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Review of environmental factors influencing distributions of selected Baltic species

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Temming, Axel; Niemax, J.; Zaiko, A.; Siaulys, A.; Törnroos, Anna; Clemmesen, Catriona; Jaspers, Cornelia; Oesterwind, D.; Bonsdorff, E.; Mittermayer, F.; Kuosa, H.; Ojaveer, Henn; Behrens, Jane; Peters, J.; Renz, J.; Kotta, J.; Dutz, Jörg; Lehtiniemi, M.; Winder, M.; Setälä, O.; Kotterba, P.; Puntila, R.; Neuenfeldt, Stefan

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BONUS



BIO-C3



BIO-C3

Biodiversity changes: causes, consequences and management implications

Deliverable No: 1.1	Workpackage number and leader: WP1, P2 DTU Aqua; Dorte Bekkevold		
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BIO-C3 overview

The importance of biodiversity for ecosystems on land has long been acknowledged. In contrast, its role for marine ecosystems has gained less research attention. The overarching aim of BIO-C3 is to address biodiversity changes, their causes, consequences and possible management implications for the Baltic Sea. Scientists from 7 European countries and 13 partner institutes are involved. Project coordinator is the GEOMAR Helmholtz Centre for Ocean Research Kiel, Germany, assisted by DTU Aqua, National Institute of Aquatic Resources, Technical University of Denmark.

Why is Biodiversity important?

An estimated 130 animal and plant species go extinct every day. In 1992 the United Nations tried countering this process with the "Biodiversity Convention". It labeled biodiversity as worthy of preservation – at land as well as at sea. Biological variety should not only be preserved for ethical reasons: It also fulfils key ecosystem functions and provides ecosystem services. In the sea this includes healthy fish stocks, clear water without algal blooms but also the absorption of nutrients from agriculture.

Biodiversity and BIO-C3

To assess the role of biodiversity in marine ecosystems, BIO-C3 uses a natural laboratory: the Baltic Sea. The Baltic is perfectly suited since its species composition is very young, with current salt level persisting for only a few thousand years. It is also relatively species poor, and extinctions of residents or invasions of new species is therefore expected to have a more dramatic effect compared to species rich and presumably more stable ecosystems.

Moreover, human impacts on the Baltic ecosystem are larger than in most other sea regions, as this marginal sea is surrounded by densely populated areas. A further BIO-C3 focus is to predict and assess future anthropogenic impacts such as fishing and eutrophication, as well as changes related to global (climate) change using a suite of models.

If talking about biological variety, it is important to consider genetic diversity as well, a largely neglected issue. A central question is whether important organisms such as zooplankton and fish can cope or even adapt on contemporary time scales to changed environmental conditions anticipated under different global change scenarios.

BIO-C3 aims to increase understanding of both temporal changes in biodiversity - on all levels from genetic diversity to ecosystem composition - and of the environmental and anthropogenic pressures driving this change. For this purpose, we are able to exploit numerous long term data sets available from the project partners, including on fish stocks, plankton and benthos organisms as well as abiotic environmental conditions. Data series are extended and expanded through a network of Baltic cruises with the research vessels linked to the consortium, and complemented by extensive experimental, laboratory, and modeling work.

From science to management

The ultimate BIO-C3 goal is to use understanding of what happened in the past to predict what will happen in the future, under different climate projections and management scenarios: essential information for resource managers and politicians to decide on the course of actions to maintain and improve the biodiversity status of the Baltic Sea for future generations.

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Executive Summary

This report presents a brief overview of ecologically or economically important species of different habitats and trophic levels in the Baltic. It supplies the modeling groups within BIO C3 with species specific information on environmental tolerances and preferences and identifies some gaps in knowledge. Where possible, information was provided on the distribution of species in relation to depth, salinity, temperature and oxygen concentrations, in some cases supplemented with experimental results. The species were chosen according to their ecological or economic importance for the Baltic Sea and their relevance for modeling tasks in BIO-C3.

The results of this Task feed into WP 2, 3 and 4.

Introduction

The Baltic Sea with its extreme hydrographic conditions is an area of low species diversity with about 70 species forming self-sustained populations. However, due to the low number of species and the limited complexity of the food web the Baltic ecosystem is considered as a scientifically interesting test case to study the ecosystem effects of changing pressures, namely a combination of climate related changes in hydrography, fishing and eutrophication. Out of these 70 species almost 50% were selected for a review of their physiological tolerances and limits. The species, 9 benthic, 13 planktonic and 8 fish were chosen either because of their abundance in the system or because they were considered relevant, e.g. because of increasing biomass trends etc. Specific emphasis was given on species that are to be included in subsequent modelling exercises. One of the key applications of this rather unique compilation of information is the envelop modelling of their potential habitats using hydrodynamic models, both in hind cast and for future scenarios derived from down-scaled climate model predictions. These applications (WP 3, D3.3) will produce insights into the expected magnitude of spatial distribution shifts and related effects on species assemblages and trophic interactions. The review also identifies the variable degree of available information and identifies especially a severe lack of experimental results on physiological limits and thresholds in many species.

1. Benthos

1.1 *Amphibalanus improvisus* (Darwin, 1854), Bay barnacle

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1. Importance for the Baltic Sea

Amphibalanus improvisus is one of the mostly spread non-indigenous species in the Baltic Sea. It is considered as one of the keystone organisms and acts as biodiversity promoter, bioconstructor which increases the 3-dimensional surface available for associated macro- and meiofauna in shallow-water hard bottoms and can enhance detritus-based food chains by additional supply of particulate detritus. *A. improvises* can promote the settlement success and further development of filamentous algae. On the other hand it is a strong competitor for space (Smith et al. 2014).

2. Distribution in the Baltic

A. improvises is widely distributed in the Baltic Sea. Its current northernmost limit of distribution at the Northern Quark is about 63°N, The easternmost point is about 25°E in the Gulf of Finland (east of Helsinki, Weidema 2000). It occupies depths from the upper littoral to approximately 90 m, where any suitable substrate is present. Elsewhere the species has been recorded from the depths of 500 m (Jarvekiulg 1979; Foster 1987).

3. Environmental tolerances and preferences

As other successful non-indigenous species, bay barnacle has wide range of environmental tolerances. It may survive at the temperatures from 0 to 27°C, the optimum conditions for free swimming nauplius larvae is around 14 °C (Jarvekiulg 1979; Nasrolahi et al. 2012).

Amphibalanus improvises is the most freshwater tolerant barnacle. It is extremely euryhaline species and was recorded even at salinities of 40. In the Baltic is found at high abundances from about 0.5. Activity optimum however is between 6 and 30 (Jarvekiulg 1979; Weidema 2000; Zaiko et al. 2007).

Not much known about its tolerance to low oxygen levels.

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1.2 Dreissena polymorpha (Pallas 1771), Zebra mussel

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1. Importance for the Baltic Sea

Zebra mussel *Dreissena polymorpha* is known as a powerful habitat engineer species in the most aquatic ecosystems it has invaded (Stewart et al. 1998; Karatayev et al. 2002). It modifies the morphological and physical properties of benthic habitats, by forming dense colonies and beds of empty shells and overfouling different submerged hydrotechnical constructions. It affects the local biodiversity by e.g. overgrowing native bivalves, forming patches of high biodiversity on the otherwise monotonous soft bottoms. Dense zebra mussels may also enhance water quality by their biofiltration activity and modify the biogeochemical properties of the sediments (Zaiko et al. 2009; Minchin & Zaiko 2013). Therefore, presence of this species in an ecosystem may cause biased environmental quality assessment and should be taken into account when developing and validating relevant indicators (Zaiko & Daunys 2015).

2. Distribution in the Baltic

Zebra mussel is one of the most widely distributed species in the oligohaline southern and eastern coastal regions of the Baltic Sea, namely CA15, CA17, CA21, CA23, CA25, CA26 and CA28 (Zaiko et al. 2011; Fenske et al. 2013). In lagoons along coastal regions of the southern Baltic Sea, zebra mussels occur in highest densities on soft-bottom habitats at a depth of 2–4 m, but the actual depth range in the Baltic is from the upper littoral to 12 m (Grim 1971; Zaiko et al. 2009).

3. Environmental tolerances and preferences

Zebra mussel can tolerate temperatures from the freeze point to 33°C. However for spawning initiation they require water temperatures to rise above 10°C and at high temperatures the filtration activity of adult mussels decreases. Therefore the optimum range is considered to be between 10 and 22°C (Karatayev 1995; McMahon 1996; Fenske et al. 2013).

So far, *D. polymorpha* does not occur in the open Baltic Sea at salinity >5 ppt, but in experiments with a gradual increase in salinity, dreissenids from the Caspian Sea and Gulf of Finland were able to tolerate salinities even up to 14–15 ppt. The optimum salinity is considered between 0 and 4 (McMahon 1996; Orlova et al. 1998).

Zebra mussels are quite sensitive to oxygen deficiency, however can survive for a short time at dissolved oxygen concentrations as low as 1.8 mg/l (Shkorbatov et al. 1994)

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1.3 Macoma balthica, Baltic Clam, (Linnaeus)

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1. Importance for the Baltic Sea

Macoma balthica is considered a key species in the Baltic Sea and most of its circumboreal range (Segerstråle, 1962; Beukema et al., 1977; Petersen, 1978). The species constitutes an important trophic node through its facultative suspension- and deposit feeding mode (Riisgård and Kamermans, 2001, Törnroos et al. 2015), as well as its role as a major prey species for invertebrate and vertebrate consumers in coastal habitats (Ejdung et al. 2000; Elmgren et al. 1986; Piersma and Beukema, 1993; Aarnio et al., 1996; Nordström et al., 2010).

2. Distribution in the Baltic

Found throughout the Baltic Sea (>4 psu), from shallow (0.5 m) to deep (below halocline), and on habitats ranging from coarse and vegetated to soft mud and glacial clay.

3. Environmental tolerances and preferences

Temperature tolerance: >0 to ca 25
The salinity tolerance: 3- 30
The oxygen tolerance: tolerant to moderate hypoxia

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1.4 Marenzelleria spp. (Mesnil, 1896), Red-gilled mudworm

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1. Importance for the Baltic Sea

Marenzelleria spp. three most successful invasive species (*M. arctia*, *M. neglecta* and *M. viridis*) in the Baltic Sea (Zaiko et al. 2011). Their success was favoured by the broad feeding strategy, extreme tolerance to varying environmental conditions, and planktonic larval stage. *Marenzelleria spp.* can outcompete local soft bottom macrozoobenthos species, modify soft-bottom habitats by the intensive bioturbation activity and affect the ecosystem services by altering the feeding grounds of demersal fish (Šiaulys et al. 2012). *Marenzelleria* species are listed among the keystone species of the Baltic Sea (Smith et al. 2014) and considered in several ongoing BIO-C3 activities.

2. Distribution in the Baltic

Marenzelleria spp. complex is found in most parts of the Baltic Sea (Zaiko et al. 2011, Kauppi et al. 2015), both in the deep zones and coastal areas. The depth range of habitats where the species are found is from upper littoral (ca. 0.2 m) to 90 m (Kube et al. 1996; Gruszka 1999; Sikorski & Bick 2004).

3. Environmental tolerances and preferences

Marenzelleria spp. has wide temperature tolerance it ranges from 0 °C up to 30 °C. The optimum temperature is at 10 °C (George 1966, Bochert et al. 1996).

The salinity tolerance of adult individuals ranges from 0.03 to 32 ppt, the optimum is at 3.5-25 ppt (George 1966, Bochert et al. 1996, Daunys et al. 2004, Kauppi et al. 2015).

The oxygen limit is indicated with 0.5 mg l⁻¹, however adults can tolerate anoxia for short periods of time (Bochert et al. 1997).

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1.5 Monoporeia (previously Pontoporeia) affinis (Lindström)

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1. Importance for the Baltic Sea

Monoporeia affinis is a surface detritivore and predator on meiofauna and juvenile settling bivalves (Ejdung & Elmgren 2001). It is a glacial relict species that dwells in the top-2 cm of the soft sediments, but it is also a capable swimmer (in particular during spawning season). It has a central role in the benthic food web linked both to the invertebrate and the fish part of the food web (e.g. important food for herring) (Aljetlawi & Leonardsson 2002; Andersinn et al. 1978, Ejdung & Elmgren 1998; Ejdung et al. 2000; Elmgren et al. 1986; Elmgren et al. 2001; Hill 1992; Johnson & Wiederholm 1992; Leonardsson 1994; Sarvala 1986; Uitto & Sarvala 1991).

2. Distribution in the Baltic

Coastal low-saline regions of the entire Baltic Sea, deep waters in GoF, GoB and northern Central Baltic.

3. Environmental tolerances and preferences

Temperature tolerance: 0 (fresh water) to 6

Salinity tolerance: ≤ 5 ‰ (Byrén 2004); 0 (fresh water) to 6

Oxygen tolerance: 0.8 - 1.6 mg (Byrén 2004); sensitive to hypoxia

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1.6 *Mytilus edulis/trossulus* (Rafinesque, 1815), Blue mussel

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1. Importance for the Baltic Sea

The hybrid population *Mytilus edulis/trossulus* is considered important in the Baltic Sea, being characterized by relatively high secondary production and supporting high benthic diversity (Martin et al. 2010). Blue mussels are the keystone species in the Baltic. They are important habitat bioconstructors, providing additional living space for macroalgae and invertebrates and also serves as a feeding ground for invertebrates, fish and birds. However, in some areas of the Baltic Sea *Mytilus* can act as a 'reducer' as it is a competitor for living space with perennial macroalgae and is, to a certain point, more favoured by nutrient and organic enrichment compared to perennial macroalgae (Smith et al 2014). Habitats formed by blue mussels have conservational value in the Baltic Sea and are included in the Habitat Directive Annex I list.

2. Distribution in the Baltic

Mytilus species are distributed in the coastal areas from the Quark to the Kattegat: CA3-14 and 16-42. The reported depth range is from upper littoral to 57 m (Kautsky 1981, 1982; Kotta et al. 2015).

3. Environmental tolerances and preferences

In experimental conditions, blue mussels could withstand freezing (-15°C) and tolerate up to 28°C in the wild. The optimum range is 10-20 °C (Read & Cumming 1967; Williams 1970; Schulte 1975; Widdows 1978).

The registered salinity tolerance ranges from 4.5 (the lowest salinity at which the species found in the Baltic) to ca. 40. The optimum range is 15-25 (Westerbom et al. 2002; Qiu et al. 2002).

The lowest recorded oxygen tolerance limit is 0.5 mg/l (Altieri 2006).

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1.7 Palaemon elegans (Rathke, 1837), Rockpool shrimp/prawn

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1. Importance for the Baltic Sea

Rockpool shrimp is a non-native and locally invasive species with a wide geographical range. It is one of the key species in BIO-C3.

2. Distribution in the Baltic

Rockpool shrimp has been detected in HELCOM coastal areas CA34, CA7, CA9, CA13, CA31, CA26, CA24, CA28, CA14, CA12, CA21, CA16. (Grabowski 2006, Kotta and Kuprijanov 2012, Katajisto et al. 2013, "Finnish Alien Species Database" 2014). The rockpool shrimp has been found in depths 0.5 to 15 m, but its most abundant in 0.5 to 3 m depths (Kotta and Kuprijanov 2012, Lesutiene et al. 2014).

3. Environmental tolerances and preferences

Rockpool shrimp has wide tolerance to environmental conditions. Its temperature tolerance ranges from 2 °C up to 34 °C. The optimum temperature range is somewhat 10-20 °C (Janas and Spicer 2008, Madeira et al. 2012, Janas et al. 2013). The salinity tolerance range from 0.6 to 45 ppt, and the optimum is at 7 to 25 ppt. The osmoregulation capacity of the species depends heavily from prevailing temperatures (de Isla Hernandez and Taylor 1985, Grabowski 2006, Janas and Spicer 2008, 2010). The lethal oxygen limit is indicated at 10 [torr] (0.716 mg L⁻¹) and the species has been reported to tolerate moderate hypoxia, 30 [torr] (2.148 mg L⁻¹) well (Taylor and Spicer 1993).

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1.8 Rhithropanopeus harrisii (Gould, 1841), Harris mud crab

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1. Importance for the Baltic Sea

Harris mud crab is widely spread invasive species both globally and in the Baltic Sea region and it is one key species in the BIO-C3 project.

2. Distribution in the Baltic

The Harris mud crab is abundant in Helcom subdivisions SB4, SB7, SB8, SB9, SB11, SB14, SB3 and in coastal areas CA9, CA40, CA37, CA26, CA21, CA16, CA28. (Bacevicius and Gasiunaite 2008, Czerniejewski 2009, Hegele-Drywa and Normant 2009, Fowler et al. 2013, Kotta et al. 2015). The Harris mud crab has been found at depths ranging from 0.5-38 m (Roche and Torchin 2007, Hegele-Drywa and Normant 2014a, Kotta et al. 2015).

3. Environmental tolerances and preferences

The Harris mud crab is very tolerant to different abiotic conditions. It has wide temperature tolerance from 1 °C up to 35 °C, the optimum temperature range is 15-25°C (Turoboyski 1978, Hegele-Drywa and Normant 2014b).

The salinity tolerance range from 0.5 to 30 ppt, the optimum is at 0.5 to 18 ppt (Turoboyski 1978, Paavola et al. 2005).

The lethal oxygen limit is around 2.65 [PPM] or 37.3 % SAT (Stickle et al. 1989)

4. References

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1.9 Saduria entomon (Linnaeus, 1758)

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1. Importance for the Baltic Sea

Saduria entomon is a mobile subsurface- and surface-feeding carnivore, scavenger and cannibal that has been observed to feed on conspecifics, and on *Monoporeia affinis*, *Pontoporeia femorata* *Bathyporeia pilosa*, *Macoma balthica* and other mussels (eg. Leonardsson 1991; Sparrevik & Leonardsson 1998, 1999). NB: there are fresh-water populations in certain lakes, and there is an Arctic variety of the species, i.e. *Saduria* is a glacial relict-species, with broad tolerance- and distribution limits. The role of *Saduria* for the Baltic Sea food web is large, but the exact importance is still under investigation (food for fish, e.g. Cod, but also an important omnivore – predator, scavenger – in the sedimentary system, as well as in the lower parts of the pelagic).

2. Distribution in the Baltic

The species lives in saline, brackish and fresh waters in the boreal and subarctic regions. It lives buried in the surface and can dig in favoured ooze and fine sand. (Ilpo Haahtela 1990)In the Baltic Sea it is found from shallow waters to 300 m depth. The main depth of occurrence is 50-85m. Some coastal populations live at a depth of about 5m (Ilpo Haahtela 1990). Main area of distribution: GoB, GoF, N Baltic Proper.

3. Environmental tolerances and preferences

Saduria entomon is a stenothermal cold water species but also can stand warmer temperature. Its temperature tolerance ranges from 0-20°C (Ilpo Haahtela 1990). The species lives in the entire Baltic Sea within a salinity range of about 1 to 20 ‰ (Ilpo Haahtela 1990).

The species can resist to severe hypoxia (6% O₂). After 41 days 81% tested animals were still alive. Animals exposed to anoxia (1% O₂) showed a LT₅₀ depending on size between 18 and 12 days (Normant & Szaniawska 1999). Further *Saduria entomon* spent most of its time in the sediment at oxygen concentrations >7%. Below 7% it is most often found on the sediment surface. (Johansson 1997)

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2. Plankton

2.1 *Acartia bifilosa* (Giesbrecht, 1881)

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1. Importance for the Baltic Sea

The copepod *Acartia bifilosa* is an indigenous species in the Baltic Sea, and important as prey for planctivorous fish and fish larvae.

2. Distribution in the Baltic

Acartia bifilosa is common from Kiel Bight to the Bothnian Sea (SB 4 – SB 15) but missing in the inner parts of the Gulf of Finland and the Bothnian Bay (Hernroth & Ackefors 1977, Hernroth 1981, Viitasalo 1992, Viitasalo et al. 1995 Ojaveer et al. 1998, Mudrak & Žmijewska 2007. Dutz et al. unpubl., Lehtiniemi, unpubl.). It is also abundant in the coastal areas of the Basins in which it occurs (CA 1, 8, 9, 13, 18, 26, 30, 36, 37; Eriksson et al. 1977, Schnack 1978, Kankaala 1987, Viitasalo 1992 Ojaveer et al. 1998, Chojnacki et al 2007, Paturej et al. 2012, Diaz-Gil et al. 2014).

3. Environmental tolerances and preferences

Acartia bifilosa has wide temperature tolerance ranging from < 4 °C to 24 °C. Reports on the optimal temperature vary with 13-18 °C for egg production and 1-18 °C for egg hatching (Koski & Kuosa 1999, Katajisto 2003). The limit for oxygen tolerance is temperature dependent with < 7 mg L⁻¹ at 18°C, while no limit was detected at 3 °C (Kuosu 1989).

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2.2 Acartia longiremis (Lilljeborg, 1853)

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1. Importance for the Baltic Sea

The copepod *Acartia longiremis* is one of the very abundant species in the sub-basins. *Acartia* spp. are important prey for planktivorous fish and fish larvae.

2. Distribution in the Baltic

Acartia longiremis has been reported from the open sea sub-basins SB 1, 4-7, 8-9, 12-15 (Eriksson 1973, Hernroth 1981, Hernroth & Ackefors 1977, Viitasalo 1992, Mudrak & Żmijewska 2007, Dutz unpubl., Lehtiniemi, unpubl) and coastal areas CA 9, 18, 26, 30, 36, 37, 40 (Schnack 1978, Viitasalo 1992, Chojnacki et al 2007, Paturej et al. 2012, Diaz-Gil et al. 2014).

3. Environmental tolerances and preferences

The environmental tolerance of *Acartia longiremis* is unknown.

4. References

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2.3 *Acartia tonsa* (Giesbrecht, 1881)

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1. Importance for the Baltic Sea

The copepod *Acartia tonsa* is a non-indigenous species in the Baltic Sea.

2. Distribution in the Baltic

Acartia tonsa is common in the open sea sub-basins SB 1 - SB 6 and rare in sub-basins SB 7-SB 15 (Viitasalo 1992, Mudrak & Żmijewska 2007, Dutz et al. unpubl., Lehtiniemi, M., unpubl). It is also found in the coastal areas CA 13, 18, 26, 30, 36, 37 (Schnack 1978, Arndt & Schneese 1986, Viitasalo 1992, Chojnacki et al 2007, Paturej et al. 2012, Diaz-Gil et al. 2014).

3. Environmental tolerances and preferences

Acartia tonsa has broad temperature tolerance ranging from 5 °C to 34 °C, the optimum temperature is 23 °C (Holste & Peck 2006). It has also a broad salinity tolerance ranging from < 6 to > 33; the optimum salinity is 10-33 (Calliari et al. 2006, Holste & Peck 2006, Peck & Holste 2006).

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2.4 *Aurelia aurita* (Linnaeus, 1758), Moon jelly

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Aurelia aurita from Kiel Fjord, August 2014. Photo: Cornelia Jaspers

1. Importance for the Baltic Sea

The moon jelly *Aurelia aurita* is one of the two naturally occurring scyphozoan species in the Baltic Sea. Scyphozoans are characterized by a complex life cycle with an alteration between a benthic polyp and a pelagic medusa stage. Adults release planula larvae which settle on hard substrate and form the sessile polyp stage, which asexually produce either sister polyps or small pelagic ephyra, which grow into adults (sexually reproducing medusa). Due to the potential to form dense blooms and their passive accumulation into high abundance patches, *A. aurita* medusa can have a substantial impact on food web dynamics. *A. aurita* has been shown to be a direct predator of fish eggs and larvae (Hansson *et al.*, 2005) as well as being a competitor with pelagic fish for the same prey, removing up to 2/3rd of the daily secondary production in the western Baltic Sea during bloom years (Schneider & Behrends, 1994). It is unknown if abundances in the Baltic Sea are on their rise due to global change as has been shown for other jellyfish species around the world with large consequences for food web dynamics and ecosystem functioning (Richardson *et al.*, 2009).

2. Distribution in the Baltic

Aurelia aurita is common in the entire Baltic Sea (Barz *et al.*, 2006, Gröndahl, 1988, Hosia *et al.*, 2012, Lischka, 1999, Möller, 1980b, Wikström, 1932). They are primarily present in coastal waters but also found in surface waters of the central basins (0-40m) with few animals being found at depths >50 m (Barz & Hirche, 2005, Lischka, 1999, Möller, 1980b). Polyp populations have been confirmed in the Skagerrak (Gröndahl, 1988), the Danish Straits (Olesen *et al.*, 1994), the SW Baltic (Thiel, 1962) and SW Finland (Wikström, 1932). No substantial recruitment is suggested to take place along the southern Baltic coastline due to the lack of suitable hard substrate (Barz *et al.*, 2006, Barz & Hirche, 2005, Janas & Witek, 1993) and no published records of *A. aurita* polyp populations from the Swedish east coast are available. Therefore, *A. aurita* present in the Baltic Sea are seeded from two different polyp sub-populations, the high saline Western Baltic/Skagerrak population on the one hand (Olesen *et al.*, 1994, Thiel, 1962) and the SW Finish coastline population on the other hand

(Wikström, 1932). These sub-populations show differences in their phenology as well as their physiological tolerance/preference.

3. Environmental tolerances and preferences

Previous work has shown high tolerance of ephyra, medusa and planula larvae to low salinities (Thill, 1937, Wikström, 1932). For example it has been shown that planula larvae produced from adults caught at a salinity of 7 from the Greifswalder Bodden, develop into polyps at salinities >4 and that larvae first disintegrated at salinities <2 (Thill 1937). Overall, a general optimum salinity range was determined between 5 – 15 PSU, while salinities >18 were lethal for *Aurelia aurita* polyp populations from the Baltic (Thill, 1937). On the other hand, active polyp populations are known from higher saline areas of the Baltic Sea such as the Danish Straits, Kattegat and Skagerrak (Grøndahl, 1988, Möller, 1980a, Olesen, 1995, Olesen *et al.*, 1994). For example, active strobilation has been documented at salinities of ca. 15-20 in Kiel Bight (Thiel, 1962).

This shows that *Aurelia aurita* is not restricted to high saline recruitments areas (Barz *et al.*, 2006) but that an active recruiting, low saline population exists in SW Finland (Wikström, 1932). Both populations show different salinity tolerances (Thill, 1937). However, Thill (1937) concluded that *A. aurita* present in the Baltic Sea is an ecological modification of the *Aurelia 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. Further experiments and molecular analyses 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 (Thiel, 1962). Surprisingly, partly frozen animals continued to beat after they were transferred to warmer water (Thiel, 1962). This large temperature range supports that *A. aurita* is well adapted to life in the entire Baltic Sea including northern, sub-arctic areas. Lower oxygen level at which animals died was 0.14 mg O₂ L⁻¹ and reduced activity was already observed at oxygen concentrations below 1.4 mg L⁻¹ (Thill, 1937).

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2.4 *Cyanea capillata* (Linnaeus, 1758), Lion's mane jellyfish

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Cyanea capillata from Kiel Fjord, Sept. 2014. Photo: Cornelia Jaspers

1. Importance for the Baltic Sea

The Lion's mane jellyfish *Cyanea capillata* is one of the two naturally occurring scyphozoan species in the Baltic Sea, being characterized by a complex life cycle with an alteration between asexual reproducing benthic (polyp) and sexually reproducing pelagic (medusa) stages. 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 (Lischka, 1999). Further, *Cyanea capillata* has a large stinging capacity, thereby negatively impacting the tourism industry and a nuisance to people enjoying swimming.

2. Distribution in the Baltic

Cyanea capillata is distributed in sub-division 1-10 and 12-14 of the Baltic Sea (Barz *et al.*, 2006, Barz & Hirche, 2005, Gröndahl & Hernroth, 1987, Holst & Jarms, 2010, Haahtela & Lassig, 1967, Möller, 1980, Verwey, 1942). Animals show primarily an offshore distribution and are found at depths around the halocline (Möller, 1980). In the Bornholm Basin, *C. capillata* was only found at depth (>45m) (Barz *et al.*, 2006, Barz & Hirche, 2005, Lischka, 1999, Möller, 1980), which has been related to drift recruitment from higher saline areas (Barz *et al.*, 2006). Occasionally, *C. capillata* specimens have been sighted in the northern Baltic Proper as far north as the Gulf of Finland and the Åland Sea (Gröndahl & Hernroth, 1987, Haahtela & Lassig, 1967, Möller, 1980, Verwey, 1942). In the Polish fisheries zone of the southern Baltic Sea, *C. capillata* was only sporadically present in the samples (Janas & Witek, 1993).

For the Baltic Sea, polyp populations of *C. capillata* have so far only been confirmed from Gullmar Fjord, Skagerrak (Gröndahl, 1988, Gröndahl & Hernroth, 1987). However, lately sexually mature animals with developed planula larvae in their brood pouches have been observed in the south western Baltic Sea (Holst & Jarms, 2010). This indicates that polyp colonies might exist in higher saline areas of the Baltic Sea (Holst & Jarms, 2010).

3. Environmental tolerances and preferences

Very little is known about environmental tolerances and preferences of *Cyanea capillata* in the Baltic Sea. Based on field observations it has been shown that animals do not occur at oxygen concentrations $<2.8 \text{ mg L}^{-1}$ (Barz & Hirche, 2005). However, lethal oxygen concentrations are unknown. Also 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. 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 (Barz *et al.*, 2006, Möller, 1980).

Intensive investigations in the Skagerrak showed that the western coast of Sweden is the geographical border for active recruitment of *C. capillata* (Gröndahl & Hernroth, 1987). Gröndahl and Hernroth (1987) 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 (2010) 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. This is of special importance since *C. capillata* is known to be dependent on gelatinous prey, especially ctenophores for ephyra growth (Båmstedt *et al.*, 1997). 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 (Lischka, 1999), this will have negative economic impacts.

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2.5 *Dinophysis acuminata* (Claparède & Lachmann, 1859) and *Dinophysis norvegica* (Claparède & Lachmann, 1859)

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1. Why is this species important for the Baltic Sea

Dinoflagellates of the genus *Dinophysis* produce toxic compounds commonly known as diarrhetic shellfish poisoning (DSP) toxins. The DSP toxins frequently contaminate filter-feeding shellfish in marine coastal areas causing great economic losses and public health problems. In the northern Baltic Sea such problems do not exist, since the brackish water mussels are too small for commercial use, but in the southernmost parts they already pose a threat. *Dinophysis acuminata* and *D. norvegica* occur commonly in the northern Baltic Sea. In the northern Baltic Sea, DSP toxins were first detected by Pimiä et al. (1998), who found okadaic acid (OA) in blue mussels and in the common flounder (Sipiä et al. 2000) from the Gulf of Finland. Studies in the northern Baltic have found other *Dinophysis*-derived toxins such as pectenotoxins (PTX2), and dinophysistoxins (DTX1 and DTX3) in phytoplankton samples containing *Dinophysis* spp. (Goto et al. 2000, Kozłowski-Suzuki et al. 2006, Kuuppo et al. 2006).

2. Species distribution in the Baltic

The *Dinophysis* spp. abundances in Baltic Sea vary typically between 1 and 5 cells ml⁻¹, but also layers of higher concentrations of up to 150 cells ml⁻¹ have been found (Carpenter et al. 1995). The species seem to have different depth maxima, *D. acuminata* being concentrated at or above thermocline and *D. norvegica* at or below (Hällfors et al. 2011). Both species occur almost in the whole Baltic Sea area. No frequent observations of *Dinophysis* spp. exist from the northernmost parts of Bothnian Bay (data from SYKE monitoring station in Hailuoto) and eastern Gulf of Finland.

3. Environmental tolerances and preferences of the species

Dinophysis norvegica and *D. acuminata* are warm water species. For *D. norvegica* a study on its tolerance for temperature and salinity (with *D. norvegica* from truly marine conditions; Australia) has been carried out (O'Loughlin et al. 2006). In that study the temperature limits were 3.2-17.8 and for salinity 6 – 34 (however the reliability of this information was considered low). Field studies from Baltic Sea have reported abundant occurrence of *D. norvegica* in temperatures 10.0-17.0, while *D. acuminata* is abundant between 5 and 20 °C. *D. acuminata* has also been found in sea-ice (-1.7 °C, Huttunen & Niemi 1986). Both species are abundant in oceanic waters, but tolerate well brackish water conditions. *D. acuminata* has been found in salinities down to 2.7.

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2.6 Eurytemora affinis (Poppe, 1880)

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1. Importance for the Baltic Sea

The calanoid copepod *Eurytemora affinis* is a dominant zooplankton species in the Baltic Sea, a main grazer of phytoplankton and major food source for fish (Viitasalo et al. 1995). This copepod species is the primary prey for herring (*Clupea harengus*) and important for its growth and survival (Cardinale et al. 2009).

2. Distribution in the Baltic

Eurytemora affinis is distributed throughout the entire Baltic Sea, with highest abundances in the euphotic depth zone (upper 20-30m) but has been observed as deep as 150 m.

3. Environmental tolerances and preferences

This species has a broad thermal window and successful hatching has been shown at temperature ranging from 0 and 25°C³⁶. In the Baltic Sea, maximum abundances of this species are reached at a temperature optimum around 15°C (Diekmann et al. 2012).

Eurytemora affinis can tolerate a wide salinity range and is distributed in waters with salinities ranging from 0 to 40 (Roddie et al. 1984, Winkler et al. 2011). In the Baltic, *E. affinis* is encountered at salinities between 0.2 and 12, and declines rapidly above 19 (Viitasalo et al. 1994). Tolerance limits for temperature and salinity can vary between populations. Laboratory experiments indicate that combined effects of temperature increase and salinity decrease are stressful conditions for this species.

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2.7 Mertensia ovum (Fabricius, 1780), Sea nut

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1. Importance for the Baltic Sea

The comb jelly *Mertensia ovum* is an arctic relict species in the Baltic Sea and has lately been confirmed to reach seasonally high abundances – especially during winter (Jaspers *et al.*, 2012, Lehtiniemi *et al.*, 2013). 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 (Majaneva *et al.*, 2014). This path way might be important especially during winter, when mesozooplankton abundances are low.

2. 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 (Jaspers *et al.*, 2013, Lehtiniemi *et al.*, 2013). During winter and spring, animals have also been confirmed from high saline regions such as the Kattegat and Skagerrak (Jaspers *et al.*, 2013). The depth distribution has been shown to change with season with a deeper distribution around the halocline during warm seasons, while animals are distributed throughout the water column during cold seasons (Jaspers *et al.*, 2013, Lehtiniemi *et al.*, 2013). Due to the difficulty of morphological identification, *M. ovum* was previously misidentified as either *Pleurobrachia pileus* or *Mnemiopsis leidyi* larvae (Gorokhova *et al.*, 2009, Lehtiniemi *et al.*, 2013).

3. Environmental tolerances and preferences

The knowledge about *M. ovum* is largely descriptive due to its late discovery and because Baltic animals have never been cultivated in the laboratory. Therefore, few studies have been conducted regarding its distribution in relation to environmental parameters, which included on board measurements of feeding and reproduction rates.

M. ovum matures at a much smaller size compared to the non-native ctenophore *Mnemiopsis leidyi* but has 3 orders of magnitude lower reproduction rates than *M. leidyi* (Jaspers *et al.*, 2013, Lehtiniemi *et al.*, 2013). 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 (Jaspers *et al.*, 2012). Further results show that *M. ovum* significantly preys on microbial loop components, thereby representing a potential link between lower and higher trophic level in the food web which might be an important pathway especially during winter (Majaneva *et al.*, 2014).

The abundance of *M. ovum* is regulated by both salinity and temperature (Jaspers *et al.*, 2013, Lehtiniemi *et al.*, 2013), with highest abundances found in sea areas and water layers at temperatures <7°C, salinities >5.5 and oxygen levels >5.7 mg L⁻¹ (Lehtiniemi *et al.*, 2013).

Animals were found at oxygen concentrations down to 1.4 mg L⁻¹ (Lehtiniemi *et al.*, 2013), which is assumed to represent their lower oxygen limit.

Throughout 13 monthly sampling events covering 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 absence of animals at shallow water stations during summer where water temperatures reached 16-18°C (Jaspers *et al.*, 2012). Generally, highest densities were observed during winter (Jaspers *et al.*, 2013).

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2.8 Mesodinium rubrum [(Lohmann 1908) Jankowski 1976]

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1. Why is this species important for the Baltic Sea

Mesodinium rubrum (= *Myrionecta rubra*) is a cosmopolitan ciliate. It is common and abundant and easily identified from water samples both live and stained with ordinary fixatives. Its distribution covers truly oceanic areas as well as brackish waters, like the Baltic Sea. *M. rubrum* possesses many distinct features that separate it from any other ciliate species in the world. Most importantly, it is photosynthetic and can significantly contribute to planktonic primary production. Photosynthesis of *M. rubrum* is made possible because it possesses chloroplasts that are robbed from cryptophycean algae (Gustafson et al. 2000). *M. rubrum* is a small but very quick ciliate that moves in jumps at a speed of almost 10 mm per second. It has regularly been found in layers below halocline in the northern Baltic Sea (Setälä et al. 2005, Majaneva et al. 2014). *M. rubrum* can form dense blooms that color the water red (red tides, first observed by Charles Darwin). Such blooms are common in shallow bays for example in the Åland archipelago.

Although a ciliate, *M. rubrum* belongs functionally together with photosynthetic phytoplankton, and it is usually included in phytoplankton counts. It is thus most likely the only ciliate species that is regularly monitored in field survey campaigns in many countries. Also in the Baltic Sea, *M. rubrum* is monitored e.g. at least in Finland, Sweden and Estonia.

2. Species distribution in the Baltic

M. rubrum is present almost throughout the whole Baltic Sea. Only the very coastal fresh water areas of Bothnian Bay and eastern Gulf of Finland lack observations of *M. rubrum*. It is usually abundant in the surface waters, but has also been found in the deep layers of e.g. Gotland Basin and Åland Sea, depth maxima being 220m (Majaneva et al. 2014).

3. Environmental tolerances and preferences of the species

M. rubrum is present in the water column of the Baltic Sea throughout the year, although its abundance during autumn/winter is low. In the Baltic Sea it has been found in temperatures down to 4 °C, and in salinities between 3 and 33.6. Field Populations of *M. rubrum* in the Åland archipelago have been under extensive studies since 1970s. Density maxima of *M. rubrum* and associated peaks in chlorophyll a have been observed both near the surface and at the interface of the anoxic layer in shallow meromictic bays of Åland. Surprisingly, living *M. rubrum* cells also occurred in anoxic layers that contained phototrophic bacteria (Lindholm 1978).

4. References

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2.9 *Mnemiopsis leidyi* (Agassiz, 1860), Sea walnut

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Mnemiopsis leidyi from the Kattegat, Baltic Sea. Photo: Cornelia Jaspers

1. Importance for the Baltic Sea

The comb jelly *Mnemiopsis leidyi*, native to the east coast of America, has been present in Northern Europe since 2005 - including Oslo Fjord, Skagerrak (Oliveira, 2007). This simultaneous hermaphrodite is characterized by extraordinary high reproduction rates of $> 10,000$ eggs $\text{ind.}^{-1} \text{d}^{-1}$ (Jaspers *et al.*, 2015a), high feeding rates (Colin *et al.*, 2010, Colin *et al.*, 2015) and bloom abundances of up to 1 ind. L^{-1} as observed in the extended Baltic Sea area (e.g. Limfjorden, Riisgård *et al.*, 2007). These attributes makes *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.

2. Distribution in the Baltic

Mnemiopsis leidyi is one of the two major ctenophore species being present in the Baltic Sea (Jaspers *et al.*, 2013, Lehtiniemi *et al.*, 2013). Previous records of *Pleurobrachia pileus* being present throughout the entire Baltic Sea have been revised to be *Mertensia ovum*, as confirmed by molecular techniques analyzing old sample libraries (Gorokhova *et al.*, 2009, Lehtiniemi *et al.*, 2013). Occasionally, other ctenophore species can be present in the Skagerrak and Kattegat area such as *Euplokamis* sp. (Granhag *et al.*, 2012), *Bolinopsis infundibulum*, *Pleurobrachia pileus*, *Beroe cucumis* (Jaspers *et al.*, 2013) and *Beroe ovata* (Shiganova *et al.*, 2014). However, these species are only rarely reported south of the Danish Straits (Jaspers *et al.*, 2013). *M. leidyi* extends its range into the Baltic Sea as far as the Bornholm Basin and the south western (SB9) - Eastern Gotland Basin (Haraldsson *et al.*, 2013, Jaspers *et al.*, 2013, Schaber *et al.*, 2011). Animals are primarily located above the halocline in high saline areas (SB1-3+6) and mainly below the halocline in lower saline regions (SB7), though they occasionally occur in upper water layers during peak abundance season - SB7, Sept. and Oct. (Haraldsson *et al.*, 2013, Schaber *et al.*, 2011). Abundances in the central Baltic are 60 fold lower compared to higher saline areas such as the Kattegat and Skagerrak (Haraldsson *et al.*, 2013). Extremely high abundances are recorded in Limfjorden, an eutrophicated Danish fjord system connecting the North Sea with the Kattegat (Riisgård *et al.*, 2007, Riisgård *et al.*, 2012).

It has been documented that the distribution of *M. leidy* is linked to higher saline areas of the Baltic Sea, hence the fraction of recruits is drastically reduced along the reduced salinity gradient into the Baltic Sea (Jaspers *et al.*, 2013). Reproduction rates are significantly regulated by salinity with no active reproduction at salinities <10 (Jaspers *et al.*, 2011a). This explains the observed 60 fold lower *M. leidy* abundance in the central Baltic as opposed to higher saline areas (Haraldsson *et al.*, 2013). Similarly, drift recruitment has been suggested as source for the observed *M. leidy* population in the Bornholm Basin as inferred from monitoring data in the central Baltic Sea (Haraldsson *et al.*, 2013, Schaber *et al.*, 2011).

Based on molecular analyses, *M. leidy* larvae have been confirmed to be present throughout the year in high saline regions of the Baltic Sea (Jaspers *et al.*, 2013). Adult *M. leidy*, on the other hand, first occur during late summer, peak in abundances during autumn and remain present until spring (Haraldsson *et al.*, 2013). During 2009 and 2010, 80 % of the observed *M. leidy* were found at salinities between 22 to 29 with 75 % of the observations representing water temperatures >11°C (Haraldsson *et al.*, 2013).

3. Environmental tolerances and preferences

Although temperatures of 12°C have been used as temperature threshold for reproduction in *M. leidy* for modeling studies (Lehtiniemi *et al.*, 2011), evidence has lately accumulated that *M. leidy* has an optimal temperature range between 8 to 27°C, with maximum growth rates of $\mu=0.9\text{ d}^{-1}$ at 27°C (Gambill *et al.*, 2015). Regarding reproduction, invasive and native *M. leidy* 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 (C. Jaspers unpublished, Costello *et al.*, 2006). Furthermore, Jaspers *et al.* (2011b) showed active prey capture of *M. leidy* at 7°C. Starvation experiments further confirm that *M. leidy* 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 and animals have been shown to actively start feeding following 7 weeks of starvation at 6°C (Granhag & Hosia, 2015). Further, 'degrowth' in *M. leidy* underlies its high reproduction rates and *M. leidy* have been shown to keep reproducing for up to 12 days without food, and low food levels generally below what is characteristic of summer food concentrations in invaded areas of northern Europe, are sufficient for egg production (Jaspers *et al.*, 2015b). This indicates that temperature effects on physiological rates need to be better incorporated into future modeling studies. However, salinity is an important parameter restricting the range expansion in the Baltic Sea and experimental studies have shown that *M. leidy* from the Baltic Sea do not reproduce at salinities <10 and that highest reproduction rates are attained at high salinities of 25 to 33 (Jaspers *et al.*, 2011a).

In its native range, *M. leidy* has been shown to perform equally well at oxygen concentration >1.5 mg L⁻¹ (Kolesar *et al.*, 2010). Further, *M. leidy* in NE USA survived for 96 hours at dissolved oxygen concentrations of 0.5 mg L⁻¹ at relatively high temperatures of 22.4 to 24.2°C (Breitburg *et al.*, 2003) which indicates a large oxygen tolerance of *M. leidy*. Together, these life history traits and broad environmental tolerances allow *M. leidy* to survive, reproduce and thrive under variable conditions in invaded northern Europe.

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2.10 *Oithona similis* (Claus 1866)

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1. Importance for the Baltic Sea

The small cyclopoid copepod *Oithona similis* is an important predator and prey zooplankton for fish.

2. Distribution in the Baltic & Environmental tolerances and preferences

This species has a strong preference for oceanic water. In the Baltic Sea, it is an abundant cyclopoid copepod at higher salinities and is absent in the Northern Baltic Sea. In the Bornholm Basin, the depth distribution is determined by the salinity stratification (Hansen et al. 2004). Maximum abundance were observed between 60 and 70 m depth, indicating that this copepod species is vertically restricted to a depth layer of high salinity and sufficient oxygen (>2 mg L⁻¹).

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2.11 Prorocentrum minimum [(Pavillard) Schiller]

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1. Why is this species important for the Baltic Sea

Prorocentrum minimum (Pavillard) Schiller (1933) is a marine, planktonic, bloom-forming dinoflagellate. *P. minimum* is a harmful species, and may also be toxic, although any specific toxic compound has not been characterized (Saba et al. 2011). Hazards for marine organisms possibly due to their presence with *P. minimum* have been observed (Grzebyk et al. 1997; Heil et al. 2005; Wikfors 2005). However, these may also be the result of increased bacterial metabolism during the decay of the bloom. *P. minimum* is a “recent” invader in the Baltic Sea system. Most of the harm of *P. minimum* is due to its heavy blooms. The maximum abundance of *P. minimum* in the Baltic Sea (350 million cells L⁻¹) was observed in the Gulf of Gdansk (Witek and Plinski, 2000). Heavy blooms of *P. minimum* can harm the e.g. native phytoplankton in the pelagic communities if it dominates the phytoplankton biomass. *P. minimum* is regarded as an efficient competitor for nutrients. Harm can also take place in the benthic community, where anoxia can take place during the decay of the bloom.

2. Species distribution in the Baltic

The first bloom at the entrance to the Baltic took place in 1979 (Tangen, 1980), after which its distribution has moved northwards. In the 1980s it was observed in the southern, central, and northern Baltic proper (Hajdu et al., 2000) and in the Gulf of Finland. It has also invaded Finnish Archipelago Sea in 2000s.

3. Environmental tolerances and preferences of the species

P. minimum has been reported to grow in salinities of 5-37 and a temperature range of 4-31 °C has been reported (Berland & Grzebyk 1991).

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2.12 *Pseudocalanus acuspes* (Giesbrecht, 1881)

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1. Importance for the Baltic Sea

Pseudocalanus acuspes is an arctic relict species in the Baltic Sea that serves as prey for planktivorous fishes and fish larvae (e.g., herring, sprat, cod larvae). It is one of the focus species in Bio-C3. Formerly often referred to as *Pseudocalanus elongatus*, the species is now considered to be *Pseudocalanus acuspes* (Holmborn et al. 2011), although an occasional occurrence of *P. elongatus* cannot be excluded (Grabbert et al. 2010).

2. Distribution in the Baltic

Pseudocalanus acuspes is abundant in Helcom subdivisions SB 4-16 and in small numbers in SB 17 (e.g., Bucklin et al., 2003, Holmborn et al. 2011; Margonski unpublished; Lehtiniemi unpublished). It is distributed in the upper 100m, showing an ontogenetic vertical distribution with nauplii and younger copepodites in upper water layers above the halocline and older stages and adults preferably occurring in the region of the halocline and below.

3. Environmental tolerances and preferences

The temperature tolerance of *Pseudocalanus acuspes* in the Baltic ranges from approx. 2 to 19°C for nauplii and copepodites stages I-V. Adult stages tolerate a range from 1 to 15°C (Renz and Hirche 2006; Margonski unpublished; Lehtiniemi unpublished). Outside the Baltic Sea all stages occur at temperatures down to 1°C (Hopcroft and Kosobokhova 2010).

The salinity tolerance ranges from 5-10 ppt for nauplii, from 5-16 ppt for copepodites stages CI-III and from 7-16 and 7-18 ppt for CIV-V and adults, respectively. Outside the Baltic Sea all stages occur at marine conditions with salinities of 31-33 psu (e.g., Hopcroft and Kosobokhova 2010).

The oxygen limit for all stages is approx. 1 mg/L.

The arctic, marine origin of *Pseudocalanus acuspes* indicates that the physiological preferences should point towards high salinity and low temperature. Considering the specific hydrographic conditions in the Baltic Sea distribution might therefore be largely determined by a combination of food availability and optimal physiological requirements for growth and reproduction. E.g., nauplii might be able to grow at higher salinities but phytoplankton availability is optimal only in upper layers at lower salinities. On the other hand older stages, which can utilize microzooplankton as food source in deeper layers, prefer lower temperatures and higher salinity. Long term series from Poland and Finland investigating the vertical distribution of developmental stages show, however that smaller portions of adults are also often found at temperatures up to 15°C (Margonski unpublished; Lehtiniemi unpublished). This indicates at least a certain tolerance towards higher temperature. Highest temperature where egg reproduction occurred in lab investigations was 6°C (Renz et al. 2007).

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2.13 Temora longicornis (O.F.Müller, 1785)

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1. Importance for the Baltic Sea

The copepod *Temora longicornis* is an indigenous species in the Baltic Sea, and important as prey for planctivorous fish and fish larvae.

2. Distribution in the Baltic

Temora longicornis occurs in open sea sub-basins SB 1, 4-9, 11-15 (Eriksson 1973, Hernroth & Ackefors 1977, Hernroth 1981, Viitasalo 1992, Ojaveer et al. 1998, Mudrak & Žmijewska 2007, Dutz et al. unpubl., Lehtiniemi, M., unpubl.) and coastal areas CA 9, 13, 14, 18, 26, 30, 36, 37, 42 (Eriksson et al. 1977, Schnack 1978, Viitasalo 1992, Ojaveer et al. 1998, Chojnacki et al 2007, Paturej et al. 2012, Diaz-Gil et al. 2014).

3. Environmental tolerances and preferences

Temora longicornis has wide temperature tolerance ranging from < 2.4 °C to 24 °C, the optimal temperature is 16.6 °C (Holste et al. 2009). The lower salinity limit is unknown, while the optimal and upper limits are 14-26 and >26, respectively (Holste et al. 2009).

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3. Fish

3.1 *Clupea harengus* (L.), Herring, adult and larval fish

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1. Importance for the Baltic Sea

Herring, *Clupea harengus* L., is an important commercial fish species which can be used as a bio-indicator of climate-driven changes in marine systems due to its short life span and its tight coupling to zooplankton dynamics and sensitivity to mesoscale hydrodynamic features (Mehner et al. 2012).

2. Distribution in the Baltic

Herring are found in the whole Baltic Sea (Klinkhardt 1996). They are composed of three large stocks: the Bothnian Sea, the central Baltic and the western Baltic stock with the western Baltic stock being the largest and mostly responsible for the recruitment in the whole Baltic Sea (Oeberst et al. 2009). It is composed of a meta-population recruiting from various inshore spawning grounds in estuaries, bays and lagoons along coastal transitional waters showing a high spawning site fidelity (homing) (Bekkevold et al. 2005, Ruzzante et al. 2006). Spawning times occur in spring and autumn, the majority of herring spawn nearshore in spring, fewer spawners are found in the autumn in deeper waters offshore (Von Dorrien et al. 2013).

3. Environmental tolerances and preferences

Baltic herring was observed in the field to avoid oxygen saturation levels below 67 % (Sjøblom 1961). Yet, Lake Rossfjord herring in Norway occurred at oxygen saturations down to 22 % (Hognestad 1994). In the Bornholm Basin in February/March 1998 to 2001, herring did not occur below ca. 50% oxygen saturation (Neuenfeldt 2002, Neuenfeldt and Beyer 2006), while herring was caught in the basin at very low oxygen saturation of ca. 10 % in July 1999 (Neuenfeldt and Beyer 2003).

Field studies have indicated a temperature range of 5- 22°C for low and high temperature tolerances of adult herring with the peak showing the same range (Stepputis 2006). Baltic herring cross the halocline twice daily during their vertical migrations without any obvious salinity-related avoidance behaviour (Orlowski 2000, Nilsson *et al.* 2002, Stepputis 2006).

Herring larvae have a broad environmental envelope in respect to both temperature and salinity, -1.8° to 24° C (Holliday & Blaxter 1960) and 1-4 to 60 psu (Blaxter 1960) respectively, most values originate from the north sea and the Clyde of Firth. Additionally Yin & Blaxter (1987) give thresholds of 20.5°-23.5° C and 3.5 to 4.5 psu salinity for the same populations.

Laboratory experiments performed by Peck et al. (2012) with southwest Baltic herring showed that larvae successfully hatched at temperatures between 5-17°C, low hatching

was observed at 3°C and no hatch occurred at 21.8°C. The authors defined low and high critical temperatures for hatching of herring larvae at 2.8°C and 18.28 °C.

Blaxter and Hempel (1961) found reduced hatching rates at 14°C compared to those at 5°C–11°C. Based on growth rates of herring larvae in the Baltic (Greifswalder Bodden, Oeberst et al. 2009) concluded that Rügen herring is tolerant to relatively high temperatures and values up to 17.5°C. Larval herring growth data from the Kiel canal, a herring spawning ground in the western Baltic Sea, indicate a temperature tolerance up to 18.3°, since this temperature didn't result in a growth depression, potentially buffered by an adequate food availability (Matthias Paulsen pers. Communication). Unfortunately no data on the particular environmental envelope of Baltic Sea herring larvae or on the physiological thresholds in regard to oxygen are available.

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3.2 *Gadus morhua* (L.), Cod, adult and larval fish

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1. Importance for the Baltic Sea

Cod is one of the most important fish species in the Baltic Sea and a top predator in the system as well as one of the major species in the BIO-C3 project. The eastern Baltic cod stock declined to its lowest stock size on record in 1992 due to a reduction in reproductive success influenced by the hydrographic conditions in the spawning areas, in combination with increasing fishing pressure. Since the mid-2000s the stock sizes have increased but this is coupled to a decline in condition factor and the loss of larger adult fish, signaling that the stock is in distress even though the numbers have increased (Bagge et al. 1994, Köster et al. 2003, Eero et al. 2015).

2. Distribution in the Baltic

Cod are generally distributed throughout the western Baltic Sea. The depth distribution of the adult fish is set by the environmental variables (Tomkiewitz et al. 1998). Two distinct stocks of cod exist in the Baltic Sea which spawn in the deep basins (Helcom subdivisions SB 2, SB4, SB5, SB6, SB7, SB8, SB 9, SB10). Genotypic and phenotypic characteristics indicate that the two stocks occur on either side of longitude 14°30E, immediately west of Bornholm with the zone of overlap between the two stocks being rather narrow. The area of distribution of the eastern Baltic cod stock extends north to about 63°N latitude. The western cod stock extends to the southernmost part of the Kattegat (Bagge et al. 1994). Newly hatched cod larvae are mostly found in the spawning grounds in deeper layers <50m where the eggs are neutrally buoyant in the region of the permanent halocline (Köster et al. 2005). Of all Baltic Sea basins the Bornholm Basin (SB7) is the most important Baltic cod spawning ground under present environmental situation, as the lack of inflows caused severe oxygen depletion in the more eastern historical spawning areas, i.e. the Gdansk Deep (SB8) and Gotland Basin (SB10) (Bagge et al. 1994, Köster et al. 2005).

3. Environmental tolerances and preferences

Both laboratory experiments and field observations (using data storage tags, DST) have shown that adult Baltic cod tolerate temperatures ranging between 1°C and 17°C. In the lab the optimum temperature (measured as maximal aerobic scope) has been determined to range between 10 and 15°C, whereas fish in the field seem to prefer somewhat lower temperatures at 8-10°C (Righton et al 2010; Tirsgaard et al 2015).

A wide salinity tolerance is likewise evident, as cod thrive in salinities ranging from 7 to 18 psu (Neuenfeldt & Beyer 2003; own trawl survey observations) with the optimum salinity level being around 9 psu, i.e. corresponding to ambient salinity (Larsen et al 2012). This latter result was deduced from investigating gene expression patterns of osmoregulatory genes of Baltic and North Sea cod in a reciprocal common garden experiment, with significant differences in the expression of the Na/K-ATPase (a gene in gill tissue) between North Sea and Baltic cod indicating an adaptation to local salinity conditions (Larsen et al 2012). The critical oxygen level, determined as the point of ambient O₂ where the fish can no longer maintain standard metabolic rate (SMR), is 16, 23 and 30% O₂ saturation, at 10°C,

15°C and 20°C, respectively (Schurmann & Steffensen 1997), whereas the specific dynamic action (SDA) can occur unhindered when the fish is exposed to ambient oxygen levels of 35% sat for up to 90 min (Behrens et al 2012). Baltic cod will, as deduced from DSTs, expose themselves to these latter conditions during short feeding migrations. However, when exposed to oxygen levels of 60-70 % sat for long-term periods, appetite is reduced with negative impacts on growth (Neuenfeldt et al 2009).

The reproductive success of the eastern Baltic cod stock is coupled to hydrographic conditions in spawning areas. Laboratory experiments confirmed that at least 2 ml/L oxygen is needed for successful egg development (Nissling 1994, Wieland et al. 1994). Additionally a minimum salinity of 11 psu for activation of spermatozoa and thus successful fertilization in Baltic cod was shown in laboratory experiments by Westin & Nissling (1991). Based on these oxygen and the salinity thresholds, Köster et al. (2005) defined the so-called "reproductive volume" (RV) which is the water volume allowing for successful cod egg development. The size of the RV in the deep Baltic basins depends on the frequency and the magnitude of inflows and the temperature of the inflowing water which influences the oxygen solubility (Hinrichsen et al. 2002).

Only limited data on the environmental tolerance of cod larvae particular on Baltic cod larvae are available, one exception being the salinity tolerances as significant work has been done on the buoyancy of Baltic cod eggs. This work suggests a lower salinity threshold of 7 (Nissling & Westin 1991), while work from the North Sea and the Firth of Clyde suggest a lower salinity tolerance threshold of 2-3 (Yin & Blaxter 1987a). An upper salinity threshold is given by Holliday (1965) as 60 for an undefined stock. Nissling (2004) further gives lower and upper temperature threshold as $> 3^{\circ}\text{C}$ and $< 9^{\circ}\text{C}$ for newly hatched cod larvae. An upper threshold is further given as 15.8° to 16°C for cod larvae from the north Sea and the Firth of Clyde (Yin & Blaxter 1987b). No data are available to assess an environmental envelope in regard to oxygen concentration for cod larvae based on laboratory experiments.

Field observations based on depth specific sampling with multiple opening and closing nets revealed that depth distribution patterns are related to developmental stages showing an ontogenetic migration pattern with an upwards shift in relation to increase in size with size groups < 4.5 mm, 4.5 – 5.5 mm, 5.5 – 7.5 mm (GrønkJaer & Wieland 1997). Feeding cod larvae were generally found above the halocline with a maximum abundance around 30 m depth and started diurnal migration at a length of 6-9mm ((GrønkJaer & Wieland 1997, GrønkJaer et al. 1997). However, in certain years no diurnal migration was detected. Larger larvae stayed in the upper water layers (ca. 0-20m) also during day-time, potentially taking advantage of the higher ambient temperatures favoring metabolism and growth (Huwer et al. 2011). Other studies have reported various depth ranges of peak abundances of Baltic cod larvae, ranging from 20 to 30 to 70-80m (Wieland and Zuzarte, 1991).

Environmental preferences based on realized/observed distributions from the Bornholm Basin range from 11-16°C for high temperatures (GrønkJaer & Wieland 1997, GrønkJaer et al. 1997, Köster et al. 2005, Huwer et al. 2011) and from 2.9°C to 4°C for the lower temperatures (GrønkJaer & Wieland 1997, GrønkJær & Schytte 1999). Salinity preferences for cod larvae range from 13-17 psu in the high and at 7 psu in the low salinity range with the peak larval distribution occurring at 7.5 – 17 psu (GrønkJaer & Wieland 1997, Huwer et al. 2011). Center of mass distribution data for cod larvae in the Bornholm basin show an oxygen range between 4.5 and 7.8 mg/liter (GrønkJær & Schytte 1999).

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3.3 *Gasterosteus aculeatus* (Linnaeus, 1758), Threespine stickleback

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1. Importance for the Baltic Sea

Gasterosteus aculeatus exhibits high abundances in coastal areas and inshore systems of the entire Baltic Sea and can also form extensive shoals in the pelagic zone of Baltic offshore areas. The species represents a dominating component in many littoral habitats along the Baltic coast. In general, the omnivorous feeding habits of threespine sticklebacks cause a diversified insertion of the species into the distinct coastal food webs. Furthermore, sticklebacks are considered to influence economically important fish species of the Baltic Sea, e.g. through food web interactions such as predation (Kotterba et al., 2014) and competition (Peltonen et al., 2004).

2. Distribution in the Baltic

Gasterosteus aculeatus is abundant within the entire Baltic Sea (HELCOM subdivision SB 1-17, coastal areas 1-42) showing a very high variability in abundance between the different locations and over time (Wootton, 1976; Winkler & Thiel 1993).

3. Environmental tolerances and preferences

As indicated by its broad distribution range from approximately 35°N to 70°N in Eurasia, from Northern Mexico to Alaska at the Eastern Pacific coast and from North Carolina to Greenland in the North-Western Atlantic *Gasterosteus aculeatus* is a eurythermal species (Wootton, 1976). The toleration of temperatures between 1°C and 34.6 °C (critical thermal maximum) has been shown in experimental studies whereby freshwater populations appeared to tolerate a broader range of temperatures than marine populations (Feldmeth & Baskin, 1976; Barrett et al., 2011).

Gasterosteus aculeatus populations can be found in freshwater lakes as well as in coastal marine waters; however the breeding success of marine populations depends on the anadromous migration into mesohaline or freshwater spawning areas (Wootton, 1976). Accordingly, the species is euryhaline with the capability to tolerate different salinities (0.5‰ to 35‰) and ionic compositions in the ambient medium (Wootton, 1976).

Hypoxia is a common phenomenon occurring in extended areas of the Baltic Sea, but it is a less severe factor in well mixed shallow littoral zones of the Baltic coast. However, *Gasterosteus aculeatus* is also common in eutrophicated inshore habitats and small scale freshwater systems which can become oxygen limited as well, particularly in summer. Feldmeth and Baskin (1976) found critical oxygen levels at $1.32 \text{ mg}\times\text{l}^{-1}$ for fish kept at 18.6°C. Comparable thresholds were found by Giles (1986) who observed the initiation of aquatic surface respiration (ASR) by sticklebacks at oxygen levels of 1.6 – 2.0 $\text{mg}\times\text{l}^{-1}$ and an ambient water temperature of 20.5 to 22°C. Considering both observations, a critical minimum oxygen saturation between 15 and 20% can be assumed for *Gasterosteus aculeatus*.

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3.4 *Neogobius melanostomus* (Palas, 1814), Round goby

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1. Importance for the Baltic Sea

Round goby is a demersal species with Ponto- Caspian origin. It is one of the most successful invaders in the Baltic Sea. *N.m.* is prey for piscivorous fishes (e.g. cod, turbot, perch, and pike perch) (Skabeikis 2015, unpub.) First unpublished analysis of a cod stomach content database show an increasing amount of gobiids within the last 2-3 years. Almqvist et al 2010 found that round goby is for medium sized cod in Gulf of Gdansk an important prey. Additionally *Perca fluviatilis* almost exclusively feeds on gobiids in that area. Round goby in the Western Baltic prey on eg. Amphipoda, Decapoda, Ostracoda Mysidae, Barnacles, Bivalvia, Gastropoda, Annelids and Insecta (Larvae) (Mattern, 2015 unpub.)

2. Distribution in the Baltic

Neogobius melanostomus was first found in the Baltic in the early 1990's in polish coastal waters (Skora&Stolarski 1993). In the past years this species managed to expand its range dramatically and is now found at nearly the complete coast of Poland, Lithuania, Latvia and Estonia. It is partly present in coastlines of Germany, Denmark, Sweden and Finland. (Helcom subdivision SB 1-17 except 16) (Kontula et al. 2012). It is also missing in the coastal areas CA2, CA3, CA4, CA6, CA8, CA39, CA40 and CA42 (Kotta et al. 2015). In the Great Lakes (USA) highest densities occur on rocky grounds (Ray & Corkum 2001) nevertheless they are also using mud and sand as habitat (Johnson et al 2005). The preferred depth in the Great Lakes changes with season, during spawning they prefer shallow waters 0.7-3m and migrate to deep waters (down to 130m) in winter (Kornis et al 2012). For the Baltic there are no published data available that show a depth preference. Unpublished own observations suggest a preferred depth < 20m, with abundance decreasing with depth. Further juveniles were found only in shallow areas.

3. Environmental tolerances and preferences

Adult *Neogobius melanostomus* have a wide temperature tolerance ranging from -1 °C up to 30 °C. The energetic optimum temperature is estimated to be at 26 °C (Lee & Johnson, 2005 as cited in Kornis et al, 2012). The salinity tolerance ranges from 0 to 25 ppt, the optimum is in the range between 5 to 10 ppt. This was found by Karsiotis et al 2012 in a long term survivorship experiment. All other salt concentrations had a higher mortality. The critical lethal oxygen limit is indicated with 0.4- 1.3/ 1.4 [mg/l] (Charlebois et al. 1997 as cited in Kornis et al 2012)

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3.5, *Platichthys flesus* (Linnaeus, 1758), European flounder

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1. Importance for the Baltic Sea

The European flounder (*Platichthys flesus*) is a commercial fish species and the most widely distributed among all flatfish species in the Baltic Sea. It is landed mainly as bycatch in the demersal fisheries (ICES 2013). Official landings in the Baltic in 2014 were about 20.6 thousand tonnes (ICES 2015).

2. Distribution in the Baltic

ICES (2013) describes the distribution throughout the whole Baltic except for the eastern part of the Gulf of Finland and the Bothnian Bay, while other literature describes a distribution in the Baltic without any exceptions (HELCOM 2012).

3. Environmental tolerances and preferences

The European flounder is a highly euryhaline species that occurs between 0 and 35 ‰ salinity and moderately tolerate hypoxic conditions (Lundgreen et al. 2008). In freshwater the minimum oxygen conditions are at 20 °C at 2.0 mg O₂/l and the optimum is about 5.0 – 6.0 mg O₂/l, while the optimum temperature for adults is between 15 and 18 °C with a critical temperature of 20 °C (Wolter et al. 2003). Other literature describe a temperature range of 5 to 25 °C (Baensch & Rhiel, 1997, as cited in Froese & Pauly 2015).

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3.6 Pomatoschistus minutus (Pallas, 1770), Sand Goby & Pomatoschistus microps (Krøyer, 1838), Common goby

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1. Importance for the Baltic Sea

Compared to commercial fish, there is relatively limited information available about the dynamics of non-commercial fish that very often play important structural and functional roles in marine ecosystems. Gobies *Pomatoschistus* spp. are small-sized short-living abundant fish (Fonds, 1973) by constituting a significant part of demersal fish communities from the Mediterranean up to Norway including the Baltic Sea (Hesthagen, 1977; Psuty-Lipska and Garbacik-Wesolowska, 1998).

In the Baltic Sea, *Pomatoschistus* spp. is shown to serve several important functions, like being a prey for upper trophic levels (Uzars, 1994, Lundsrtöm et al., 2010), acting as an intermediate hosts of parasites (Zander et al. 1993) and influencing stock performance of commercially exploited predatory fish – pikeperch *Zander lucioperca* – (Müller-Karulis et al., 2013).

2. Distribution in the Baltic

In the Baltic Sea, there are at least two *Pomatoschistus* species: sand goby *P. minutus* and common goby *P. microps*. They are well-adapted to the brackish conditions prevailing in the estuaries and have achieved pan-Baltic distribution (Zander 1979; Jansson et al. 1985; Nellbring 1985; Thorman 1986; Aarnio and Bonsdorff 1993; Winkler and Thiel 1993). Because identification to a species level is impossible at larval stage, analyses are often carried out at the genus level (Laur et al. 2014; Parmanne and Lindström 2003).

3. Environmental tolerances and preferences

When *P. minutus* and *P. microps* tolerate broadly similar salinity range (from 0.9 to 45 PSU; Fonds 1973), there is a difference in temperature preference between the species: while *P. minutus* avoids temperatures starting from 19 °C (Fonds 1973; Hesthagen 1977; Nellbring 1985), *P. microps* tolerates higher temperatures (Fonds 1973; Wiederholm 1987).

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3.7 *Scophthalmus maximus* (Linnaeus, 1758), Turbot

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1. Importance for the Baltic Sea

Turbot is a commercial fish species. In the Baltic, it is mainly landed in the southern and western parts as a valuable bycatch, but in some areas target fisheries exists as well. Prey consists of demersal and pelagic fish species like sandeel, herring and gobies (ICES 2015, ICES 2011, Golani et al. 2015)

2. Distribution in the Baltic

Turbot occurs in the western and southern Baltic up to the Sea of Aland frequently (HELCOM 2013), but regularly observations exists in the Bothnian Bay while temporary existence is described for the Quark as well (HELCOM 2012).

3. Environmental tolerances and preferences

Based on the distribution area turbot tolerates a salinity between 35 ‰ and 5 ‰ (Karås & Klingsheim 1997). Temperature and salinity for optimal egg development and viable hatch were published in various studies; with optimal conditions for turbot from the North Sea between 12 and 18 °C at salinities between 20 and 35 ‰ while corresponding data from the southern Baltic proper show a sharply decrease in turbot survival in temperatures below 14 °C and a high survival in salinities between 10 to 15 ‰ (Karås & Klingsheim 1997). Other investigations show that eggs from the Belt Sea have an optimal development at 17 °C and 15 ‰ while incubation in 5 ‰ or of less than 10 °C was lethal (Kuhlmann & Quantz, 1980). Studies on turbot caught along the coast off Gotland show a minimum salinity of 5.5 – 6 psu and an optimum salinity of ≥ 7 psu for fertilization and egg development with an optimum condition for egg developemen at 12 – 18 °C (Nissling et al. 2006).

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3.8 *Sprattus sprattus* (L.), Sprat, adult and larval fish

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1. Importance for the Baltic Sea

Sprat (*Sprattus sprattus*) is an ecologically- and commercially important pelagic fish species in the Baltic Sea (Kornilovs et al. 2001) since it is preyed on by top predators like Atlantic cod (*Gadus morhua*) and is a predator on zooplankton and fish eggs (Arrhenius & Hansson 1993, Cardinale et al. 2002). Clupeid fish, like sprat can be used as bio-indicators of climate-driven changes in marine systems, since they show strong changes in stock size and distribution and are tightly coupled to zooplankton dynamics and sensitive to mesoscale hydrodynamic features (Mehner et al. 2012) At present, sprat also represents the most abundant, commercially-exploited fish species in the Baltic Sea benefiting from the decreased predation pressure by cod and the reduced fishing pressure (Voss et al. 2012).

2. Distribution in the Baltic

The different Baltic basins (Bornholm Basin (SB7), the Gdansk Deep (SB8) and the Gotland Basin (SB9, SB10) as well as the estuarine habitats are used by sprat as spawning areas and represent the species' most northern spawning and distribution areas (Voss et al. 2012, Peck et al. 2012)

In the deep basins sprat spawn pelagic eggs that sink below the halocline (6–15 psu) located at intermediate water in depths of 30–60 m (Wieland and Zuzarte, 1991). Field studies performed in 1989-1990 revealed that sprat larvae perform diel vertical migration down to 70 m, whereas studies from 1999 to 2001 suggest a loss of this migration pattern and a concentration of the larvae in the upper 30 m (Voss et al. 2007).

3. Environmental tolerances and preferences

Laboratory experiments on temperature and salinity tolerance for adult sprat larvae are lacking so far. No oxygen tolerances estimates under experimental conditions in the laboratory are available.

To evaluate preferences to environmental parameters, field observations of distribution pattern of adult sprat were investigated. 22°C and 5°C were found as the upper and lower temperature threshold for adult sprat with the peak also occurring at 5-22°C (Stepputis 2006). Maximum salinity experienced by adult sprat in the field was 23 psu and the lowest salinity level was 3psu. No clear optimum or peak value was determined. Lowest oxygen concentration determined in the adults' distribution area was 1 mg/L (Stepputis 2006). In a field study in Swedish waters Cardinale et al. 2002 analyzed the effect of temperature and salinity on the condition factor of adult Baltic sprat in Subdivision 25 and 27 from a time series from 1986 – 2000 using the environmental condition in the months September and October. Within the time series temperature ranged from 8.4- 11°C with a mean of 9.8°C and a mean salinity of 7.7. (range 7.3 -7.7 psu) in Subdivision 25 and from 6.7 -10.1°C with an mean of 8.6°C and a mean salinity of 6.8 psu (range 6.4-7.2 psu) for subdivision 27. No effect of temperature or salinity on the condition factor (except for salinity in subdivision

27) was shown indicating favorable environmental condition for adult sprat. Mackenzie und Köster (2004) analysed data on sprat recruitment (numbers of 1-yr olds) from a time series (1973–1999) in ICES Subdivisions 22–32 together with temperature data in May representing the midpoint of the historical sprat spawning season in the Baltic Sea. The temperature used in the regression model was the mean temperatures for the depth interval 45-65 m, the water body where sprat eggs are mainly distributed (Köster & Möllmann 2000). It could be shown that sprat recruitment was positively correlated with an increase in temperature ranging from 1-6°C, indicating that even these low temperatures can be tolerated by adult sprat while spawning.

Larval sprat show a wide tolerances range for temperature and salinities. Laboratory experiments performed by Nissling (2004), with eggs and larvae of Baltic sprat showed increased mortality at temperatures ($\leq 5^\circ\text{C}$). Upper and lower temperature threshold for eggs and larvae have been determined in laboratory experiments to be at 14.7°C and 3.4°C respectively with an optimal temperature of 6.8°C (Petereit 2009). Sprat larvae have a salinity thresholds between 5 psu and 35 psu and an optimum of 8-14 psu (Petereit et al. 2009). Data on oxygen tolerances are lacking.

Environmental preferences based on realized/observed distributions from the Bornholm Basin show a range between 4°C and 16°C , 4-15.5 psu salinity levels and 2-9 mg/L oxygen for low and high values (Voss et al. 2007).

Temperature values, where sprat larvae have their peak distribution, determined by plotting the depth of highest abundance and the mean weighted depth of sprat larvae $> 10\text{mm}$, ranged from 4.5°C to 6.25°C and 6.25°C to 16.5°C depending on the season. Peak distribution of sprat larvae indicated optimum salinity ranges from 7 psu to 9 psu and oxygen levels of 6-7 mg/L (Voss et al. 2007).

Analyses of physiological data and temperature dependent growth predictions synthesized in Peck et al. 2012 have shown that yolk sac sprat larvae have an optimum for growth between $6-12^\circ\text{C}$, feeding larvae grow best at $5-11^\circ\text{C}$, whereas schooling 12-16mm sprat larvae have a growth optimum at $9-17^\circ\text{C}$.

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Discussion

This unique compilation of physiological tolerances and limits for 30 relevant Baltic species provides a service to the modelling teams within BIOC3. The information will mainly be used in WP 3 in combination with hydrographic data from model output representing present and future condition to describe the changing envelopes of the species habitats. These applications (WP 3, D3.3) will produce insights into the expected magnitude of spatial distribution shifts and related effects on species assemblages and trophic interactions. The review has further identified knowledge gaps for a number of species.

Appendix

For a better readability is appendix online available:

<https://docs.google.com/spreadsheets/d/11zBNyIWvdaQ8fEZ0JRgF6Ac5p75NbFWZcneknku m8Hc/edit?pli=1#gid=2117449428>