high feeding rates [101].

In the Bornholm Basin, where *M. leidyi* occurs primarily below the halocline, a high overlap with eggs of commercially important fish species was observed in May 2007. This has led to a suggested large negative impact on fish stock recruitment in the Bornholm

Basin [99]. However, analyses of seasonal data indicate that spatio-temporal overlap between *M. leidyi* and fish eggs/larvae is limited [97]. In combination with laboratory experiments, where a very low feeding rates on cod eggs under environmental conditions characteristic for the Bornholm Basin have been documented [104], a negligible direct predation impact on fish eggs in the Bornholm Basin is expected under current conditions.

Abundances of adult *M. leidyi* in the central Baltic are 60-fold lower compared to higher saline areas such as the Kattegat and Skagerrak [94]. Extremely high abundances are recorded in the Limfjord, a eutrophicated Danish fjord system connecting the North Sea with the Kattegat [93,105], where 867 ± 121 *M. leidyi* m^{-3} have been caught on replicated tows in Skive Fjord during Aug. 2007 [93]. Furthermore, in the southern Kattegat, high abundances of ca. 600 *M. leidyi* m^{-3} have been observed in Kerteminde Fjord during November 2008 [54]. For the SW Baltic Sea, maximum abundances were recorded in Kiel Fjord with single observations of 400-500 larval/adult *M. leidyi* m^{-3} in 2007, with the suggested onset of bloom events at salinities and temperatures (°C) >15 [106]. Though abundance comparisons are hampered by including larval stages or not. It is remarkable to note that *M. leidyi* disappeared from the Baltic Sea and large areas of NW Europe in 2010 [43]. Hence, animals were absent during the years 2011–2013 [43,44], which were characterized by cold winter temperatures [43]. First, after the exceptionally warm winter 2014 (January–March), animals were sighted in the Baltic Sea and other north European waters again. No significant population structure between animals caught off Belgium, Norway, nor the Baltic Sea was found during the re-invasion, indicating a novel re-introduction from a single source population in the North Sea with local extinction of the previously present genotypes in the Baltic Sea [43].

It has been documented that the distribution of *M. leidyi* is linked to higher saline areas of the Baltic Sea, hence the fraction of recruits is drastically reduced along the salinity gradient into the Baltic Sea [13]. Reproduction rates are significantly regulated by salinity with no active reproduction at salinities <10, as confirmed from laboratory-controlled and *in situ* reproduction experiments [107]. This explains the observed 60-fold lower *M. leidyi* abundance in the central Baltic, as opposed to higher saline areas [94]. Similarly, drift recruitment has been suggested as a source for the observed *M. leidyi* population in the Bornholm Basin, as inferred from monitoring depth distribution data in the central Baltic Sea [94,96].

Based on molecular analyses, *M. leidyi* larvae have been confirmed to be present throughout the year in high saline regions of the Baltic Sea [13]. Adult *M. leidyi*, on the other hand, first occur during late summer, peak in abundances during autumn, and remain present until spring [94]. However, local overwintering in the SW Baltic Sea might be possible, as suggested for Kiel Fjord during 2007 [106] and as observed during winter/spring 2020 (C. Jaspers pers. observation, 2020). Covering the extended salinity gradient of the Baltic Sea and adjacent waters, it was confirmed that 80% of the observed *M. leidyi* were found at salinities between 22 to 29, with 75% of the observations representing water temperatures >11 °C during 13 monthly monitoring cruises conducted in 2009/2010 [94]. Though temperatures of 12 °C have been used as temperature threshold for reproduction in *M. leidyi* for modelling studies [108], evidence has lately accumulated that *M. leidyi* has an optimal temperature range between 8 to 27 °C [109]. Regarding reproduction, invasive and native *M. leidyi* populations have been shown to actively reproduce at temperatures as low as 7 °C and 6 °C in the Danish Straits and NE USA, respectively ([110] and C. Jaspers, unpublished). Furthermore, Jaspers et al. [104] showed active prey capture of *M. leidyi* at 7 °C. Also, Jaspers et al. [111] show that 'degrowth' in *M. leidyi* can underlie its high reproduction rates with maximum measured daily reproduction of 11,232 eggs in one day in the higher saline Skagerrak area [112]. This leads to an average carbon-specific egg production of 8.4 ± 1.4% per day for the largest sized animals [90]. Similar rates are attained by laboratory-controlled experiments, where small-sized animals, during the onset of reproduction invest ca 8 to 15% of their body carbon into egg production per day [112]. One of the reasons why *M. leidyi* can build up large population densities

and bridge unfavorable conditions could be related to their ability to shrink and keep up reproduction for up to 12 days without food [111]. Calculations indicate that summer food concentrations in invaded areas of northern Europe are, on average, sufficient for sustaining high egg production rates [111]. Lately, it has been suggested that *M. leidyi* preys on its own offspring to maintain high population growth rates [113]. However, unrealistically high prey densities along with very small experimental container volumes (2L), where *M. leidyi* filtered the water >10 times during the investigation by Javidpour et al. [113], need further substantiation to confirm the significance of their observations on an ecosystem level. Taken together, it becomes evident that temperature and salinity effects on physiological rates need to be better incorporated into future modelling studies.

3.1.3. Environmental Tolerances and Preferences

Gambill et al. [109] show that the larvae of the invasive northern European *M. leidyi* population has a broad realized temperature growth range between 8 and 27 °C with maximum growth rates of $\mu = 0.9\ d^{-1}$ at 27 °C. Starvation experiments further confirm that *M. leidyi* adults, kept at 6 °C, can survive for 10 weeks without food and do so by reducing their body carbon content to 20–40% of original values [114]. Further, 'degrowth' in *M. leidyi* underlies its high reproduction rates, and *M. leidyi* have been shown to keep reproducing for up to 12 days without food [111]. However, salinity is an important parameter restricting the range expansion in the Baltic Sea, and experimental studies have shown that *M. leidyi* from the Baltic Sea do not reproduce at salinities <10 and that the highest reproduction rates are attained at high salinities of 25 to 33 [107].

In its native range, *M. leidyi* has been shown to perform equally well at oxygen concentration >1.5 mg $O_2\ L^{-1}$ [115]. Further, *M. leidyi* in NE USA survived for 96 h at dissolved oxygen concentrations of 0.5 mg $O_2\ L^{-1}$ at relatively high temperatures of 22.4 to 24.2 °C [27], which indicates a large oxygen tolerance of *M. leidyi*. Together, these life-history traits and broad environmental tolerances allow *M. leidyi* to survive, reproduce, and thrive under variable conditions in invaded northern Europe, where only salinity is setting a limit to its range expansion into the central and northern Baltic Sea [107]. It remains to be seen if *M. leidyi* can adapt to those low saline conditions, as populations are known to thrive in other, low-saline environments such as the Caspian Sea and Sea of Azov [95].

3.2. Sea Nut Mertensia ovum (Fabricius, 1780)

3.2.1. Distribution in the Baltic

Mertensia ovum is present throughout the entire Baltic Sea apart from the Gulf of Riga, coastal areas of the Gulf of Finland, and the western Baltic Sea—but only during summer and autumn [11,13]. During winter and spring, animals have also been confirmed from high-saline regions such as the Kattegat and Skagerrak [13]. The depth distribution has been shown to change seasonality, with a deeper distribution around the halocline during warm seasons, while animals are distributed throughout the water column, including surface waters, during cold seasons [11,13]. Due to the difficulty of morphological identification, *M. ovum* was previously misidentified as either *Pleurobrachia pileus* or *Mnemiopsis leidyi* larvae [10,11]. However, molecular re-analyses of previous *Pleurobrachia pileus* identifications from Finish waters confirmed the exclusive presence of *Mertensia ovum* [10,11]. It is noted that *P. pileus* can be found in the SW Baltic Sea during winter under certain weather conditions with offshore winds, which favor local upwelling [2]. Möller [2] found a maximum of 1.5 *P. pileus* 100 m^{-3} in Kiel Bight during January 1977.

3.2.2. Importance for the Baltic Sea

The comb jelly *Mertensia ovum* (Figure 8) is an arctic relict species in the Baltic Sea and has lately been confirmed to reach seasonally high abundances—especially during winter [11,12]. So far, this species has been largely overlooked in food web investigations, though laboratory experiments confirm that *M. ovum* consumes microbial loop components, thereby efficiently channeling energy to higher trophic levels [9]. This pathway might be

important for the Baltic Sea ecosystem, especially during winter, when meso-zooplankton abundances are low.

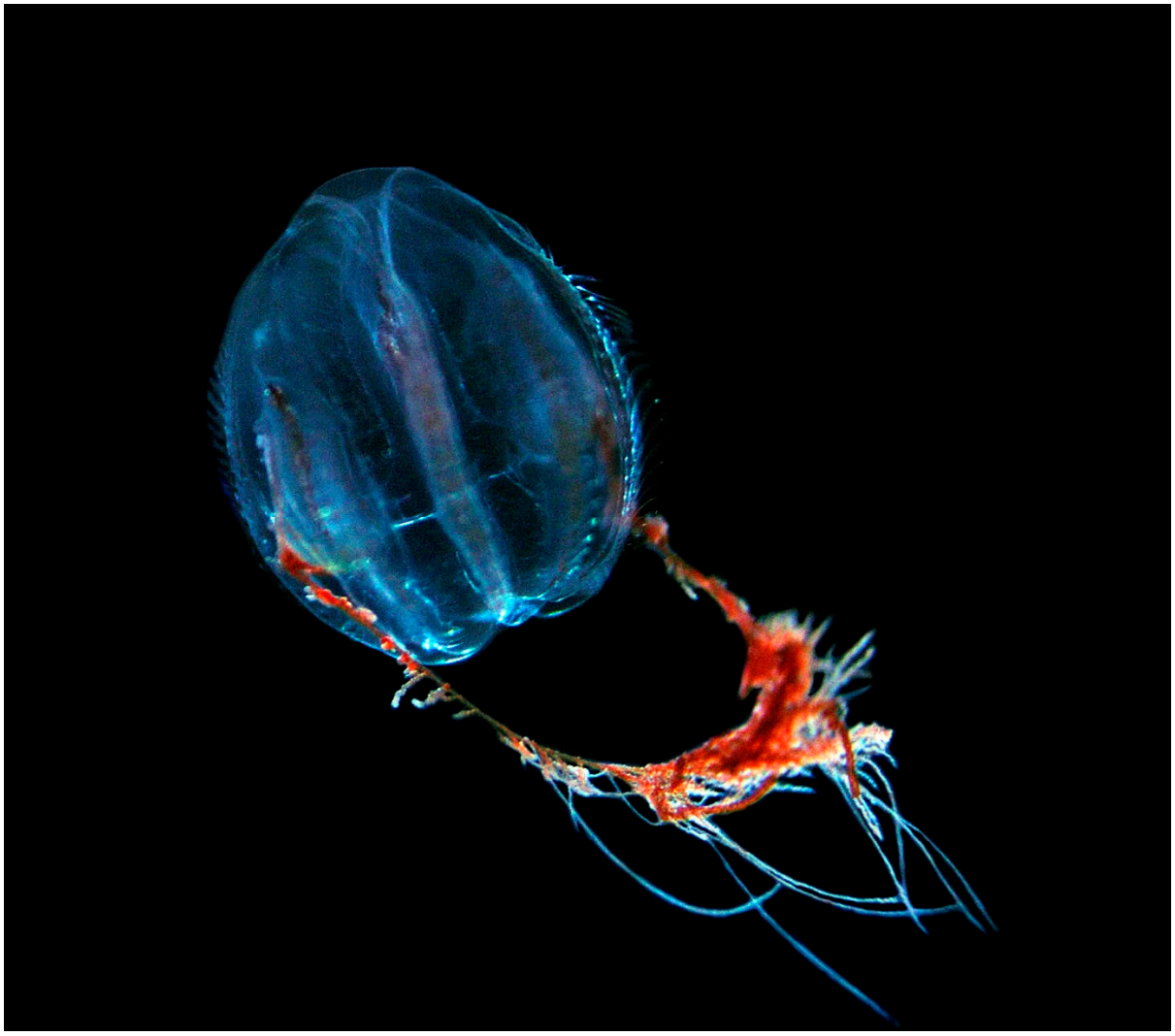


Figure 8. Native comb jelly *Mertensia ovum*, which is only present as larvae in the Baltic Sea. 5 mm *M. ovum* from West Greenland waters. Image credit: C. Jaspers.

3.2.3. Distribution in the Baltic

The knowledge about *M. ovum* is largely descriptive due to its late discovery and lack of sophisticated laboratory experiments. Therefore, few studies have been conducted regarding its distribution in relation to environmental parameters, which included onboard measurements of feeding and reproduction rates (but see [11,12]).

M. ovum matures at a much smaller size compared to the non-native ctenophore *Mnemiopsis leidyi* with reproduction rates three orders of magnitude lower than *M. leidyi* [11,12]. However, year-round reproduction in combination with early reproductive activity are sufficient to maintain this arctic relict species in the Baltic Sea and constitutes a first-time proof that a ctenophore population can sustain through larval reproduction on population level [12]. Further results show that *M. ovum* significantly preys on microbial loop components, thereby representing a potential link between lower and higher trophic levels in the food web, which might be an important pathway, especially during winter [9].

The abundance of *M. ovum* is regulated by both salinity and temperature [11,13]. Throughout 13 monthly sampling events covering the area from the Skagerrak to the

Northern Baltic Proper, *M. ovum* has been confirmed to be present at temperatures ranging from −0.3 to 11.6 °C, with the absence of animals at shallow water stations during summer where water temperatures reached 16–18 °C [12]. Highest abundances of *M. ovum* were observed in water layers with temperatures <7 °C, salinities >5.5, and oxygen levels >5.7 mg O_2 L^{-1} [11]. Minimum oxygen concentrations were recorded with 1.4 mg O_2 L^{-1} [11], which is assumed to represent their lower oxygen limit. Generally, the highest densities were observed during winter [13].

4. Conclusions

The Baltic Sea is a hydrographically complex system with large changes in the physical environment over small spatial scales. As a result of this extreme environment, the Baltic Sea can be regarded as relatively species poor. This is exemplified by the limited number of gelatinous macro-zooplankton species, where only three native species exist in the Baltic Sea. Even though *M. leidyi* do not form self-sustaining populations in most areas of the Baltic Sea as a consequence of salinity constraints on reproduction rates [107], they attain very high abundances in higher saline waters of the SW Baltic and Kattegat region. In those areas, this invasive species is representing a severe food competitor to fish. In contrast to *M. leidyi*, the non-native hydromedusae *Blackfordia virginica* is not constrained by low salinity and occurs in the Kiel Canal from early summer throughout autumn. Therefore, negative impacts on fish recruits could be expected via food competition as well as direct predation, especially for coastal areas of the Baltic, where, e.g., Herring is spawning [72]. This highlights that the new record of this non-indigenous species in northern Europe is a matter of concern for the entire Baltic Sea, including low saline areas of central and northern regions. It remains highly debated, if jellyfish and ctenophore abundances are on a rise due to global change. For the Baltic Sea we can conclude that non-indigenous gelatinous zooplankton species are on the rise and represent a matter of concern due to their high abundances and novel grazing impact on ecosystem level. If the same trend holds true for native gelatinous zooplankton species, represents a knowledge gap and needs further investigation across the entire Baltic Sea. This review is envisioned to highlight the importance of jellyfish and comb jellies in the Baltic Sea and aims to encourage including them into ongoing monitoring activities to elucidate their impact on fish communities and response to global change.

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