BIO-C3
Biodiversity changes: causes, consequences and management implications

Deliverable No: 4.3		Workpackage number and leader: 4.3, Monika Winder, P4	
Date:		Delivery due date: 31.10.2017	Month 46
Title:		Projection of impacts of changed drivers on future biodiversity	
Lead partner for deliverable:		Monika Winder (P4) Stockholm University	
Other contributing partners		P2, P5, P6, P7, P8, P9, P12, P13	
Authors		M Winder, K Aarnio, H Andersson, B Bauer, E Bonsdorff, C Björklund, D Costalago, M Gogina, , M Gröger, K Herkül, E Kock Rasmussen, J Kotta, V Lauringson, K Lundström, B R MacKenzie, P Margonski, T Möller, K Nyström, H Ojaveer, H Orav-Kotta, R Puntila, M Pärnoja, H Skov, MT Tomczak, A Törnroos, J Warzocha, I Wåhlström, A Zaiko, M L Zettler	

Dissemination level (PU=public, PP=Restricted to other programme participants, including the BONUS Secretariat, CO=confidential)	PU
Nature of the Deliverable (RE=Report, OT=Other)	RE

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.

CONTENT

Executive Summary of BIO-C3 Task 4.3

The objectives of BIO-C3 Task 4.3 is to investigate how distributions and abundances of species and populations important for food web functioning in the Baltic Sea might change under different scenarios of anticipated changes of major drivers. The work contributing to this task are summarized here:

Climate change and eutrophication impacts on reproductive habitat: The ability of the Baltic Sea biota and ecosystems to provide goods and services depends on which species continue to be present in the Baltic Sea under future climate change, eutrophication and exploitation, and which species can successfully enter and esstablish new populations. A key prerequisite for the continued presence of existing species and the potential for new species to become established is whether they will be able to reproduce under the probable abiotic conditions of the future Baltic Sea. It is likely that temperature, salinity and oxygen conditions are going to change systematically during the 21st century; furthermore successful reproduction by all species is constrained physiolgoically by species- and sometimes population-species ranges of these same variables. As a result some species could suffer while others benefit as the abiotic environment of the Baltic Sea progressively changes during the coming decades. Here and together with P12 we have used experimental results from other BIO-C3 tasks and literature data to derive the ranges of temperature, salinity and oxygen concenctration at which several key species representing different functional groups and salinity tolerances (i. e., freshwater, marine) can reproduce sucessfully, and then used integrated climate-ocean-biogeochemical models to derive the sizes and locations of reproductive habitat by month for a historical and future climate period. These habitat estimates have furthermore been estimated for different nutrient-loading scenarios so that habitat sizes for combinations of climate change-eutrophication can be derived and compared. Our results show that many key components of the Baltic biodiversity will experience conditions which can potentially lead to major decreases or increases in reproductive success. As a consequence, species distributions will have to change, or pressure for adaptation to the changing conditions will increase. The results suggest that changes to Baltic biodiversity both in terms of species and functions, and the structure and functioning of foodwebs, are vulnerable to expected 21st century climate change and eutrophication.

The extent to which increasing populations of seals are ecologically interacting with fisheries, and how these trophic interactions will change in the future has rarely been explored. This is an important question for the Baltic Sea presents as it is a highly exploited system with an increasing population of seals interacting with some fisheries. Here, using an Ecopath with Ecosim food-web model for the Baltic Proper we investigated the trophic role of grey seals and their effect on some fish stocks. Aiming at providing new insights for an ecosystem-approach to management and conservation in regions where fisheries and seals interact, we predicted the changes in the fish and seal populations under different future scenarios. We showed that fish biomass is affected primarily by fishing mortality rather than by seals, and that seal predation pressure on cod is highest under low fish biomass. We thus demonstrated that healthy populations of both fish and seals would help to sustain the most important commercial species in the region. Our results from the Baltic Sea can also serve as a basis for studies aiming to offer management and conservation advice elsewhere.

In another study Boosted Regression Trees modelling was used to relate the cover of submerged aquatic vegetation to the abiotic environment in the brackish Baltic Sea. The analyses showed that the majority of the studied submerged aquatic species are most sensitive to changes in water temperature, current velocity and winter ice scour. Surprisingly, water

salinity, turbidity and eutrophication have little impact on the distributional pattern of the studied biota. Both small and large scale environmental variability contributes to the variability of submerged aquatic vegetation. When modelling species distribution under the projected influences of climate change, all of the studied submerged aquatic species appear to be very resilient to a broad range of environmental perturbation and biomass gains are expected when seawater temperature increases. This is mainly because vegetation develops faster in spring and has a longer growing season under the projected climate change scenario.

In a different study, we applied the species marginality index and species distribution modeling in the northern Baltic Proper to determine (a) if environmental niche spaces at habitat scale differ between taxonomically and functionally closely related invasive and native gammarid species, and (b) whether the observed pattern relates to the species distribution overlap. Both methods agreed in notably narrower and more segregated realized niche of invasive *Gammarus tigrinus* compared to the studied native gammarids. Among native species, the distribution of *G. zaddachi* overlapped the most with *G. tigrinus*. Our results confirm that widespread colonization does not require a wide niche of the colonizer, but may rather be a function of other biological traits and/or the saturation of the recipient ecosystem. The niche divergence and wider environmental niche space of native species are likely to safeguard their existence in habitats less suitable for *G. tigrinus*.

We also assessed the role of invasive species in the food web. In specific, the food web interactions of invasive species were assessed conceptually using the round goby (*Neogobius melanostomus*) and Harris mud crab (*Rhithropanopeus harrisii*) as examples. Both species have established in the Baltic Sea and especially the round goby is widespread. Conversely, the Harris mud crab is locally abundant in the Archipelago Sea (Finland) and Pärnu bay (Estonia) with potentially significant impacts to the important littoral ecosystems. Based on the studies, the species have both predatory and prey roles in the food webs and their increasing abundances may cause impacts cascading both down and up in their respective food webs. The impacts of the invasions will be further studied using Ecopath and Ecosim food web models.

Downscaled benthic-pelagic food-web model for the Gulf of Riga (GoR) has been applied in hindcast and forecast mode to study the past and future levels of nutrient control of the carrying capacity of macrobenthos (bivalves) in coastal areas of the Baltic Sea. The model data were analysed using one climate scenario and two eutrophication scenarios (reference/Baltic Sea Action Plan (BSAP)) from BONUS Ecosupport. The impact was assessed by analysing spatio-temporal trends in modelled concentrations of dissolved nutrients and chl *a* and in the biomass of two species of bivalves (*Mytilus edulis, Macoma baltica*) which dominate the overall zoobenthic biomass in the region. During the period between 1990 and 2020, a descending trend (0.075 mg/l per year) in the concentration of chl *a* was predicted for the BSAP scenario and a slightly weaker downward trend (0.050 mg/l per year) was predicted for the reference scenario. In the BSAP scenario the downward trend in chl *a* concentrations continued after 2020. The biomass of *Mytilus* bivalves was predicted to decline in the reference scenario over the whole period, but intensified after 2050. By 2020, the level of *Mytilus* biomass in the BSAP scenario was predicted to be 70% of the biomass in 2008. No clear trend was identified in the predicted biomass of *Macoma* during the period.

Knowledge about non-indigenous species biology and ecology is particularly important for impact prediction and projections of future changes as well as legislation and marine management. We therefore experimentally and empirically assessed the trophic positioning of a recent invader, Harris mud crab (*Rhitropaneus harrisii*), gathered the current biological

and ecological trait knowledge of this species worldwide and qualitatively compared traits with those of the native macrofaunal community. The findings show a temporally and spatially stable trophic position of the crab as well as overall similar functional role of the species compared to native invertebrate species. This work serves as a basis for further assessment of the functional role of the species, as well as an example of the trait-based approach for disentangling non-indigenous species roles in the Baltic Sea.

I) Introduction

The goal of deliverable 4.3 is to investigate how distributions and abundances of species and populations important for food web functioning and how entire species assemblages in the Baltic Sea might change under different scenarios of anticipated changes of major drivers.

The future biodiversity of the Baltic Sea depends crucially on the ability of species and populations being able to successfully reproduce and maintain viable populations as abiotic conditions trend away from historical levels. Some of the most likely changes will involve increases in temperature, a reduction in salinity and continued frequent periods of anoxia. Species and populations which are unable to reproduce under future abiotic conditions will no longer remain as viable components of foodwebs and communities thereby leading to changes in structure and function of foodwebs. Data compilation and habitat modelling under past and future climate was conducted to evaluate how the sizes and locations of reproductive habitats (as defined by laboratory studies of successful reproduction at combinations of temperature, salinity and oxygen concentration) in the Baltic Sea would change for combinations of CO_2 emission and nutrient-loading scenarios. Analyses were conducted for a range of species across trophic levels and functional groups. We have furthermore developed ways to evaluate and quantify the risk that the Baltic Sea will become more vulnerable to non-indigenous species due to ongoing climate change and eutrophication.

We assessed the interactions of grey seals and fisheries in the Baltic Sea and projected trophic impact of fisheries and seal predation under different climate, nutrient and fishing scenarios. The exponential increase in the number of grey seals in the Baltic Sea since the 1980s has raised concerns in the fisheries sector, and there is a growing alarm regarding the impact that grey seals might have on the declining stocks of the commercially most important fish species (e.g. cod, herring and sprat). Although the majority of the interactions recorded between seals and fisheries in the Baltic are described as operational (i.e. loss or damage to catch or fishing gear caused by seals). We used the Baltic Proper as a model system to investigate the role of seals in a highly exploited system aiming at providing new insights for an ecosystem-approach to management and conservation in regions where fisheries and seals interact. Using Ecopath with Ecosim (EwE) modeling we elucidated top-down effects of grey seals under different future environmental conditions. We highlight some of the factors that might have a great impact on the Baltic food-web, the commercial fish species and the seals and thus need the researchers' attention.

The Baltic Sea hosts a mixture of submerged aquatic vegetation of marine, brackish or fresh water origin; each species characterised by its specific tolerance to environmental conditions. Located at the margins of typical marine environments, the Baltic Sea is a vulnerable ecosystem and predicted dramatic climate change will challenge all the submerged aquatic species. Our goal was to (1) identify the most important environmental variables defining the cover of submerged aquatic vegetation, (2) specify the spatial scales where such relationships

are the stongest and (3) predict changes in the distributional pattern of the submerged aquatic vegetation from the current to future climate (Kotta et al. 2014). The modelling approach aims to identify possible critical tipping points of all these variables where regime shifts in species distribution may occur, to provide a better understanding of the ecological frames in which outbreaks or local extinction are more likely to occur.

Invasions of non-indigenous species (NIS) are considered among the most serious threats to global biodiversity. To date, studies comparing multidimensional niche overlaps of invasive and native guild members are almost lacking. The Baltic Sea is heavily trafficked and in terms of salinity it resembles estuarine conditions of many of the world's ports. The high dispersal connectivity for estuarine NIS between the Baltic Sea and potential donor regions yields high rates of invasion. However, the Baltic Sea is still a relatively species-poor ecosystem due to its geological youth, and therefore represents an excellent model system to study different aspects of species invasions, including relationships with native congenerics and the recipient environment. In this study, we asked why *Gammarus tigrinus* is a successful invader in the north-eastern Baltic Sea, and if this could be explained by similar or divergent niche breadth when compared to native gammarids. Specifically, we addressed the following research questions by applying multivariate ordination and species distribution modeling: (1) Do environmental niche spaces differentiate between taxonomically and functionally closely related sympatric species? (2) Does similarity in niche space result in species distribution overlap? (3) Are there any particular differences in the niche width and segregation between invasive and native species? Does the invasive species have wider or narrower environmental niche? (Herkül et al. 2016).

Non-indigenous species, especially when they become invasive, are known to induce a variety of changes to the ecosystems of their new environments. The impacts of invasive non-indigenous species in aquatic environments often draw attention (e.g., Carlton and Geller 1993, Ricciardi and Rasmussen 1998, Cohen and Webb 2002, Molnar et al. 2008), and the majority of the studies concentrate on the top-down predatory impacts of an invader on native prey. Although many species have both predatory and prey roles in the ecosystem, food web wide impacts of the invasions have been far less studied. In the BIO-C3, many of the key ecological interactions were studied and here we reviewed the results in food web context.

A fine-scale ecosystem model complex has been set up in BIO-C3 for the Gulf of Riga covering the period between 1970 and 2100. Reconstruction of past ecosystem changes in the Gulf (WP 4.2) revealed nutrient-driven localised decline in productivity affecting the entire benthic food web after mid 1990es. One of the main aims of the study has been to project key functional interactions in the benthic-pelagic food web to future scenarios based on large-scale models developed and executed in the BONUS Ecosupport project. We anticipated to be able to determine the relative contribution of the BSAP to eutrophication control and declining supply of nutrients during the 21st century.

We studied the food web positioning of a non-native invasive epibenthic invertebrate, the Harris mud crab (*Rhitropanopeus harrisii*), and showed clear ontogenetic shifts between juvenile and adult stages of the crab (Aarnio et al 2015). Moreover, we reviewed and outline additional functional characteristics of the species, apart from the assessed feeding-related ones, and compared these qualitatively with the functional characteristics of the native invertebrate communities in the region, in order to discuss its possible functional and future impacts in the coastal ecosystems of the Baltic Sea. We conclude that traits expressed by the crab is similar to the trait composition of the native coastal community, although being a taxonomically new species to the system. This means that, currently in the area and base on a

qualitative assessment, the Harris mud crab is essentially only contributing to the functional richness and functions. In addition, and in collaboration with P2 (lead) and P12, we have reviewed reproductive tolerance limits (and in some cases where no information exists, adult stages) in regard to especially temperature and salinity for a number of key benthic invertebrates and algae and angiosperm species. This information will be used with scenarios of future climatic and HELCOM BSAP targets to project spatial distribution of taxa and essentially functional attributes or even functions.

Due to the wealth of new information and detail outputs of the different studies, the key results are highlighted in the core deliverable text and the detailed material and result descriptions are provided as appendices.

II) Core Activities

Focus areas of this task were the Baltic Proper, the Gulf of Riga, the West Estonian Archipelago Sea, and the Gulf of Finland, the Gulf of Gdańsk.

Major activities of Task 4.3 per partner were as follows:

P2 has developed databases and conducted analyses of how reproductive habitats will change for several species under combinations of expected climate change and nutrient loadings. The work is a collaboration among many BIO-C3 partners including major contributions from SMHI (**P12**) regarding oceanographic modelling and data processing. Specific activities are as follows:
1) Derived a large database (> 20,000 observations) of abundance and distribution of a key benthic species, *Saduria entomon*, based on national and international databases (e. g., ICES, Helcom), and used these data together with an external collaborator, IOW, Germany to derive a habitat model for this species; used this model under future climate-eutrophication condtions provided by **P12** to estimate the change in its distribution, abundance and biomass for end of 21st century. See Appendix 7.
2) Compiled from other BIO-C3 tasks and literature the temperature, salinity and oxygen concentration limits for successful reproduction for several species and functional groups.
3) Derived estimates of sizes and locations of reproductive habitat together with **P12** for selected species under future climate change and eutrophication scenarios, and based on physiological limits for reproduction. See Appendices 8 and 9, and Deliverable Report 3.4.
4) Developed together with **P8** and **P6** an approach for assessing the consequences of three inter-linked drivers (climate change, eutrophication, introduction of non-indigenous species) of change in future Baltic Sea biodiversity. See Appendix 10.

P4 updated the existing Baltic Sea Proper Ecopatch with Ecosim (EwE) model for studying seal-fisheries interactions in order to be able to simulate the trophic effect of grey seals on the fish populations and on the fisheries. We introduced current population size estimations derived from the number of counted seals during four decades of surveys obtained from the Baltic Marine Environment Protection Commission (HELCOM) and from the Swedish Museum of Natural History (SMNH). Ecosim was used to create time-dynamic simulations of the food-web in response to observed biomass data (1974-2015) and fishing mortality, seal abundance, nutrient load and climate scenarios (2016-2098). See Appendix 1.

P5 tested for <u>zooplankton</u> in the southern part of the Baltic Sea, changes in key copepod

species biomass against the environmental and climatic potential descriptors and assessed <u>macrobenthic community composition</u> in relation to environmental conditions in the southern part of the Bornholm Deep and the Gulf of Gdańsk.

P6 built spatial model on the distribution and abundances of a selection of benthic macrophyte species under current and future climate conditions for the West Estonian Archipelago Sea; and performed the analysis of sensitivity of different functional traits to separate and combined effects of climate and eutrophication variables, combining verious mapping technologies (e.g. hyperspectral remote sensing, habitat identification using video analysis) with probability mapping and machine learning. See Appendix 2.

P6 assessed <u>niche breadth</u> and separation of habitat niche between <u>native and invasive</u> gammarid species. P6 also run <u>spatial predictive models</u> of the probability of occurrence of the studied gammarid species. See Appendix 3.

P7 reviewed the <u>role of benthic invasive species</u> in food webs based on literature and studies conducted in BIO-C3 and using the round goby and the Harris mud crabs as examples. The work will continue with modelling applications. See Appendix 4.

P9 conducted <u>downscaled ecosystem models</u> for the Gulf of Riga of three interlinked components for different scenarios; an eutrophication model based on a coupled local biophysical and ecosystem model, a mussel population model and a seaduck energetics module. See Appendix 5.

P13 experimentally and empirically assessed feeding preferences and trophic positioning of the non-indigenous Harris mud crab (*Rhitropanopeus harrisii*) in the Northern Baltic Sea and Finnish archipelago, in order to evaluate its current and potential future ecological and functional role in the coastal ecosystem. Additionally, P13 also contributed to ongoing work in collaboration with P2 and P12 on assessments of current and future distribution of reproductive areas based on tolerance limits of e.g. temperature and salinity. See Appendix 6.

III) Scientific highlights

Future climate change and nutrient loading alter reproductive habitat size and location for Baltic Sea species (for details see Appendices 8, 9, 10)
Together with several other partners in BIO-C3 and especially P12, we have developed estimates of how the reproductive habitats for a large number of species at different trophic levels and functional groups will change in the Baltic Sea under scenarios of cclimate change and eutrophication. The models are based mostly on process-oriented studies of how combinations of temperature, salinity and oxygen concentration affect reproudctive success. Those results are then used with a coupled climate-ocean-biogeochemical model RCO-SCOBI for the Baltic Sea to estiamte how habitats defined on the basis of physiological tolerance for reproduction will change. We found large differences (i. e., 50-60% decreases for some species and several-fold increases for other species), which imply that some species must change distributions, adapt relatively quickly to keep pace with expected changes (already-locally adapted populatons must increase their productivities), or alter their phenologies to avoid local extinction. The changes imply that should species fail to adapt, major changes in foodweb structure and functioning will occur, partly due to changes in abiotic conditions in habitats which affect reproductive success.

Are grey seals affecting fish biomass in the Central Baltic Sea? (for details see Appendix 1)

The extent of interaction of the increasing grey seals population with fisheries, and how seal population and interactions will be affected by future changing conditions is largely unexplored for the Baltic Sea. The Baltic Sea presents an excellent opportunity to study these relationships, as it is a highly exploited system with an increasing population of seals interacting with some fisheries and there are food-web and environmental models already developed for the region. Here, using an Ecopath with Ecosim food-web model for the Baltic Proper we investigated the trophic role of grey seals and their effect on some fish stocks. Aiming at providing new insights for an ecosystem-approach to management and conservation in regions where fisheries and seals interact, we predicted the changes in the fish and seal populations under different future scenarios. We showed that fish biomass is affected primarily by fishing mortality rather than by seals, and that seal predation pressure on cod is highest under low fish biomass. We thus demonstrated that healthy populations of both fish and seals would help to sustain the most important commercial species in the region. Our results from the Baltic Sea can also serve as a basis for studies aiming to offer management and conservation advice elsewhere.

Realized niche width of a brackish water submerged aquatic vegetation under current environmental conditions and projected influences of climate change (for details see Appendix 2)

Little is known about how organisms might respond to multiple climate stressors and this lack of knowledge limits our ability to manage coastal ecosystems under contemporary climate change. Ecological models provide managers and decision makers with greater certainty that the systems affected by their decisions are accurately represented. In this study Boosted Regression Trees modelling was used to relate the cover of submerged aquatic vegetation to the abiotic environment in the brackish Baltic Sea. The analyses showed that the majority of the studied submerged aquatic species are most sensitive to changes in water temperature, current velocity and winter ice scour. Surprisingly, water salinity, turbidity and eutrophication have little impact on the distributional pattern of the studied biota. Both small and large scale environmental variability contributes to the variability of submerged aquatic vegetation. When modelling species distribution under the projected influences of climate change, all of the studied submerged aquatic species appear to be very resilient to a broad range of environmental perturbation and biomass gains are expected when seawater temperature increases. This is mainly because vegetation develops faster in spring and has a longer growing season under the projected climate change scenario.

Specialization among amphipods: the invasive *Gammarus tigrinus* has narrower niche space compared to native gammarids (for details see Appendix 3)

Human mediated invasions of non-indigenous species are modifying global biodiversity. Despite significant interest in the topic, niche separation and specialization of invasive and closely related native sympatric species are not well understood. It is expected that combined use of various methods may reveal different aspects of niche space and provide stronger evidence for niche partitioning as compared to a single method. We applied the species marginality index (OMI) and species distribution modeling (SDM) in the northern Baltic Proper to determine (a) if environmental niche spaces at habitat scale differ between taxonomically and functionally closely related invasive and native gammarid species, and (b) whether the observed pattern relates to the species distribution overlap. Both methods agreed in notably narrower and more segregated realized niche of invasive *Gammarus tigrinus* compared to the studied native gammarids. Among native species, the distribution of *G. zaddachi* overlapped the most with *G. tigrinus*. Our results confirm that widespread

colonization does not require a wide niche of the colonizer, but may rather be a function of other biological traits and/or the saturation of the recipient ecosystem. The niche divergence and wider environmental niche space of native species are likely to safeguard their existence in habitats less suitable for *G. tigrinus*.

Role of invasive species in the food webs (for details see Appendix 4)
The roles of the selected invasive species were reviewed conceptually based on literature and results of the studies conducted within BIO-C3. Based on the results, the round goby has successfully established in the various coastal ecosystems in the Baltic Sea. They are simultaneously both predators for native prey and prey for native predators as well as competitors to some native species. In addition, they are a host for native generalist parasites. In some areas, run down consumption of *Mytilus trossulus* has been reported, which may have cascading impacts in the ecosystem. The interactions with the surrounding ecosystem (e.g., predation and parasites) do not seem to limit the population growth of the round goby and their range and abundance is increasing in most of the locations.

Based on the studies in the northern Baltic Sea range of the Harris mud crab, the species has established in the ecosystems and they are both predators and prey in the food webs. The implications to the other trophic levels including detritus consumption are still unknown. Run down consumption of grazers may result in impacts on *Fucus vesiculosus*, where grazing is naturally an important phenomenon. The decline in grazing may lead to changes in the algal composition in these hard bottom habitats. Also, the crabs may compete with some local fish species, such as perch and roach, for prey.

Predicted impacts of changes in intensity of eutrophication on future carrying capacity of the Gulf of Riga (for details see Appendix 5)
Downscaled benthic-pelagic food-web model for the Gulf of Riga (GoR) has been applied in hindcast and forecast mode to study the past and future levels of nutrient control of the carrying capacity of macrobenthos (bivalves) in coastal areas of the Baltic Sea. The model data were analysed using one climate scenario and two eutrophication scenarios (reference/Baltic Sea Action Plan (BSAP)) from BONUS Ecosupport. The model data covered the period between 1970 and 2100. The impact was assessed by analysing spatio-temporal trends in modelled concentrations of dissolved nutrients and chl *a* and in the biomass of two species of bivalves (*Mytilus edulis, Macoma baltica*) which dominate the overall zoobenthic biomass in the region. A steep decline (0.0085 mg/l per year) in the concentration of dissolved inorganic nitrogen (DIN) and a moderate decline (0.00015 mg/l per year) in the concentration of inorganic phosphorus (DIP) was predicted in the BSAP scenario between 1990 and 2020. After 2020, the concentration of DIN stabilised, whereas the concentration of DIP showed a weak but continuous downward trend. The decreasing trends in nutrient concentrations during this period for the reference scenario were predicted to be approximately 30% less steep than in the BSAP scenario. During the period between 1990 and 2020, a descending trend (0.075 mg/l per year) in the concentration of chl *a* was predicted for the BSAP scenario and a slightly weaker downward trend (0.050 mg/l per year) was predicted for the reference scenario. In the BSAP scenario the downward trend in chl *a* concentrations continued after 2020. The biomass of *Mytilus* bivalves was predicted to decline in the reference scenario over the whole period, but intensified after 2050. During the BSAP scenario, the decline in predicted *Mytilus* biomass started earlier and amplified the trend in the reference scenario. By 2020, the level of *Mytilus* biomass in the BSAP scenario was predicted to be 70% of the biomass in 2008. No clear trend was identified in the predicted biomass of *Macoma* during the period. A spatial assessment of the predicted dramatic decline in the

carrying capacity of *Mytilus* revealed that the decline will be focused on the Gulf of Riga rather than the Irbe Strait and the coastal areas west of the Gulf.

Food web positioning of a recent coloniser: the North American Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) in the northern Baltic Sea (for details see Appendix 6)

Identifying resource use and functional traits of non-indigenous species are promising means to increase the ability to predict ecological consequences of invasions. One of the most widely spread brachyuran crab species, and a recent invader in the northern Baltic Sea, is the North American Harris mud crab, *Rhithropanopeus harrisii* (Gould, 1841). Although spread, establishment, and population structure have been studied for this species, little is known about its role and impact in a new environment. We investigated the position and role of *R. harrisii* in the coastal food web by combining spatial and temporal estimates of trophic position using stable isotopes ($\delta^{13}C$ and $\delta^{15}N$), with short-term food- and habitat-choice experiments. We observed a stable pattern in the trophic position between two environmentally different locations in the Archipelago Sea over the production season. The identification of a natural breakpoint in carbon stable isotopes at the size of 12 mm carapace width suggested a presence of an ontogenetic diet shift, which was confirmed by isotope signatures positioning large *R. harrisii* among secondary consumers and small individuals with primary consumers. The generalist consumer nature of *R. harrisii* and preference for structured habitat was supported by an active habitat and food choice, revealing no preference for prey species (polychaetes versus amphipod), but selection of brown algae over bare mud. To broaden the understanding of the functional role of *R. harrisii*, we combined our findings with other known biological and ecological traits of the species and qualitatively compared these to characteristics of other benthic organisms in the northern Baltic Sea, suggesting a general similarity in traits.

IV) Progress and next steps

Studies and work-tasks were performed according to the workplan and original objectives were obtained. The progress and outstanding next steps are as follow:

The sizes and locations of the historical and future reproductive habitats for a large number of species and functional groups of the Baltic Sea have been quantified for combinations of climate change and nutrient-loading scenarios. Most of these analyses have only recently been completed and further work in the remaining months will be used to quantify and analyse the changes in further detail, include a few additional species from especially the benthos and habitat-forming species whose reproductive thresholds have only recently been located or been provided and to prepare results for the final BIO-C3 project report and for peer-review publication in international journals. Furthermore, analyses to assess how the Baltic may become more vulnerable to non-indigenous species from estuarine areas under climate change and eutrophication has been started with P8 and P6, and is expected to be completed in the coming 1-2 months in time for the final report (Appendix 10).

EcoPath and EcoSim modeling and future predictions of Baltic Sea seals and fisheries interactions have been performed and finalized according to work plan. A draft manuscript is finished and will be submitted within the next weeks for publication in a peer review journal.

The impacts of invasions on food web processes will be further studied with food web modelling (EwE).

A study on the functionality of non-native species was performed according to the work plan and original objectives. Work on assessment and construction of functional properties, based on reproduction tolerances, of zoobenthos under future scenarios has been initiated as planned, and is still in progress. Scenario outcomes for a larger set of key invertebrates will be interpreted, as well as any potential overarching functional changes will be discussed and highlighted in a manuscript for publication in a peer review journal, to be reported in the final project report.

V) Methods and results

Major results are highlighted in section (*i*), detailed methods and results for each respective study are described in the Appendices. A list of all attached appendices is given in section (*v*).

VI) Recommendations

Estimates of reproductive habitat size have been derived for a range of species in the Baltic Sea. The estimates are based partly on somewhat limited experimental data of the tolerances for reproduction across temperature, salinity and oxygen concentration ranges; for example population-specific differences within species which could represent adaptation potential were usually not available and could not be directly accounted for. Furthermore the reproductive requirements for some key species in the foodweb have never been experimentally investigated (e. g., S. entomon) and other habitat modelling approaches were employed. New experimental studies of the reproductive success of selected species and populations with major roles in Baltic foodwebs are necessary to fill knowledge gaps.

Reproductive habitat size as determined from temperature, salinity, oxygen and potentially other abiotic variables (e. g., depth, substrate type) can be relatively easily quantified given background experimental or field data and climate-ocean-biogeochemical models available in the Baltic scientific community. Habitat sizes for some selected species could potentially be useful indicators of population and environmental status and food web functioning and could potentially contribute to MFSD and GES monitoring protocols.

It is also recommended that monitoring and data collection be continued and expanded for the distribution and abundance of key biota. Regular and frequent observations are needed to detect changes, to enable attribution of such changes to changes in potential drivers and to compare with and validate models of habitat and abundance changes. Biological monitoring should be accompanied by continued development of integrated climate-ocean-biogeochemical models of the Baltic Sea to reduce uncertainties in model outputs and improve estimates of habitat sizes and locations.

Our model projections showed that seal abundance will level off at about 140000 individuals in the year 2038 individuals, which his likely close to the carrying capacity of the system for grey seals. Our results provide evidence that at their current population size, consumption by grey seals do not affect fish biomass in the Baltic Proper in a significant manner. Should the grey seal population remain stable in the future, or even increase substantially, it is still unlikely that grey seals will have a greater effect on the cod biomass. Also, we have demonstrated that maintaining fish populations at relatively high abundance levels in the Baltic Sea would reduce cod predation mortality by seal, and thereby healthy populations of

both fish and seals would help to sustain the most important commercial species in the region. Our results from the Baltic Sea can thus serve as a basis for studies aiming to offer management and conservation advice elsewhere.

Deliverable 4.1 reported the unfavorable changes in benthic community structure, and even a complete disappearance of macrozoobenthic organisms on the muddy bottom of the southern part of the Bornholm Deep and the Gulf of Gdańsk, also above the halocline. These changes are related to oxygen depletion in those parts of the Baltic Sea. Thus, any scenario influencing the distribution and extension of anoxic areas will have an impact on dynamics of benthic communities. Profound changes in zooplankton community were recorded at the deep-water stations in the southern part of the Baltic Sea, which is mostly caused by a decrease in abundance of *Pseudocalanus* copepods responding to the salinity changes in-between of the inflows from the North Sea. Biomasses of all key copepod species were significantly correlated with hydrological parameters (especially with salinity) and winter NAO, suggesting that reduced future inflow will change zooplankton community composition.

Our study suggests that practically all of the studied submerged aquatic species benefit from the projected influences of climate change with no indication of local extinction in the West Estonian Archipelago Sea. The individualistic response of species to the environmental change was expected and this was confirmed by the spatial predictive models. Non-linearities between environment and biota result in situations where even gradual changes in future climate may provoke sudden and unpredictable biological responses as populations shift from one state to another. The observed results are study area specific and possibly cannot be extrapolated to other seas.

All predictions of future climate are far from certain and opposite changes in the abiotic environment might also occur under other climate change scenarios. Nevertheless, our modelling study showed that the submerged aquatic vegetation is very resilient to a broad range of environmental perturbation and biomass gains are expected when seawater temperature increases. This is mainly because vegetation develops faster in spring and has a longer growing season under the projected climate change scenario.

The distribution and niche assessment of NIS by combining spatial modeling and multivariate ordination in the present study proved to be a highly relevant approach to reveal patterns of invasion process. Environmental niche analysis (OMI) offers complementary information about biotic patterns in available environmental space compared to more traditional species distribution modelling. Our study reminds that wide environmental tolerance of a species does not necessarily result in a wide realized niche in the course of an invasion process. Our results also suggest that colonization success and wide distribution do not necessarily require a broad environmental niche of the colonizer, but may instead rely on the saturation of the recipient ecosystem and the novelty of the pre-adaptations of the colonizer: an ability to optimally utilize previously under-occupied environmental niche can support the apparent luck of the draw. Despite the decline in specialist species worldwide, anthropogenic introductions may thus regionally increase the proportion of relatively specialized taxa.

Both investigated invasive species, the round goby and the Harris mud crab, have successfully established into their ecosystems and play both predatory and prey roles in the food webs. Their presence has top down impacts on their prey, leading to both competition with native species and potentially cascading changes in the lower tropic levels. Furthermore, they are prey for native predators adding a new links into the food web, currently with unknown consequences. Further studies will concentrate in modelling the cascading impacts of these

growing populations on food web processes such as energy transfer. These potential changes in the food web processes will be examined in the future by utilizing modelling tools in the Ecopath with Ecosim (EwE) framework.

The model predictions for the development of the benthic ecosystem in the Gulf of Riga indicated significant impacts of the continued control of eutrophication and derived reductions in nutrient concentrations. With the implementation of the mitigation measures through the BSAP these impacts will be amplified with a knock-on effect on the carrying capacity of bivalves, most notably blue mussels in the part of the model area focused on the Gulf of Riga. Obviously, local ecosystem models like this one for the Gulf of Riga may provide useful decision support tools in order to achieve future synergies between targets for water quality and biodiversity conservation in many coastal areas of the Baltic Sea.

The study supports the fact that identifying resource use and functional traits of non-indigenous species are promising means to increase the ability to predict ecological consequences of invasions. The experimentally and empirically observed stable pattern in the trophic position of Harris mud crab between two environmentally different locations in the Archipelago Sea over the production season, serves as important knowledge for further Baltic Sea wide studies and for management purposes. Moreover, the demonstrated ontogenetic switch between feeding as a primary consumer to feeding as a secondary consumer, at 12 mm carapace width, illustrates two distinct trophic roles of Harris mud crab. The fact that reproductive females smaller than 12 mm was found means that this shift is not strictly related to a transition from juveniles to adults, which is valuable information especially for ecosystem modelling studies. The compilation of the specie's traits beyond feeding and habitat use, and the qualitative comparison of these to the native faunal assemblage highlighted the need for further quantification of the species' other roles for ecosystem functioning in order to clarifying any negative as well as positive contributions and proper management measures.

VII) References

Aarnio K, A Törnroos, C Björklund, E Bonsdorff (2016) Food web positioning of a recent coloniser: the North American Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) in the northern Baltic Sea. Invasions, 10, 399-413.

Kotta, J.; Möller, T.; Orav-Kotta, H.; Pärnoja, M. 2014. Realized niche width of a brackish water submerged aquatic vegetation under current environmental conditions and projected influences of climate change. Marine Environmental Research, 102, 88–101.

Herkül, K.; Lauringson, V.; Kotta, J. 2016. Specialization among amphipods: the invasive Gammarus tigrinus has narrower niche space compared to native gammarids. Ecosphere, 7, e01306.

VIII) Appendices

APPENDIX 1: Are grey seals affecting fish biomass in the Central Baltic Sea?
> *By*: David Costalago, Barbara Bauer, Maciej T. Tomczak, Karl Lundström, Monika Winder, *submitted manuscript*; *contact*: monika.winder@su.se
> The content was embargoed until publication of the manuscript; please contact the communicating author for more information.

APPENDIX 2: Realized niche width of a brackish water submerged aquatic vegetation under current environmental conditions and projected influences of climate change
Published manuscript

APPENDIX 3: Specialization among amphipods: the invasive *Gammarus tigrinus* has narrower niche space compared to native gammarids
Published manuscript

APPENDIX 4: Role of invasive species in the food webs – the cases of the round goby and
Report

APPENDIX 5: Predicted impacts of changes in intensity of eutrophication on future carrying capacity of the Gulf of Riga
Report

APPENDIX 6: Food web positioning of a recent coloniser: the North American Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) in the northern Baltic Sea
Published manuscript

APPENDIX 7: Inter-annual and spatial variability in the abundance and distribution of a benthic trophic connector species, *Saduria entomon*, in the Baltic Sea
Report

APPENDIX 8: The past and future habitats of a key benthic animal, *Saduria entomon*, in the Baltic Sea – combined impacts of climate change and nutrient loading scenarios
By: Brian R. MacKenzie, Mayya Gogina, Michael L. Zettler, Karin Nyström, Irene Wåhlström, Helén Andersson, *manuscript in prep.*; *contact*: brm@aqua.dtu.dk
The content was embargoed until publication of the manuscript; please contact the communicating author for more information.

APPENDIX 9: Future climate change and nutrient loading alter reproductive habitat size and location for Baltic Sea species
By: Brian R. MacKenzie, Matthias Gröger, Irene Wåhlström, Helén Andersson, *manuscript in prep.*; *contact*: brm@aqua.dtu.dk
The content was embargoed until publication of the manuscript; please contact the communicating author for more information.

APPENDIX 10: An approach for estimating the potential exposure of the Baltic Sea to future invasion success of non-indigenous species
By: Brian R. MacKenzie, Anastasija Zaiko, Henn Ojaveer, Matthias Gröger, Irene Wåhlström, Helén Andersson, *manuscript in prep.*; *contact*: brm@aqua.dtu.dk
The content was embargoed until publication of the manuscript; please contact the communicating author for more information.

Realized niche width of a brackish water submerged aquatic vegetation under current environmental conditions and projected influences of climate change

Jonne Kotta[*], Tiia Möller, Helen Orav-Kotta, Merli Pärnoja

Estonian Marine Institute, University of Tartu, Mäealuse 14, 12618 Tallinn, Estonia

A B S T R A C T

Little is known about how organisms might respond to multiple climate stressors and this lack of knowledge limits our ability to manage coastal ecosystems under contemporary climate change. Ecological models provide managers and decision makers with greater certainty that the systems affected by their decisions are accurately represented. In this study Boosted Regression Trees modelling was used to relate the cover of submerged aquatic vegetation to the abiotic environment in the brackish Baltic Sea. The analyses showed that the majority of the studied submerged aquatic species are most sensitive to changes in water temperature, current velocity and winter ice scour. Surprisingly, water salinity, turbidity and eutrophication have little impact on the distributional pattern of the studied biota. Both small and large scale environmental variability contributes to the variability of submerged aquatic vegetation. When modelling species distribution under the projected influences of climate change, all of the studied submerged aquatic species appear to be very resilient to a broad range of environmental perturbation and biomass gains are expected when seawater temperature increases. This is mainly because vegetation develops faster in spring and has a longer growing season under the projected climate change scenario.

© 2014 Elsevier Ltd. All rights reserved.

1. Introduction

Seagrasses and other plants of higher order are unique by occupying the subtidal photic zone of soft sediments. They form extensive habitats in sheltered near coastal zones (Reusch et al., 2005; Larkum et al., 2006) and are among the most productive habitats worldwide (Duarte, 2002). Furthermore, they provide a range of ecological functions such as coastline protection, sediment stabilization, wave attenuation, land-derived nutrient filtration, and carbon fixation, just to name a few; thereby providing some of the most valuable ecosystem services on Earth (Costanza et al., 1997; Short et al., 2011). The submerged aquatic species are also important as food, shelter and space for many invertebrates and fish, many of which are socioeconomically important (Hemminga and Duarte, 2000).

Human use of the coastal marine environment is increasing and diversifying worldwide. Given its multiple stresses, submerged aquatic species have gone through an unusually fast transition in terms of areal decline in habitat (Orth et al., 2006; Waycott et al., 2009). Although large scale processes on the formation of biotic patterns is not well known, it is plausible that contemporary climate change, interacting with other anthropogenic stressors, accounts for a large part of the observed decline. Ecologists have typically interpreted the composition of communities as the outcome of local-scale processes. However, in recent decades this view has been challenged emphasizing the importance of large-scale processes, including climate change, that may result in dramatic shifts in species distribution patterns and thereby affect community species composition, diversity, structure and productivity (Hawkins et al., 2013). Concurrent with recent climate change effects, large-scale fluctuations in water temperature is considered likely to control the distribution of submerged aquatic vegetation because with increasing temperature the photosynthesis-to-respiration ratio steadily decreases (Glemarec et al., 1997; Marsh et al., 1986; Zimmerman et al., 1989). In addition, heavy storms may create physical disturbance capable of reducing seagrass cover and increasing fragmentation of seagrass beds (Fonseca and Bell, 1998; Fonseca et al., 2000). At northern latitudes, elevated ice scouring likewise destroys submerged aquatic vegetation (Robertson and Mann, 1984; Schneider and Mann, 1991) but

* Corresponding author.
  E-mail address: jonne@sea.ee (J. Kotta).

contemporary climate change may release vegetation from such a disturbance.

Non-independent effects are common in nature (Hoffman et al., 2003; Reynaud et al., 2003) and therefore it is expected that the combined effects of two or more variables cannot be predicted from the individual effect of each. However, anticipating the future consequences of the interacting pressures is a pre-requisite to sustainable management of coastal ecosystems under current environmental conditions and contemporary climate change. In recent years large investments have been made towards modelling of ecological systems and predicting their future behaviour (e.g. Müller et al., 2009). However, many of these models perform poorly because very little is known about how organisms might respond to multiple climate stressors (e.g. temperature and wave induced currents) and it is difficult to deal with complex and non-linear systems, such as those seen in the marine environment (see Byrne and Przeslaswki (2013) for an overview). Specifically, traditional statistical models tend to oversimplify the reality and/or statistical modelling itself may not be the most reliable way to disentangle the relationships between environmental variables and species distributional patterns because it begins by assuming an appropriate data model and the associated model parameters are estimated from the data. By contrast, machine learning avoids starting with a data model and rather uses an algorithm to discover the relationship between the response and its predictors (Hastie et al., 2009). The novel predictive modelling technique called Boosted Regression Trees (BRT) combines the strength of machine learning and statistical modelling. BRT has no need for prior data transformation or elimination of outliers and can fit complex non-linear relationships. The BRT method also avoids overfitting the data, thereby providing very robust estimates. What is most important from the ecological perspective is that it automatically handles interaction effects between predictors. Due to its strong predictive performance, the BRT method is increasingly being used in ecological studies (Elith et al., 2008).

The Baltic Sea hosts a mixture of submerged aquatic vegetation of marine, brackish or fresh water origin; each species characterized by its specific tolerance to environmental conditions (Snoeijs, 1999). Located at the margins of typical marine environments, the Baltic Sea is a vulnerable ecosystem and predicted dramatic climate change will challenge all the submerged aquatic species (Koch et al., 2013). Moreover, in the Northern Hemisphere high-latitude regions are expected to experience more severe warming compared to low-latitude regions (IPCC, 2013). In addition climate change is expected to prolong growing season, reduce ice cover as well as alter wind and precipitation patterns. Such changes are likely to have profound influences on water turbidity and salinity (Short and Neckles, 1999 and references therein). Due to the non-linear response of biota to the environment, even gradual changes in future climate may provoke sudden and perhaps unpredictable shifts in submerged aquatic plant communities as many are close to their physiological tolerance limit and different species have different response mechanisms. For example many submerged plant species are of fresh water origin but have a wide salinity tolerance and thus are often competitively superior over seagrasses under fluctuating salinity regimes (Stevenson, 1988; van den Berg et al., 1998).

Hydrodynamic conditions (Schanz and Asmus, 2003), nature of the substrate (Viaroli et al., 1997; De Boer, 2007), light (Peralta et al., 2002), temperature (Glemarec et al., 1997), salinity (Wortmann et al., 1997), water transparency (Krause-Jensen et al., 2008) and nutrient concentrations in the water column (Orth, 1977) are the key environmental variables affecting the distribution of submerged aquatic vegetation. In addition to this, ice conditions are also important in high-latitude regions (Robertson and Mann, 1984). Most of these variables are expected to change with changes in future climate; however, the strength of environment—biota relationships is likely a

function of spatial scale. To date, the relationships between these environmental variables and the distributional patterns of aquatic vegetation have mostly been specified at one spatial scale but ignoring an infinite variety of other possibilities (Krause-Jensen et al., 2003; Appelgren and Mattila, 2005). In order to take into account these scale-specific effects, both small- and large-scale environmental variability should be incorporated into the models.

Seascape-scale (1–10 km) abiotic processes contribute to broadscale distributional patterns. Within these patterns smaller-scale processes (1–10 m) operate at a lower intensity to modify the distribution of species (Steele and Henderson, 1994). Among physical disturbances changes in water temperature and wave-induced current velocity are the key large-scale processes that are expected to alter species distributions. Specifically, elevated water temperatures favour plant growth and result in increased cover of submerged aquatic species (Xiao et al., 2010). Elevated wave stress affects sediment characteristics and water turbidity (Madsen et al., 2001), thereby favouring opportunistic species and disfavouring the pristine water species (Burkholder et al., 2007). The reduction of ice cover is also expected to have direct and indirect consequences. A direct consequence is the prolongation of the growth season and elevated macrophyte cover/biomass values. Currently, the co-existence of species is granted due to the presence of moderate ice disturbance that removes a significant amount of vegetation annually. In the absence of such disturbance, however, fast growing species are favoured over slow growing species. Finally, increased fresh water inputs favour higher order plants of fresh water origin over seagrasses (Touchette, 2007). But increased riverine inputs may also elevate sedimentation rates that impact negatively on the whole macrophyte community (Chambers et al., 1991). As species are shown to have strong individualistic responses to their environment we also expect large variability of responses among species (Bulleri et al., 2012).

The aims of this paper are to (1) identify the most important environmental variables defining the cover of submerged aquatic vegetation, (2) specify the spatial scales where such relationships are the strongest and (3) predict changes in the distributional pattern of the submerged aquatic vegetation from the current to future climate. The modelling approach aims to identify possible critical tipping points of all these variables where regime shifts in species distribution may occur, to provide a better understanding of the ecological frames in which outbreaks or local extinction are more likely to occur.

2. Material and methods

2.1. Study area

The study was carried out in the different sub-basins of the north-eastern Baltic Sea: the Baltic Proper, the Gulf of Riga, the West Estonian Archipelago Sea, and the Gulf of Finland (Fig. 1). The Baltic Sea is a geologically young semi-enclosed sea and one of the largest brackish water basins in the world. Due to short evolutionary history, low salinity and strong seasonality in temperature and light conditions, the number of submerged aquatic plant species is small, characterised by a mixture of marine, brackish or fresh water origin (Hällfors et al., 1981).

In the study area there is a strong permanent salinity gradient from west to east with western areas having higher salinity values. In coastal areas the dynamics of seawater temperatures is directly coupled with air temperatures. The average sea surface temperature is around 2 °C in winter and may rise up to 20 °C in August. The study area is characterized by a wide coastal zone with diverse bottom topography and underwater habitats (Kotta et al., 2008a; 2008b) (Table 1).

Fig. 1. Map of the sampling stations in the study area.

Table 1

List of environmental variables with their average, minima and maxima in different water bodies around the Estonian coastal sea given ambient and projected climate conditions. Water basins are denoted as follows: GOF — Gulf of Finland, WEAS — West Estonian Archipelago Sea, GOR — Gulf of Riga, BP — Baltic Proper. Environmental variables are as follows: Temperature — average water temperature, Salinity — average water salinity, Velocity — average current velocity, K_d — average water attenuation coefficient, Chlorophyll a — average chlorophyll a content in water, Slope — inclination of coastal slope, Soft sediment — percentage cover of soft sediment fractions, Ice cover — average ice cover over the study site.

Variable	Unit	Descriptive statistics	Current conditions				Projected climate conditions			
			GOF	WEAS	GOR	BP	GOF	WEAS	GOR	BP
Temperature	°C	Mean	12.9	14.2	13.4	12.8	16.9	18.2	17.4	16.8
		Minimum	10.3	11.4	10.2	11.0	14.3	15.4	14.2	14.9
		Maximum	17.3	19.1	18.5	18.1	21.3	23.1	22.5	22.1
Salinity	Unitless	Mean	5.3	7.0	5.5	7.3	3.9	5.2	4.1	5.5
		Minimum	3.3	6.0	3.4	6.4	2.5	4.5	2.6	4.8
		Maximum	7.5	7.3	6.8	7.8	5.6	5.5	5.1	5.9
Velocity	cm s^{-1}	Mean	1.9	5.5	2.8	4.0	1.9	5.5	2.8	4.0
		Minimum	0.1	0.1	0.2	0.1	0.1	0.1	0.2	0.1
		Maximum	5.2	11.7	7.4	9.7	5.2	11.7	7.4	9.7
K_d	Unitless	Mean	1.4	1.3	1.2	1.1	1.7	1.5	1.5	1.3
		Minimum	0.8	0.6	0.7	0.4	1.0	0.7	0.9	0.5
		Maximum	2.7	2.7	2.9	2.9	3.3	3.2	3.5	3.5
Chlorophyll a	mg m^{-3}	Mean	25.4	17.9	20.3	12.1	38.2	26.9	30.5	18.2
		Minimum	6.8	7.6	8.5	3.8	10.2	11.4	12.8	5.7
		Maximum	45.0	47.7	47.2	45.8	67.5	71.6	70.8	68.7
Slope	°C	Mean	0.5	0.1	0.1	0.2	0.5	0.1	0.1	0.2
		Minimum	0.0	0.0	0.0	0.0	0	0	0	0
		Maximum	22.9	5.1	5.9	11.1	22.9	5.1	5.9	11.1
Soft sediment	%	Mean	66.9	86.6	68.7	48.7	66.9	86.6	68.7	48.7
		Minimum	3.1	12.2	12.0	1.1	3.1	12.2	12.0	1.1
		Maximum	98.8	99.2	96.0	95.4	98.8	99.2	96.0	95.4
Ice cover	%	Mean	30.1	32.6	33.5	15.9	15.1	16.3	16.7	8.0
		Minimum	19.4	23.4	19.4	4.7	9.7	11.7	9.7	2.3
		Maximum	38.1	36.3	41.9	32.7	19.0	18.1	20.9	16.4
Depth	M	Mean	38.0	4.9	26.0	61.8	38.0	4.9	26.0	61.8
		Minimum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
		Maximum	115.0	24.0	67.0	181.0	115.0	24.0	67.0	181.0

2.2. Predicted climate change

According to most climate change scenarios mean global surface temperatures will rise by 1.4—4.0 °C in the next 100 years, primarily depending on the amount of carbon dioxide emissions from anthropogenic sources (IPCC, 2013). However, in the Northern Hemisphere high-latitude regions are expected to experience even more dramatic warming estimated at up to 10 °C increases in air temperature (Heino et al., 2009; IPCC, 2013). Similarly, projected changes in future climate of the north-eastern Baltic Sea differ widely between various regional models. On average, oceanographic studies demonstrate that changes in temperature would be 5 °C in winter and 4 °C in summer. Such shifts in temperature may have no pronounced direct effect on biological quality elements considering the large natural temperature fluctuation of the Baltic Sea basin. However, the increase in temperature significantly affects ice conditions reducing the ice extent by some 50% and therefore indirectly amplifying the effects of wind conditions. Furthermore, it is also expected that the mean daily wind speed over sea areas would increase up to 18% in winter. Finally, the average salinity of the Baltic Sea is projected to decrease by 25% of the recent level (BACC, 2008). Such shifts plausibly result in the doubling of phytoplankton biomass (Hense et al., 2013). Besides, water transparency is expected to be reduced as a function of water salinity (Stramska and Świrgoń, 2014). These stressors do not act in isolation but in combination their impacts on submerged aquatic vegetation may be greater than the sum of the single factor effects (Crain et al., 2008; Holmer et al., 2011). The modelling exercise used in this study incorporated all important environmental variables both at current and future climate levels. Hence our models suggest those stress-combinations and environmental conditions where impacts are synergistic and ecosystem degradation may occur.

2.3. Biotic and environmental data

2.3.1. Field sampling

The depth limit of submerged aquatic vegetation does not exceed 10 m in the Baltic Sea (Nielsen et al., 2002; Boström et al., 2003; Steinhardt and Selig, 2007) and therefore the sampling was carried out between seashore down to 10 m depth. Altogether, 6516 stations were sampled during the summers between 2005 and 2012 (Fig. 1). The dataset contains 1891 stations that include submerged aquatic vegetation. Using a remote underwater video device the cover patterns of submerged aquatic vegetation was estimated. The camera was set at an angle of 35° below horizontal to maximize the field of view and the range of the forward view was approximately 2 m in clear waters. The camera sled was towed from a 5-m-long boat 1 m above the sea floor at an average speed of 50 cm s^{-1}. Real-time video was captured with a digital video recorder. For each site a 50 m length transect was recorded. Depth and navigational data (from GPS) were recorded at 1-s intervals during camera deployments. In each transect the coverage of different sediment type (rock, boulders, pebbles, gravel, sand, silt) and submerged aquatic vegetation was estimated. Six different submerged plant species were investigated: *Myriophyllum spicatum* L., *Potamogeton perfoliatus* L., *Ruppia maritima* L., *Stuckenia pectinata* (L.) Börner, *Zannichellia palustris* L. and *Zostera marina* L. When it was difficult to identify submerged vegetation species in field, community samples were collected by diver for later taxonomic analysis.

2.3.2. Supporting environmental data

In the following paragraphs we describe environmental proxies that were used to link physical environment to the coverage of the submerged aquatic plants (for detailed modelling procedures see Section 2.4). The Baltic Sea lacks important biotic modifiers of seabed structure such as corals and oysters that are commonly present in true marine areas. Furthermore, the seabed sediment depends on the bedrock formations, glacial and post-glacial sediments, hydrodynamic conditions and seabed topographic features. The geographic information system (GIS) layer of the proportion of soft sediment was derived from a generalized additive model (GAM) where depth, wave exposure, seabed slope and large-scale geological seabed types (stored at the database of the Estonian Marine Institute) were used as predictive variables. The package mgcv (Wood, 2006) in statistical software R (RDC Team, 2013) was used to build the GAM. Data from nearly 10,000 benthos sampling points from the north-eastern Baltic Sea were used as input data for the proportion of soft sediment. Altogether 90% of the data were used as model training data and 10% for validating the model predictions using Pearson correlation (0.72 for the final model). After fitting the model, the GIS layers of predictive variables were used to produce the spatial prediction of the proportion of soft sediment at a resolution of 200 m (Herkül et al., 2013).

Based on bathymetry charts (available at the Estonian Marine Institute, University of Tartu) the inclination of coastal slopes was calculated at 50 m pixel resolutions using the Spatial Analyst tool of ArcInfo software (ESRI, 2011). High values of coastal slopes indicate the occurrence of topographic depressions or humps at the measured spatial scale. Low values refer to flat bottoms.

The values of water temperature, salinity and water velocity were obtained from the results of hydrodynamical model calculations from summers 2005—2012. The calculations were based on the COHERENS model which is a primitive equation ocean circulation model. It was formulated with spherical coordinates on a $1' \times 1'$ minute horizontal grid and 30 vertical sigma layers. The model was forced with hourly meteorological fields of 2 m air temperature, wind speed, wind stress vector, cloud cover and relative humidity. The meteorological fields were obtained from an operational atmospheric model. The model was validated against water level, temperature, salinity and water velocity measurements from the study area (Bendtsen et al., 2009).

Finnish Meteorological Institute provided ice cover over the study area for the investigated period. Ice cover was produced on daily basis at a nominal resolution of 500 m and was based on the most recent available ice chart and synthetic aperture radar (SAR) image. The ice regions in the ice charts were updated according to a SAR segmentation and new ice parameter values were assigned to each SAR segment based on the SAR backscattering and the ice range at that location.

As a proxy of eutrophication we used the MODIS satellite derived water transparency (K_d) and water chlorophyll a values. The frequency of satellite observations was generally weekly over the whole ice-free period, however, several observations were discarded due to cloudiness. The spatial resolution of satellite data was 1 km. False zeroes were removed from the data prior to the statistical analysis.

The ESRI Spatial Analyst tool was used to calculate the average of all abiotic and biotic variables (those obtained from field sampling as well as from modelling) for local i.e. sampling scale, 1 km and 10 km spatial scales. These values were used to link environmental and biotic patterns at larger spatial scales. The abiotic environmental variables with means, minima and maxima are presented in Table 1.

2.4. Modelling

2.4.1. Environmental niche analysis

All abiotic and biotic geo-referenced environmental data was used for environmental niche analysis. Niche breadth and

separation of habitat niche between submerged aquatic plant species were assessed using analysis of outlying mean index (OMI). OMI measures the distance between the mean habitat conditions used by the species (niche centre), and the mean habitat conditions of the sampling area (Dolédec et al., 2000). The higher the value of OMI index of a species, the higher its habitat specialization. OMI analysis is a multivariate coinertia analysis that unlike canonical correspondence analysis and redundancy analysis, can handle non-unimodal and non-linear species–environment relationships. Compared to the traditional multivariate methods, OMI gives a more even weight to all sampling units even if they exhibit low number of species or individuals. Thus, OMI captures more adequately the multivariate environmental space represented by sampling units (Dolédec et al., 2000). The package "ade4" (Dray and Dufour, 2007) was used for running OMI analysis in the statistical software R (RDC Team, 2013). The environmental niche space of submerged aquatic vegetation was visualized by drawing a convex hull over the points of OMI ordination where the species were present. When drawing the border of niche space, a total of 5% of the most distant observations of species occurrences were considered as outliers and excluded in the analysis.

2.4.2. Species distribution modelling

The contribution of different environmental variables on the coverages of submerged aquatic plant species was explored using the Boosted Regression Tree method (BRT) and the BRT models were also used to predict the species coverages for the whole study area given ambient and projected climate conditions. BRT models are capable of handling different types of predictor variables and their predictive performance is superior to most traditional modelling methods. The BRT method iteratively develops a large ensemble of small regression trees constructed from random subsets of the data. Each successive tree predicts the residuals from the previous tree to gradually boost the predictive performance of the overall model. Although BRT models are complex, they can be summarized in ways that give powerful ecological insight (Elith et al., 2008).

In the BRT models, all studied environmental variables were regressed to predict the coverage of submerged aquatic plant species. When fitting a BRT the learning rate and the tree complexity must be specified. The learning rate determines the contribution of each successive tree to the final model, as it proceeds through the iterations. The tree complexity fixes whether only main effects (tree complexity = 1) or interactions are also included (tree complexity >1). Ultimately, the learning rate and tree complexity combined determine the total number of trees in the final model. For each species, multiple models were run varying both the model learning rate (between 0.1 and 0.001) and the number of trees (between 1000 and 10,000). Then the optimum model was selected based on model performance. Typically, optimal learning rates, number of trees and interaction depth were 0.01, 2000 and 5, respectively. In order to avoid potential problems of overfitting, unimportant variables were dropped using a simplify tool. Such simplification is most useful for small data sets where redundant predictors may degrade performance by increasing variance. As a consequence, our final models did not include any autocorrelating variables. Model performance was evaluated using the cross validation statistics calculated during model fitting (Hastie et al., 2009). A random 20% of the data was assigned for testing model accuracy. The best models were then used for making the spatial prediction of the cover of submerged aquatic plant species in the Estonian coastal sea area. In order to model the cover of submerged aquatic vegetation in the predicted future climate we used the established relationships of today's plants to the environmental factors (and their interactions) in interpreting the influence of the future climate. Both present and future predictions were modelled over a 200 × 200 m grid covering water depths of 0–10 m. The BRT modelling was done in the statistical software R using the gbm package (RDC Team, 2013).

3. Results

Submerged aquatic vegetation was found at 1891 stations out of 6516. Other sites were devoid of vegetation or dominated by perennial or ephemeral algae. Altogether, six submerged aquatic plant species were observed with the number of records indicated in brackets: *M. spicatum* (437), *P. perfoliatus* (381), *R. maritima* (333), *S. pectinata* (1274), *Z. palustris* (433) and *Z. marina* (293). Both single species and mixed stands of submerged aquatic vegetation were observed.

The distributional range of the submerged plant species was similar and they inhabited practically the whole Estonian coastal range. In general the studied species were not found in the easternmost parts of the Gulf of Finland and *Z. marina* also tended to avoid the turbid and diluted Pärnu Bay area. Plants were recorded up to 8 km distance from the shore (Fig. 2). Higher order plants prevailed on soft and mixed substrates; *R. maritima* and *Z. palustris* were recorded also on rock crevices. No higher order plants were recorded deeper than 7 m and usually they were found at the depth range of 0.3 and 4.5 m. Similarly, the niche modelling indicated that there was a large overlap in niche space among all submerged plant species. Only *Z. marina* and *P. perfoliatus* inhabited somewhat opposing niche space. *P. perfoliatus* and *M. spicatum* had the narrowest niche space whereas *Z. palustris* had the broadest niche space (Fig. 3).

The BRT modelling described a significant proportion of variability in the cover of submerged aquatic vegetation and as expected the model performance varied among plant species. In general, the majority of the studied species are sensitive to changes in water temperature, current velocity and winter ice scour. Surprisingly, water salinity, turbidity and trophic state have a low impact on the biota. For the majority of submerged aquatic plant species, the distributional pattern is a function of a few environmental variables. Only *Z. palustris* and *R. maritima* are equally described by many environmental variables (Table 2).

Both local and seascape-scale environmental variability are important in the models of submerged aquatic plant species with local-scale variability, in general, exceeding that of 1 and 10 km scale variability. The contribution of 1 km scale variability is as important as local-scale variability in the models of *S. pectinata* and *Z. palustris* and that of 10 km scale in the model of *P. perfoliatus*, respectively (Table 3). In general there is no difference between the studied variables in how they contributed to the models along spatial scale. The only difference is due to their relative contribution.

When modelling species distribution under the projected influences of climate change, all of the studied submerged aquatic species seem to benefit from climate change with no indication of local extinction. Only the coverage of *Z. palustris* does not change in time (Figs. 4 and 5). Interestingly, this species has the lowest OMI index value i.e. broadest niche space.

All submerged plant species benefit from the warming climate. In general there is an abrupt increase in the vegetation cover over a certain threshold value and such a tipping point varied among species. Those species that have the highest temperature threshold value are mostly favoured by the future climate. If the temperature is too high, the coverage of *R. maritima* decreases again. *Z. palustris* have a narrow depth range whereas other species have either moderate to large depth range. Except for *S. pectinata* and *Z. marina*, all submerged plant species reduce their depth range under the
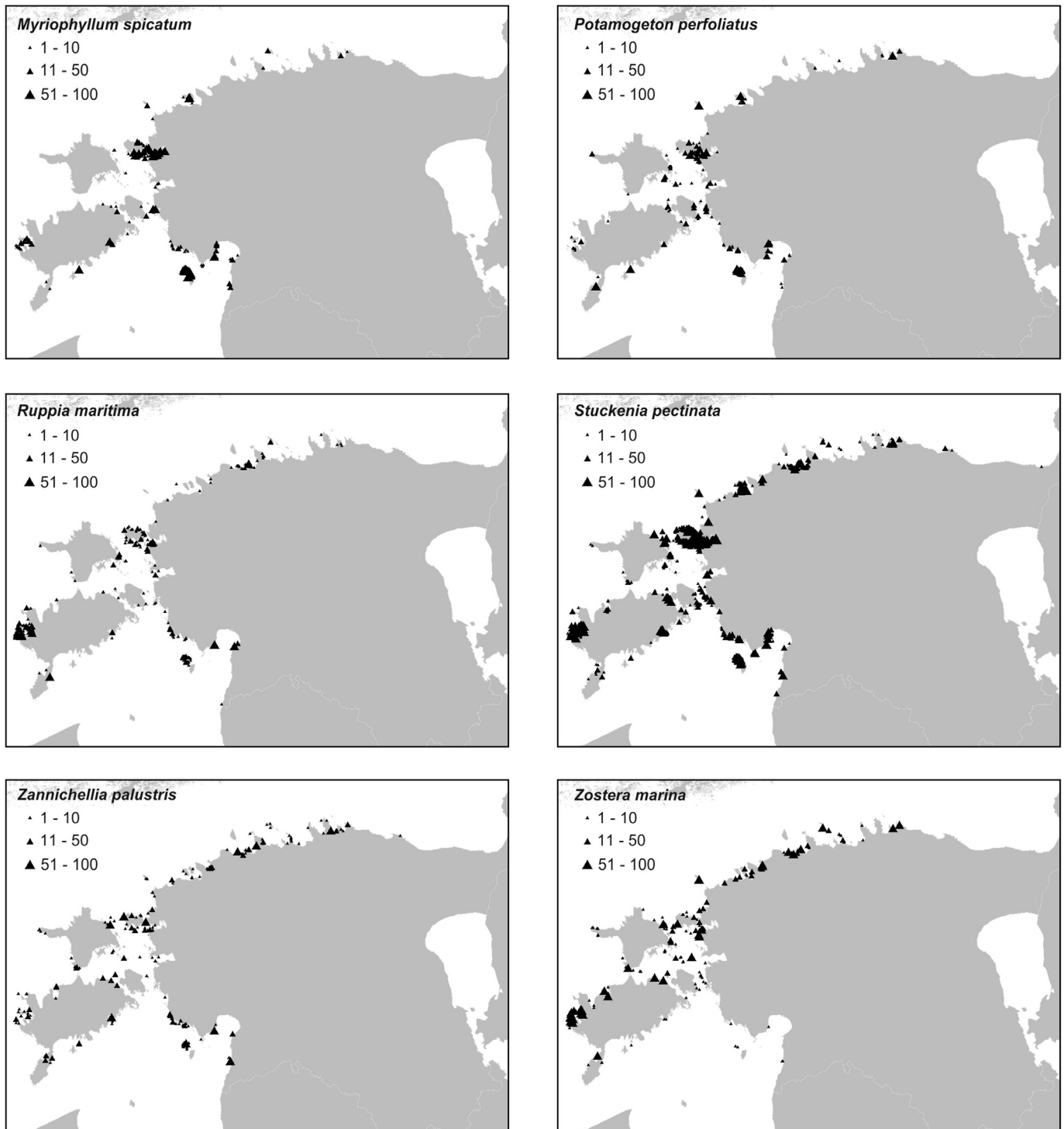
Fig. 2. The coverage of submerged aquatic plant species (%) in the study area.

projected influences of climate change. The majority of species are confined to areas where the wave-induced current velocity is the lowest. Only *M. spicatum* benefits from the elevated exposure to waves. *P. perfoliatus*, *M. spicatum* and *S. pectinata* reduce their cover and *Z. marina*, *R. maritima* and *Z. palustris* increase their cover under a reduced ice extent of the projected climate change (Fig. 6). To conclude, an overall increase in the cover of submerged aquatic vegetation under the projected influences of climate change is triggered both by a separate effect of seawater warming and an interactive effect of temperature and other environmental variables.

4. Discussion

Our study suggests that (1) local and seascape-scale environmental variability affect the cover patterns of submerged aquatic species with local variability exceeding seascape-scale variability, (2) physical disturbance such as seawater warming, elevated wave-
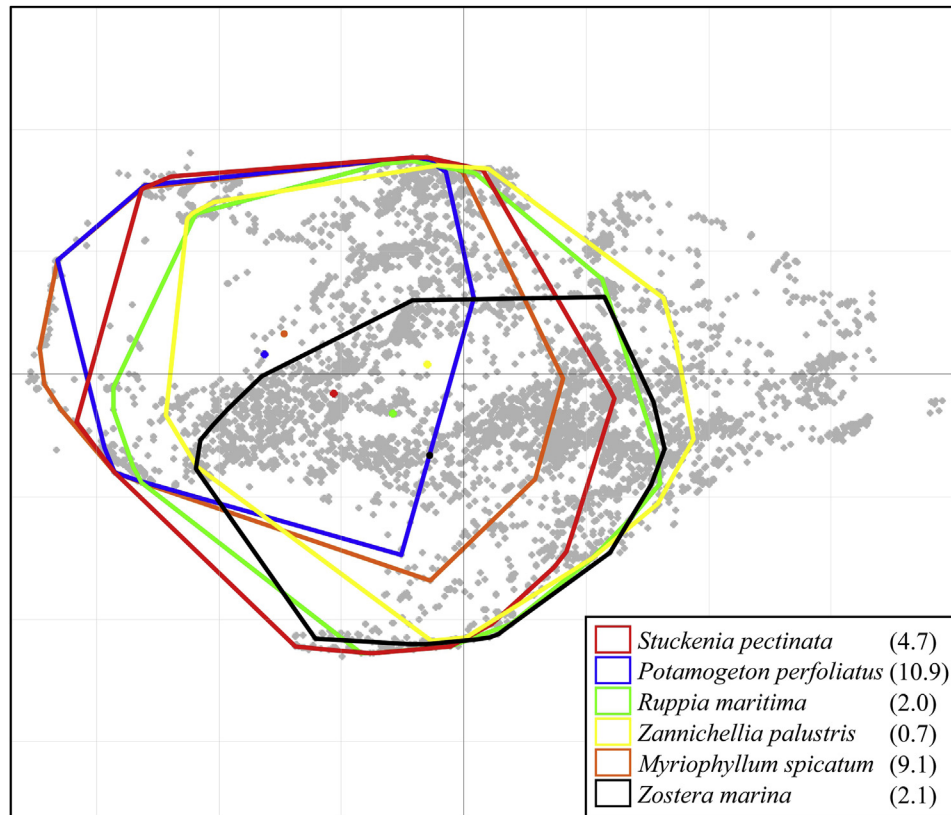
Fig. 3. Niche breadth analysis of the studied species. The borders of niche space and separation of habitat niche between the studied submerged aquatic species are shown by coloured lines. Coloured dots on the plot indicate the centres of niche space of the species. Grey dots represent sampling sites. The value of outlying mean index (OMI) is shown in brackets. OMI measures the distance between the mean habitat conditions used by species (niche centre), and the mean habitat conditions of the sampling area. The higher is the value of OMI index of a species, the higher is its habitat specialization. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

induced current velocity and reduced ice scour override the effects of salinity reduction, elevated turbidity and pelagic production and (3) finally, practically all of the studied submerged aquatic species benefit from the projected influences of climate change with no indication of local extinction.

These findings suggest that there is no key spatial factor affecting the distributional patterns of submerged plant species and that in fact, the species distributional patterns seemingly having scale invariance in the Baltic Sea (in sensu Halley, 1996; Gisiger, 2001). This is not in accordance with earlier observations from various marine areas and for different organisms. Often the variation of physical characteristics at larger spatial scales (e.g. from hundreds of metres to hundreds of kilometres) has been seen to have a significant effect on species abundance (Turner et al., 1999; Witman et al., 2004), whereas small-scale environmental variability explained only a little of the variation in species abundance, especially when considered independently of large-scale variability (e.g. Zajac et al., 2003). More recently, however, it has been shown that the submerged plant species interacted with the environment across multiple spatial scales. In results similar to our study, the response to environmental forcing varied among different macrophyte species and many species showed constant variability through a wide range of spatial scales (Kendrick et al., 2008).

It is likely that high variability in submerged plant species at small scales is related to the mosaic of sediment and bottom topography at this scale in the study area (Kotta et al., 2008a; 2008b). Firstly, the availability of soft substrate is a pre-requisite for the establishment of the species. Secondly, sediment

Table 2

The percentage of variance explained by the BRT species models. Environmental variables are as follows: T − average water temperature, Vel − average current velocity, D − sampling depth, Ice − average ice cover over the study site, Slope − inclination of coastal slope, Chl − average chlorophyll a content in water, K_d − average water attenuation coefficient, Sed − percentage cover of soft sediment fractions, Sal − average water salinity. Total variance of the BRT models explained by the models is given in bold.

Species	T	Vel	D	Ice	Slope	Chl	K_d	Sed	Sal	Total
Myriophyllum spicatum	27	30	6	13	7	7	0	7	3	**0.81**
Potamogeton perfoliatus	40	28	5	8	6	6	2	4	1	**0.75**
Ruppia maritima	27	16	12	11	6	13	10	2	3	**0.50**
Stuckenia pectinata	22	30	12	4	8	9	5	5	5	**0.83**
Zannichellia palustris	20	18	17	18	10	0	17	0	0	**0.64**
Zostera marina	32	16	12	4	16	4	6	5	5	**0.61**
Average	**28**	**23**	**11**	**10**	**9**	**7**	**7**	**4**	**3**	**0.69**

Table 3

The percentage of explained variance by the BRT species models by different spatial scales.

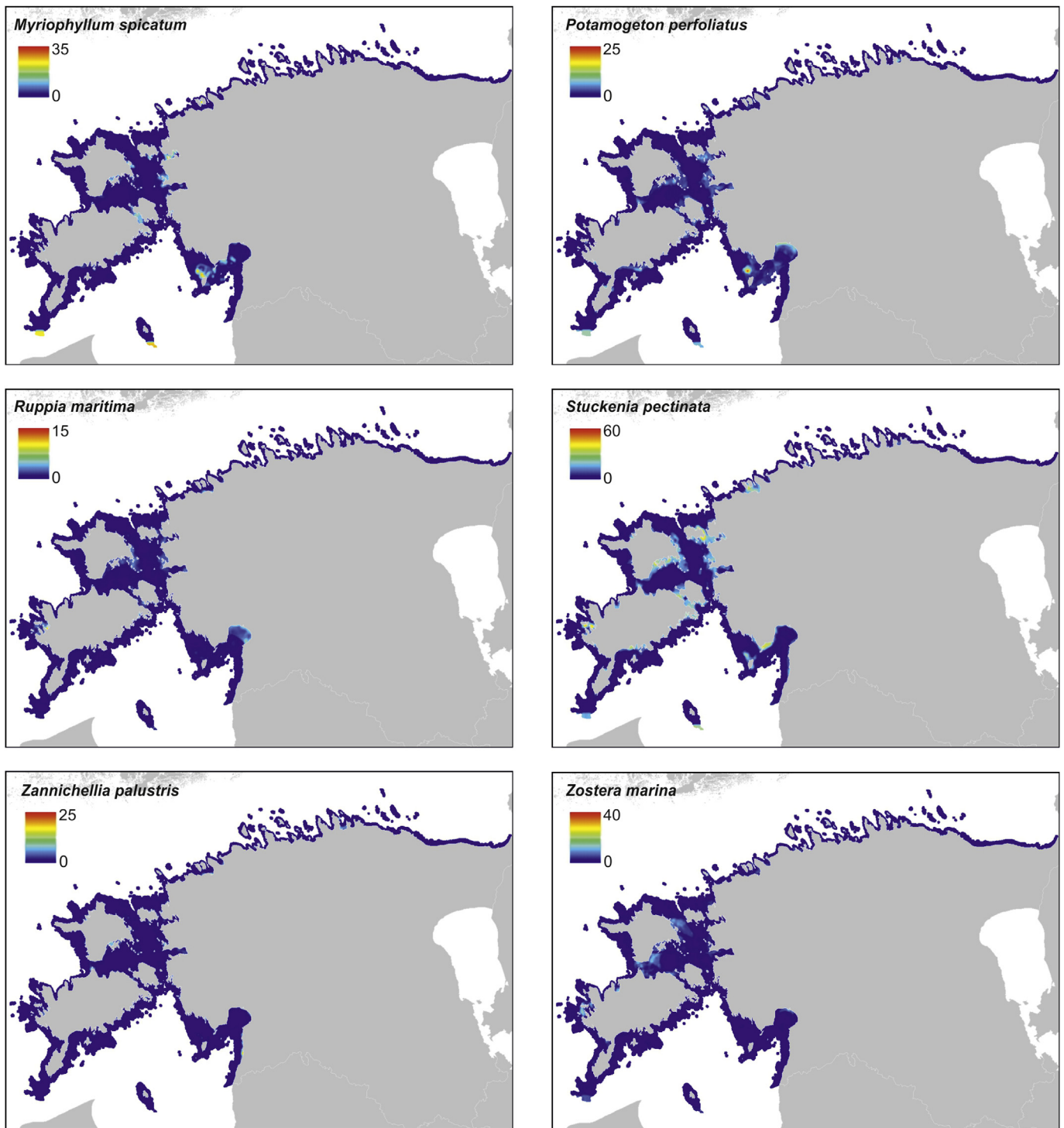| Species	Local	1 km	10 km
Myriophyllum spicatum	42	35	23
Potamogeton perfoliatus	38	22	40
Ruppia maritima	53	22	25
Stuckenia pectinata	40	36	24
Zannichellia palustris	38	38	24
Zostera marina	45	26	29
Average	43	30	28

Fig. 4. Modelled distribution of the submerged aquatic plant species for current climate conditions. For modelling the Boosted Regression Tree technique (BRT) was used. Colour diagram shows the species cover in percentage. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

modulates the flow above the seabed (e.g. Prasad et al., 2000; Håkanson and Eckhéll, 2005) and the intensity of flows is directly related to the cover pattern of the macrophytes (van Katwijk and Hermus, 2000; Madsen et al., 2001). In soft sediments, water flow also determines the light climate; i.e., large waves may cause considerable re-suspension of sediments and prolonged periods of poor light conditions (Madsen et al., 2001). Thirdly, small scale topographic heterogeneity may provide the

species refuges against physical disturbances including ice scouring and mechanical stress due to waves (Kautsky, 1988; Heine, 1989). For some submerged aquatic species the contribution of seascape-scale variability was as important as local-scale variability. Those species were characterised by lower sensitivity to the variability in substrate characteristics compared to others. For example, *Z. palustris* inhabits different types of soft bottoms but also hard substrates i.e. rock crevices. In such habitats, this species
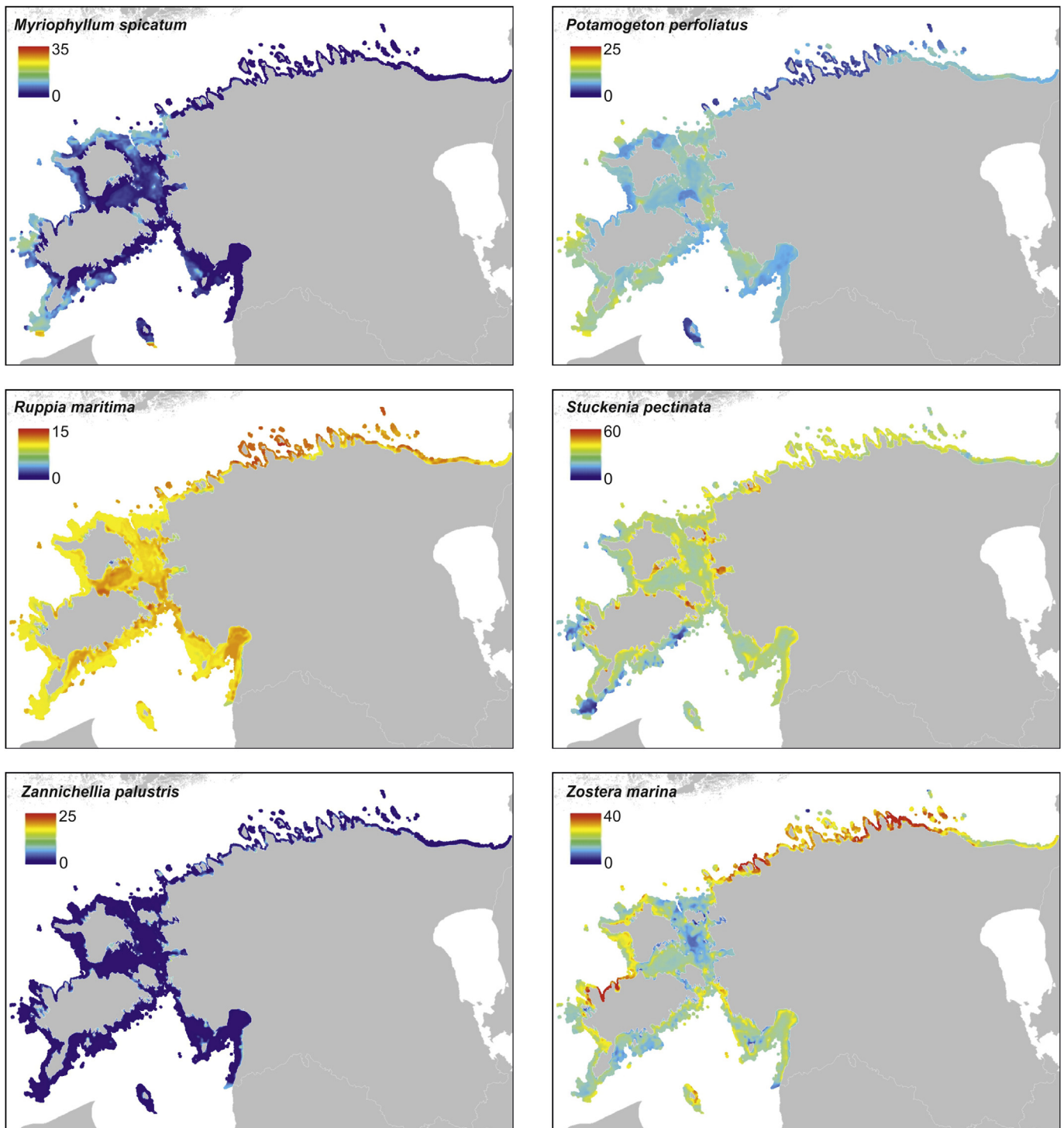
Fig. 5. Modelled distribution of the submerged aquatic plant species for projected future climate. The projected future scenario is described in the section "2.2. Predicted climate change." For modelling the Boosted Regression Tree technique (BRT) was used. Colour diagram shows the species cover in percentage. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

can actually grow outside of its "normal" environment i.e. at exposed conditions and far away from the coast. High variability in macrophyte communities at seascape-scales is related to broad patterns of seawater warming, exposure to waves and winter ice scour and an interaction of all these variables defines the suitability of seascape for the growth of submerged aquatic vegetation (Kautsky and van der Maarel, 1990).

One of the fundamental challenges facing ecologists is to understand how natural systems will respond to environmental conditions that have no analogue at present or in the recent past (Harley et al., 2006). There is always a risk of non-linearities that are specific to climatic conditions we have not yet experienced. Although such source of error is acknowledged, the study area covered a large gradient of water temperature, salinity, wave
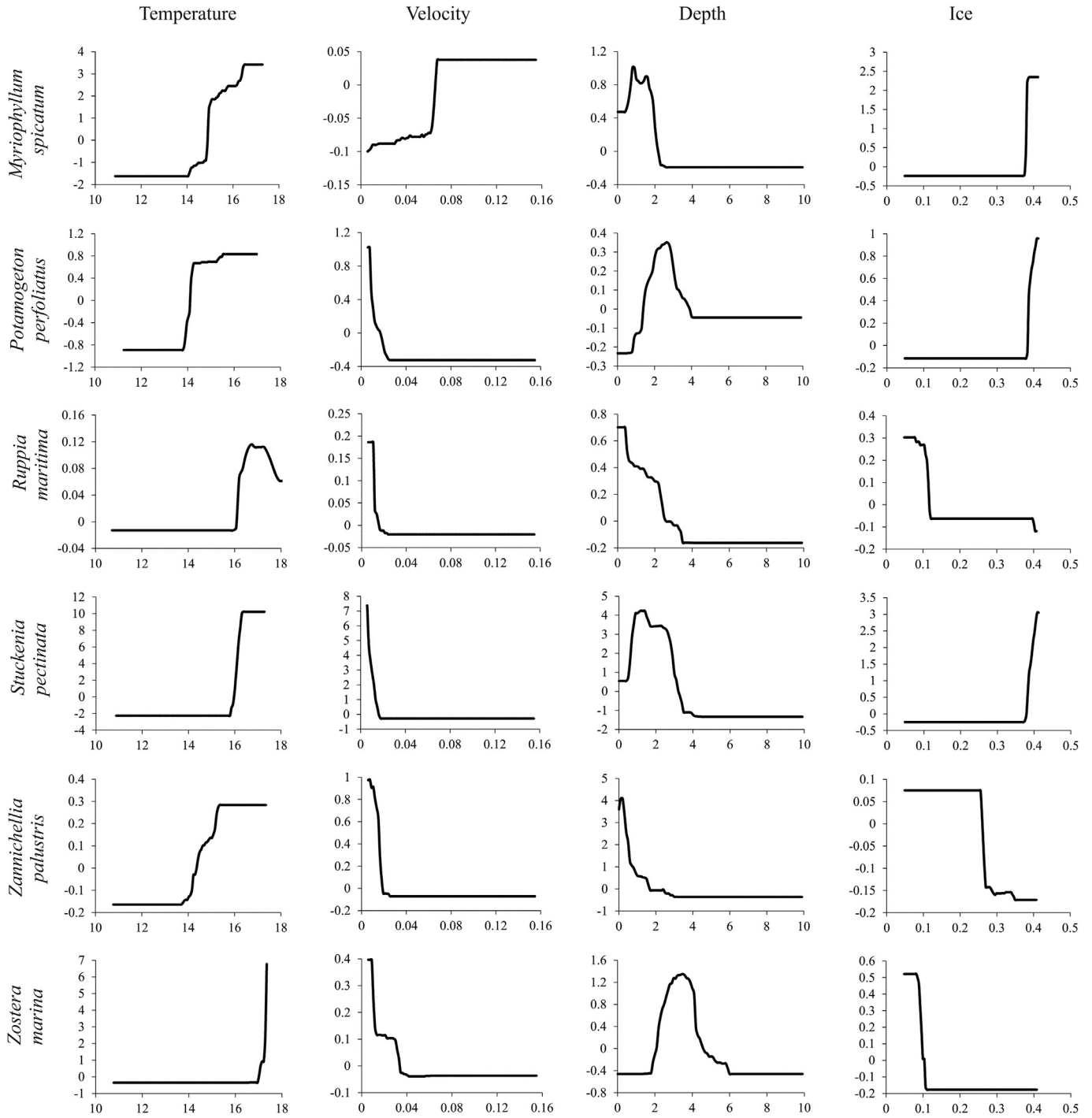
Fig. 6. "Partial dependence" plots of the Boosted Regression Tree technique modelling (BRT) showing the effect of environmental variables on the cover of submerged aquatic plant species whilst all other variables are held at their means.

exposure, etc. and the modelled ranges of environmental variability did not exceed those observed in the field.

The individualistic response of species to the environmental change was expected (e.g. Schiel, 2004; Bulleri et al., 2012) and this was confirmed by the BRT models (e.g. Fig. 6). The future climate would be also expected to be highly idiosyncratic and therefore shift in the patterns of submerged vegetation be species-specific. However, this was not the case as our future climate models showed a generic increase of the cover of submerged aquatic vegetation.

As expected, non-linearities between environment and biota result in situations where even gradual changes in future climate may provoke sudden and perhaps unpredictable biological responses as populations shift from one state to another. Moreover, the combined influence of several stressors might push population beyond a critical threshold that would not be reached via variation in any forcing variable operating in isolation (e.g. Hoffman et al., 2003).

This study shows that the species that has the broadest niche space is insensitive to the projected influences of climate change.

However, moderate to high selectivity to environmental conditions does not couple with the species sensitivity to climate change. It is expected that species with a broad environmental tolerance can cope with different stresses including those subjected by the future climate. The lack of differences in responses to the future climate among medium to highly selective species may be attributed to the species-specific reaction of environmental change (e.g. Schiel, 2004; Bulleri et al., 2012). Specifically, S. pectinata and Z. marina have the strongest responses to the projected influences of climate change. Both species have relatively broad depth range and this attribute may facilitate the species to persist under impoverished light conditions induced by the future climate. In fact, although the distribution maps of the submerged aquatic vegetation show that the majority of species benefit from the future climate, all species except for S. pectinata and Z. marina also retract from the deepest parts of their distributional range. Those species that can naturally inhabit broad depth ranges i.e. different light conditions, are insensitive to the impoverished light conditions and thereby are disproportionally favoured by a reduction of ice scour and an increment of temperature and nutrient availability as compared those species acclimated to the narrower ranges of light conditions and/or depth ranges. As an extreme, Z. palustris has a very narrow depth range inhabiting only at the shallowmost study areas. Concurrent with the declined transparency of the future climate, the species cannot possibly migrate into shallower areas and benefit from e.g. reduced ice disturbance and prolonged vegetative season.

This study suggests that elevated coverages of submerged vegetation associated to the future climate are largely triggered by elevated temperatures. A primary effect of increased global temperature on seagrasses but likely other submerged vegetation is related to the alteration of growth rates of the plants themselves (Short and Neckles, 1999). In general net photosynthesis of macrophytes increases with temperature up to an optimum value and then decreases dramatically. For seagrasses the rate of leaf respiration increases more rapidly with rising temperature than does that of photosynthesis, leading to both a steady decrease in the photosynthesis-to-respiration ratio with increasing temperature. A sharp decline of gross photosynthesis, however, is reached beyond $30\,°C$ (Marsh et al., 1986). Obviously, the Baltic Sea is far too cold an environment characterised by a short vegetation season. Any elevated temperatures of the projected influences of climate change only prolong the vegetation season i.e. increase growth of the submerged aquatic vegetation and shoot to root ratio (Zimmerman et al., 1989) with no adverse effects on their carbon balances.

Water motion is known to affect the plant structure of submerged aquatic vegetation (Fonseca et al., 1983; Worcester, 1995) with elevating current velocity increasing leaf biomass, width, and canopy height (Fonseca and Kenworthy, 1987; Short, 1987). However, our study shows opposite results with only the cover of M. spicatum being facilitated by increased current velocities. This pattern may be due to specific light conditions in our study area. Specifically, clayey bottom deposits prevail in deeper parts of the study area and wind speeds higher than $5\,m\,s^{-1}$ already result in considerable resuspension of these sediments and, thus, the reduction of water transparency in the coastal water. M. spicatum, however, can thrive in nutrient rich turbid habitats where other submerged aquatic plant species are missing due to poor light conditions (Menéndez and Comin, 1989; Eriksson et al., 2004; Gustafsson, 2013). In addition, M. spicatum is also very resistant to different mechanical disturbances e.g. a clipping experiment by Cohen et al. (1986) demonstrated that M. spicatum regenerated from below the damaged point, while other submerged plant species regenerated from the roots. Finally, M. spicatum can remain photosynthetically active through winter opposing to other

submerged aquatic vegetation (Aiken and Walz, 1979). This wintertime growth allows the species to outcompete other submerged algal species especially in exposed areas where light conditions due to the lack of ice cover is relatively good all year round. On the other hand, there is also evidence that the resource allocation of some submerged plant species such as S. pectinata is strongly influenced by wave exposure. At sheltered areas more resources are allocated to vegetative shoots and rhizomes whereas at exposed sites more resources are allocated to reproduction (Kautsky, 1987).

Submerged aquatic vegetation is affected by changing salinity values by water and nutrient imbalance resulting from large difference in osmotic potentials between internal and external environments (Gorham et al., 1985). Salinity resistance is related to diverse physiological adaptations (Flowers et al., 1977; Greenway and Munns, 1980). Although seagrass photosynthesis is maintained at low salinities, a large reduction in productivity has been measured for various species at reduced salinities (Pinnerup, 1980; Kerr and Strother, 1985; Dawes et al., 1987). The submerged aquatic vegetation of fresh water origin are expected to increase their photosynthetic performance and hence their growth together with reduction in salinity (Riddin and Adams, 2010). Within a range of the projected influences of climate change, salinity seemed to have only a minor effect on the distributional patterns of submerged aquatic plant species. Plausibly, the submerged aquatic vegetation inhabiting the Baltic Sea range are adapted to a broad range of salinity variation and a 25% reduction of salinity values did not overweigh the gains resulted from elevated seawater temperature, prolonged vegetative season and reduced winter time ice scour. Other authors have also demonstrated a marginal role of salinity in the models of benthic vegetation compared to its potential role for species distributions in the brackish Baltic Sea (Rosqvist et al., 2010).

The models in this study demonstrate that different submerged aquatic species respond differently to changing winter ice cover. Winter ice scouring periodically destroys submerged aquatic vegetation. During harsh winters, prevailing fast growing species such as M. spicatum, P. perfoliatus and S. pectinata are favoured as those species can gain a large size and/or high biomass within a short vegetative season. Moreover, harsh winters seemingly bury the seeds of submerged vegetation deep in sediment and thereby dramatically reduces the species germination percentage, especially those of slow growing species (Xiao et al., 2010). The reduction of ice cover, in turn, favours slow growing species. The slow growing species are often the late successional species i.e. being once established they keep fast growing species away from the community.

The current study also suggests that those species that are weakly related to the multitude of environmental variables have a broad distributional range. For example, among the studied species R. maritima is the most widely distributed seagrass, occurring in tropical and temperate zones in a wide variety of habitats (Short et al., 2007). Weak responses of R. maritima to a range of environment variables may be related to the opportunistic character of the species. Specifically, it has been demonstrated that the response of submerged aquatic vegetation to the environmental perturbation is often a function of organism size (Kotta et al., 2013). For example, the large Mediterranean seagrass species Posidonia oceanica requires centuries for recolonization due to slow rhizome elongation rates and rare sexual reproduction (Duarte, 1995; Meehan and West, 2000). On the other hand, small, fast-growing seagrass species such as R. maritima recover within just one or a few years (Duarte, 1995). Moreover, submerged aquatic vegetation is known to modify their local abiotic environment by trapping and stabilizing suspended sediments and thereby improving water clarity and plant growth conditions (van

der Heide et al., 2011). This effect is expected to increase with the size of plants. Thus, the distribution of large submerged species is expected to be less coupled with their adjacent abiotic environment compared to their smaller counterparts and, their cover is therefore a function of a colonization history that spans decades to centuries (Kendrick et al., 2000).

The observed results are study area specific and possibly cannot be extrapolated to other seas. This is because different seas (e.g. Baltic Sea and the Atlantic coast) differ greatly with respect to salinity and wave exposure, and that the range of the studied environmental variables defines how those factors influence the distribution of a species. This is also because the habitat selection of seagrasses are known to vary among water bodies e.g. *Z. marina* having different habitat requirements in the Atlantic coasts and the Baltic Sea (Boström et al., 2003; Bekkby et al., 2008). The mechanisms behind the niche differentiation among brackish and marine seagrass populations stem from differences in both interspecific competition and genetic background. Although our study did not account for genetic adaptation, this likely does not affect our main conclusions. Specifically, many seagrass and other submerged plant populations are highly clonal, largely relying on asexual reproduction for population maintenance (Rasheed, 1999; Waycott et al., 2006). In the Baltic Sea submerged aquatic vegetation has very small genetic variability, often consisting of one or a few clones only (Reusch et al., 1999). Therefore, they are expected to be highly sensitive to extrinsic stressors and potentially have very low genetic adaptation potential (Lasker and Coffroth, 1999; Santamaría, 2002). Nevertheless, considering of a large variability in salinity, ice cover and eutrophication in the Baltic Sea range in last thousands of years these genotypes are characterised by wide reaction norms enabling the persistence of species under highly fluctuating environmental conditions. This is also supported by our study suggesting a strong resistance of vegetation to a dramatic change in the environment.

Besides genetic variability, our study did not account for the elevated growth of ephemeral epiphytic macroalgae stimulated by increased temperature under the projected climate change scenario (Lotze et al., 1999; Taylor et al., 2001). Nevertheless, the Baltic Sea is one of the most eutrophicated water basins in the world and the blooms of filamentous algae and the formation of the drifting macroalgal mats have not shown to have a dramatic consequence on the submerged aquatic vegetation including seagrasses (Lauringson and Kotta, 2006; Lyons et al., in press). However, such blooms likely reduce light availability and consequently lead to a reduced depth penetration and abundance of submerged vegetation (Duarte, 1991). The consequences of such interspecific interaction are expected to be much weaker compared to the facilitative effects of seawater warming. The most dramatic macroalgal blooms are developing during the summer months. Since then, however, the submerged aquatic vegetation has gained their maximum size and the algal blooms just reduce the photosynthetic performance of the host plant.

5. Conclusions

Our study did not confirm the hypothesis that large scale abiotic processes define broad patterns of distribution and are the most significant factors in community variability. Instead, small and large-scale environmental variability both interactively contribute to the variability in the cover of submerged aquatic vegetation. Physical disturbance such as seawater warming, elevated wave-induced current velocity and reduced ice scour override the effects of salinity reduction, elevated turbidity and pelagic production.

All predictions of future climate are far from certain and opposite changes in the abiotic environment might also occur under other climate change scenarios. Nevertheless, our modelling study showed that the submerged aquatic vegetation is very resilient to a broad range of environmental perturbation and biomass gains are expected when seawater temperature increases (e.g. Asaeda et al., 2001). This is mainly because vegetation develops faster in spring and has a longer growing season under the projected climate change scenario.

Although it is impossible to halt global warming within the coming years, a modelling of the cover of submerged aquatic species under the future climate is essential in order to help managers to establish marine protected areas that can resist the projected influences of climate change and thereby minimizing the risk of population collapses.

References

Aiken, S.G., Walz, K.F., 1979. Turions of *Myriophyllum exalbescens*. Aquat. Bot. 6, 357–363.

Appelgren, K., Mattila, J., 2005. Variation in vegetation communities in shallow bays of the northern Baltic Sea. Aquat. Bot. 83, 1–13.

Asaeda, T., Trung, V.K., Manatunge, J., Bon, T.V., 2001. Modelling macrophytes-nutrient-phytoplankton interactions in shallow eutrophic lakes and the evaluation of environmental impacts. Ecol. Eng. 16, 341–357.

BACC, 2008. Assessment of Climate Change for the Baltic Sea Basin. In: Regional Climate Studies, vol. 22. Springer, 474 pp.

Bekkby, T., Rinde, E., Erikstad, L., Bakkestuen, V., Longva, O., Christensen, O., Isaeus, M., Isachsen, P.E., 2008. Spatial probability modeling of eelgrass *Zostera marina* L. distribution on the west coast of Norway. ICES J. Mar. Sci. 65, 1093–1101.

Bendtsen, J., Gustafsson, K.E., Söderkvist, J., Hansen, J.L.S., 2009. Ventilation of bottom water in the North Sea–Baltic Sea transition zone. J. Mar. Syst. 75, 138–149.

Boström, C., Baden, S.P., Krause-Jensen, D., 2003. The seagrasses of Scandinavia and the Baltic Sea. In: Green, P., Short, F.T. (Eds.), The World Atlas of Seagrasses. University of California Press, Berkeley, USA, pp. 27–37.

Bulleri, F., Benedetti-Cecchi, L., Cusson, M., Maggi, E., Arenas, F., Aspden, R., Bertocci, I., Crowe, T.P., Davoult, D., Eriksson, B.K., Fraschetti, S., Golléty, C., Griffin, J.N., Jenkins, S.R., Kotta, J., Kraufvelin, P., Molis, M., Sousa Pinto, I., Terlizzi, A., Valdivia, N., Paterson, D.M., 2012. Temporal stability of European rocky shore assemblages: variation across a latitudinal gradient and the role of habitat-formers. Oikos 121, 1801–1809.

Burkholder, J.M., Tomasko, D.A., Touchette, B.W., 2007. Seagrasses and eutrophication. J. Exp. Mar. Biol. Ecol. 350, 46–72.

Byrne, M., Przeslawski, R., 2013. Multistressor impacts of warming and acidification of the ocean on marine invertebrates' life histories. Integr. Comp. Biol. 53, 582–596.

Chambers, P.A., Prepas, E.E., Hamilton, H.R., Bothwell, M.L., 1991. Current velocity and its effect on aquatic macrophytes in flowing waters. Ecol. Appl. 1, 249–257.

Cohen, Y., Moen, R., Schecterly, M., 1986. Interspecific interactions between *Potamogeton pectinatus* and *Myriophyllum exalbescens* in the face of grazing in a simulated ecosystem. In: Freshwater Wetlands and Wildlife: Perspectives on Natural, Managed and Degraded Ecosystems. Ninth Symposium, 24–27 March 1986. University of Georgia, Savanah River Ecological Laboratory 169.

Costanza, R., d'Arge, R., Groots, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, R.V., Paruelo, J., Raskin, R.G., Sutton, P., van den Belt, M., 1997. The value of the worlds ecosystem services and natural capital. Nature 387, 253–260.

Crain, C.M., Kroeker, K., Halpern, B.S., 2008. Interactive and cumulative effects of multiple human stressors in marine systems. Ecol. Lett. 11, 1304–1315.

Dawes, C., Chan, M., Chinn, R., Koch, E.W., Lazar, A., Tomasko, D., 1987. Proximate composition, photosynthetic and respiratory responses of the seagrass *Halophila engelmanni* from Florida. Aquat. Bot. 27, 195–201.

De Boer, W.F., 2007. Seagrass-sediment interactions, positive feedbacks and critical thresholds for occurrence: a review. Hydrobiologia 591, 5–24.

Dolédec, S., Chessel, D., Gimaret-Carpentier, C., 2000. Niche separation in community analysis: a new method. Ecology 81, 2914–2927.

Dray, S., Dufour, A.B., 2007. The ade4 package: implementing the duality diagram for ecologists. J. Stat. Softw. 22, 1–20.

Duarte, C.M., 1991. Seagrass depth limits. Aquat. Bot. 40, 363–377.

Duarte, C.M., 1995. Submerged aquatic vegetation in relation to different nutrient regimes. Ophelia 41, 87–112.

Duarte, C.M., 2002. The future of seagrass meadows. Environ. Conserv. 29, 192–206.

Elith, J., Leathwick, J.R., Hastie, T., 2008. A working guide to boosted regression trees. J. Anim. Ecol. 77, 802–813.

Eriksson, B.K., Sandström, A., Isæus, M., Schreiber, H., Karås, P., 2004. Effects of boating activities on aquatic vegetation in the Stockholm archipelago, Baltic Sea. Estuar. Coast. Shelf Sci. 61, 339–349.

ESRI, 2011. ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA.

Flowers, T.J., Troke, P.F., Yeo, A.R., 1977. The mechanism of salt tolerance in halophytes. Annu. Rev. Plant Physiol. 28, 89–121.

Fonseca, M.S., Bell, S.S., 1998. Influence of physical setting on seagrass landscapes near Beaufort, North Carolina. Mar. Ecol. Prog. Ser. 171, 109–121.

Fonseca, M.S., Kenworthy, W.J., 1987. Effects of current on photosynthesis and distribution of seagrass. Aquat. Bot. 27, 59–78.

Fonseca, M.S., Kenworthy, W.J., Whitfield, P.E., 2000. Temporal dynamics of seagrass landscapes: a preliminary comparison of chronic and extreme disturbance events. In: Pergent, G., Pergent-Martini, C., Buia, M.C., Gambi, M.C. (Eds.), Proceedings of the Fourth International Seagrass Biology Workshop. September 25–October 2, 2000, Corsica, France. Biologia Marina Mediterranea, Instituto di Zoologia, Genova, Italy, pp. 373–376.

Fonseca, M.S., Zieman, J.C., Thayer, G.W., Fisher, J.S., 1983. The role of current velocity in structuring eelgrass *Zostera marina* meadows. Estuar. Coast. Shelf Sci. 17, 367–380.

Gisiger, T., 2001. Scale invariance in biology: coincidence or footprint of a universal mechanism? Biol. Rev. 76, 161–209.

Glemarec, M., LeFaou, Y., Cuq, F., 1997. Long-term changes of seagrass beds in the Glenan Archipelago (South Brittany). Oceanol. Acta 20, 217–227.

Gorham, J., Wyn Jones, R.G., McDonnell, E., 1985. Some mechanisms of salt tolerance in crop plants. Plant Soil. 89, 15–40.

Greenway, H., Munns, R., 1980. Mechanisms of salt tolerance in nonhalophytes. Annu. Rev. Plant Physiol. 31, 149–190.

Gustafsson, C., 2013. Biodiversity and Ecosystem Functioning in Angiosperm Communities in the Baltic Sea (PhD thesis). Åbo Akademi University, Department of Biosciences, Environmental and Marine Biology, Åbo, Finland, 59 pp.

Håkanson, L., Eckhéll, J., 2005. Suspended particulate matter (SPM) in the Baltic Sea – new empirical data and models. Ecol. Model. 189, 130–150.

Halley, J.M., 1996. Ecology, evolution and 1/f-noise. Trends Ecol. Evol. 11, 33–37.

Hällfors, G., Niemi, Å., Ackefors, H., Lassig, J., Leppäkoski, E., 1981. Biological oceanography (chapter 5). In: Voipio, A. (Ed.), The Baltic Sea, Elsevier Oceanography Series, vol. 30, pp. 219–274. Amsterdam, The Netherlands.

Harley, C.D.G., Hughes, A.R., Hultgren, K.M., Miner, B.G., Sorte, C.J., Thornber, C.S., Rodriguez, L.F., Tomanek, L., Williams, S.L., 2006. The impacts of climate change in coastal marine systems. Ecol. Lett. 9, 228–241.

Hastie, T., Tibshirani, R., Friedman, J., 2009. The Elements of Statistical Learning: Data Mining, Inference, and Prediction. Springer-Verlag, New York, 744 pp.

Hawkins, S.J., Firth, L.B., McHugh, M., Poloczanska, E.S., Herbert, R.J.H., Burrows, M.T., Kendall, M.A., Moore, P.J., Thompson, R.C., Jenkins, S.R., Sims, D.W., Genner, M.J., Mieszkowska, N., 2013. Data rescue and re-use: recycling old information to address new policy concerns. Mar. Policy 42, 91–98.

Heine, J.N., 1989. Effects of ice scour on the structure of sublittoral marine algal assemblages of St. Lawrence and St. Matthew Islands, Alaska. Mar. Ecol. Prog. Ser. 52, 253–260.

Heino, J., Virkkala, R., Toivonen, H., 2009. Climate change and freshwater biodiversity: detected patterns, future trends and adaptations in northern regions. Biol. Rev. Camb. Philos. Soc. 84, 39–54.

Hemminga, M.A., Duarte, C.M., 2000. Seagrass Ecology. Cambridge University Press, Cambridge, UK; New York, NY, USA, 198.

Hense, I., Meier, H.E.M., Sonntag, S., 2013. Projected climate change impact on Baltic Sea cyanobacteria. Climate change impact on cyanobacteria. Clim. Change 119, 391–406.

Herkül, K., Kotta, J., Kutser, T., Vahtmäe, E., 2013. Relating remotely sensed optical variability to marine benthic biodiversity. PLoS One 8 (2), e55624.

Hoffman, J.R., Hansen, L.J., Klinger, T., 2003. Interactions between UV radiation and temperature limit inferences from single-factor experiments. J. Phycol. 39, 268–272.

Holmer, M., Wirachwong, P., Thomsen, M.S., 2011. Negative effects of stress-resistant drift algae and high temperature on a small ephemeral seagrass species. Mar. Biol. 158, 297–309.

International Panel on Climate Change (IPCC), 2013. Climate Change 2013: the Physical Science Basis. Cambridge University Press, Cambridge, UK.

Kautsky, H., van der Maarel, E., 1990. Multivariate approaches to the variation in phytobenthic communities and environmental vectors in the Baltic Sea. Mar. Ecol. Prog. Ser. 60, 169–184.

Kautsky, L., 1988. Life strategies of aquatic soft bottom macrophytes. Oikos 53, 126–135.

Kendrick, G.A., Hegge, B.J., Wyllie, A., Davidson, A., Lord, D.A., 2000. Changes in seagrass cover on Success and Parmelia Banks, Western Australia between 1965 and 1995. Estuar. Coast. Shelf Sci. 50, 341–353.

Kendrick, G.A., Holmes, K.W., van Niel, K.P., 2008. Multi-scale patterns of three seagrass species with different growth dynamics. Ecography 31, 191–200.

Kerr, E.A., Strother, S., 1985. Effects of irradiance, temperature and salinity on photosynthesis of *Zostera muelleri*. Aquat. Bot. 23, 177–183.

Koch, M., Bowes, G., Ross, C., Zhang, X.-H., 2013. Climate change and ocean acidification effects on seagrasses and marine macroalgae. Glob. Change Biol. 19, 103–132.

Kotta, J., Jaanus, A., Kotta, I., 2008a. Haapsalu and Matsalu Bays. In: Schiewer, U. (Ed.), Ecology of Baltic Coastal Waters, Ecological Studies, vol. 197. Springer, pp. 245–258.

Kotta, J., Kutser, T., Teeveer, K., Vahtmäe, E., Pärnoja, M., 2013. Predicting species cover of marine macrophyte and invertebrate species combining hyperspectral remote sensing, machine learning and regression techniques. PLoS One 8 (6), e63964.

Kotta, J., Lauringson, V., Martin, G., Simm, M., Kotta, I., Herkül, K., Ojaveer, H., 2008b. Gulf of Riga and Pärnu Bay. In: Schiewer, U. (Ed.), Ecology of Baltic Coastal Waters, Ecological Studies, vol. 97. Springer, pp. 217–243.

Krause-Jensen, D., Pedersen, M.F., Jensen, C., 2003. Regulation of eelgrass (*Zostera marina*) cover along depth gradients in Danish coastal waters. Estuaries 26, 866–877.

Krause-Jensen, D., Sagert, S., Schubert, H., Boström, C., 2008. Empirical relationships linking distribution and abundance of marine vegetation to eutrophication. Ecol. Indic. 8, 515–529.

Larkum, A.W.D., Orth, R.J., Duarte, C.M., 2006. Seagrasses: Biology, Ecology, and Conservation. Springer.

Lasker, H.R., Coffroth, M.A., 1999. Responses of clonal reef taxa to environmental change. Am. Zool. 39, 92–103.

Lauringson, V., Kotta, J., 2006. Influence of the thin drift algal mats on the distribution of macrozoobenthos in Kõiguste Bay, NE Baltic Sea. Hydrobiologia 554, 97–105.

Lotze, H.K., Schramm, W., Schories, D., Worm, B., 1999. Control of macroalgal blooms at early developmental stages: *Pilayella littoralis* versus *Enteromorpha* spp. Oecologia 119, 46–54.

Lyons, D.A., Arvanitidis, C., Blight, A.J., Chatzinikolaou, E., Guy-Haim, T., Kotta, J., Orav-Kotta, H., Queirós, A.M., Rilov, G., Somerfield, P.J., Crowe, T.P., 2014. Effects of macroalgal blooms on marine biodiversity and ecosystem functioning: a global meta-analysis. Glob. Change Biol. in press.

Madsen, J.D., Chambers, P.A., James, W.F., Koch, E.W., Westlake, D.F., 2001. The interaction between water movement, sediment dynamics and submersed macrophytes. Hydrobiologia 444, 71–84.

Marsh Jr., J.A., Dennison, W.C., Alberte, R.S., 1986. Effects of temperature on photosynthesis and respiration in eelgrass (*Zostera marina* L.). J. Exp. Mar. Biol. Ecol. 101, 257–267.

Meehan, A.J., West, R.J., 2000. Recovery times for a damaged *Posidonia australis* bed in South Eastern Australia. Aquat. Bot. 67, 161–167.

Menéndez, M., Comin, F.A., 1989. Seasonal patterns of biomass variation of *Ruppia cirrhosa* (Petagna) Grande and *Potamogelon pectinatus* L. in a coastal lagoon. Sci. Mar. 53, 633–638.

Müller, R., Laepple, T., Bartsch, I., Wiencke, C., 2009. Impact of oceanic warming on the distribution of seaweeds in polar and cold-temperate waters. Bot. Mar. 52, 617–638.

Nielsen, S.L., Sand-Jensen, K., Borum, J., Geertz-Hansen, O., 2002. Depth colonization of eelgrass (*Zostera marina*) and macroalgae as determined by water transparency in Danish coastal waters. Estuaries 25, 1025–1032.

Orth, R.J., 1977. Effect of nutrient enrichment on growth of the seagrass *Zostera marina* in the Chesapeake Bay, Virginia, USA. Mar. Biol. 44, 187–194.

Orth, R., Carruthers, T.J.B., Dennison, W.C., Duarte, C.M., Fourqurean, J.W., Heck, J.K.L., Hughes, A.R., Kendrick, G., Kenworthy, W.J., Olyarnik, S., Short, F.T., Waycott, M., Williams, S.L., 2006. A global crisis for seagrass ecosystems. BioScience 56, 987–996.

Peralta, G., Perez-Llorens, J.L., Hernandez, I., Vergara, J.J., 2002. Effects of light availability on growth, architecture and nutrient content of the seagrass *Zostera noltii* Hornem. J. Exp. Mar. Biol. Ecol. 269, 9–26.

Pinnerup, S.P., 1980. Leaf production of Zostera marina L. at different salinities. Ophelia 1, 219–224.

Prasad, S.N., Pal, D., Römkens, M.J.M., 2000. Wave formation on a shallow layer of flowing grains. J. Fluid Mech. 413, 89–110.

Rasheed, A.M., 1999. Recovery of experimentally created gaps within a tropical *Zostera capricorni* (Aschers.) seagrass meadow, Queensland, Australia. J. Exp. Mar. Biol. Ecol. 235, 183–200.

RDC Team, 2013. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available. http://www.R-project.org/ (accessed 20.07.13.).

Reusch, T.B.H., Boström, C., Stam, W.T., Olsen, J.L., 1999. An ancient eelgrass clone in the Baltic Sea. Mar. Ecol. Prog. Ser. 183, 301–304.

Reusch, T.B.H., Ehlers, A., Hämmerli, A., Worm, B., 2005. Ecosystem recovery after climatic extremes enhanced by genotypic diversity. Proc. Natl. Acad. Sci. U. S. A. 102, 2826–2831.

Reynaud, S., Leclercq, N., Romaine-Lioud, S., Ferrier-Pagès, C., Jaubert, J., Gattuso, J.-P., 2003. Interacting effects of CO_2 partial pressure and temperature on

photosynthesis and calcification in a scleractinian coral. Glob. Change Biol. 9, 1660–1668.

Riddin, T., Adams, J.B., 2010. The effect of a storm surge event on the macrophytes of a temporarily open/closed estuary, South Africa. Estuar. Coast. Shelf Sci. 89, 119–123.

Robertson, A.I., Mann, K.H., 1984. Disturbance of ice and life-history adaptations of the seagrass *Zostera marina*. Mar. Biol. 80, 131–141.

Rosqvist, K., Mattila, J., Sandstrom, A., Snickars, M., Westerbom, M., 2010. Regime shifts in vegetation composition of Baltic Sea coastal lagoons. Aquat. Bot. 93, 39–46.

Santamaría, L., 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. Acta Oecol. 23, 137–154.

Schanz, A., Asmus, H., 2003. Impact of hydrodynamics on development and morphology of intertidal seagrasses in the Wadden Sea. Mar. Ecol. Prog. Ser. 261, 123–134.

Schiel, D.R., 2004. The structure and replenishment of rocky shore intertidal communities and biogeographic comparisons. J. Exp. Mar. Biol. Ecol. 300, 309–342.

Schneider, F.I., Mann, K.H., 1991. Rapid recovery of fauna following simulated ice rafting in a Nova Scotian seagrass bed. Mar. Ecol. Prog. Ser. 78, 57–70.

Short, F.T., 1987. Effects of sediment nutrients on seagrasses: literature review and mesocosm experiment. Aquat. Bot. 27, 41–57.

Short, F., Carruthers, T., Dennison, W., Waycott, M., 2007. Global seagrass distribution and diversity: a bioregional model. J. Exp. Mar. Biol. Ecol. 350, 3–20.

Short, F.T., Neckles, A.H., 1999. The effects of global climate change on seagrasses. Aquat. Bot. 63, 169–196.

Short, F.T., Polidoro, B., Livingstone, S.R., Carpenter, K.E., Bandeira, S., Bujang, J.S., Calumpong, H.P., Carruthers, T.J.B., Coles, R.G., Dennison, W.C., Erftemeijer, P.L.A., Fortes, M.D., Freemen, A.S., Jagtap, T.G., Kamal, A.H.M., Kendrick, G.A., Kenworthy, W.J., Nafie, Y.A.L., Nasution, I.M., Orth, R.J., Prathep, A., Sanciangco, J.C., van Tussenbroek, B., Vegara, S.G., Waycott, M., Zieman, J.C., 2011. Extinction risk assessment of the world's seagrass species. Biol. Conserv. 144, 1961–1971.

Snoeijs, P., 1999. Marine and brackish waters. In: Snoeijs, P., Diekmann, M. (Eds.), Swedish Plant Geography, Acta Phytogeographica Suecica 84. Opulus Press, Uppsala, pp. 187–212.

Steele, J.H., Henderson, E.W., 1994. Coupling between physical and biological scales. Philos. Trans. R. Soc. Lond. B 343, 5–9.

Steinhardt, T., Selig, U., 2007. Spatial distribution patterns and relationship between recent vegetation and diaspore bank of a brackish coastal lagoon on the southern Baltic Sea. Estuar. Coast. Shelf Sci. 74, 205–214.

Stevenson, J.C., 1988. Comparative ecology of submersed grass beds in freshwater, estuarine, and marine environments. Limnol. Oceanogr. 33, 867–893.

Stramska, M., Świrgoń, M., 2014. Influence of atmospheric forcing and freshwater discharge on interannual variability of the vertical diffuse attenuation coefficient at 490 nm in the Baltic Sea. Rem. Sens. Environ. 140, 155–164.

Taylor, R., Fletcher, R.L., Raven, J.A., 2001. Preliminary studies on the growth of selected 'Green Tide' algae in Laboratory Culture: effects of irradiance, temperature, salinity and nutrients on growth rate. Bot. Mar. 44, 327–336.

Touchette, B.W., 2007. Seagrass-salinity interactions: physiological mechanisms used by submersed marine angiosperms for a life at sea. J. Exp. Mar. Biol. Ecol. 350, 194–215.

Turner, S.J., Hewitt, J.E., Wilkinson, M.R., Morrisey, D.J., Thrush, S.F., Cummings, V.J., Funnell, G., 1999. Seagrass patches and landscapes: the influence of wind-wave dynamics and hierarchical arrangements of spatial structure on macrofaunal seagrass communities. Estuaries 22, 1016–1032.

van den Berg, M., Coops, H., Simons, J., de Keizer, A., 1998. Competition between *Chara aspera* and *Potamogeton pectinatus* as a function of temperature and light. Aquat. Bot. 60, 241–250.

van der Heide, T., van Nes, E.H., van Katwijk, M.M., Olff, H., Smolders, A.J.P., 2011. Positive feedbacks in seagrass ecosystems – evidence from large-scale empirical data. PLoS One 6, e16504.

van Katwijk, M.M., Hermus, D.C.R., 2000. Effects of water dynamics on *Zostera marina*: transplantation experiments in the intertidal Dutch Wadden Sea. Mar. Ecol. Prog. Ser. 208, 107–118.

Viaroli, P., Bartoli, M., Fumagalli, I., Giordani, G., 1997. Relationship between benthic fluxes and macrophyte cover in a shallow brackish lagoon. Water Air Soil Pollut. 99, 533–540.

Waycott, M., Duarte, C.M., Carruthers, T.J.B., Orth, R.J., Dennison, W.C., Olyarnik, S., Calladine, A., Fourqurean, J.W., Heck, J.K.L., Hughes, A.R., Kendrick, G.A., Kenworthy, W.J., Short, F.T., Williams, S.L., 2009. Accelerating loss of seagrasses across the globe threatens coastal ecosystems. Proc. Natl. Acad. Sci. U. S. A. 106, 12377–12381.

Waycott, M., Procaccini, G., Les, D.H., Reusch, T.B.H., 2006. Seagrass evolution, ecology, and conservation: a genetic perspective. In: Larkum, A.W.D., Orth, R.J., Duarte, C. (Eds.), Seagrasses: Biology, Ecology, and Conservation. Springer, The Netherlands, pp. 25–50.

Witman, J.D., Etter, R.J., Smith, F., 2004. The relationship between regional and local species diversity in marine benthic communities: a global perspective. Proc. Natl. Acad. Sci. U. S. A. 101, 15664–15669.

Wood, S.N., 2006. Generalized Additive Models: an Introduction with R. Chapman and Hall/CRC.

Worcester, S.E., 1995. Effects of eelgrass beds on advection and turbulent mixing in low current and low shoot density environments. Mar. Ecol. Prog. Ser. 126, 223–232.

Wortmann, J., Hearne, J.W., Adams, J.B., 1997. A mathematical model of an estuarine seagrass. Ecol. Model. 98, 137–149.

Xiao, C., Wang, X., Xia, J., Liu, G., 2010. The effect of temperature, water level and burial depth on seed germination of *Myriophyllum spicatum* and *Potamogeton malaianus*. Aquat. Bot. 92, 28–32.

Zajac, R.N., Lewis, R.S., Poppe, L.J., Twichell, D.C., Vozarik, J., DiGiacomo-Cohen, M.L., 2003. Responses of infaunal populations to benthoscape structure and the potential importance of transition zones. Limnol. Oceanogr. 48, 829–842.

Zimmerman, R.C., Smith, R.D., Alberte, R.S., 1989. Thermal acclimation and whole-plant carbon balance in *Zostera marina* L. (eelgrass). J. Exp. Mar. Biol. Ecol. 130, 93–109.

Specialization among amphipods: the invasive *Gammarus tigrinus* has narrower niche space compared to native gammarids

Kristjan Herkül,† Velda Lauringson, and Jonne Kotta

Estonian Marine Institute, University of Tartu, Mäealuse 14, 12618 Tallinn, Estonia

Abstract. Human-mediated invasions of nonindigenous species are modifying global biodiversity. Despite significant interest in the topic, niche separation and specialization of invasive and closely related native sympatric species are not well understood. It is expected that combined use of various methods may reveal different aspects of niche space and provide stronger evidence for niche partitioning as compared to a single method. We applied the species marginality index (OMI) and species distribution modeling (SDM) in the northern Baltic Proper to determine (1) if environmental niche spaces at habitat scale differ between taxonomically and functionally closely related invasive and native gammarid species, and (2) whether the observed pattern relates to the species distribution overlap. Both methods agreed in notably narrower and more segregated realized niche of invasive *Gammarus tigrinus* compared to the studied native gammarids. Among native species, the distribution of *G. zaddachi* overlapped the most with *G. tigrinus*. Our results confirm that widespread colonization does not require a wide niche of the colonizer, but may rather be a function of other biological traits and/or the saturation of the recipient ecosystem. The niche divergence and wider environmental niche space of native species are likely to safeguard their existence in habitats less suitable for *G. tigrinus*.

† **E-mail:** kristjan.herkul@ut.ee

INTRODUCTION

Invasions of nonindigenous species (NIS) are considered among the most serious threats to global biodiversity (Costello et al. 2010). When establishing in the recipient ecosystem, NIS may cause significant, unpredictable and irreversible changes to abiotic and biotic environment as well as result in severe economic damage in a variety of waterbodies worldwide (e.g., Carlton 1996, Vitousek et al. 1997, Sala et al. 2000). Despite of their importance, the knowledge on the extent to which NIS actually affect biodiversity and species co-existence is still vague (Gurevitch and Padilla 2004, McGill et al. 2015).

Much of ecological theory predicts that species differ in their niches. It has been speculated that sympatric populations of taxonomically closely related species rely on niche separation to reduce competition pressure that, in turn, facilitates long term co-existence (Schoener 1974, Pianka 1978, Fenchel and Kolding 1979, Kolding 1981). The outcome of this niche difference is that species limit their own populations more than they limit others or that niche separation causes intraspecific effects to be more negative than interspecific effects (Chesson 2000). However, there exists an alternative theory that all species are identical in their fitness and in their effects on one another, thus the primary driver of population dynamics

is random variation in births, deaths, and dispersal (Bell 2000, Hubbell 2001). Based on this theory, high diversity can occur if extinction rates are slow enough to be balanced by speciation.

Surprisingly, very few studies have successfully quantified the importance of either mechanism (functional difference among species vs. demographic stochasticity and dispersal limitation) for maintaining the diversity we observe in natural communities. Though, classic views of community saturation have been challenged by recent mass invasions (Sax et al. 2007), and the apparent "unsaturation" of communities may indicate our lack of knowledge on basic assembly rules of ecological systems. Many alternative views have been developed in order to take the first steps toward a generic theory of how species niche space and species invasiveness are related. Some authors have shown that successful invaders are expected to have broad environmental tolerance or a wide environmental niche space (Marvier et al. 2004). Even more, mass invasions have provided evidence that invasive species can adapt to the recipient environment and quickly widen their niche space (Dlugosch and Parker 2008), possibly due to the lack of enemies in the recipient environment (Callaway and Ridenour 2004). Other authors have shown that coexistence is supported by niche differentiation and only those invasive species that are different from natives are able to establish successfully (Strauss et al. 2006). Such niche separation between invasive and native species has been confirmed over a few environmental gradients (e.g., Priddis et al. 2009) and the widening of niche in this context may indicate niche separation to secure co-existence. However, there is also a diametrically opposing view that invaders that are more similar to native species should be more likely to establish as their trait characteristics allow them to succeed in the recipient environment (Duncan and Williams 2002). This has also been shown in many empirical examples (Bruno et al. 2005).

To date, studies comparing multidimensional niche overlaps of invasive and native guild members are almost lacking. It is expected though that increasing the dimensionality of models will guide us closer to ecological reality and enable a better understanding of the mechanisms and consequences of environmental change (Clark et al. 2007). Niche width is also an important concept in conservation biology, as habitat specialization has been considered an important determinant of species vulnerability to global changes, and worldwide decline in specialist species has been noticed (Clavel et al. 2011). Nevertheless, niche width has received limited attention in invasion studies (Evangelista et al. 2008).

The Baltic Sea is heavily trafficked and in terms of salinity it resembles estuarine conditions of many of the world's ports. The high dispersal connectivity for estuarine NIS between the Baltic Sea and potential donor regions yields high rates of invasion (Leppäkoski et al. 2002*a*). However, the Baltic Sea is still a relatively species-poor ecosystem due to its geological youth, and therefore represents an excellent model system to study different aspects of species invasions, including relationships with native congenerics and the recipient environment (Leppäkoski et al. 2002*b*). Several nonindigenous amphipods have been recorded in the northern Baltic Sea in recent years (Herkül et al. 2006*a*, 2009). Six sympatric species of the crustacean amphipod genus *Gammarus* are found in these brackish waters. Among them are five native gammarids: *G. zaddachi* Sexton, *G. salinus* Spooner, *G. oceanicus* Segerstråle, *G. duebeni* Liljeborg, and *G. locusta* (Linnaeus), and an invasive species *G. tigrinus* Sexton that originates from North America. *G. tigrinus* was found for the first time in the northern Baltic Sea in 2003 and its range has been continuously expanding (Grabowski et al. 2006, Herkül et al. 2006*b*, Paavola et al. 2008, Kotta et al. 2013). A notable decrease in the diversity and density of native amphipods has been observed concurrent with the invasion of *G. tigrinus* in the region (Grabowski et al. 2006, Jänes et al. 2015).

Approaches for estimating environmental niche are mainly based on either ordination methods or species distribution models (SDM) (Broennimann et al. 2012). Species distribution models (SDM) are numerical methods that relate observations of species occurrences or abundances to environmental variables (Elith and Leathwick 2009). These relationships are further used to predict species distribution across different spatial and/or temporal scales (Elith and Leathwick 2009). Unlike in the case of simple plotting of species occurrences on a map, modeled distribution maps enable assessment of (1) surface area of habitats, (2) distribution of spe-

cies in areas that were not sampled or sampled sparsely, and (3) spatial overlap of distributions of different species. In contrast, ordinations enable assessment of niche in multidimensional environmental space by constructing synthetic axes from measured environmental variables (e.g., principal component analysis, canonical correspondence analysis, outlying mean index; ter Braak and Verdonschot 1995, Dolédec et al. 2000). We used both approaches in this study to address the environmental niche separation in the case of gammarids in the northern Baltic Proper. Applying both approaches yields a more robust insight into the potential niche separation among species than applying only one approach (Broennimann et al. 2012). We are not aware of any previous studies that combine these approaches to clarify the possible niche separation between taxonomically closely related native and invasive species. To this end, improved knowledge about the connection of species distribution maps with multidimensional niche space would be a highly rewarding approach.

In this study, we asked why *G. tigrinus* is a successful invader in the north-eastern Baltic Sea, and if this could be explained by similar or divergent niche breadth when compared to native gammarids. Specifically, we addressed the following research questions by applying multivariate ordination and species distribution modeling:

(1) Do environmental niche spaces differentiate between taxonomically and functionally closely related sympatric species?
(2) Does similarity in niche space result in species distribution overlap?
(3) Are there any particular differences in the niche width and segregation between invasive and native species? Does the invasive species have wider or narrower environmental niche?

Methods

Study area

Abiotic environment.—The Baltic Sea is a tideless and brackish water body. This study was conducted in the coastal water of western Estonia, northern Baltic Proper (Fig. 1). The area

is characterized by complex topography with numerous islands, islets, bays, and peninsulas. Most of the study area is very shallow with water depths seldom exceeding 25 m. Strong gradients of wave exposure and salinity exist in the area. The sea areas west of the islands Saaremaa and Hiiumaa are exposed to the open Baltic Proper and have a wave fetch of hundreds of kilometers. In contrast, the inner reaches of the bays of the mainland (e.g., Matsalu and Haapsalu bays, see Fig. 1) are very sheltered both by the mainland and by islands. Similar to wave exposure, the salinity gradient generally follows an east-west direction. Salinity reaches 7 in the westernmost study area while it falls to almost 0 in the inner parts of bays with riverine inflow in the eastern study area. Hard limestone substrate and granite boulders dominate in the most exposed areas. Different combinations of mixed sediments comprised of sand, gravel, and pebbles can be found in the mid-range of the exposure gradient. Fine sand and mud dominates in the most sheltered bays. Scattered single boulders or boulder fields can be found throughout the area in shallow waters. Regardless of the relatively small spatial extent of the study area, important environmental gradients (depth, salinity, wave exposure, seabed sediments) were well represented because of the high heterogeneity of the area that encompasses the Gulfs of Finland and Riga, the Baltic Proper, and the West Estonian Archipelago Sea.

Benthic communities.—Variability in the abiotic environment is also reflected in the structure of macrobenthic communities. Species of marine origin dominate in the areas of medium and high salinity while freshwater species dominate in the eastern bays with riverine inflow. Among algal species, the brown alga *Fucus vesiculosus* and the red alga *Furcellaria lumbricalis* are the most important perennial species on hard substrates. *F. vesiculosus* usually grows in depth of 1–4 m, whereas *F. lumbricalis* inhabits deeper areas (>4 m). Several annual and perennial filamentous green, brown, and red algae like *Ulva intestinalis*, *Cladophora glomerata*, *Pilayella littoralis*, *Ceramium tenuicorne*, *Polysiphonia* spp are very common. Many species of vascular plants are common on soft substrate: *Zostera marina*, *Stuckenia pectinata*, *Potamogeton perfoliatus*, *Zannichellia palustris*, *Myriophyllum spicatum*, *Ruppia maritima*. Charo-
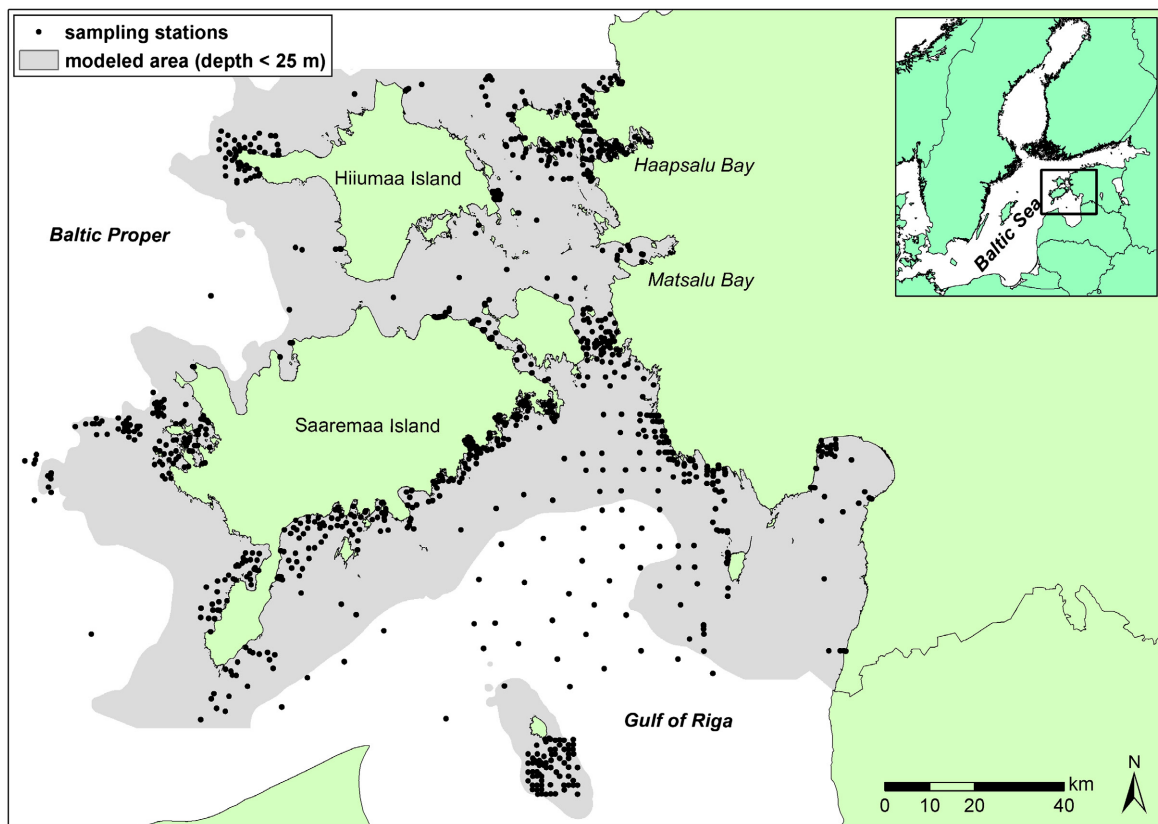
Fig. 1.   Study area and locations of sampling sites.

phytes (*Chara* spp., *Tolypella nidifica*) are common on sandy and muddy sediments in the shallow waters of the most sheltered bays. Extensive growth of ephemeral filamentous algae and formation of drift algal mats as a result of eutrophication are common phenomena in the area (Kotta et al. 2008).

Among the invertebrates, the bivalve *Mytilus trossulus* and the barnacle *Amphibalanus improvisus* prevail on hard bottoms. Gammarid amphipods, idoteid isopods, the snails *Peringia ulvae*, *Radix balthica*, and *Theodoxus fluviatilis* are common in vegetated areas. Common infaunal species in soft sediments are the bivalves *Macoma balthica* and *Cerastoderma glaucum* and polychaetes *Hediste diversicolor* and *Marenzelleria neglecta*. Various insect larvae inhabit shallow coastal areas with low salinity.

All five species of native gammarids are present in the study area but *G. duebeni* and *G. locusta* are very rare in benthic samples compared to the other native species (*G. salinus*, *G. oceanicus*,

G. zaddachi) and the nonindigenous *G. tigrinus*. Therefore, only *G. salinus*, *G. oceanicus*, *G. zaddachi*, and *G. tigrinus* were included in this study. The nonindigenous *G. tigrinus* has been common in the study area since 2006 (Herkül et al. 2009).

Benthic sampling

The macrobenthos database of the Estonian Marine Institute, University of Tartu was used as a data source on the distribution of gammarids and key phytobenthic species. Only quantitative samples from the period of 2005–2012 were used. Data were averaged when several samples were collected from the same sampling station. Samples from soft bottoms were predominantly collected using Ekman type or Van Veen type bottom grab samplers. Samples from hard substrate were collected by divers by harvesting all material inside a 20 × 20 cm metal frame. Samples were sieved through a 0.25 mm mesh and all retained material was

stored deep frozen (−18°C) until analysis. In the laboratory, all samples were sorted under a binocular microscope (20–40× magnification). All macrobenthic organisms were identified to species level except for oligochaetes, chironomids, and juveniles of gammarid amphipods (length <5 mm). Sampling and analysis followed the guidelines developed for the HELCOM COMBINE program (HELCOM 2015). The locations of sampling sites (n = 1329) are shown in Fig. 1.

Environmental niche analysis

Niche breadth and separation of habitat niche between gammarid species was assessed using analysis of outlying mean index (OMI). OMI, or species marginality, measures the distance between the mean habitat conditions used by the species (niche center), and the mean habitat conditions of the sampling area (Dolédec et al. 2000). The higher the value of the OMI index of a species, the higher is its habitat specialization. OMI analysis is a multivariate coinertia analysis that unlike canonical correspondence analysis (CCA) and redundancy analysis (RDA), can handle nonunimodal and nonlinear species–environment relationships. Compared to the traditional multivariate methods, CCA and RDA, OMI gives a more even weight to all sampling units even if they exhibit a low number of species or individuals. Thus, OMI more adequately captures the multivariate environmental space represented by sampling units (Dolédec et al. 2000). The package "ade4" (Dray and Dufour 2007) was used for running OMI analysis in the statistical software R 2.15.1 (R Core Team 2012). Occurrence (i.e., presence-absence) data of gammarids was used as a species matrix input (n = 1329). A permutation test with 9999 permutations was used to calculate the statistical significance of the values of OMI of each gammarid species. The environmental niche space of gammarid species was visualized based on a principal component analysis (PCA) ordination of sampling sites on two synthetic axes and by drawing a convex hull over the points where a given species was present. Five percent of species occurrences that were most distant from niche center were considered as outliers and were excluded when drawing the border of niche space.

Abiotic and biotic georeferenced environmental data was used for environmental niche analysis. The abiotic environmental variables included different bathymetrical (depth, slope of seabed), topographic (distance to land), hydrodynamic (wave exposure), geological (seabed substrate), and physico-chemical (temperature, salinity, transparency, ice conditions) variables. The biotic variables included chlorophyll content and modeled probability of occurrence of key phytobenthic species (*Fucus vesiculosus*, *Furcellaria lumbricalis*, and charophytes). Altogether 20 environmental variables were used that were all available as raster layers in a geographical information system (grid size 50–200 m). The full list of variables with additional information (data source) is presented in Table 1.

Species distribution models (SDM)

The same environmental variables were used in the SDMs as in the OMI analysis. The spatial distribution (probability of occurrence) of all studied gammarid species was modeled. Several candidate models were built for each species using the following algorithms: generalized additive models (GAM), random forests (RF), and boosted regression trees (BRT); descriptions of the algorithms are given below. The candidate model with the best predictive performance was chosen to produce the final distribution maps. All distribution modeling exercises were done in the statistical software R 2.15.1 (R Core Team 2012). During modeling, 80% of the input data was randomly selected and used as model training data while 20% of the data was reserved for validation. The predictive performance of the candidate models was validated by calculating the area under the receiver operating curve (AUC, Fielding and Bell 1997). Following Hosmer and Lemeshow (2000), AUC values over 0.9 indicate excellent, 0.8–0.9 very good, 0.7–0.8 satisfactory, and below 0.7 poor discriminative ability. The algorithm that produced models with the highest AUC value over all the studied species was then used to build final models for all species using 100% of the input data. The approach of selecting a single best-performing algorithm to produce the final models for all species was chosen in order to get comparable distribution predictions and to achieve a more balanced interpretation of

Table 1. Variables used in the environmental niche analysis and species distribution models. Five variables with the highest importance in the final random forest (RF) models are indicated for each gammarid species (higher rank indicates higher importance).

Variable	Source†	Five variables with the highest importance in RF models			
		G. oceanicus	*G. salinus*	*G. zaddachi*	*G. tigrinus*
Depth	a	4	4	2	1
Average depth in 500 m radius	a		5	3	2
Average depth in 2000 m radius	a				4
Slope of seabed	a				
Slope of seabed in 500 m radius	a	3		5	
Slope of seabed in 2000 m radius	a				
Distance to land	b				
Distance to 20 m depth isoline	b				
Proportion of soft sediment (modeled)	b	1	2	1	
Salinity	b	5			
Wave exposure	c				
Chlorophyll a content based on satellite imagery; average over 2009–2010	b				
Water transparency estimated as attenuation coefficient based on satellite imagery; average over 2010–2012	b				5
Water temperature based on satellite imagery; average over 2009–2010	b				
Number of ice days per year; average over 2009–2011	d				
Ice coverage; average over 2009–2011	d				
Ice thickness; average over 2009–2011	d				
Probability of occurrence of *Furcellaria lumbricalis* (modeled)	b		3		
Probability of occurrence of *Fucus vesiculosus* (modeled)	b	2	1	4	
Probability of occurrence of charophytes (modeled)	b				3

† Data sources: a – Bathymetric raster, developed at the Estonian Marine Institute. b – Databases of the Estonian Marine Institute. c – Wave exposure calculations for the Estonian coast (Nikolopoulos and Isæus 2008). d – Finnish Meteorological Institute.

differences in distributions. The distribution predictions were produced with 100 m grid size over a depth zone of 0-25 m (Fig. 1). The depth limitation was set because gammarid amphipods very rarely inhabit areas of greater depth.

Generalized additive models (GAM) are a semiparametric extension of generalized linear models that enables the user to fit complex non-linear relationships and handle different types of error distributions (Hastie and Tibshirani 1990). Due to these characteristics, GAM has been one of the most widely used methods for SDM (Elith et al. 2006). The package "mgcv" was used for building GAMs (Wood 2006). The models were built using penalized regression splines as the smoothing function, binomial error distribution, and automatic calculation of smoothing parameters. The maximum degree of freedom was set

to four for each variable. At first, single predictor models were built. Predictors were then added into the final model in the decreasing order of explained deviances of single variable models.

Random forests (RF) is a machine learning method that generates a large number of regression trees, each calibrated on a bootstrap sample of the original data (Breiman 2001). Each node is split using a subset of randomly selected predictors and the tree is grown to the largest possible extent without pruning. For predicting the value of a new data point, the data are run through each of the trees in the forest and each tree provides a value. The model prediction is then calculated as the average value over the predictions of all the trees in the forest (Breiman 2001). The package "party" (Hothorn et al. 2006) was used to run RF models in R. Two parameters must be set in RF models: the number of predictor variables to

be randomly selected at each node (*mtry*) and the number of trees in a forest (*ntree*). *mtry* was set to one-third of the number of predictor variables as suggested by Liaw and Wiener (2002). *ntree* was set to 1000 as 500 trees usually yield stable results (Liaw and Wiener 2002). The importance of predictor variables was assessed by using the AUC-based permutation (*n* = 1000) routine (Janitza et al. 2012) in the package "party" (Hothorn et al. 2006).

Boosted regression trees (BRT) is an ensemble method that combines the strength of two algorithms: regression trees and boosting (Elith et al. 2008). Regression trees are good at selecting relevant predictor variables and can model interactions. Boosting enables building of a large number of trees in a way that each successive tree adds small modifications in parts of the model space to fit the data better (Friedman et al. 2000). The algorithm keeps adding trees until finding the optimal number of trees that minimizes the predictive deviance of a model. The predictive performance of BRT has been shown to be superior to most other modeling methods (Elith et al. 2006, Revermann et al. 2012). The BRT modeling was performed using packages "gbm" (Ridgeway 2012) and "dismo" (Hijmans et al. 2012). Important parameters in building BRT models are learning rate, tree complexity, and bag fraction (Elith et al. 2008). Learning rate determines the contribution of each tree to the growing model and tree complexity defines the depth of interactions allowed in a model. Bag fraction determines the proportion of data to be selected randomly at each iteration. Different combinations of these parameters may yield variable predictive performance but generally a lower learning rate and inclusion of interactions gives better results. For each species, two groups of BRT models were built that had tree complexity of 1 and 5, respectively. A tree complexity of 1 fits a model without interactions between predictors while a tree complexity of 5 fits a model with up to five-way interactions. In both groups, models with learning rates of 0.0001, 0.0005, 0.001, 0.005, 0.01, 0.05, and 0.1 were built. The bag fraction was set at 0.5 which is the recommended default value for presence–absence models (Elith et al. 2008). This design resulted in 14 models for each species.

Schoener's D was used to assess the overlaps of distributions of gammarid species based on the results of SDMs. There are many metrics for measuring the distribution overlap but Schoener's D was chosen because of its simplicity, long history of use and good performance (Warren et al. 2008, Rödder and Engler 2011). Schoener's D varies between zero and one. Zero indicates no overlap while one indicates full distribution overlap between species.

RESULTS

Environmental niche analysis

According to OMI analysis, *G. salinus* had the largest environmental niche space followed by *G. zaddachi*, *G. oceanicus*, and *G. tigrinus*. The niche space of invasive *G. tigrinus* was notably smaller than that of the native species *G. salinus* and *G. zaddachi* (Fig. 2). The centers of niche positions of native species almost coincided while that of *G. tigrinus* laid notably farther apart (Fig. 2). Based on the values of OMI, *G. tigrinus* had the highest habitat specialization among the studied gammarid species, whereas *G. salinus* had the lowest specialization (Fig. 2). OMI values of all species were statistically significant (*P* < 0.001).

Species distribution models (SDMs)

The predictive accuracy of models was very high, as the AUC values of all models exceeded 0.8. GAM showed somewhat lower accuracy than BRT and RF, whereas the AUC values of BRT and RF were very similar (Table 2). Among the models of native species, RF had the highest AUC values. BRT was only fractionally better than RF in the case of *G. tigrinus*. As RF produced the best models among three of four species and gave essentially equally good result in the case of one species, RF was chosen as the method for modeling the spatial distribution of gammarid species. In the final RF models, depth was among five most important predictor variables for each gammarid species. In addition to depth, modeled distributions of macrophytes proved to have high importance in predicting the distribution of gammarids (Table 1).

The predicted distributions clearly differed between gammarid species in terms of both the distribution area and distribution pattern (Fig. 3). Based on SDMs, *G. salinus* had the most extensive distribution area. The distribution
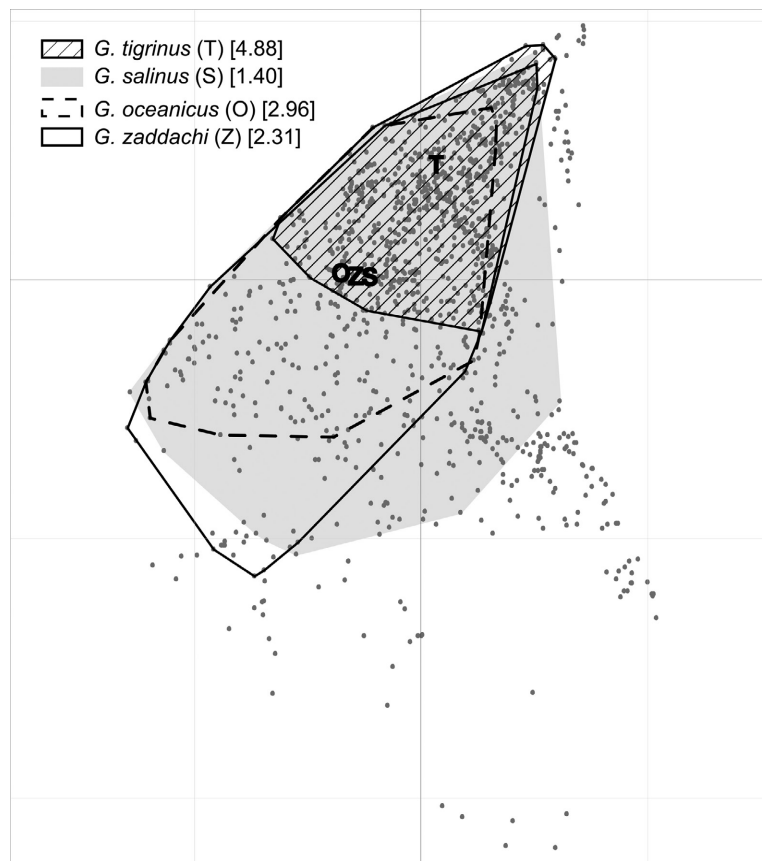
Fig. 2. Environmental niche characteristics of the studied gammarid species based on PCA ordination of the values of environmental variables in sampling sites. Dots represent sampling sites, polygons represent the realized niche breadths, and letters on the plot indicate the centers of niche spaces of the species. The values of OMI are shown in square brackets.

Table 2. AUC values of species distribution models.

Species	GAM	BRT	RF
G. tigrinus	0.884	0.898	0.896
G. oceanicus	0.824	0.847	0.857
G. salinus	0.816	0.858	0.865
G. zaddachi	0.815	0.821	0.829

Notes: GAM – generalized additive model, BRT – boosted regression trees, RF – random forest. Higher AUC value indicates better performance of model. RF was chosen to model the spatial distribution of all gammarid species based on the best overall performance.

pattern of the invasive *G. tigrinus* clearly distinguished from the distributions of the native gammarids: the probability of occurrence of *G. tigrinus* was highest in sheltered bays where the probability of occurrence of native species was very low (Fig. 3).

Based on the SDMs, the overlap of distribution was larger among native species than between *G. tigrinus* and native species (Table 3). Among distribution overlaps between native species and invasive *G. tigrinus*, Schoener's D scores suggest that the overlap was largest between *G. zaddachi* and *G. tigrinus* and smallest between *G. oceanicus* and *G. tigrinus*.

DISCUSSION

Our data showed that invasive species may have narrower environmental niche space than native species in a particular area, with the invasive *Gammarus tigrinus* being more specialized than any of the native gammarid species. The difference in the values of OMI was more than three-fold between the most specialized
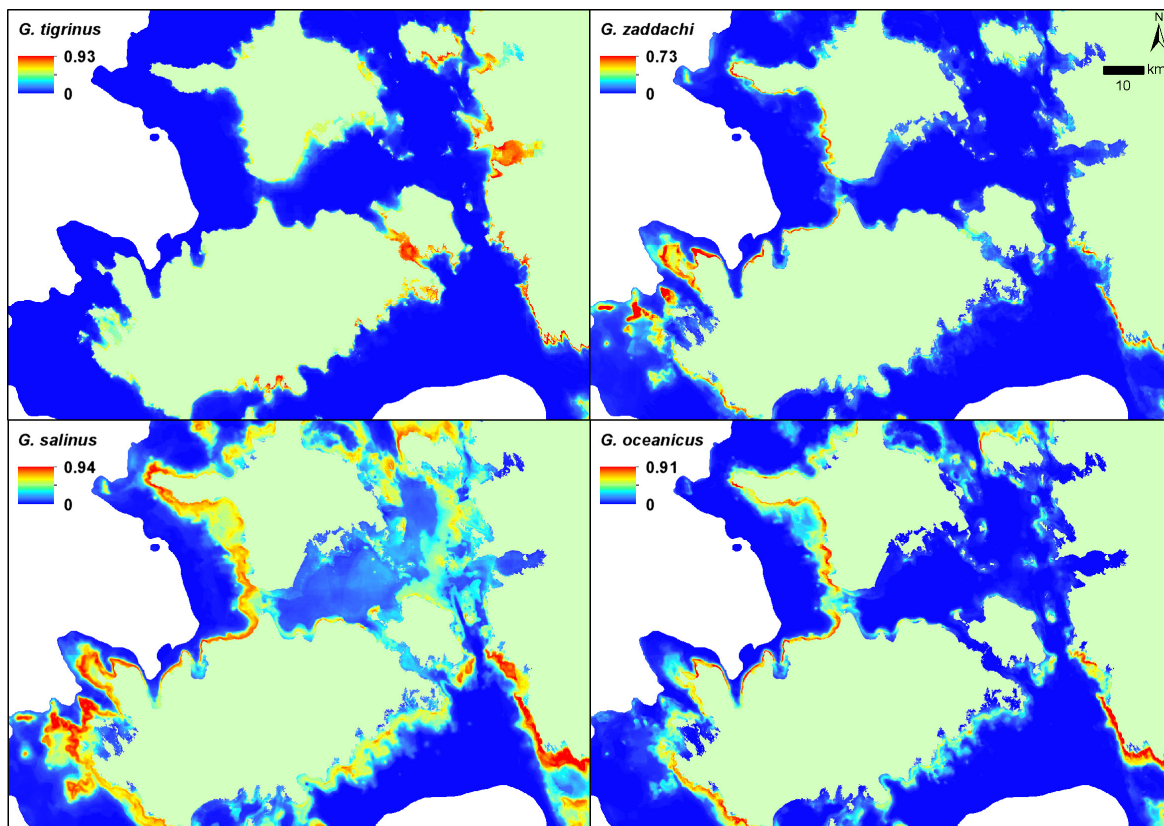
Fig. 3. Modeled distributions of the studied gammarid species. The color gradient indicates the probability of occurrence of a given species. The central part of the study area is zoomed in for easier comparison.

Table 3. Schoener's D values between modeled distributions of gammarid species. Higher value indicates larger overlap of distributions.

	G. tigrinus	G. oceanicus	G. salinus
G. oceanicus	0.277		
G. salinus	0.265	0.670	
G. zaddachi	0.380	0.596	0.526

species, *G. tigrinus*, and the least specialized species, *G. salinus*. In addition to higher specialization, the centroid of the niche of the nonindigenous species departed strongly from all the other species, indicating niche segregation. Our results suggest that successful nonindigenous species do not necessarily have to be habitat generalists and species with narrow niche space may become a pest species. This also suggests that high similarity in environmental niche space between native and invasive

species may reduce the success of invading species (Callaway et al. 2004, Vivanco et al. 2004). Therefore, the degree of segregation in environmental niche space between an invader and native community may provide a predictive tool for invasiveness as shown for the phylogenetic relatedness in terrestrial habitat (Strauss et al. 2006). There exist two potential mechanisms explaining the observed segregation in environmental niche space between invasive and native species. First, species that highly overlap within their niche space should not coexist because they highly overlap in resource use (Fargione et al. 2003). Second, natural enemies (e.g., parasites or predators) are expected to switch to close relatives of their host and/ or prey more easily than to distantly related taxa. Consequently, larger differences in environmental niche space between native and invasive species result in more complete release of invasive species from enemies (Strong et al.

1984). For the gammarid amphipod perspective, a direct competitive inhibition of *G. tigrinus* by natives of their own functional guild is not likely as *G. tigrinus* has been experimentally shown to be competitively superior over natives (Orav-Kotta et al. 2009). However, indiscriminate predation on juveniles by all gammarid species is very strong in the study area (Jänes et al. 2015) and weakening of such predation gives the invasive species a clear advantage.

Earlier studies have demonstrated that *G. tigrinus* is rather euryoecious in its native distribution range (Steele and Steele 1972, Bousfield 1973) as well as more tolerant toward some physical and chemical factors like salinity, hypoxia, and thermal stress compared to other gammarids in Europe (Grabowski et al. 2006, Lenz et al. 2011, Sareyka et al. 2011). Nevertheless, the environmental space occupied by the invasive species was significantly narrower compared to the native species in the eastern Baltic Sea. This leads to another important implication of this study: wider tolerance limits do not necessarily translate to wider occupied niche of an invasive species in an area subject to invasion.

There may be several reasons why the invasive gammarid has narrower habitat niche compared to local species. One plausible explanation may be preadaptation of the invasive species to warmer and more sheltered habitats that have emerged in the Baltic Sea during postglacial period but are under-occupied by the native Baltic species. The native fauna of the contemporary Baltic Sea is assembled by the most euryoecious species from the Arctic and northern Atlantic faunal groups (Segerstråle 1957). Thus, the native gammarids are probably more tolerant to low water temperatures characteristic to the eastern Baltic Sea with the exception of the shallowest bays. Contrastingly, for *G. tigrinus* several experiments have confirmed tolerance to high temperatures and optimal developmental temperatures as high as 25 °C (Savage 1982, Lenz et al. 2011). The other possible explanation for the narrower niche may be lower genetic diversity of the species in the invasive range due to recent bottleneck effects (Lee 2002). However, the Baltic population of *G. tigrinus* is characterized by high genetic diversity resulting from an invasion history combining separate invasion events from distinct source populations (Kelly et al. 2006).

In addition to the named reasons, it is probable that the new species is still expanding its distribution in the study area. In the case of *G. tigrinus* and the spatial scale of this study, range expansion may not necessarily result from time-consuming distribution strategies as has been shown for several terrestrial species (Svenning and Skov 2004), as the Eastern European populations of *G. tigrinus* have displayed fast spatial expansion in new areas at scales comparable to the extent of our study area (Pinkster et al. 1977, Kotta et al. 2013). Further range expansion may rather result from rapid evolutionary postinvasion responses to new environments (Lee 2002), and in such case, future niche changes may be expected.

The relatively narrower niche of an invasive species compared to sympatric congeners seemingly contradicts several previous studies that found larger niche in invaders (Scott and Panetta 1993, Goodwin et al. 1999, Sultan 2001) or an enlargement of niche presumably due to invader's successful escape from biotic suppressors (Callaway and Ridenour 2004). However, the spatial scale of niche studies must be considered before drawing conclusions. The spatial extent of our study area was about 200 km while the whole extent of the European range of *G. tigrinus* is more than one order of magnitude larger covering also freshwater populations (Kelly et al. 2006). Therefore, a local pattern of niche breadth does not necessarily coincide with the regional or global pattern, and analysis on the scale of the whole invasive range of *G. tigrinus* would have possibly revealed a notably larger niche space.

Both ordination and distribution modeling showed partial overlap of the niches of *G. tigrinus* and native gammarids. This indicates that no complete competitive exclusion exists among the studied sympatric species. This may be a product of large temporal variability in the Baltic Sea environment represented by many stochastic disturbances at multiple spatial and temporal scales with abiotic disturbance enabling the coexistence of species (Roxburgh et al. 2004). Previous experimental evidence suggests that there is no strong interference competition among adult individuals of gammarid species in the northern Baltic Sea (Kotta et al. 2011), although adult predation on juvenile gammarids has been observed in all of the studied species (Jänes et al. 2015). Contrast-

ingly, there are cases from European fresh waters where superior intraguild predators *G. duebeni* or *Dikerogammarus villosus* may outcompete *G. tigrinus* in certain habitats resulting in a strict habitat segregation (MacNeil and Prenter 2000, MacNeil et al. 2008). The width of the realized niche of an invader in a new geographic range most likely results from an interplay between available niche space and biotic interactions with resident species within the framework of this particular niche space.

Our results indicate that *G. tigrinus* is not occupying a new niche totally devoid of other gammarids in the northern Baltic Sea, although its environmental preferences clearly distinguish it from all the native species. An addition of a species with differing preferences may, however, lead to competitive dominance and accordingly high densities of the newcomer at environmental combinations favored distinctly by it. This seems to be the case in the Baltic Sea, as *G. tigrinus* has been reported to dominate in several areas with native gammarid species present at very low numbers (Packalén et al. 2008, Herkül et al. 2009, Kotta et al. 2013). In areas of niche overlap, microhabitat segregation is the likely cause for density patterns, as has also been shown for native gammarids with highly overlapping niches (Korpinen and Westerbom 2010).

The spatial resolution of the used environmental data sets was generally in a magnitude of 100 m. Higher resolution of environmental data may very likely reveal stronger niche separation between the studied species. Environmental variability in a submeter spatial scale can be driving micro-habitat selection in small-sized invertebrates (Platvoet et al. 2009). However, due to practical reasons such a small-scale variability can seldom be recorded during standard benthos sampling and neither can environmental GIS-layers achieve that high spatial resolution. Specially targeted field work is needed to record very small-scale environmental variability, and the results of such detailed data collection may likely reveal stronger niche separation between the species than this study.

The species distribution models (SDMs) produced predictions with high accuracy and thus proved to be useful for comparing the distribution of gammarid species. The high prediction accuracy can be explained by several reasons: (1) the input data set of the presence and absence of gammarid species was very representative including thousands of records and covering all important environmental gradients; (2) modern modeling algorithms like RF and BRT have proved to produce highly accurate predictions (e.g., Elith et al. 2006, Lindegarth et al. 2014); (3) the elaborate set of environmental variables (including biotic predictors) for model building reflected well the heterogeneity and natural gradients of the study area.

Most studies on species distribution modeling have focused only on abiotic drivers of species distribution (Zimmermann et al. 2010). However, inclusion of biotic predictors like competitors or facilitators, may increase the predictive power of models (Araújo and Luoto 2007, Pellissier et al. 2010). In this study, the distributions of key phytobenthic species were highly important predictors in distribution models of gammarids: the probability of occurrence of *Fucus vesiculosus*, *Furcellaria lumbricalis*, and charophytes were among the top four predictors in the models of every gammarid species (Table 1). This proves that available species distribution maps can be a rewarding input for species distribution modeling. Charophytes grow on soft sediments in the most sheltered bays. *F. vesiculosus* and *F. lumbricalis* grow on hard substrate but in different depths and wave exposure levels. Based on the importance of predictor variables in SDMs, *G. tigrinus* is most related to charophytes and native gammarids to *F. vesiculosus* and *F. lumbricalis* indicating habitat separation between the invasive and native species. The included three key macrophytes may have caused the exclusion or decreased importance of abiotic variables like wave exposure from SDMs in this study because the distribution of different plant groups reflect certain gradients in many abiotic drivers like depth, wave exposure, substrate, and salinity. However, compared to the cumulative and interactive effects of abiotic variables, the distribution of vegetation showed higher predictive power. This indicates that the modeled biotic variables (vegetation in this study) carry additional information compared to the sum of effects of underlying abiotic variables.

Modeled distribution maps (Fig. 3) enabled assessment of the spatial aspect of niche over-

lap between gammarid species in the study area. Based on the pairwise comparisons of distribution overlap (Schoener's D), the distribution of *G. tigrinus* had the smallest overlap with all the other species. This result complied well with the analysis of niche specialization (OMI values) which indicated that *G. tigrinus* has the highest habitat specialization. Among native gammarids, the distribution of *G. zaddachi* had the largest overlap with *G. tigrinus* and this clearly indicates that *G. zaddachi* is the most affected by the competitive and predation pressure by *G. tigrinus*. Compared to OMI analysis, the modeled distributions reflect the actual geographic dimensions where biological interactions take place. The geographic nature of SDM and SDM-based analyses makes the approach easily comprehendible in a management point of view.

Tolerance to stress is sometimes considered less important for invasiveness than reproduction following the r-selection strategy (McMahon 2002). Our study suggests that tolerance does not necessarily convert to wider environmental niche or distribution in the invaded range. Instead, larger tolerance of invasive species compared to local species along some environmental gradient may translate to niche and habitat segregation in the invaded range. However, the situation is far from static (Simberloff 2014), and not only are the species evolving but also the available niche space is constantly transforming in geographic space. Warming climate prospects may change the amount of available niche space for both native and non-native co-occurring species and accelerate changes in the arrangement of occupied niches (Williams and Jackson 2007), with probable retraction of niches of more cold-adapted resident species like *G. zaddachi* and possible protrusion of invaders favored by or more tolerant to warmer conditions.

Conclusions

The distribution and niche assessment of NIS by combining spatial modeling and multivariate ordination in this study proved to be a highly relevant approach to reveal patterns of invasion process. Environmental niche analysis (OMI) offers complementary information about biotic patterns in available environmental space compared to more traditional species distribution modeling. The occupied niche space of the nonindigenous gammarid *G. tigrinus* was narrower than those of native gammarids. Also, niche centers of the native species almost coincided while the one of *G. tigrinus* was situated notably apart. This differentiation was also well reflected in the modeled distributions: the highest probability of occurrence of *G. tigrinus* was spatially restricted to shallow and sheltered areas that are predominantly warmer and of lower salinity. These findings indicate that the success of the invasion of *G. tigrinus* has been facilitated by specific habitats in the recipient area that are highly suitable for the species due to favorable preadaptations. Considering intraguild interactions, the invasion of *G. tigrinus* may have the strongest effect on *G. zaddachi*, as the distribution overlap between these two congeners is the largest. However, the observed niche divergence and wider realized niche of the native species are likely to aid survival in habitats less suitable for *G. tigrinus*. Our study reminds that wide environmental tolerance of a species does not necessarily result in a wide realized niche in the course of an invasion process. Our results also suggest that colonization success and wide distribution do not necessarily require a broad environmental niche of the colonizer, but may instead rely on the saturation of the recipient ecosystem and the novelty of the preadaptations of the colonizer: an ability to optimally utilize previously under-occupied environmental niche can support the apparent luck of the draw. Despite the decline in specialist species worldwide (Clavel et al. 2011), anthropogenic introductions may thus regionally increase the proportion of relatively specialized taxa.

Council. The authors thank Holger Jänes for revising the text of the manuscript.

Literature cited

Araújo, M. B., and M. Luoto. 2007. The importance of biotic interactions for modelling species distributions under climate change. Global Ecology and Biogeography 16:743–753.

Bell, G. 2000. The distribution of abundance in neutral communities. American Naturalist 155:606–617.

Bousfield, E. L. 1973. Shallow-water Gammaridean Amphipoda of New England. Comstock Publishing Associates, Cornell University Press, Ithaca, New York, USA.

Breiman, L. 2001. Random forests. Machine Learning 45:5–32.

Broennimann, O., et al. 2012. Measuring ecological niche overlap from occurrence and spatial environmental data. Global Ecology and Biogeography 21:481–497.

Bruno, J. F., J. D. Fridley, K. Bromberg, and M. D. Bertness. 2005. Insights into biotic interactions from studies of species invasions. Pages 13–40 *in* D. F. Sax, J. J. Stachowicz and S. D. Gaines, editors. Species invasions: insights into ecology, evolution, and biogeography. Sinauer, Sunderland, Massachusetts, USA.

Callaway, R. M., and W. M. Ridenour. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. Frontiers in Ecology and the Environment 2:436–443.

Callaway, R. M., G. C. Thelen, A. Rodriguez, and W. E. Holben. 2004. Soil biota and exotic plant invasion. Nature 427:731–733.

Carlton, J. T. 1996. Pattern, process, and prediction in marine invasion ecology. Biological Conservation 78:97–106.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Clark, J. S., M. Dietze, S. Chakraborty, P. K. Agarwal, I. Ibanez, S. LaDeau, and M. Wolosin. 2007. Resolving the biodiversity paradox. Ecology Letters 10:647–662.

Clavel, J., R. Julliard, and V. Devictor. 2011. Worldwide decline of specialist species: Toward a global functional homogenization? Frontiers in Ecology and the Environment 9:222–228.

Costello, M. J., M. Coll, R. Danovaro, P. Halpin, H. Ojaveer, and P. A. Miloslavich. 2010. Census of marine biodiversity knowledge, resources, and future challenges. PLoS ONE 5:e12110.

Dlugosch, K. M., and I. M. Parker. 2008. Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. Molecular Ecology 17:431–449.

Dolédec, S., D. Chessel, and C. Gimaret-Carpentier. 2000. Niche separation in community analysis: a new method. Ecology 81:2914–2927.

Dray, S., and A. B. Dufour. 2007. The ade4 package: implementing the duality diagram for ecologists. Journal of Statistical Software 22:1–20.

Duncan, R. P., and P. A. Williams. 2002. Ecology: Darwin's naturalization hypothesis challenged. Nature 417:608–609.

Elith, J., and J. R. Leathwick. 2009. Species distribution models: ecological explanation and prediction across space and time. Annual Review of Ecology, Evolution, and Systematics 40:677–697.

Elith, J., et al. 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29:129–151.

Elith, J., J. R. Leathwick, and T. Hastie. 2008. A working guide to boosted regression trees. Journal of Animal Ecology 77:802–813.

Evangelista, P. H., S. Kumar, T. J. Stohlgren, C. S. Jarnevich, A. W. Crall, J. B. III Norman, and D. T. Barnett. 2008. Modelling invasion for a habitat generalist and a specialist plant species. Diversity and Distributions 14:808–817.

Fargione, J., C. S. Brown, and D. Tilman. 2003. Community assembly and invasion: an experimental test of neutral versus niche processes. Proceedings of the National Academy of Sciences 100:8916–8920.

Fenchel, T. M., and S. Kolding. 1979. Habitat selection and distribution patterns of five species of the amphipod genus *Gammarus*. Oikos 33:316–322.

Fielding, A. H., and J. F. Bell. 1997. A review of methods for the assessment of prediction errors in conservation presence/absence models. Environmental Conservation 24:38–49.

Friedman, J. H., T. Hastie, and R. Tibshirani. 2000. Additive logistic regression: a statistical view of boosting. Annals of Statistics 28:337–407.

Goodwin, B. J., A. J. McAllister, and L. Fahrig. 1999. Predicting invasiveness of plant species based on biological information. Conservation Biology 13:422–426.

Grabowski, M., A. Konopacka, K. Jazdzewski, and E. Janowska. 2006. Invasions of alien gammarid species and retreat of natives in the Vistula Lagoon (Baltic Sea, Poland). Helgoland Marine Research 60:90–97.

Gurevitch, J., and D. K. Padilla. 2004. Are invasive species a major cause of extinctions? Trends in Ecology & Evolution 19:470–474.

Hastie, T. J., and R. J. Tibshirani. 1990. Generalised additive models. Chapman & Hall, New York, New York, USA.

HELCOM. 2015. Manual for marine monitoring in the COMBINE programme of HELCOM. http://www.helcom.fi/action-areas/monitoring-and-assessment/manuals-and-guidelines/combine-manual

Herkül, K., J. Kotta, and I. Kotta. 2006a. Distribution and population characteristics of the alien talitrid amphipod *Orchestia cavimana* in relation to environmental conditions in the northeastern Baltic Sea. Helgoland Marine Research 60:121–126.

Herkül, K., J. Kotta, I. Kotta, and H. Orav-Kotta. 2006b. Effects of physical disturbance, isolation and key macrozoobenthic species on community development, recolonisation and sedimentation processes. Oceanologia 48(S):267–282.

Herkül, K., J. Kotta, T. Püss, and I. Kotta. 2009. Crustacean invasions in the Estonian coastal sea. Estonian Journal of Ecology 58:313–323.

Hijmans, R. J., S. Phillips, J. Leathwick, and J. Elith. 2012. dismo: Species distribution modeling. R package version 0.7-23. http://CRAN.R-project.org/package=dismo

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression. Second edition. John Wiley & Sons, New York, New York, USA.

Hothorn, T., P. Buehlmann, S. Dudoit, A. Molinaro, and M. Van Der Laan. 2006. Survival ensembles. Biostatistics 7:355–373.

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. Princeton University Press, Princeton, New Jersey, USA.

Jänes, H., J. Kotta, and K. Herkül. 2015. High fecundity and predation pressure of the invasive *Gammarus tigrinus* cause decline of indigenous gammarids. Estuarine, Coastal and Shelf Science 165:185–189.

Janitza, S., C. Strobl, and A.-L. Boulesteix. 2012. An AUC-based permutation variable importance measure for random forests. Department of Statistics: technical reports No.130, LMU Muenchen. http://epub.ub.uni-muenchen.de/14206/

Kelly, D. W., J. R. Muirhead, D. D. Heath, and H. J. MacIsaac. 2006. Contrasting patterns in genetic diversity following multiple invasions of fresh and brackish waters. Molecular Ecology 15:3641–3653.

Kolding, S. 1981. Habitat selection and life cycle characteristics of five species of the amphipod genus Gammarus in the Baltic. Oikos 37:173–178.

Korpinen, S., and M. Westerbom. 2010. Microhabitat segregation of the amphipod genus *Gammarus* (Crustacea: Amphipoda) in the northern Baltic Sea. Marine Biology 157:361–370.

Kotta, J., T. Paalme, T. Püss, K. Herkül, and I. Kotta. 2008. Contribution of scale-dependent environmental variability on the biomass patterns of drift algae and associated invertebrates in the Gulf of Riga, northern Baltic Sea. Journal of Marine Systems 74:S116–S123.

Kotta, J., H. Orav-Kotta, K. Herkül, and I. Kotta. 2011. Habitat choice of the invasive *Gammarus tigrinus* and the native *Gammarus salinus* indicates weak interspecific competition. Boreal Environmental Research 16:64–72.

Kotta, J., M. Pärnoja, T. Katajisto, M. Lehtiniemi, S. A. Malavin, G. Reisalu, and V. E. Panov. 2013. Is a rapid expansion of the invasive amphipod *Gammarus tigrinus* Sexton, 1939 associated with its niche selection: a case study in the Gulf of Finland, the Baltic Sea. Aquatic Invasions 8:319–332.

Lee, C. E. 2002. Evolutionary genetics of invasive species. Trends in Ecology & Evolution 17:386–391.

Lenz, M., et al. 2011. Non-native marine invertebrates are more tolerant towards environmental stress than taxonomically related native species: results from a globally replicated study. Environmental Research 111:943–952.

Leppäkoski, E., S. Olenin, and S. Gollasch. 2002a. The Baltic Sea — a field laboratory for invasion biology. Pages 253–259 *in* E. Leppäkoski, S. Gollasch, and S. Olenin, editors. Invasive aquatic species of Europe. Distribution, impacts and management. Springer, Dordrecht, Netherlands.

Leppäkoski, E., S. Gollasch, P. Gruszka, H. Ojaveer, S. Olenin, and V. Panov. 2002b. The Baltic — a sea of invaders. Canadian Journal of Fisheries and Aquatic Sciences 59:1175–1188.

Liaw, A., and M. Wiener. 2002. Classification and regression by randomforest. R News 2(3):18–22.

Lindegarth, M., et al. 2014. Testing the potential for predictive modeling and mapping and extending its use as a tool for evaluating management scenarios and economic valuation in the Baltic Sea (PREHAB). Ambio 43:82–93.

MacNeil, C., and J. Prenter. 2000. Differential microdistributions and interspecific interactions in coexisting native and introduced *Gammarus* spp. (Crustacea: Amphipoda). Journal of Zoology 251:377–384.

MacNeil, C., D. Platvoet, and J. T. A. Dick. 2008. Potential roles for differential body size and microhabitat complexity in mediating biotic interactions within invasive freshwater amphipod assemblages. Fundamental and Applied Limnology 172:175–182.

Marvier, M., P. Kareiva, and M. G. Neubert. 2004. Habitat destruction, fragmentation, and disturbance promote invasion by habitat generalists in a multispecies metapopulation. Risk Analysis 24:869–878.

McGill, B. J., M. Dornelas, N. J. Gotelli, and A. E. Magurran. 2015. Fifteen forms of biodiversity trend in the Anthropocene. Trends in Ecology & Evolution 30:104–113.

McMahon, R. F. 2002. Evolutionary and physiological adaptations of aquatic invasive animals: r selection versus resistance. Canadian Journal of Fisheries and Aquatic Sciences 59:1235–1244.

Nikolopoulos, A., and M. Isæus. 2008. Wave exposure calculations for the Estonian coast. AquaBiota Water Research AB, Stockholm, Sweden.

Orav-Kotta, H., J. Kotta, K. Herkül, I. Kotta, and T. Paalme. 2009. Seasonal variability in the grazing potential of the invasive amphipod *Gammarus tigrinus* and the native amphipod *Gammarus salinus* in the northern Baltic Sea. Biological Invasions 11:597–608.

Paavola, M., A. O. Laine, M. Helavuori, and P. Kraufvelin. 2008. Profiling four brackishwater harbours: zoobenthic composition and invasion status. Boreal Environment Research 13:159–175.

Packalén, A., S. Korpinen, and K. K. Lehtonen. 2008. The invasive amphipod species *Gammarus tigrinus* (Sexton 1939) can rapidly change littoral communities in the Gulf of Finland (Baltic Sea). Aquatic Invasions 3:405–412.

Pellissier, L., K. A. Bråthen, J. Pottier, C. F. Randin, P. Vittoz, A. Dubuis, G. Yoccoz, T. Alm, N. E. Zimmermann, and A. Guisan. 2010. Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants. Ecography 33:1004–1014.

Pianka, E. R. 1978. Evolutionary ecology. Harper and Row, New York, USA.

Pinkster, S., H. Smit and Brandse-de Jong N. 1977. The introduction of the Alien Amphipod *Gammarus tigrinus* Sexton, 1939, in the Netherlands and its competition with indigenous species. Crustaceana, Supplement No 4:91–105.

Platvoet, D., J. T. A. Dick, C. MacNeil, M. C. van Riel, and G. van der Velde. 2009. Invader–invader interactions in relation to environmental heterogeneity leads to zonation of two invasive amphipods, *Dikerogammarus villosus* (Sowinsky) and *Gammarus tigrinus* Sexton: amphipod pilot species project (AMPIS) report 6. Biological Invasions 11:2085–2093.

Priddis, E., R. Rader, M. Belk, B. Schaalje, and S. Merkley. 2009. Can separation along the temperature niche axis promote coexistence between native and invasive species? Diversity and Distributions 15:682–691.

R Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Revermann, R., H. Schmid, N. Zbinden, R. Spaar, and B. Schröder. 2012. Habitat at the mountain tops: How long can Rock Ptarmigan (*Lagopus muta helvetica*) survive rapid climate change in the Swiss Alps? A multi-scale approach. Journal of Ornithology 153:891–905.

Ridgeway, G. 2012. gbm: Generalized Boosted Regression Models. R package version 1.6-3.2. http://CRAN.R-project.org/package=gbm

Rödder, D., and J. O. Engler. 2011. Quantitative metrics of overlaps in Grinnellian niches: advances and possible drawbacks. Global Ecology and Biogeography 20:915–927.

Roxburgh, S. H., K. Shea, and J. B. Wilson. 2004. The intermediate disturbance hypothesis: patch dynamics and mechanisms of species coexistence. Ecology 85:359–371.

Sala, O. E., et al. 2000. Global biodiversity scenarios for the year 2100. Science 287:1770–1774.

Sareyka, J., P. Kraufvelin, M. Lenz, M. Lindström, R. Tollrian, and M. Wahl. 2011. Differences in stress tolerance and brood size between a non-indigenous and an indigenous gammarid in the northern Baltic Sea. Marine Biology 158:2001–2008.

Savage, A. A. 1982. The survival and growth of *Gammarus tigrinus* Sexton (Crustacea: Amphipoda) in relation to salinity and temperature. Hydrobiologia 94:201–212.

Sax, D. F., et al. 2007. Ecological and evolutionary insights from species invasions. Trends in Ecology & Evolution 22:465–471.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

Scott, J. K., and F. D. Panetta. 1993. Predicting the Australian weed status of southern African plants. Journal of Biogeography 20:87–93.

Segerstråle, S. G. 1957. Baltic Sea. Geological Society of America Memoirs 67:751–800.

Simberloff, D. 2014. The "balance of nature" – evolution of a panchreston. PLoS Biology 12:e1001963.

Steele, V. J., and D. H. Steele. 1972. The biology of *Gammarus* (Crustacea, Amphipoda) in the northwestern Atlantic. VI. *Gammarus tigrinus* Sexton. Canadian Journal of Zoology 50:1063–1068.

Strauss, S. Y., C. O. Webb, and N. Salamin. 2006. Exotic taxa less related to native species are more invasive. Proceedings of the National Academy of Science 103:5841–5845.

Strong, D. R., J. H. Lawton, and T. R. E. Southwood. 1984. Insects on plants: community patterns and mechanisms. Harvard University Press, Cambridge, Massachusetts, USA.

Sultan, S. E. 2001. Phenotypic plasticity for fitness components in *Polygonum* species of contrasting ecological breadth. Ecology 82:328–343.

Svenning, J.-C., and F. Skov. 2004. Limited filling of the potential range in European tree species. Ecology Letters 7:565–573.

ter Braak, C. J. F., and P. F. M. Verdonschot. 1995. Canonical correspondence analysis and related

multivariate methods in aquatic ecology. Aquatic Sciences 57:255–289.

Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human domination of Earth's ecosystems. Science 277:494–499.

Vivanco, J. M., H. P. Bais, F. R. Stermitz, G. C. Thelen, and R. M. Callaway. 2004. Biogeographical variation in community response to root allelochemistry: novel weapons and exotic invasion. Ecology Letters 4:285–292.

Warren, D. L., R. E. Glor, and M. Turelli. 2008. Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution 62:2868–2883.

Williams, J. W., and S. T. Jackson. 2007. Novel climates, no-analog communities, and ecological surprises. Frontiers in Ecology and the Environment 5:475–482.

Wood, S. N. 2006. Generalized additive models: an introduction with R. Chapman and Hall/CRC, Boca Raton, Florida, USA.

Zimmermann, N. E., T. C. Edwards Jr., C. H. Graham, P. B. Pearman, and J.-C. Svenning. 2010. New trends in species distribution modelling. Ecography 33:985–989.

Role of invasive species in the food webs – the cases of the round goby and Harris mud crab

Riikka Puntila, Marine research centre, Finnish environment institute

Non-indigenous species, especially when they become invasive, are known to induce a variety of changes to the ecosystems of their new environments. The impacts of invasive non-indigenous species in aquatic environments often draw attention (e.g., Carlton and Geller 1993, Ricciardi and Rasmussen 1998, Cohen and Webb 2002, Molnar et al. 2008), and the majority of the studies concentrate on the top-down predatory impacts of an invader on native prey. Although many species have both predatory and prey roles in the ecosystem, more comprehensive food web wide impacts of the invasions had been far less studied. In the BONUS BIO-C3, many of the key ecological interactions were studied in detail and here the results are reviewed in the food web context.

The round goby

The invasive round goby, *Neogobius melanostomus*, is known as an aggressive, territorial and voracious benthivorous fish species observed to have profound impacts on ecosystems, especially where numerous (e.g., Dubs and Corkum 1996, Balshine et al. 2005, Almqvist et al. 2010). They are generalist predators but often prefer bivalves when available (Skora and Rzeznik 2001, Karlson et al. 2007, Rakauskas et al. 2008, Raby et al. 2010, Järv et al. 2011). The diets and prey preference of the round goby were studied in BONUS BIO-C3 in several locations throughout the Baltic Sea, representing very different biotic (including prey field) and abiotic conditions (e.g., Oesterwind et al. 2017, Skabeikis and Lesutiene 2015, Nurkse et al. 2016, and others reviewed in Lehtiniemi et al. 2017). In general the studies also show that the feeding behavior of round goby is very flexible and they are preying usually on the most abundant prey and the availability of the prey in each of the locations is therefore reflected to the stomach contents. In areas where bivalves were abundant, they often were the most prevalent prey, but in other locations round gobies willingly feed on other benthic prey such as polychaetes, gastropods, and even barnacles. In Mariehamn, the presence of sticklebacks in the round goby stomachs was elevated (Herlevi et al. in review). Furthermore, the results from the various studies show that round goby undergoes ontogenetic diet shifts and there is both temporal (seasonal) and spatial variation in their prey use. While most studies show no direct prey impact on other fish species a case study in a very important herring spawning site with a combined lab experiment could show that small round goby are able to feed on herring eggs (Wiegleb et al. in prep). When overlapping, the round gobies consume also the other invasive species of interest, Harris mud crabs (Puntila et al. in prep a). In one of the locations (Lithuania), the round goby population was very dense and prey field appeared to be limited (Skabeikis and Lesutiene 2015) leading intraspecific competition and even to cannibalism at times (Puntila et al. in prep a). Finally, prey choice appears to have very little impact on the condition of the fish, indicating that round goby populations are not relying on presence of any specific prey organisms and are capable of maintaining growing populations under very different environmental conditions.

Furthermore, the food web positioning of the round goby comparing a new invasive population in Mariehamn, Åland Islands in the northern Baltic Sea to an older population in the Gulf of Gdansk, Poland showed that overall the round goby positioned as a second order consumer among other predatory benthic-feeding fish. The round goby experiences significant intraspecific competition as well as competition with other predatory fish in the new invasive area. The trophic position of round gobies in Mariehamn is significantly higher than in the Gulf of Gdansk, likely due to different prey items in these areas (e.g., their diet in Mariehamn includes more fish, mostly sticklebacks). Furthermore, the ontogenetic patterns differ between the two invasive populations, suggesting more intraspecific competition in the Gulf of Gdansk. (Herlevi et al. in review).

Previous studies in the Baltic Sea had identified over 30 parasite taxa infecting the invasive round goby. A study comparing parasite assemblages and infection rates (prevalence and intensity) in

different populations across the invasive range in the Baltic Sea (Denmark, Lithuania, Estonia and Finland (Åland Islands)), revealed that infection rates were 56-60 % across all locations except Lithuania (28%)(Herlevi et al. 2016). Most of the parasites were generalists commonly infecting native fish species and the round goby has not retained parasites from its area of origin, but instead has been successively colonized by native generalist parasites reflecting the parasite assemblage at each site. Furthermore, there is small scale variation in parasite assemblages as shown between populations in Estonia (Ojaveer et al. 2017). Although variable, overall parasite richness is still quite low around the Baltic compared to the native areas and similarly prevalence and mean infection intensities in the Baltic Sea are significantly lower than in the native areas.

Furthermore, the role of the round goby as a prey for piscivorous fish and avian predators was studied in different regions in the Baltic Sea. The round goby was found to be prey for cod (*Cadus morhua*), but its significance varied seasonally (Skabeikis et al. in prep). In coastal areas, the most predominant predator was the Eurasian perch (*Perca fluviatilis*) and their proportion in cormorants (*Phalacrocorax carbo sinensis*) diets have also increased (Oesterwind et al. 2017). Furthermore, the presence of round gobies in perch (*Perca fluviatilis*) stomachs has also been noticed in Lithuanian and Estonian coasts (Skabeikis et al. in prep, Liversage et al. 2017).

Competition with native species has been detected with many species as their diets and habitat preferences overlap (e.g., Herlevi et al. in review, Järv et al. 2011). The round goby appears to have impact on the biomass densities of the flounder (*Platichthys flesus*) in Poland (Smolinski 2017). In addition, they seem to compete with the long tailed duck (*Clangula hyemalis*) over preferred prey, bivalves, in Lithuania (Skabeikis et al. in prep).

Based on the results, the round goby has successfully established in the various coastal ecosystems in the Baltic Sea. They are simultaneously both predators for native prey and prey for native predators as well as competitors to some native species. In addition, they are a host for native generalist parasites (Fig 1). In some areas, run down consumption of *Mytilus trossulus* has been reported, which may have cascading impacts in the ecosystem. The interactions with the surrounding ecosystem (e.g., predation and parasites) do not seem to limit the population growth of the round goby and their range and abundance is increasing in most of the locations.
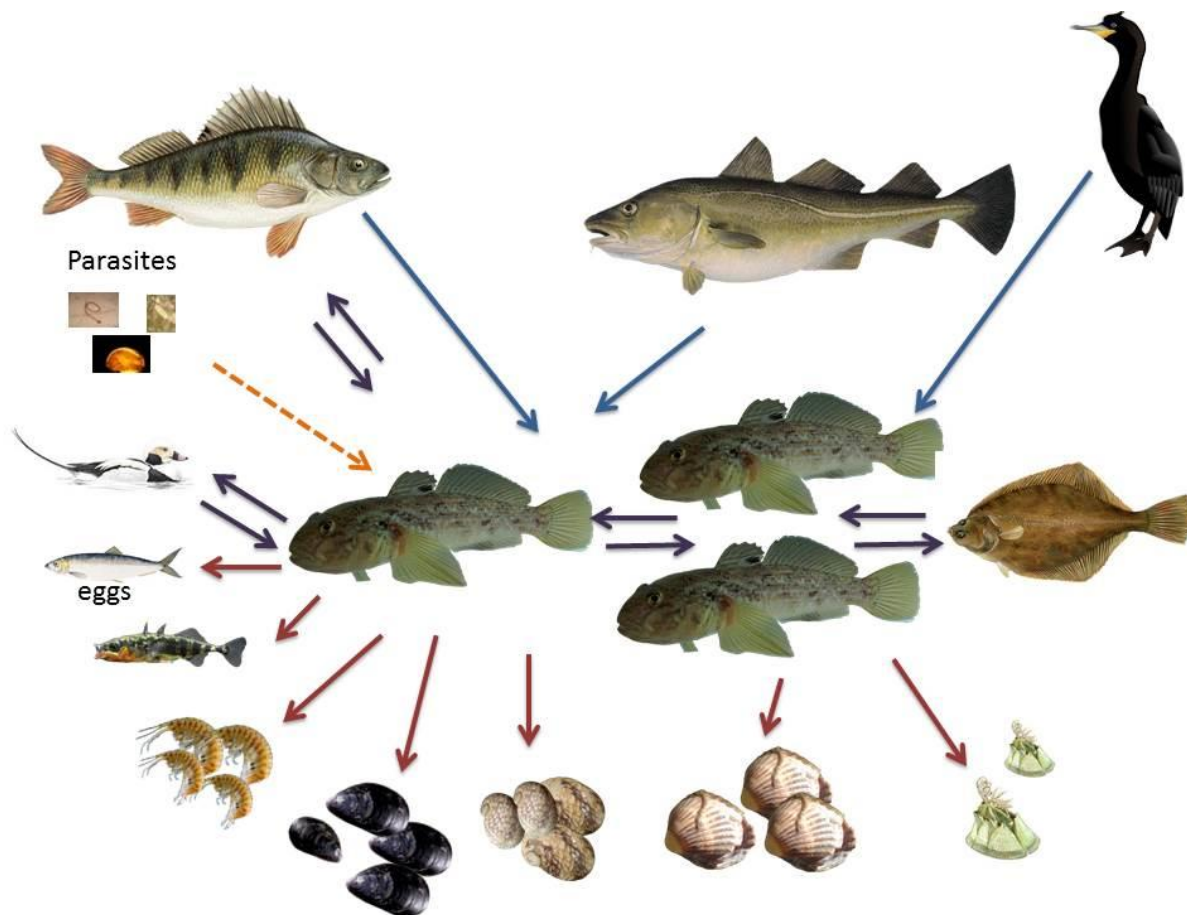
Figure 1. The role of the invasive round goby in the coastal food webs in the Baltic Sea. Red arrows indicate prey consumption, blue arrows role as prey for native predators and purple arrows competition with native species.

The Harris mud crab

The Baltic Sea, especially the northern parts are naturally low in species diversity, which increases the likelihood of obtaining a species that is novel to the system. Good example of a novel non-native species that has settled successfully to the Baltic Sea is the Harris mud crab (*Rhithropanopeus harrisii*). The Harris mud crab was first introduced to the western Baltic in the late 19th century, most likely via ballast originating from the eastern United States. The first observation of the crab in the Baltic Sea was made in the 1930's in the Kiel Channel in Germany (Schubert 1936) and in 1950 in Poland (Demel 1953). In the 2000's, they began to spread northward, and it was recorded in Lithuania in 2000 (Bacevicius and Gasiunaite 2008), Finland in the Archipelago Sea in 2009 (Fowler et al. 2013) and in Estonia 2011 (Kotta and Ojaveer 2012).

The Harris mud crab is highly omnivorous, feeding on detritus and plant material, as well as, mobile crustaceans depending on the habitat they occupy (Turoboyski 1978, Czerniejewski and Rybczyk 2008, Hegele-Drywa and Normant 2009). In their native area, they are mostly scavengers and predation on crustaceans is more common among the small crabs (Odum and Heald 1972). In the Archipelago Sea they have been reported to impact gastropod abundance (Forsström et al. 2015, Jormalainen et al. 2016) and their stable isotope ratio places them mostly among second degree consumers (Aarnio et al. 2015). In the Baltic Sea the crab has invaded many locations with submerged aquatic vegetation (Gagnon and Boström 2016) and associated grazer communities (Nurkse et al. 2015).

Since the establishment in the northern Baltic Sea in Lithuania, Estonia and Finland, the Harris mud crab has steadily increased its range in most locations. The area lacks native crab species, providing an excellent opportunity to observe how a novel species establishes into the local food webs.

Based on recent studies on the diet of the Harris mud crab in the northern Baltic Sea, they appear to preferentially consume mobile crustaceans and gastropods (Nurkse et al. 2015, Forsström et al. 2015, Jormalainen et al. 2016, Puntila et al. in prep b). Results of a mesocosm study, conducted within BONUS BIO-C3 project (reviewed in Lehtiniemi et al. 2017) indicate that the mud crabs predate preferentially and rapidly, on the isopod *Idotea baltica* (Pallas, 1772), one of the key species in the ecosystem. Furthermore, the predation on most of the offered prey was intense even in the lower crab density treatment implying that their predatory impacts in naïve systems may be significant as implied by Jormalainen et al. (2016).

Nearly all non-indigenous species eventually begin experiencing predation by native predators, which may even exert population control on them (e.g., Hunt and Yamada 2003; Jensen et al. 2007). Based on fishermen reports and an extensive field survey the crabs are prey for several fish (perch, pikeperch, four-horned sculpin, burbot, ruffe and bentic feeding cyprinids). Of the species inspected, most crabs were found in the four-horned sculpin stomachs, followed by the perch and roach. Even though the Harris mud crab is prey for many native fish species, their range and abundance is increasing in the Archipelago Sea (Puntila et al. in prep c).

Based on the studies in the area, the Harris mud crab has established in the Archipelago Sea ecosystem and they are both predators and prey in the food web. The implications to the other trophic levels including detritus consumption are still unknown. Run down consumption of grazers may result in impacts on *Fucus vesiculosus*, where grazing is naturally an important phenomenon (Eriksson et al. 2011). The decline in grazing may lead to changes in the algal composition in these hard bottom habitats. Also, the crabs may compete with some local fish species, such as perch and roach, for prey. Furthermore, the crabs are not necessarily a good prey item for the predators: they have hard shells and offer very little energy (Wiszniewska et al. 1998). Slow moving predators such as sculpins may obtain enough of them to justify the feeding on crabs, whereas in stomachs of quick-moving and efficient predators, such as perch, they may take space from better quality prey. Also, the prey currently targeted by the mud crabs traditionally have been prey for the same fish species now preying on the mud crab. Therefore, following the invasion trophic transfer may be less efficient due to the added step in the food web (Hairston Jr. and Hairston Sr. 1993).
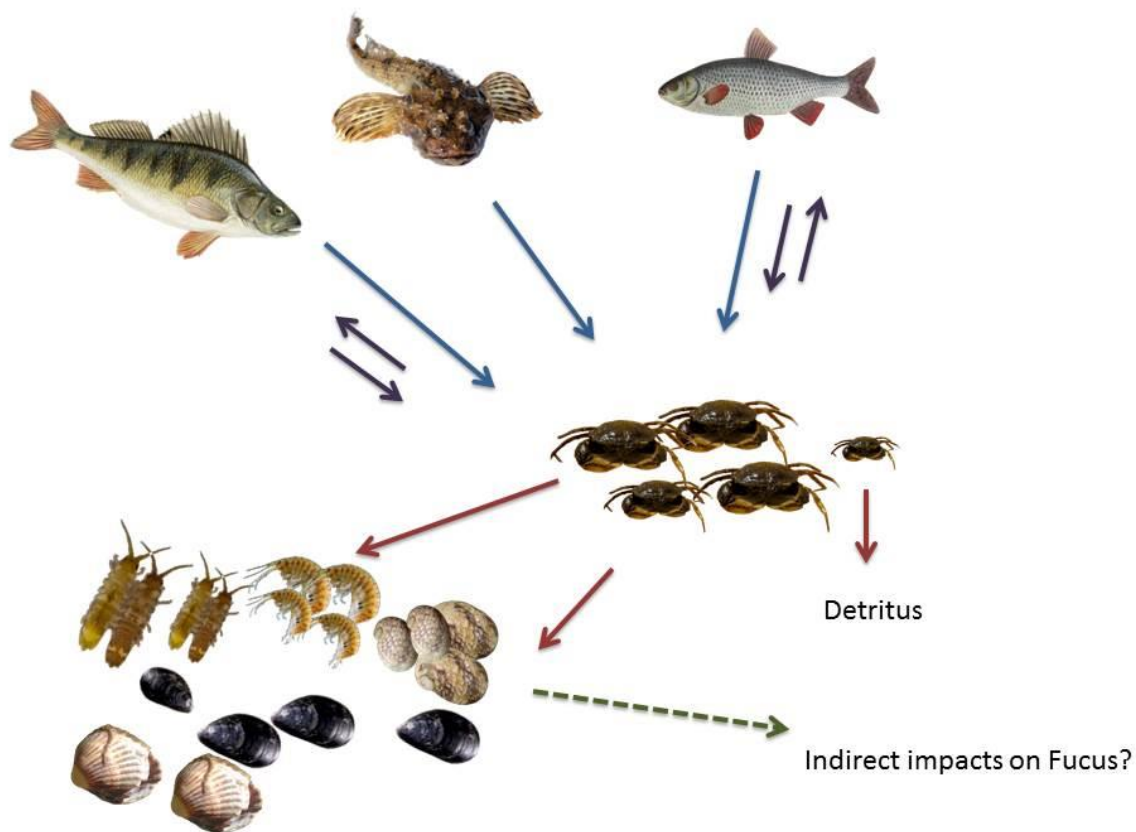
Figure 2 The role of the Harris mud crab in the coastal food web in the northern Baltic Sea. Red arrows indicate prey consumption, blue arrows role as prey for native predators, purple arrows competition with native species and green arrow potential indirect impacts.

Conclusions

Both investigated invasive species, the round goby and the Harris mud crab, have successfully established into their ecosystems and play both predatory and prey roles in the food webs. Their presence has top down impacts on their prey at least locally, leading to both competition with native species and potentially cascading changes in the lower tropic levels. Furthermore, they are prey for native predators adding a new links into the food web, currently with unknown consequences. Further studies will concentrate in modelling the cascading impacts of these growing populations on food web processes such as energy transfer in the different parts of the Baltic Sea.

References

Aarnio, K., A. Törnroos, C. Björklund, and E. Bonsdorff. 2015. Food web positioning of a recent coloniser: the North American Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) in the northern Baltic Sea. Aquatic Invasions 10:399–413.

Almqvist, G., A. K. Strandmark, and M. Appelberg. 2010. Has the invasive round goby caused new links in Baltic food webs? Environmental Biology of Fishes 89:79–93.

Bacevicius, E., and Z. R. Gasiunaite. 2008. Two crab species-Chinese mitten crab (*Eriocheir sinensis* Edw.) and mud crab (*Rhithropanopeus harrisii* (Gould) *ssp. tridentatus* (Maitland) in the Lithuanian coastal waters, Baltic Sea. Transitional Waters Bulletin 2:63–68.

Balshine, S., A. Verma, V. Chant, and T. Theysmeyer. 2005. Competitive interactions between round gobies and logperch. Journal of Great Lakes Research 31:68–77.

Blackburn, T. M., P. Pyšek, S. Bacher, J. T. Carlton, R. P. Duncan, V. Jarošík, J. R. U. Wilson, and D. M. Richardson. 2011. A proposed unified framework for biological invasions. Trends in Ecology & Evolution 26:333–9.

Carlton, J. T., and J. B. Geller. 1993. Ecological roulette: the global transport of nonindigenous marine organisms. Science 261:78–82.

Cohen, A. N., and S. K. Webb. 2002. Biological Invasions in Aquatic Ecosystems : Impacts on Restoration and Potential for Control. Page 30. Proceedings of a Workshop April 25 1998 Sacramento California. San Francisco Estuary Institute, Oakland, California.

Czerniejewski, P., and A. Rybczyk. 2008. Body weight, morphometry, and diet of the mud crab, *Rhithropanopeus harrisii tridentatus* (Maitland, 1874) in the Odra estuary, Poland. Crustaceana 81:1289–1299.

Demel, K. 1953. Nowy gatunek w faunie Baltyku. Kosmos 2:105–106.

DeRivera, C. E., G. M. Ruiz, A. Hines, and P. Jivoff. 2005. Biotic Resistance to Invasion: Native Predator Limits Abundance and Distribution of an Introduced Crab. Ecology 86:3364–3376.

Dubs, D. O. L., and L. D. Corkum. 1996. Behavioral Interactions Beween Round Gobies (*Neogobius melanostomus*) and Mottled Sculpins (*Cottus bairdi*). Journal of Great Lakes Research 22:838–844.

Eriksson, B. K., C. van Sluis, K. Sieben, L. Kautsky, and S. Råberg. 2011. Omnivory and grazer functional composition moderate cascading trophic effects in experimental Fucus vesiculosus habitats. Marine Biology 158:747–756.

Forsström, T., A. E. Fowler, I. Manninen, and O. Vesakoski. 2015. An introduced species meets the local fauna: predatory behavior of the crab *Rhithropanopeus harrisii* in the Northern Baltic Sea. Biological Invasions 17:2729–2741.

Fowler, A., T. Forsström, M. von Numers, and O. Vesakoski. 2013. The North American mud crab *Rhithropanopeus harrisii* (Gould, 1841) in newly colonized Northern Baltic Sea: distribution and ecology. Aquatic Invasions 8:89–96.

Gagnon, K., and C. Boström. 2016. Habitat expansion of the Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) in the northern Baltic Sea: potential consequences for the eelgrass food web. BioInvasions Records 5.

Hairston Jr., N. G., and N. G. Hairston Sr. 1993. Cause-effect relationships in energy flow, trophic structure, and interspecific interactions. The American Naturalist 142:379–411.

Hegele-Drywa, J., and M. Normant. 2009. Feeding ecology of the American crab *Rhithropanopeus harrisii* (Crustacea, Decapoda) in the coastal waters of the Baltic Sea. Oceanologia 51:361–375.

Herlevi, H., R. Puntila, H. Kuosa, and H.-P. Fagerholm. 2016. Infection rates and prevalence of metazoan parasites of the non-native round goby (*Neogobius melanostomus*) in the Baltic Sea. Hydrobiologia 792:265–282.

Herlevi, H., Aarnio, K., Puntila, R., Bonsdorff, E. (in review): The food web positioning and ontogenetic diet shifts of the non-indigenous round goby in a recently established population in a low-diversity system in the northern Baltic Sea.

Järv, L., J. Kotta, I. Kotta, and T. Raid. 2011. Linking the structure of benthic invertebrate communities and the diet of native and invasive fish species in a brackish water ecosystem. Annales Zoologici Fennici 2450:129–141.

Jormalainen, V., K. Gagnon, and E. Rotha. 2016. The invasive mud crab enforces a major shift in a rocky littoral invertebrate community of the Baltic Sea. Biological Invasions 18:1409–1419.

Karlson, A. M. L., G. Almqvist, K. E. Skora, and M. Appelberg. 2007. Indications of competition between non-indigenous round goby and native flounder in the Baltic Sea. Ices Journal of Marine Science 64:479–486.

Kotta, J., and H. Ojaveer. 2012. Rapid establishment of the alien crab *Rhithropanopeus harrisii* (Gould) in the Gulf of Riga. Estonian Journal of Ecology 61:293.

Lehtiniemi M., Bonsdorff E., Funk S., Herlevi H., Huwer B., Jaspers C., Kotta J., Kotterba P., Lesutienė J., Margonski P., Mattern S., Niemax J., Nurkse K., Oesterwind D., Ojaveer H., Puntila R., Skabeikis A., Smoliński S., Temming A., Törnroos A., Warzocha J. (2017) Report assessing the effects of key NIS on ecosystem functioning. BIO-C3 Deliverable, D2.3. EU BONUS BIO-C3, 37 pp + Annex 196 pp.

Liversage, K., K. Nurkse, and J. Kotta. 2017. The interaction of perch and round goby involves characteristics of physical environment and macrophyte habitat. The Book of Abstracts from the BONUS Symposium.

Molnar, J. L., R. L. Gamboa, C. Revenga, and M. D. Spalding. 2008. Assessing the global threat of invasive species to marine biodiversity. Frontiers in Ecology and the Environment 6:485–492.

Nurkse, K., J. Kotta, H. Orav-Kotta, and H. Ojaveer. 2016. A successful non-native predator, round goby, in the Baltic Sea: generalist feeding strategy, diverse diet and high prey consumption. Hydrobiologia.

Nurkse, K., J. Kotta, H. Orav-Kotta, M. Pärnoja, and I. Kuprijanov. 2015. Laboratory analysis of the habitat occupancy of the crab *Rhithropanopeus harrisii* (Gould) in an invaded ecosystem: The north-eastern Baltic Sea. Estuarine, Coastal and Shelf Science 154:152–157.

Odum, W. E., and E. J. Heald. 1972. Trophic Analyses of an Estuarine Mangrove Community. Bulletin of Marine Science 22:671–738.

Oesterwind, D., C. Bock, A. Förster, M. Gabel, C. Henseler, P. Kotterba, M. Menge, D. Myts, and H. M. Winkler. 2017. Predator and prey: the role of the round goby *Neogobius melanostomus* in the western Baltic. Marine Biology Research 13:188–197.

Ojaveer, H., A. Turovski, and K. Nurkse. 2017. Parasite infestation of the round goby in two localities in the NE Baltic Sea. The Book of Abstracts from the BONUS Symposium.

Puntila, R., Herlevi, H., Arciszewski, B., Lozys, L., Behrens, J. and Ojaveer, H. (in prep a): Feeding preferences of the invasive Round goby (*Neogobius melanostomus*) in the Baltic Sea.

Puntila R., Fowler A., Riipinen K., Vesakoski O. & Lehtiniemi M. (in prep b): Invasive Harris mud crab (*Rhithropanopeus harrisii*) prefers isopod prey in the Northern Baltic Sea.

Puntila, R., Loisa, O., Fowler, A. & Riipinen, K. (in prep c): A taste for aliens? Incorporation of a novel prey item into native fishes diet.

Raby, G. D., L. F. G. Gutowsky, and M. G. Fox. 2010. Diet composition and consumption rate in round goby (*Neogobius melanostomus*) in its expansion phase in the Trent River, Ontario. Environmental Biology of Fishes 89:143–150.

Rakauskas, V., E. Bacevičius, Ž. Pūtys, L. Ložys, and K. Arbačiauskas. 2008. Expansion, Feeding and Parasites of the Round Goby, *Neogobius melanostomus* (Pallas, 1811), a recent invader in the Curonian Lagoon, Lithuania. Acta Zoologica Lituanica 18:180–190.

Reise, K., S. Olenin, and D. W. Thieltges. 2006. Are aliens threatening European aquatic coastal ecosystems? Helgoland Marine Research 60:77–83.

Ricciardi, A., and J. B. Rasmussen. 1998. Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Canadian Journal of Fisheries and Aquatic Sciences 55:1759–1765.

Sakai, A. K., F. W. Allendorf, J. S. Holt, M. Lodge, J. Molofsky, K. A. With, R. J. Cabin, J. E. Cohen, C. Norman, D. E. Mccauley, P. O. Neil, M. Parker, J. N. Thompson, and S. G. Weller. 2001. The Population Biology of Invasive Species. Annual Review of Ecology and Systematics 32:305–332.

Schubert, K. 1936. *Pilumnopeus tridentatus* Maitland, eine neue Rundkrabbe in Deutschland. Zoologischer Anzeiger 116:320–323.

Skabeikis, A., and J. Lesutiene. 2015. Feeding activity and diet composition of round goby (*Neogobius melanostomus*) in the coastal waters of SE Baltic Sea. Oceanological and Hydrobiological Studies 44:508–519.

Skabeikis, A., J. Lesutienė, and R. Morkūnė et al. An effect of round goby invasion to mussel beds and its consequences to winter diet of the long-tailed duck. In prep.

Skora, K. E., and J. Rzeznik. 2001. Observations on Diet Composition of *Neogobius melanostomus* Pallas 1811 (Gobiidae, Pisces) in the Gulf of Gdansk (Baltic Sea). Journal of Great Lakes Research 27:290–299.

Turoboyski, K. 1978. Biology and ecology of the crab *Rhithropanopeus harrisii ssp. tridentatus*. Marine Biology 23:303–313.

Wiszniewska, A., A. Rychter, and A. Szaniawska. 1998. Energy value of the mud crab *Rhithropanopeus harrisii ssp. tridentatus* (Crustacea, Decapoda) in relation to season, sex and size. Oceanologia 40:231–241.

Predicted impacts of changes in intensity of eutrophication on future carrying capacity of the Gulf of Riga

Henrik Skov & Erik Kock Rasmussen - DHI

Abstract:

DHI's downscaled benthic-pelagic food-web model for the Gulf of Riga (GoR) has been applied in hindcast and forecast mode to study the past and future levels of nutrient control of the carrying capacity of macrobenthos (bivalves) in coastal areas of the Baltic Sea. The model data were analysed using one climate scenario and two eutrophication scenarios (reference/Baltic Sea Action Plan (BSAP)) from BONUS Ecosupport. The model data covered the period between 1970 and 2100. The impact was assessed by analysing spatio-temporal trends in modelled concentrations of dissolved nutrients and chl *a* and in the biomass of two species of bivalves (*Mytilus edulis, Macoma baltica*) which dominate the overall zoobenthic biomass in the region. A steep decline (0.0085 mg/l per year) in the concentration of dissolved inorganic nitrogen (DIN) and a moderate decline (0.00015 mg/l per year) in the concentration of inorganic phosphorus (DIP) was predicted in the BSAP scenario between 1990 and 2020. After 2020, the concentration of DIN stabilised, whereas the concentration of DIP showed a weak but continuous downward trend. The decreasing trends in nutrient concentrations during this period for the reference scenario were predicted to be approximately 30% less steep than in the BSAP scenario. During the period between 1990 and 2020, a descending trend (0.075 mg/l per year) in the concentration of chl *a* was predicted for the BSAP scenario and a slightly weaker downward trend (0.050 mg/l per year) was predicted for the reference scenario. In the BSAP scenario the downward trend in chl *a* concentrations continued after 2020. The biomass of *Mytilus* bivalves was predicted to decline in the reference scenario over the whole period, but intensified after 2050. During the BSAP scenario, the decline in predicted *Mytilus* biomass started earlier and amplified the trend in the reference scenario. By 2020, the level of *Mytilus* biomass in the BSAP scenario was predicted to be 70% of the biomass in 2008. No clear trend was identified in the predicted biomass of *Macoma* during the period. A spatial assessment of the predicted dramatic decline in the carrying capacity of *Mytilus* revealed that the decline will be focused on the Gulf of Riga rather than the Irbe Strait and the coastal areas west of the Gulf.

Introduction:

A fine-scale ecosystem model complex has been set up in BIO-C3 for the Gulf of Riga covering the period between 1970 and 2100 (Rasmussen et al. 2015, Figure 1). Reconstruction of past ecosystem changes in the Gulf (WP 4.2) revealed nutrient-driven localised decline in productivity affecting the entire benthic food web after mid 1990es. One of the main aims of the study has been to project key functional interactions in the benthic-pelagic food web to future scenarios based on large-scale models developed and executed in the BONUS Ecosupport project (Meier et al. 2011). The climate scenario A1B_1 with two eutrophication scenarios were used as meterological drivers and boundary conditions with DHI's ecosystem model. By comparing trends from a reference scenario with nutrient loads from 2007 with trends from a scenario with the implementation of the BSAP we anticipated to be able to determine the relative contribution of the BSAP to eutrophication control

and declining supply of nutrients during the 21st century. The model data covered the period between 1970 and 2100.
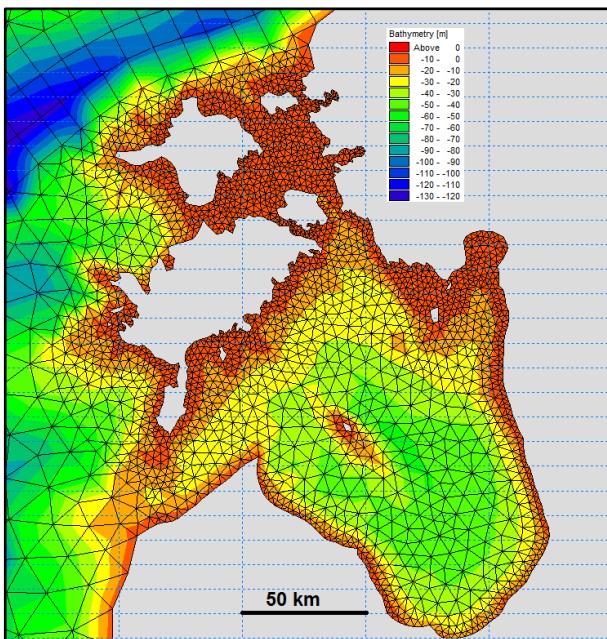

Figure 1. The model area in the Gulf of Riga. Applied bathymetry and model grid are shown.

Progress and next steps:

Analyses completed. No deviations.

Methods and Results:

The ecosystem model complex for the Gulf of Riga consists of three interlinked components; an eutrophication model based on a coupled local biophysical and ecosystem model (MIKE 3 FM & ECOLAB), a mussel population model and a seaduck energetics module. The eutrophication model describes the benthic ecosystem with phytoplankton, nitrogen (N) and phosphorus (P), chlorophyll-a, zooplankton, detritus (C, N & P), inorganic nutrients (dissolved inorganic nitrogen—DINNH4 N, NO3 N & PO4–P), total N and P nutrients (including dissolved organic N and P compounds) and dissolved Oxygen.

Weekly estimates of concentrations of dissolved inorganic nitrogen, inorganic phosphorus and chlorophyll *a* and estimates of the biomass (g DW soft tissue/m^2) of blue mussels (*Mytilus edulis*) and Baltic clams (*Macoma baltica*) were extracted and the spatio-temporal trends analysed. As benthic productivity patterns typically show seasonal trends superimposed on spatial gradients the derivation of long-term trends in spatial structure and biomass was undertaken by analysing temporal trends on deseasoned biomass values at the scale of each grid node (5 km). Deseasoning was done by subtracting the long-term average from each weekly estimate and standardising the resulting value to anomaly z-scores by dividing by the standard deviation. The non-parametric Median Trend (Theil 1950, Hoaglin et al. 2000) test was used to compute the size and significance of the trend for each of the 3040 grid nodes, which subsequently could be visualised to identify

zones with similar trends. This is a robust non-parametric trend operator, which is highly recommended for assessing the rate of change in noisy time series, as it is less sensitive to outliers than least-squares estimators . The trend is calculated by the median value of the slope between every pairwise combination. The Median Trend test was applied for the entire 92-year time series between 2008 and 2099.

Synchronous trends were predicted for both model scenarios across ecosystem components during the century. A steep decline (0.0085 mg/l per year) in the concentration of dissolved inorganic nitrogen (DIN) and a moderate decline (0.00015 mg/l per year) in the concentration of inorganic phosphorus (DIP) was predicted in the BSAP scenario between 1990 and 2020 (Figure 2). The predicted levels of nutrient concentrations in early 2000s are in line with measurements, as is the predicted decline in the concentration of nitrogen (Skov 2017). After 2020, the concentration of DIN stabilised, whereas the concentration of DIP showed a weak but continuous downward trend. The decreasing trends in nutrient concentrations during this period for the reference scenario were predicted to be approximately 30% less steep than in the BSAP scenario. During the period between 1990 and 2020, a descending trend (0.075 mg/l per year) in the concentration of chl *a* was predicted for the BSAP scenario and a slightly weaker downward trend (0.050 mg/l per year) was predicted for the reference scenario. In the BSAP scenario the downward trend in chl *a* concentrations continued after 2020. The biomass of *Mytilus* bivalves was predicted to decline in the reference scenario over the whole period, but intensified after 2050 (Figure 3). During the BSAP scenario, the decline in predicted *Mytilus* biomass started earlier and amplified the trend in the reference scenario. By 2020, the level of *Mytilus* biomass in the BSAP scenario was predicted to be 70% of the biomass in 2008. No clear trend was identified in the predicted biomass of *Macoma* during the period. A spatial assessment of the predicted dramatic decline in the carrying capacity of *Mytilus* revealed that the decline will be focused on the Gulf of Riga rather than the Irbe Strait and the coastal areas west of the Gulf (Figure 4).

Recommendations:

The model predictions for the development of the benthic ecosystem in the Gulf of Riga indicated significant impacts of the continued control of eutrophication and derived reductions in nutrient concentrations. With the implementation of the mitigation measures through the BSAP these impacts will be amplified with a knock-on effect on the carrying capacity of bivalves, most notably blue mussels in the part of the model area focused on the Gulf of Riga. Obviously, local ecosystem models like this one for the Gulf of Riga may provide useful decision support tools in order to achieve future synergies between targets for water quality and biodiversity conservation in many coastal areas of the Baltic Sea.
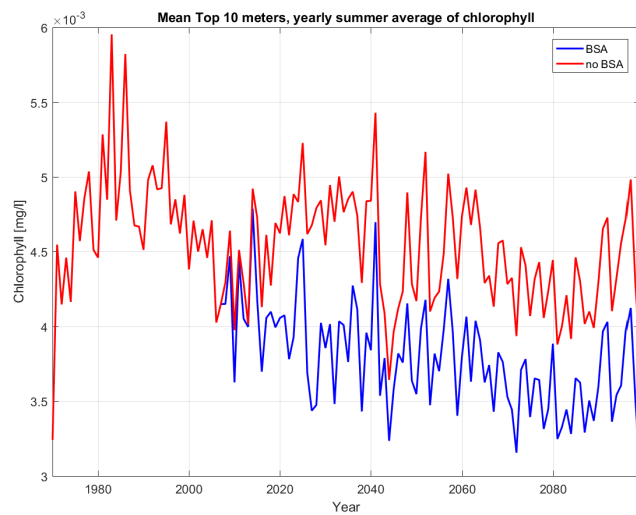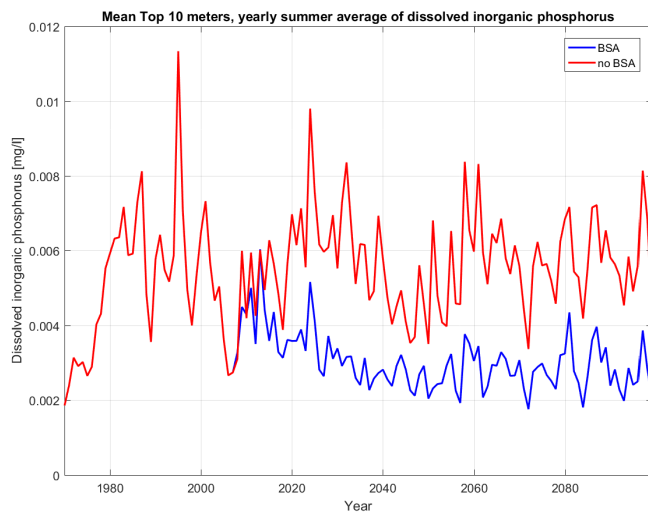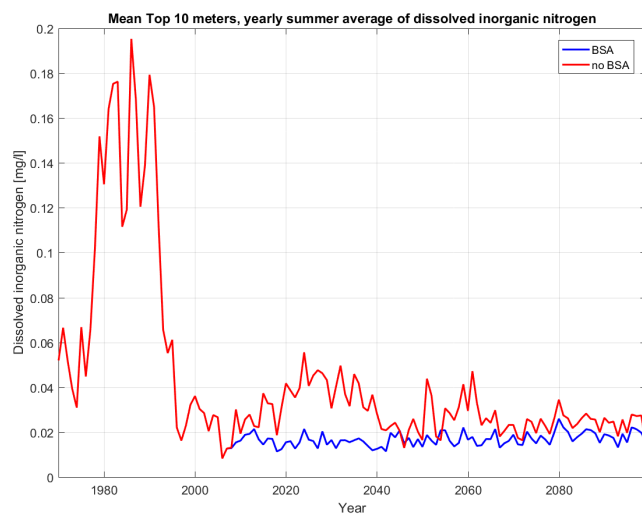
Figure 2. Trends in modelled concentrations (mg/l) of dissolved inorganic nitrogen and phosphorus and Chlorophyll a in the Gulf of Riga during the period 1970-2100 – both the BSAP and the reference (noBSA) scenarios.
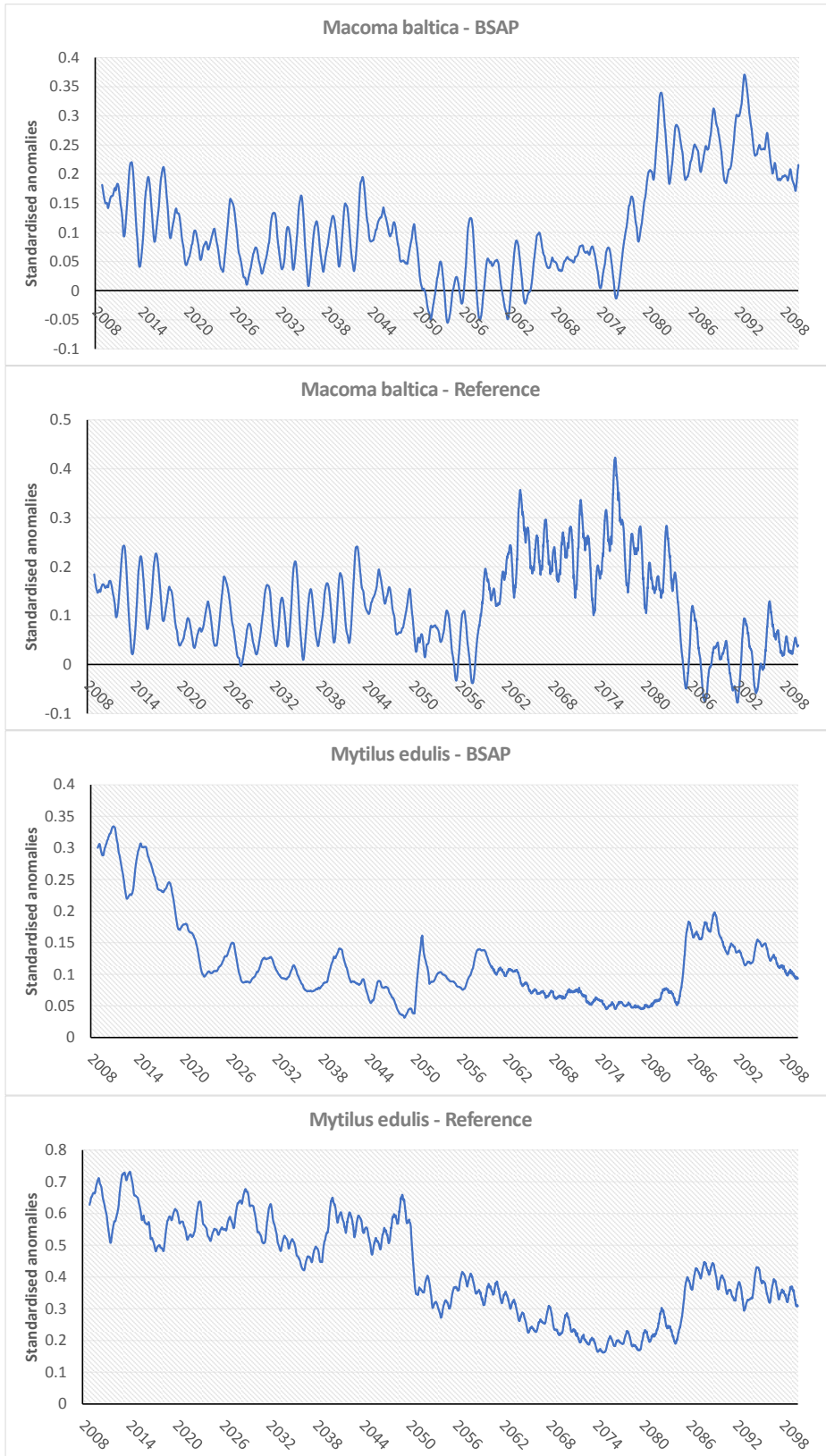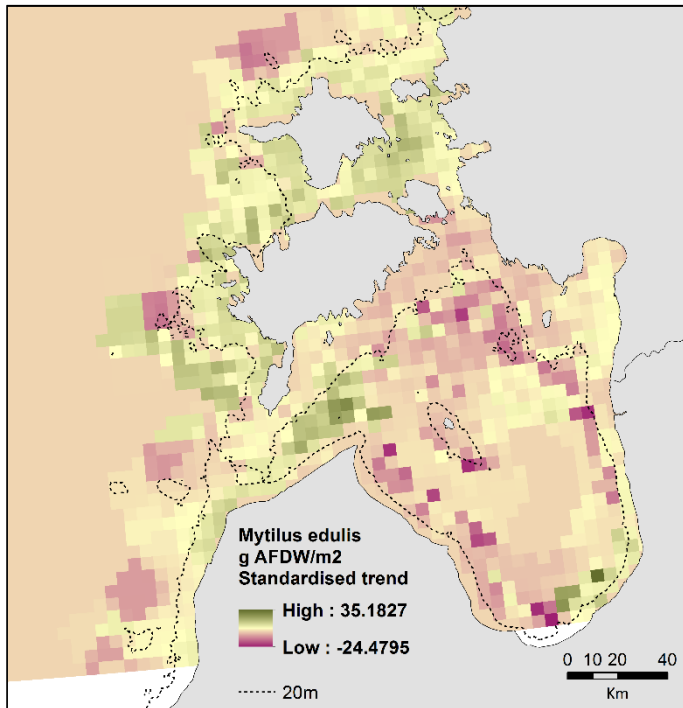
Figure 3. Modelled trends in biomass of Macoma baltica *and* Mytilus edulis *during the period 2008-2100 for the BSAP and the reference scenarios. Biomass values (g AFDW/m²) have been transformed to standardised anomalies.*

Figure 4. Spatio-temporal trends in modelled biomass of Mytilus edulis in the Gulf of Riga during the period 2008-2100. Z-scores of the Theil-Sen tests are shown. High positive value means that the mussel biomass increase significantly and negative values reductions in biomass is predicted.

Hoaglin, D.C., Mosteller, F., & Tukey, J.W. 2000. Understanding Robust and Exploratory Data Analysis. Wiley Classics Library Edition, New York, Wiley.

Meier, H. E. M., Höglund, A., Döscher, R., Andersson, H., Löptien, U., Kjellström, E., 2011. Quality assessment of atmospheric surface fields over the Baltic Sea of an ensemble of regional climate model simulations with respect to ocean dynamics. Oceanologia, 193–227.

Rasmussen, E.K. Zydelis, R., Uhrenholdt, T. & Middelboe, A. 2015. The bottom to top consumer modelling complex. In: Winder, M. (Ed.) Report on effects of changing drivers on pelagic and benthic species composition and production. Deliverable 2.1 from Bonus-BIO-C3.

Skov 2017. Pollution - nutrients. In: Oesterwind, D. (Ed.) Review on (existing knowledge of) patterns and dynamics of drivers of biodiversity (species, communities, habitats) across Baltic Sea ecosystems in space and time including socio-economy.. Deliverable 3.1 from Bonus-BIO-C3.

Theil, H. 1950. A rank-invariant method of linear and polynomial regression analysis. I, II, III", Nederl. Akad. Wetensch., Proc., 53, 386–392, 521–525, 1397–1412.

REABIC

Research Article

Food web positioning of a recent coloniser: the North American Harris mud crab *Rhithropanopeus harrisii* (Gould, 1841) in the northern Baltic Sea

Katri Aarnio*, Anna Törnroos, Charlotta Björklund and Erik Bonsdorff

Environmental and Marine Biology, Department of Biosciences, Åbo Akademi University, Artillerigatan 6, FI-20520 Turku, Finland

E-mail: *katri.aarnio@abo.fi (KA), anna.m.tornroos@abo.fi (AT), cbjorklu@abo.fi (CB), erik.bonsdorff@abo.fi (EB)*

*Corresponding author

Abstract

Identifying resource use and functional traits of non-indigenous species are promising means to increase the ability to predict ecological consequences of invasions. One of the most widely spread brachyuran crab species, and a recent invader in the northern Baltic Sea, is the North American Harris mud crab, *Rhithropanopeus harrisii* (Gould, 1841). Although spread, establishment, and population structure have been studied for this species, little is known about its role and impact in a new environment. We investigated the position and role of *R. harrisii* in the coastal food web by combining spatial and temporal estimates of trophic position using stable isotopes (δ^{13}C and δ^{15}N), with short-term food- and habitat-choice experiments. We observed a stable pattern in the trophic position between two environmentally different locations in the Archipelago Sea over the production season. The identification of a natural breakpoint in carbon stable isotopes at the size of 12 mm carapace width suggested a presence of an ontogenetic diet shift, which was confirmed by isotope signatures positioning large *R. harrisii* among secondary consumers and small individuals with primary consumers. The generalist consumer nature of *R. harrisii* and preference for structured habitat was supported by an active habitat and food choice, revealing no preference for prey species (polychaetes versus amphipod), but selection of brown algae over bare mud. To broaden the understanding of the functional role of *R. harrisii*, we combined our findings with other known biological and ecological traits of the species and qualitatively compared these to characteristics of other benthic organisms in the northern Baltic Sea, suggesting a general similarity in traits.

Key words: introduced species, feeding, habitat choice, stable isotopes, biological traits, experiment

Introduction

Human-mediated species introductions are a continuing threat to both terrestrial and marine biodiversity and thus an important part of global change (Strayer 2012; Simberloff et al. 2013; Jeschke et al. 2014). To increase our ability to predict ecological changes due to non-native species introductions, invasion ecology needs to move beyond descriptive cataloguing of establishment and impact studies and to a more mechanistic understanding and quantification of invader effects (Dick et al. 2014; Paterson et al. 2015). The most promising efforts to generalise mechanisms have focused on how non-indigenous species alter communities and ecosystems through resource use (Vitousek 1990; Parker et al. 1999; Dick et al. 2014). Differences in resource use, such as food or habitat, are reflected in practically all of the

29 hypotheses designed to explain invasion success summarised by Catford et al. (2009). For many of these hypothesis, a major factor that influence invasion success is related to the biological characteristics of the invading species and/or species in the recipient community (Catford et al. 2009; Dick et al. 2014). Recent progress in comparisons of species traits between invaders and natives is encouraging in assessing establishment and spread of invaders (Dick et al. 2014), particularly for terrestrial plant species (Van Kleunen et al. 2010) and to some degree for fish (Marchetti et al. 2004), but still remains patchy (Hayes and Barry 2008; Dick et al. 2014). Moreover, characterising and quantifying traits of non-native species to specifically assess impact is also emerging (Dobb et al. 2014; Paterson et al. 2015). In one study, a comparison between marine invasive invertebrates in only one trait, size,

revealed effects on the invading species itself (Grosholz and Ruiz 2003). Gribben et al. (2013) examined several traits in a biogeographic evaluation of the porcelain crab *Petrolisthes elongatus* (H. Milne-Edwards, 1837) while Gothland et al. (2014) described biological traits related to colonisation and distribution Asian shore crab *Hemigrapsus takanoi* Asakura and Watanabe, 2005. The current gap in the use of species' ecological knowledge between invasion ecology and other ecological fields is interesting because trait-based approaches have proven successful for disentangling marine biodiversity-ecosystem functional linkages (Solan et al. 2006), macroecological patterns (Webb et al. 2009), and anthropogenic impacts (Bremner et al. 2006; de Juan et al. 2007; Villéger et al. 2010).

Some mesohaline habitats, particularly in higher latitude areas, are characterized by relatively low species numbers and relatively weak interspecific competition interactions, which provides the opportunity for colonization by non-indigenous species (Cohen and Carlton 1998; Stachowicz et al. 2002). The Baltic Sea has abiotic and biotic conditions seemingly ideal for establishment of introduced species (Paavola et al. 2005; Gollash and Leppäkoski 2007; Leppäkoski et al. 2009). This mainly brackish (salinity 0.5–20) water body is geologically young (< 10,000 years), with a biota consisting of post-glacial immigrants (Bonsdorff 2006; Leppäranta and Myrberg 2009). Native species diversity is low, which results in simple food webs with relatively few links (Bonsdorff and Blomqvist 1993; Elmgren and Hill 1997). To date, 119 non-indigenous species have been found in the Baltic Sea, of which 20 species have been reported in the northern Baltic Sea and the Archipelago Sea area (David et al. 2013), which is the region of focus in this study. One of the more recent invaders in the northern Baltic Sea is the North American Harris mud crab, *Rhithro-panopeus harrisii* (Gould, 1841). The species is a small (adult maximum carapace width 25 mm) brachyuran crab that tolerates a wide range of temperatures (4–35°C) and salinities (0.5 to >40) (Costlow et al. 1966; Forward 2009). The native range of *R. harrisii* extends along the Atlantic coast of North America from the Gulf of St Lawrence in Canada to Veracruz in the Gulf of Mexico, where it occupies a wide variety of substrates and habitats in river mouths and estuaries (Williams 1984; Fowler et al. 2013). The species was already known in Europe in 1874, probably arriving in ballast water. *R. harrisii* was first found in the southern Baltic Sea in the 1950s, where it has since become established (Turoboyski 1973; Hegele-Drywa and Normant 2014). In the Archipelago Sea, *R. harrisii* was first recorded in 2009, and it has since established reproducing populations in more than 80 locations within a 30 km radius of the site of initial colonization (Fowler et al. 2013). Apart from the occasional adult Chinese mitten crab (*Eriocheir sinensis* H. Milne-Edwards, 1853) (Anger 1991), there were no other crab species in the northern Baltic Sea prior to the arrival of *R. harrisii* (Ojaveer et al. 2007).

The establishment and spread of *Rhithropanopeus harrisii* globally and in the Baltic Sea is well catalogued, but few studies have assessed the impact of this species on the recipient community and ecosystem. Similar to other non-indigenous crab species (e.g., Goodenough 2010; Brockernhoff and McLay 2011), there is clear evidence of competition between *R. harrisii* and native crabs and benthivorous fishes at sites in Europe and on the west coast of North America (Cohen and Carlton 1995; Zaitsev and Öztürk 2001). The species also alters the local food webs because *R. harrisii* is both a predator on, and prey for, native species (Turoboyski 1973; Cohen and Carlton 1995; Zaitsev and Öztürk 2001; Fowler et al. 2013). *R. harrisii* is an opportunistic omnivore that feeds on a mixture of animals, vegetation, and detritus (Turoboyski 1973; Czerniejewski and Rybczyk 2008; Hegele-Drywa and Normant 2009). As in its native range, the species occupies a diverse array of substrates in the northern Baltic Sea, including: bare soft sediment, stones, decaying reeds (*Phragmites australis* (Cav.) Trin. ex Steud.), brown algae (*Fucus vesiculosus* Linnaeus, 1753) and other vegetation that provide both protection and a high density and rich variety of prey (Fowler et al. 2013; Nurkse et al. 2015).

The overall aim of this study was to investigate the trophic position and role of *Rhithropanopeus harrisii* in the coastal food web of the northern Baltic Sea. We addressed this by combining spatial and temporal estimates of trophic position of *R. harrisii* with short-term habitat- and food choice experiments. More specifically, we wanted to: i) determine ontogenetic differences in trophic position of *R. harrisii*; ii) assess temporal variability of the species' consumer characteristics; and iii) identify whether *R. harrisii* displays an active choice for selected substrates and prey species. We then qualitatively compared the known biological and ecological traits of *R. harrisii* to other benthic organisms in the northern Baltic Sea as a means of evaluating the

effects of introduction of *R. harrisii* on ecosystem structure and functioning.

Acknowledging that the diet of generalist predators rely on the spatial and temporal availability of food items (Evans 1983), we assessed trophic position of Harris mud crab by investigating variability in stable isotopes ratios (^{13}C:^{12}C and ^{15}N:^{14}N, expressed as $\delta^{13}C$ and $\delta^{15}N$) (Peterson and Fry 1987). Earlier studies (e.g. Nordström et al. 2009, 2010; Karlson et al. 2015) demonstrated spatial and temporal differences in food web structure between various shallow coastal habitats in the northern Baltic Sea. Therefore, we focused our work on two habitats that differed with respect to wave exposure and substrate. To accommodate potential temporal differences during the productive season, we conducted field sampling in both early and late summer. We hypothesized that the two populations of *R. harrisii* would experience somewhat different food availability, which could reveal the plasticity of the species in their food web positioning. In accordance with present knowledge about the species' use of resources, we hypothesised that *R. harrisii* individuals would actively choose prey and favour a structurally more complex and potentially more sheltering habitat over bare substrate.

Methods

Trophic positioning through stable isotope analysis

To assess trophic position, we collected *Rhithropanopeus harrisii* individuals, fish, benthic infauna and epifauna, vascular plants, algae, and detritus from two localities in the Archipelago Sea in June and August 2012. Sampling sites were located 30 km apart in the inner archipelago zone, with a salinity of 5–6 and depth of 1–2 m. The two sites differed markedly in terms of wind and wave exposure as well as the composition of the bottom substrate. Sampling station 1 (Tuorla: 60°40′77″N; 22°44′29″E) was situated in a narrow and shallow strait in the inner archipelago, where vegetation along the shores were dominated by the European common reed *Phragmites australis*. The bottom consisted of mud, which was covered by decaying reeds, and the sediment was sometimes hypoxic under the overlying vegetation. Sampling station 2 (Lempisaari: 60°49′04″N; 21°77′90″E) was situated further out in the archipelago, still surrounded by islands but leaving it more exposed to wind and wave action. Perennial brown algae (*Fucus vesiculosus*) and common reed dominated

the vegetation in the area. The bottom consisted of mud and clay, covered by a layer of loose drifting *F. vesiculosus*.

Sampling of *R. harrisii* was accomplished using wire traps filled with shells or pieces of clay pots that allowed crabs to move in and out freely (Fowler et al. 2013). Some of the crabs at station 2 were collected by hand from drifting stands of *F. vesiculosus*. Fish were collected from some of the crab traps, and additional fish samples were collected with a wire fish-trap (20 mm mesh size). Epi- and in-faunal benthic invertebrates were sampled using an Ekman-Birge grab and push-nets. Plant material and algae were sampled with push-nets and rakes. Thirty two taxa (plants, invertebrates, and fish) were sampled in this study: 26 taxa from station 1 and 24 taxa at station 2, with 18 taxa in common (Table 1).

All samples were frozen as soon as possible and stored at -20 °C for subsequent analyses. In the laboratory, crabs were measured (carapace width, CW in mm), and the sex was determined if possible. The smallest crab for which we could determine to sex was 7 mm CW. However, sex was not determined for many crabs collected in June (station 1: 40 individuals; station 2: 50 individuals). These crabs were mostly 4–10 mm CW.

Depending on the size of the crab, claw muscle tissue, whole claws, or the whole individual was used for analysis of carbon (^{13}C/^{12}C) and nitrogen (^{15}N/^{14}N) stable isotopes. Muscle tissue was used from fish and the Baltic prawn *Palaemon adspersus* Rathke, 1837. Specimens of epi- and in-faunal benthic invertebrates were analysed whole, except bivalves and gastropods for which shell-free soft tissues were used. Three to five individuals were sampled from each species. All samples were treated with 1 M HCl to remove carbonates. The animal material was dried at 60 °C for 48 h, crushed to a powder in a mortar, and 1 (± 0.2) mg of the sample put into tin capsules for analysis. Plant material was dried, crushed to a powder, and 2–3 mg of the powder was put into tin capsules for analysis. The samples were sent to the Stable Isotope Facility of the University of California, Davis (California, USA) for analysis of carbon and nitrogen stable isotope ratios.

Habitat- and food choice experiments

The individuals of *R. harrisii* used in the laboratory experiments were collected two weeks prior to the experiments and were kept in 30 L aquaria filled with seawater (15 °C, salinity 5.5) and equipped with an aerating system. Pieces of

Table 1. List of sampled foodweb components found on Station 1 and Station 2 in 2012. A species/food web component found in only one station is indicated in bold.

Secondary consumers:	Station 1	Station 2
Rhithropanopeus harrisii	x	x
Palaemon adspersus	x	x
Perca fluviatilis	x	x
Gymnocephalus cernuus	**x**	
Gobius niger	x	x
Pomatoschistus minutus	x	x
Pungitus pungitus	**x**	
Rutilus rutilus	x	
Tinca tinca	x	x
Abramis brama	**x**	x
Blicca bjoerkna	**x**	
Scardinius erythrophthalmus	**x**	
Primary consumers:		
Asellus aquaticus	x	x
Gammarus sp.	x	x
Marenzelleria **sp.**		**x**
Hediste diversicolor		**x**
Macoma balthica	x	x
Mya arenaria		**x**
Mytilus edulis		**x**
Theodoxus fluviatilis	x	x
Lymnea stagnalis	x	x
Bithynia tentaculata	x	x
Chironomidae	x	x
Ephemeroptera	x	x
Odonata	x	x
Tricoptera	**x**	
Primary producers:		
Ceratophyllym demersum	x	x
Myriophyllum **sp.**	**x**	
Cladophora glomerata	x	x
Enteromorpha intestinalis	**x**	
Fucus vesiculosus (**apikal and**		**x**
basal)		**x**
Epiphytes (on *F. vesiculosus*)		
Detritus	x	x
Decaying *Phragmites australis*	**x**	

clay-pots were added to the aquaria to provide shelter for the crabs, and the individuals were fed frozen chironomids and clams (*Macoma balthica* (Linnaeus, 1758)) during this time. Individuals were fasted for 24 hours prior to the experiments. Both male and female crabs (mean ± SE CW: 16.1 ± 0.32 mm; range: 8.4 to 21.4 mm; n = 60) were used in the experiments but no distinction was made between the two sexes in experiments.

The habitat- and food-choice experiments were conducted in Y-shaped aquaria, which allows for a combination of two resources to be presented to the individual crab simultaneously (Bonsdorff and Vahl 1982). We used two experimental aquaria (basal area: 40 × 16 cm; each arm area: 33 × 10 cm; water height: 8 cm; water volume: 6 L) to conduct trials. A trial consisted of a combination of either two resources or a resource and a control (three possible combinations), and was repeated 15 times. Experimental trials were randomised between the two aquaria, and new individuals were used every trial to avoid any bias in individual crab behaviour or related to the experimental conditions. The aquaria was scrubbed and carefully rinsed with fresh water between trials to remove all traces of the resources. The placement of a resource (habitat or food) or control (seawater, no substrate) in the end of either of the two "arms" was randomised for each trial. The water temperature was kept at 15 °C, salinity at 5.5, and a flow-through system allowed water to flow from each "arm" to the basal area at a rate of 0.15 L/minute, resulting in 100 % water exchange every 40 minutes.

Prior to the start of the experiment, a crab was placed at the basal area, where it was allowed to acclimatize for 10 minutes. A perforated wall between the base and the "arms" prevented the crab from leaving the basal area, but exposed the individual to the water from the "arms" and thereby the potential odour from the resources. When an experimental trial started, the perforated wall was lifted, and we noted the initial choice of the crab and then documented the position of the crab every five minutes for 30 minutes, providing six observations per trial.

In the habitat choice experiment, crabs could choose between soft sediment (clay) and brown algae (*Fucus vesiculosus*). In the food choice experiment, we used the vegetation-associated amphipod *Gammarus* spp. and the sediment-dwelling polychaete *Hediste diversicolor* O. F. Müller, 1776 as food resources. Both prey species were placed inside a transparent net-bag that allowed the crabs to see and smell the prey without consuming it. The control in both the food- and habitat experiment was seawater, no substrate.

Statistical analyses

As a first step, to evaluate if there were any natural breakpoints in carbon isotope values in relation to size of the crab, we conducted a piece-wise linear regression analysis using the package Segmented (Muggeo 2008) in R (R Development Core Team 2014). The results showed that there were two breakpoints, one at 11.53 ± 0.36 mm CW and another at 12.32 ± 0.11 mm CW (mean ± SE)

Figure 1. Piecewise regression plot of *Rhithropanopeus harrisii* size (x-axis) versus $\delta^{13}C$ –values (y-axis) of all crabs sampled in June and August 2012. Two breakpoints are identified at around 12 mm carapace width size. Slopes of the lines are 0.2163 (for size up to 11.53 mm), -6.529 (11.53 – 12.32 mm) and -0.00271 (> 12.32 mm).
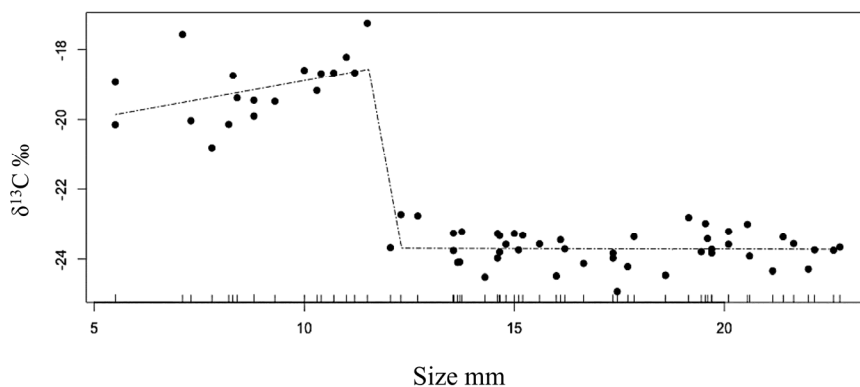
Table 2. Number, sex, and size (carapace width range and mean size, mm) of *Rhithropanopeus harrisii* sampled at Station 1 and Station 2 in June and August 2012.

	June			August		
	n	range	mean ± SE	n	range	mean ± SE
a) Station 1						
Male	17	14.3 – 22.0	18.45 ± 0.60	26	7.45 – 22.75	15.04 ± 0.96
Female	10	13.5 – 16.2	14.97 ± 0.30	15	7 – 13.55	10.32 ± 0.49
Not sexed	40	4.0 – 12.0	7.52 ± 0.28	0		
Total	67			41		
b) Station 2						
Male	6	11.7 – 19.3	16.60 ± 1.16	16	10 – 20.5	15.78 ± 0.87
Female	13	10.0 – 17.5	12.45 ± 0.77	0		
Not sexed	50	4.0 – 10.0	6.70 ± 0.24	8	10 – 15	11.49 ± 0.76
Total	69			24		

(Figure 1). Thus, for all subsequent analysis, we divided crabs into small (< 12 mm CW) and large (> 12 mm CW) size classes.

To assess spatial differences in stable isotope values of small and large size classes of *R. harrisii* and food web components (detritus, primary producers, primary and secondary consumers), separate t-tests were used. If the variances were not homogenous, a *t*-test with Welch correction was performed.

In order to assess temporal differences in isotope values between the two size classes, we conducted separate Two-way ANOVAs for station 1 and station 2 for both $\delta^{13}C$ and $\delta^{15}N$. A comparison of isotopic differences between male and female crabs was analysed with *t*-tests for the large sized crabs (> 12mm CW) in June only, as not enough data were available for comparison in August.

To analyse the first-choice (resources or control) of crabs in the aquarium experiments, we used Chi-square statistics. One-way ANOVA was used to analyse the choice of crabs made every 5 minutes

(i.e. the position of the crabs in the aquaria), during the 30 min trial. No data transformations were required as the data were normally distributed and the variances homogeneous.

Results

Trophic position and spatial variability

We collected 108 (48 large, 60 small) individuals of *R. harrisii* at station 1 and 93 (26 large and 67 small) at station 2 (Table 2). The largest number of individuals was sampled in June at both stations, and the majority were smaller than 12 mm CW (60 % at station 1 and 84 % at station 2). In August, the small size group accounted for 50 % of the individuals from station 1 and 38 % of those from station 2. The sex ratio was skewed toward more males at both sampling sites. However, in June, sex was not determined for most crabs due the small individual sizes of the animals. Five ovigerous females (38% of all female crabs, 10.7–13.6 mm CW) were obtained from
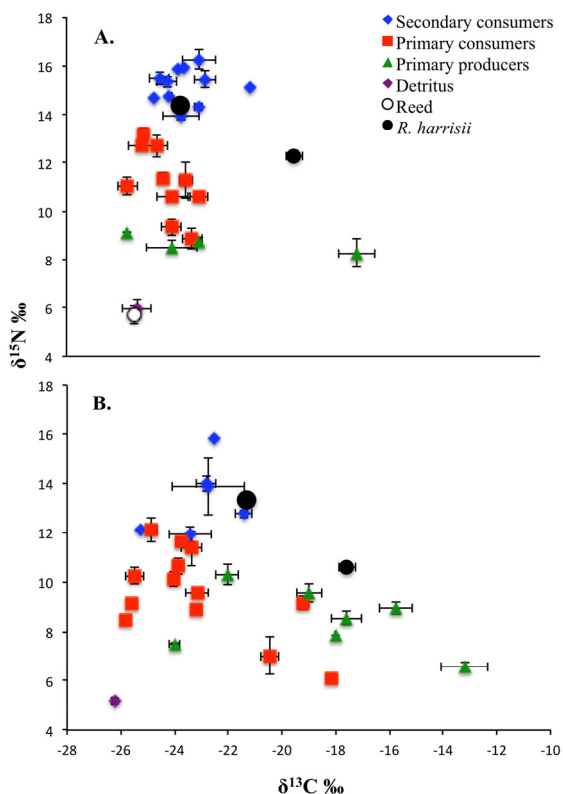
Figure 2. Isotope values ($\delta^{13}C$ & $\delta^{15}N$) for organisms sampled in June and August 2012, at A. Station 1 (Tuorla) and B. Station 2 (Lempisaari). Large (> 12 mm) and small (< 12 mm) *Rhithropanopeus harrisii* are indicated by larger and smaller symbol (•), respectively. Secondary consumers: *Abramis brama*[1], *Blicca bjoerkna*[1], *Gobius niger, Gymnocephalus cernuus*[1], *Palaemon adspersus*, *Perca fluviatilis*, *Pomatoschistus minutus*, *Pungitus pungitus*[1], *Rutilus rutilus*, *Scardinius erythrophthalmus*[1], *Tinca tinca.* Primary consumers: *Asellus aquaticus*, *Bithynia tentaculata*, Chironomidae, Ephemeroptera, *Gammarus* sp, *Lymnea stagnalis*, *Macoma balthica*, *Marenzellaria* sp[2], *Mya arenaria*[2], *Mytilus edulis*[2], *Hediste diversicolor*[2], Odonata, *Theodoxus fluviatilis*, Tricoptera[1]. Primary producers: *Ceratophyllym demersum*, *Cladophora glomerata*, *Enteromorpha intestinalis*[1], Epiphytes (on Fucus)[2], *Fucus vesiculosus* (apical)[2], *F. vesiculosus* (basal)[2], *Myriophyllum* sp. [1]= species were found on station 1 only, [2] = species were found on station 2 only.

station 1 in August, while only males were found at station 2 at that time.

The stable isotope values (June and August combined) of *R. harrisii* at station 1 varied between -24.90 and -17.58 ‰ for $\delta^{13}C$ and between 10.59 and 15.47 ‰ for $\delta^{15}N$ (Figure 2A). Crab individuals at station 2 were enriched

in carbon compared to the other station (-22.69 and -15.19 ‰ for $\delta^{13}C$) and depleted in nitrogen (between 9.07 and 14.31 ‰ for $\delta^{15}N$) (Figure 2B). This pattern was confirmed for both the large and small size class of crabs when we compared mean values of $\delta^{13}C$ of *R. harrisii* between stations (large: $t = 13.60$, df = 31, p < 0.0001, and small: $t = 3.646$, df = 35, p = 0.0009). Similarly, both size classes differed significantly in terms of $\delta^{15}N$ between stations (large: $t = 5.733$, df = 63, p < 0.0001, and small: $t = 4.383$, df = 38, p < 0.0001).

The same spatial variability in carbon and nitrogen signatures was also found within the other food web components except detritus, which did not vary between stations (Figure 2). At station 1, the values for all sampled food web components ranged between -15.4 and -27.7 for $\delta^{13}C$ and between 3.4 and 17.3 for $\delta^{15}N$. At station 2, the corresponding values were -10.7 to -26.5 for $\delta^{13}C$ and 3.6 to 15.8 for $\delta^{15}N$. Both secondary and primary consumers were significantly enriched in $\delta^{13}C$ at station 2 compared to station 1 (secondary consumers: $t = 3.251$, df = 51, p = 0.0020, primary consumers: $t = 6.099$, df = 64, p < 0.0001). Carbon stable isotope values of primary producers did not differ significantly between sites. Similarly, a significantly higher $\delta^{15}N$ value was found at station 1 for secondary ($t = 7.207$, df = 51, p < 0.0001) and primary consumers ($t = 5.800$, df = 65, p < 0.0001), as well as primary producers ($t = 3.994$, df = 9, p = 0.0031).

In terms of the spatial variability in trophic position of the two size classes, the same pattern was seen at both stations. The large size class of *R. harrisii* was located at the same trophic level as fish and other secondary consumers, while small individuals were positioned together with primary consumers, in this case invertebrates (Figure 2). This result supports the clear evidence of an ontogenetic diet change, as initially suggested in the piece-wise linear regression (Figure 1).

Temporal variability of isotope signatures

Carbon and nitrogen stable isotopes of the two size-classes varied over time but the general difference between large and small crabs were constant at both stations. At station 1, a significant interaction between crab size and month was detected for both $\delta^{13}C$ and $\delta^{15}N$ values (Table 3). The average $\delta^{13}C$ value at station 1 in June was 4 ‰ higher in large crabs than small ones (Figure 3), i.e., large crabs were more enriched in carbon. In August, the difference was almost 5 ‰ between
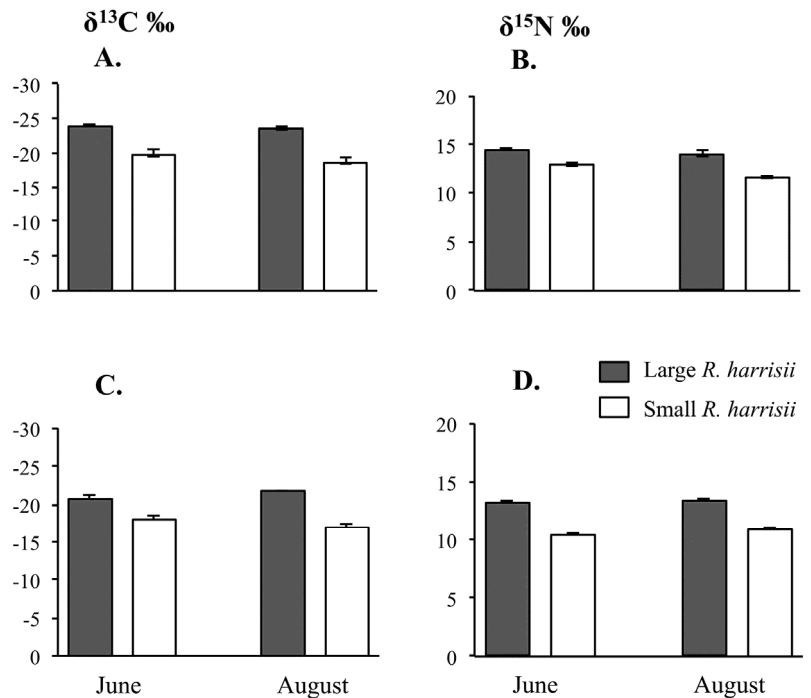
Figure 3. $\delta^{13}C$ and $\delta^{15}N$ for large (> 12 mm carapace width) and small (< 12 mm carapace width) *Rhithropanopeus harrisii* collected in June and August 2012. A. and B. Station 1, C. and D. Station 2. Values are mean ± SE. See Table 3 and Table 4 for significant differences.

Table 3. Two-factor ANOVA results of a) $\delta^{13}C$ and b) $\delta^{15}N$ in *Rhithropanopeus harrisii* of different sizes (small, large) and sampled in different months (June, August) at Station 1. Significant differences are shown in bold.

Treatment	df	MS	F	p
a) $\delta^{13}C$				
Size	1	248.5	831.0	**<0.0001**
Month	1	6.279	21.00	**<0.0001**
Size × Month	1	2.600	8.694	**0.0046**
Error	57	0.2990		
b) $\delta^{15}N$				
Size	1	52.58	119.6	**<0.0001**
Month	1	10.36	23.56	**<0.0001**
Size × Month	1	3.041	6.918	**0.0110**
Error	57	0.4396		

Table 4. Two-factor ANOVA results of a) $\delta^{13}C$ and b) $\delta^{15}N$ in *Rhithropanopeus harrisii* of different sizes (small, large) and sampled in different months (June, August) at Station 2. Significant differences are shown in bold.

Treatment	df	MS	F	p
a) $\delta^{13}C$				
Size	1	159.5	135.0	**<0.0001**
Month	1	0.9287	0.7862	0.3806
Size × Month	1	8.387	7.100	**0.0111**
Error	40	1.181		
b) $\delta^{15}N$				
Size	1	64.80	88.79	**<0.0001**
Month	1	0.1559	0.2136	0.6464
Size × Month	1	0.02149	0.02945	0.8646
Error	40	0.7298		

405

the size categories at the same station. The mean $\delta^{15}N$ was 1.57 ‰ higher in large sized crabs compared to small ones in June and 2.57 ‰ higher in August (Figure 3). The $\delta^{13}C$ values of large (> 12 mm) crabs did not differ significantly (p = 0.7630) between males and females in June, whereas $\delta^{15}N$ values were significantly higher in females than in males ($t = 2.563$, df = 25, p = 0.0154).

A slightly different pattern was observed at station 2, where a significant interaction between crab size and month was detected for $\delta^{13}C$ but not for $\delta^{15}N$ (Table 4). In parallel to station 1, large crabs were more enriched in carbon compared to small ones and this increased over time (average value of $\delta^{13}C$ in June was 3 ‰ higher for the larger size class and increased to 4.8 ‰ in August) (Figure 3). Concerning $\delta^{15}N$, values differed significantly between the two size classes but not over time (between June and August). The $\delta^{15}N$ values were about 2.5 ‰ higher in large sized crabs compared to the small ones in both months (Figure 3). The isotope values of large crabs did not differ significantly between the sexes ($\delta^{13}C$ p= 0.1017; $\delta^{15}N$ p = 0.1312).

Habitat and food choices

The laboratory experiments showed that *Rhithropanopeus harrisii* actively choose both habitat and prey. There was no significant difference in the initial choice of substrate, whether the crabs were presented with *Fucus vesiculosus* and control (p = 0.80), clay and control (p = 0.80), or between the two substrates (p = 0.45). Over the 30-minute period, however, individuals preferred *F. vesiculosus* to both control and clay (One-way ANOVAs: $F_{1,28} = 32.02$, p < 0.0001 and $F_{1,28} = 3.85$, p = 0.01, respectively). No significant difference (p > 0.05) was found between clay and control.

The initial food choice of *R. harrisii* varied depending on the prey species presented. Crab individuals chose the worm *H, diversicolor* over the control with seawater ($\chi^2 = 9.320$, df = 1, p = 0.0023), but showed no significant preference between *Gammarus* sp. and control (p = 0.44), or between *H. diversicolor* and *Gammarus* sp (p = 0.80). When observing the crabs for 30 minutes, however, the individuals spent significantly more time in the area of the aquaria with a food source than in the area with a control (*Gammarus* sp.: One-way ANOVA. $F_{1,28}=4.31$, p=0.05; *H. diversicolor*: $F_{1,28} = 11.48$, p = 0.0001). Similarly to the results of the initial choices, no clear preference of *R. harrisii* between *H. diversicolor* and *Gammarus* sp. was observed over time.

Discussion

We determined the trophic position of Harris mud crab using stable isotope ratios, and identified consistent size-specific differences over time and space. The presence of an ontogenetic diet shift was confirmed through the combination of: i) a natural breakpoint in carbon stable isotopes identified at the size of 12 mm CW; and ii) the positioning of large *Rhithropanopeus harrisii* among the secondary consumers and small individuals with primary consumers. The generalist nature of *R. harrisii* described by the stable isotope ratios was supported by an active food choice but no specific preference for the prey species presented in laboratory experiments. Our hypothesis about substrate preferences of *R. harrisii* was confirmed experimentally by the choice of the structurally more complex bladderack, *Fucus vesiculosus*, over bare mud.

The trophic role(s) resulting from ontogenetic diet shift

Depending on the diet, species may contribute to different trophic pathways and thus, express different trophic roles in an ecosystem (Blondel 2003). Moreover, ontogenetic diet shifts can result in differing juvenile and adult resource use and thus their ecological roles (Werner and Gilliam 1984). Ontogenetic changes in diet are a very common occurrence among invertebrates and fishes (Werner and Gilliam 1984) and are a means to decrease intraspecific competition for food (Aarnio et al. 1998; Arim et al. 2010; Toscano and Griffen 2012). The natural breakpoint in carbon stable isotopes of Harris mud crab at 12 mm CW suggested that large and small *R. harrisii* used different carbon sources and thus there was an ontogenetic diet shift. The analysis of *R. harrisii* stable isotope ratios in bivariate δ-space further supported this observation with small individuals acting as primary consumers while large crabs grouped with fish and other secondary consumers. The enriched $\delta^{13}C$ values of the individuals in the small size class showed that these had predominately fed on plant material, such as detritus, algae and/or macrophytes. Large crabs appeared to have fed mainly upon invertebrate fauna, which had a carbon signature about 2 ‰ lower than the signature of the crabs themselves.

Previous studies have classified the Harris mud crab as an omnivore feeding on detritus and a large variety of macrofaunal species (Turoboyski 1973). Studies based on stomach contents have had the same conclusion (Czerniejewski and Rybczyk

2008; Hegele-Drywa and Normant 2009). However, previous studies either did not take size into account (Czerniejewski and Rybczyk 2008) or focussed on crabs > 12 mm CW (Hegele-Drywa and Normant 2009). While the species *per se* can be classed as an omnivore (Pimm and Lawton 1978), our findings indicate this to be an over-simplification. The demonstrated ontogenetic switch between feeding as a primary consumer to feeding as a secondary consumer illustrates two distinct trophic roles of *R. harrisii*. In addition, ovigerous females as small as 8.4 mm CW can be found (Fowler et al. 2013; this study), which would mean that the smaller size class (<12 mm CW) includes reproductive individuals and thus is not strictly comprised of juveniles. This makes the ontogenetic diet change and the role as primary consumer interesting because it cannot be explained solely as behaviour linked to the juvenile stage.

The clear difference in trophic position with size is perhaps not surprising in the light of general invertebrate and crab ecology (Werner and Gilliam 1984; Boudreau and Worm 2012). For the invasive crab *Hemigrapsus sanguineus* (De Haan, 1835), Griffen et al. (2012) showed that herbivory decreased with increasing size for females. The shift to more animal tissue in the diet with an increase in crab age/size was assumed to reflect changes in size-specific nutritional requirements (related to molting and growth), and reflected the greater capability of larger individuals to find and handle animal prey (Griffen et al. 2012). These are also possible mechanisms for the observed shift in *R. harrisii* in this study, as are the potential need for an animal-based food source to facilitate energy need for reproduction (Kang and Poulet 2000). Nevertheless, with the existence of mature individuals < 12 mm CW, reproduction clearly occurs on a diet of detritus and other plant material. The lower consumption of animal prey by small crabs could potentially also be linked to differences in habitat usage, and thus food availability, by small and large crabs because of intra-specific competition or predation (Dittel et al. 1995; Nurkse et al. 2015).

When interpreting stable isotope signatures, nature of the tissue analysed needs to be taken into account especially for nitrogen stable isotope analysis. The lower $\delta^{15}N$ values in the small size class could be partly due to small crabs being analysed as whole organisms while only soft claw tissues were analysed for large crabs. This methodological discrepancy was inevitable because of the small amount of soft tissue material in small crabs. Søreide and Nygård (2012) showed

in their study that $\delta^{15}N$ values in arctic amphipods were significantly lower in the exoskeleton than in soft tissue, and whole organism signatures were in between the two. Also, $\delta^{15}N$ values of the whole animals were 1–2 ‰ lower than those of soft tissue, while $\delta^{13}C$ values were not significantly different between whole-animal and exoskeleton samples.

Spatial and temporal consistency in trophic position

Variability in isotopic signatures in space and time is common. In this study, the trophic structure of the assemblages sampled and the position of both size-classes of *Rhithropanopeus harrisii* were consistent in space (i.e. between two different locations, about 30 km a part). Although $\delta^{15}N$ and $\delta^{13}C$ values differed significantly between the two stations studied, both regarding the whole consumer assemblage and *R. harrisii* in particular, we perceived these as resulting from local nitrogen and carbon dynamics, rather than changes in trophic level. A similar pattern in spatial variability was identified by Nordström et al. (2010) in a study of nine shallow sandy sediment food webs in the northern Baltic Sea where the basic food web components remained the same but the trophic positioning of each varied depending on the local conditions and the local species composition. Furthermore, slight differences in trophic structure and/or positioning of individual species do not necessarily indicate altered or different functional properties of the systems (Törnroos et al. 2013). Moreover, influx of freshwater can affect the natural abundances of $\delta^{15}N$ in plant tissue as allochthonous nitrogen differs in isotopic signature from autochthonous nitrogen (Peterson and Fry 1987; McClelland and Valiela 1998), while enrichment of $\delta^{15}N$ in primary producers is known to indicate denitrification, e.g., during hypoxia (Fourqurean et al. 1997). These mechanisms may explain the higher $\delta^{15}N$ values at station 1, which is a sheltered narrow strait in the inner archipelago close to the coast with a higher volume of fresh water runoff. Additionally, we noted that the sediment at station 1 occasionally experienced hypoxic conditions during the field sampling.

To be able to extrapolate results from stable isotope analysis, it is also important to assess temporal variability in isotope signatures (Akin and Winemiller 2006; Nordström et al. 2009). In this study, we were interested in the intra-seasonal variation in the trophic role of Harris mud crab, and the consistent temporal variability in signatures of large and small *R. harrisii* over the production

period (June to August) strengthened the size-specific difference in trophic position. Temporal fluctuations in stable isotope signatures is common as primary producers often vary in isotope values several times per year (Rolff 2000), which will after a potential lag time be reflected in higher trophic levels (Goering et al. 1990; Nordström et al. 2009). Our results show that the pattern was stable over time although the difference in $\delta^{13}C$ between small and large crabs increased from June to August at both locations, possibly due to changing isotope values at the base of the food web or changes in food sources, or both (Nordström et al. 2009).

The implication of an active habitat and food choice

Investigating both habitat and feeding choices is important for disentangling invasion impacts and success (Marchetti et al. 2004). As discussed above, trophic patterns may reflect differences in habitat occupancy linked to local food availability and community interactions (Dittel 1995; Nurkse et al. 2015). The results from the laboratory experiments showed that *R. harrisii* preferred the brown alga *Fucus vesiculosus* as habitat over clay or the control (no substrate), and that the crabs were strongly attracted to the odour of both prey organisms offered as food. Crabs in general have well-developed olfactory senses (Weissburg and Zimmer-Faust 1993), and *R. harrisii* uses this trait in search for both suitable habitat and food (Kidawa et al. 2004). Surprisingly, there was no difference between the choice of clay and bare substrate as alternative habitats, although clay naturally had a stronger odour than plain seawater. The burying behaviour of Harris mud crab is well known (Petersen 2006; Fowler et al. 2013) and females in particular need access to suitable sediments when they are about to lay their eggs (Turoboyski 1973). During other periods, crabs are observed to search for shelter under shells, stones, or in vegetation (Ryan 1956; Fowler et al. 2013). We used both male and female individuals in our experiments, and both were primarily attracted to the habitat that provided overhead shelter over clay and the structure-free control. These findings are consistent with other experiments (Nurkse et al. 2015) in which *R. harrisii* chose habitats with boulders covered with *F. vesiculosus* over all other habitats provided (*Cladophora*, unvegetated boulder, silty sand).

In the food choice experiment, both prey species were chosen over the control, but no preference was found between the offered prey types. Our experimental results support previous findings that the species chooses prey according to availability (Czerniejewski and Rybczyk 2008; Hegele-Drywa and Normant 2009). The preferred first choice was the polychaete *Hediste diversicolor*, however, no statistical differences in overall choice were found. It is possible that *H. diversicolor* left a stronger chemical cue in the water than the amphipods (Velez et al. 2007) and was thus detected more easily by the crabs. In line with studies of olfactory senses in other crab species (Rittschof 1992; Keller et al. 2003) and crustaceans (Weissburg and Zimmer-Faust 1993; Lee and Meyers 2006), the strength of a food signal may be a significant factor modifying food-search behaviour of *R. harrisii*. Kidawa et al. (2004) demonstrated that *R. harrisii* uses the stimulus concentration as a source of information about their distance to a food item. Furthermore, avoidance behaviour of weak food signals may decrease the risk of encountering predators or cannibalistic conspecifics (Kidawa et al. 2004; Tran 2014). Additionally, crabs exposed to food odour repeatedly may lose their motivation to locate the food if they cannot find its source and begin feeding (Ristvey and Rebach 1999; Kidawa et al. 2004). The crabs in our experiments may have lost interest in the prey because they could not reach it through the net-bags, which could explain why there was no difference between choices of prey species over the 30 min period.

Understanding of the trophic and functional roles of non-indigenous species

Recent studies on the role of non-indigenous species in the marine environment underlines the importance of knowing their biology and ecology as a basis for legislation and marine management (Lehtiniemi et al. 2015; Ojaveer et al. 2015), as well as impact prediction (Kolar and Lodge 2001; Dick et al. 2014). We therefore gathered the current biological and ecological trait knowledge of this species worldwide (Table 5) and qualitatively compared a number of traits with those of the native macrofaunal community (from Valanko et al. 2010; Villnäs et al. 2011; Törnroos and Bonsdorff 2012; Törnroos et al. 2015). Törnroos and Bonsdorff (2012) described 12 trait categories expressed by the macrofaunal community along the entire Finnish coastline, i.e., represented the typical functional characteristics of the northern Baltic Sea benthic species. *Rhithropanopeus harrisii* shares eight of these traits with this "type organism" because *R. harrisii* is: of medium size (1–3 cm); reproduces sexually and has separate sexes; is mobile; and

Table 5. Compilation of traits and ecologically important information of *Rhithropanopeus harrisii* .

Trait	Value/category	Reference
Size	Introduced areas: Max*: ♂ 22.8 mm, ♀ 20.2 mm	*This study
	Range: ♂ 1.8–22.9, ♀ 1.8–20.2 mm	Fowler et al. 2013, Turoboyski 1973
	Native areas: ♂ 4.1–14.6 mm, ♀ 4.4–12.6 mm	Ryan 1956
Size of maturity	Introduced areas: 8.4mm*, 4–5mm	*This study, Turoboyski 1973, Williams 1984 Ryan 1956
	Native areas: ♂ 4–5 mm, ♀ 4.4–5.5 mm	
Time to maturity	0.5 yr.	Williams 1984
Reproductive type	Sexual repr. (Gonochoristic)	Derived
Developmental type	Ovoviviparous	Derived
Larval type	Lecitotrophic (actively feeding)	Williams 1984
Larval duration	16 days (~ 30d in fully marine areas), 4 stages	Williams 1984
Larval migration	Vertical migration	Petersen 2006
Reproductive season	June – August (temp. dependent)	Fowler et al. 2013, *This study
Egg production	1200–4800 eggs (environmental-dependent)	Turoboyski 1973, *This study
*Trophic level	Primary consumers: ind. < 12mm Secondary consumers: ind.>12mm	*This study
*Stable isotope values	Average(sd) Δ^{13}C: -18.4 ± 1.64 (ind.<12mm) -22.8 ± 1.4 (ind. >12mm)	*This study
	Average(sd) Δ^{15}N: 11.4 ± 1.2 (ind. <12mm) -14.0 ± 0.8 (ind. >12mm)	*This study
*Diet (include ontogenetic shift)	Polychaetes (e.g. *Hediste* sp.)	*This study, Turoboyski 1973, Czerniejewski and Rybczyk 2008,
	Crustaceans (e.g. *Gammarus* spp.)	
	Molluscs (e.g. *Macoma balthica*)	Hegele-Drywa and Normant 2009
	Detritus	
Resource capture method	Maxillipeds, maxillae, mandibles (adult), suspension feeder (larvae)	Derived, Williams 1984
Living habit	Epibenthic, Infauna	Derived
Mobility	Mobile	Derived
Movement type	Crawler, Burrower	Derived, *This study
Migration	Potentially to deeper waters in winter	Turoboyski 1973
Ecological information		
Salinity tolerance	0.5 – >20 psu	Boyle et al. 2010, Ryan 1956
	2.5 – 40 psu (larvae lab)	Costlow et al. 1966
Temperature tolerance	15 – 35 ºC (larvae lab)	Costlow et al. 1966
	at least +4 ºC (adult)	Derived from Finnish water temperatures in winter
Depth range	0–20m (max 37m)	Hegele-Drywa and Normant 2014,
Habitat preferences	Various: e.g. debris on seafloor, canopy-forming algae such as bladder-rack, mud, gravel, oyster and mussel reefs.	*This study, Fowler et al. 2013

lives in or on the top 1 cm of the sediment; and smaller crabs consume both detritus and plant material (Table 5). Furthermore, another trait that was found among the typical benthic species characteristics was diffusive mixing as a bioturbation mode (Törnroos and Bonsdorff 2012). While bioturbation by Harris mud crab at the sediment-water interface has not been investigated directly, the normal movements and feeding on the surface (Turoboyski 1973; Nurkse et al. 2015) most certainly moves sediments around (Kristensen et al. 2012). On the other hand, the burrowing behavior of *R. harrisii* (Turoboyski 1973; Peterson 2006; Fowler et al. 2013) may represent more elaborate bioturbation effect similar to regenerator or gallery-diffusers that aid bio-irrigation (Kristensen et al. 2012) such as fiddler crabs (Huang et al. 2007). *R. harrisii* matures in about half a year in the Baltic Sea (Turoboyski 1973) and has lecitotrophic larval development (Table 5), which are some of the less common characteristics of the northern Baltic Sea macrofauna (Valanko et al. 2010; Törnroos and Bonsdorff 2012), and may in part explain its success in its new environment.
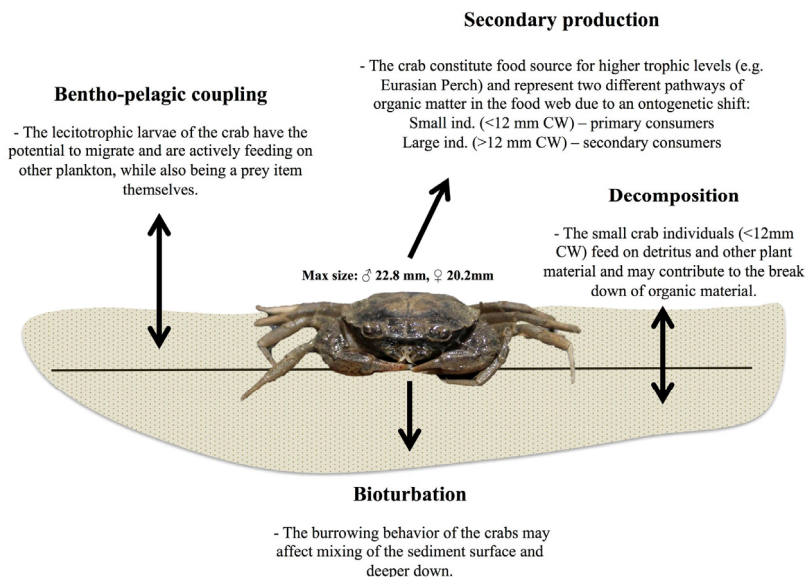
Figure 4. Conceptual figure showing ecosystem functions, to which the non-indigenous *Rhithropanopeus harrisii* potentially could contribute, based on its species-specific traits.

Sharing these traits with the natural macrofaunal community does not mean that the effect of *R. harrisii* on the functioning of the benthic ecosystem could not substantially differ from other benthic species (e.g. in terms of rates). However, it does suggest that the Harris mud crab qualitatively adds to the already present functional (trait) diversity, rather than bringing in something completely new. Disentangling this type of trait information further, in relation to ecosystem functions (Symstad et al. 2003; Violle et al. 2007; Reiss et al. 2009) will help broaden our understanding of the many roles of species in ecosystems (Hooper et al. 2005). Using the species-specific traits (Table 5), it is possible to conceptually illustrate the ecosystem functions of the non-indigenous *R. harrisii* (Figure 4). It is consumed by common predators, e.g., Eurasian perch (*Perca fluviatilis* Linnaeus, 1758), pikeperch (*Sander lucioperca* (Linnaeus, 1758)), and fourhourned sculpin (*Myoxocephalus quadricornis* (Linnaeus, 1758)) (Fowler et al. 2013), and thus contributes to secondary production. It has a role in bioturbation of the surface layer of the sediment. Due to its lecitotrophic larval mode, it would be involved in benthic-pelagic coupling as larvae both consume other zooplankton and are prey for both benthic and pelagic organisms (Marcus and Boero 1998; Raffaelli et al. 2003). Finally, the consumption of detritus and other plant material results in a breakdown and excretion of organic matter, which subsequently is available to the meiofaunal and bacterial community. Whether the net effect of *R. harrisii* on these ecosystem functions is positive and/or negative, remains to be investigated. Non-indigenous species can affect ecological processes positively and negatively (Thomsen et al. 2015). For example, modelling work (Norkko et al. 2012) suggests the introduced spionid polychaete *Marenzelleria* spp. may enhance phosphorus retention in sediments and thus reduce phosphorus release from bottom waters. This could be interpreted as positive driver of change influencing the function of the system (Norkko et al. 2012; Kauppi et al. 2015). Previously work on *R. harrisii* have stressed potential negative effects, such as the species possibility to displace native organisms (Zaitsev and Öztürk 2001; Fowler et al. 2013; Nurkse et al. 2015). As demonstrated in this study, *R. harrisii* may also contribute positively to the ecosystem functioning, especially in a species-poor system such as the Baltic Sea.

Acknowledgements

References

Aarnio K, Bonsdorff E, Rosenback N (1998) Food and feeding habits of juvenile flounder, *Platichthys flesus* (L.), and turbot, *Scophthalmus maximus* L., in the Åland Archipelago, northern Baltic Sea. *Journal of Sea Research* 36: 311–320

Akin S, Winemiller KO (2006) Seasonal variation in food web composition and structure in a temperate tidal estuary. *Estuaries and Coasts* 29(4): 552–567, http://dx.doi.org/10.1007/BF02784282

Anger K (1991) Effects of temperature and salinity on the larval development of the Chinese mitten crab *Eriocheir sinensis* (Decapoda: Grapsidae). *Marine Ecology Progress Series* 72: 103–110, http://dx.doi.org/10.3354/meps072103

Arim M, Abades SR, Laufer G, Loureiro M, Marquet PA (2010) Food web structure and body size: trophic position and resource acquisition. *Oikos* 119: 147–153, http://dx.doi.org/10.1111/j.1600-0706.2009.17768.x

Blondel J (2003) Guilds or functional groups: does it matter? *Oikos* 100: 223–231, http://dx.doi.org/10.1034/j.1600-0706.2003.12152.x

Bonsdorff E (2006) Zoobenthic diversity-gradients in the Baltic Sea: Continuous post-glacial succession in a stressed ecosystem. *Journal of Experimental Marine Biology and Ecology* 330: 383–391, http://dx.doi.org/10.1016/j.jembe.2005.12.041

Bonsdorff E, Blomqvist EM (1993) Biotic couplings on shallow water soft bottoms – examples from the northern Baltic Sea. *Oceanography and Marine Biology - An Annual Review* 31: 153–176

Bonsdorff E, Vahl O (1982) Food preference of the sea urchins *Echinus acutus* and *E. esculentus*. *Marine Behavior & Physiology* 8: 243–248, http://dx.doi.org/10.1080/10236248209387021

Boudreau SA, Worm B (2012) Ecological role of large benthic decapods in marine ecosystems: a review. *Marine Ecology Progress Series* 469: 195–213, http://dx.doi.org/10.3354/meps09862

Boyle T Jr, Keith D, Pfau R (2010) Occurrence, reproduction, and population genetics of the estuarine mud crab, *Rhithropanopeus harrisii* (Gould) (Decapoda, Panopidae) in Texas freshwater reservoirs. *Crustaceana* 83(4): 493–505, http://dx.doi.org/10.1163/001121610X492148

Bremner J, Rogers SI, Frid CLJ (2006) Methods for describing ecological functioning of marine benthic assemblages using biological trait analysis (BTA). *Ecological Indicators* 6: 609–622, http://dx.doi.org/10.1016/j.ecolind.2005.08.026

Brockerhoff A, McLay C (2011) Human-mediated spread of alien crabs. In: Galil BS, Clark PF, Carlton JT (eds), In the Wrong Place – Alien Marine Crustaceans: Distribution, Biology and Impacts. *Invading Nature, Springer Series in Invasion Ecology* 6: 27–106

Catford JA, Jansson R, Nilsson C (2009) Reducing redundancy in invasion ecology by integrating hypotheses into a single theoretical framework. *Diversity and Distributions* 15: 22–40, http://dx.doi.org/10.1111/j.1472-4642.2008.00521.x

Cohen AN, Carlton JT (1995) Biological Study, nonindigenous aquatic species in a United States Estuary: A case study of the biological invasions of the San Francisco Bay and Delta, A Report for the U.S. Fish and Wildlife Service, 246 pp

Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. *Science* 279: 555–557, http://dx.doi.org/10.1126/science.279.5350.555

Costlow JD Jr, Bookhout CG, Monroe RJ (1966) Studies on the larval development of the crab *Rhithropanopeus harrisii* (Gould). I Effect of salinity and temperature on larval development. *Physiological Zoology* 35: 79–93

Czerniejewski P, Rybczyk A (2008) Body weight, morphometry, and diet of the mud crab, *Rhithropanopeus harrisii tridentatus* (Maitland, 1874) in the Odra estuary, Poland. *Crustaceana* 81: 1289–1299, http://dx.doi.org/10.1163/156854008X369483

David M, Gollasch S, Leppäkoski E (2013) Risk assessment for exemptions from ballast water management – the Baltic Sea case study. *Marine Pollution Bulletin* 75: 205–217, http://dx.doi.org/10.1016/j.marpolbul.2013.07.031

de Juan S, Thrush SF, Demestre M (2007) Functional changes as indicators of trawling disturbance on a benthic community located in a fishing ground (NW Mediterranean Sea). *Marine Ecology Progress Series* 334: 117–129, http://dx.doi.org/10.3354/meps334117

Dick JTA, Alexander ME, Jeschke JM, Ricciardi A, MacIsaac HJ, Robinson TB, Kumschick S, Weyl OLF, Dunn AM, Hatcher MJ, Paterson RA, Farnsworth KD, Richardson DM (2014) Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. *Biological Invasions* 16: 735–753, http://dx.doi.org/10.1007/s10530-013-0550-8

Dittel AI, Hines AH, Ruiz GM, Ruffin KK (1995) Effects of shallow water refuge on behavior and density-dependent mortality of juvenile blue crabs in Chesapeake Bay. *Bulletin of Marine Science* 57: 902–916

Dobb JA, Dick JTA, Alexander ME, Macneil C, Dunn AM, Aldridge D (2014) Predicting the ecological impacts of a new freshwater invader: functional responses and prey selectivity of the 'killer shrimp', *Dikerogammarus villosus*, compared to the native *Gammarus pulex*. *Freshwater Biology* 59: 337–352, http://dx.doi.org/10.1111/fwb.12268

Elmgren R, Hill C (1997) Ecosystem Function at Low Biodiversity - The Baltic Example. In: Ormond RFG, Gage J, Angel M (eds), Marine Biodiversity: Patterns and Processes. Cambridge University Press Cambridge, pp 319–336, http://dx.doi.org/10.1017/cbo9780511752360.015

Evans S (1983) Production, predation and food niche segregation in a marine shallow soft-bottom community. *Marine Ecology Progress Series* 10:147–157, http://dx.doi.org/10.3354/meps010147

Forward RB Jr (2009) Larval biology of the crab *Rhithropanopeus harrisii* (Gould): a synthesis. *Biological Bulletin* 216: 243–256

Fourqurean JW, Moore TO, Fry B, Hollibaugh JT (1997) Spatial and temporal variation in C:N:P ratios, $\delta^{15}N$, and $\delta^{13}C$ of eelgrass *Zostera marina* as indicators of ecosystem processes, Tomales Bay, California, USA. *Marine Ecology Progress Series* 157: 147–157, http://dx.doi.org/10.3354/meps157147

Fowler AE, Forsström T, von Numers M, Vesakoski O (2013) The North American mud crab *Rhithropanopeus harrisii* (Gould, 1841) in newly colonized Northern Baltic Sea: distribution and ecology. *Aquatic Invasions* 8: 89–96, http://dx.doi.org/10.3391/ai.2013.8.1.10

Goering J, Alexander V, Haubenstock N (1990) Seasonal variability of stable carbon and nitrogen isotope ratios of organisms in a North Pacific bay. *Estuarine, Coastal and Shelf Science* 30: 239–260, http://dx.doi.org/10.1016/0272-7714(90)90050-2

Gollasch S, Leppäkoski E (2007) Risk assessment and management scenarios for ballast water mediated species introductions in the Baltic Sea. *Aquatic Invasions* 2: 313–340, http://dx.doi.org/10.3391/ai.2007.2.4.3

Gothland M, Dauvin JC, Denis L, Dufossé F, Jobert S, Ovaert J, Pezy JP, Tous Rius A, Spilmont N (2014) Biological traits explain the distribution and colonisation ability of the invasive shore crab *Hemigrapsus takanoi*. *Estuarine, Coastal and Shelf Science* 142: 41–49, http://dx.doi.org/10.1016/j.ecss.2014.03.012

Goodenough AE (2010) Are the ecological impacts of alien species misrepresented? A review of the "native good, aliens bad" philosophy. *Community Ecology* 11: 13–21, http://dx.doi.org/10.1556/ComEc.11.2010.1.3

Gribben PE, I'Ons S, Phillips NE, Geange SW, Wright JT, Murray BR (2013) Biogeographic comparisons of the traits and abundance of an invasive crab throughout its native and invasive ranges. *Biological Invasions* 15: 1877–1885, http://dx.doi.org/10.1007/s10530-013-0416-0

Griffen BD, Altman I, Bess BM, Hurley J, Penfield A (2012) The role of foraging in the success of invasive Asian shore crabs in New England. *Biological Invasions* 14: 2545–2558, http://dx.doi.org/10.1007/s10530-012-0251-8

Grosholz ED, Ruiz GM (2003) Biological invasions drive size increases in marine and estuarine invertebrates. *Ecology Letters* 6: 700–705, http://dx.doi.org/10.1046/j.1461-0248.2003.00495.x

Hayes KR, Barry SC (2008) Are there any consistent predictors of invasion success? *Biological Invasions* 10: 483–506, http://dx.doi.org/10.1007/s10530-007-9146-5

Hegele-Drywa J, Normant M (2009) Feeding ecology of the American crab *Rhithropanopeus harrisii* (Crustacea, Decapoda) in the coastal waters of the Baltic Sea. *Oceanologia* 51: 361–375, http://dx.doi.org/10.5697/oc.51-3.361

Hegele-Drywa J, Normant M (2014) Non-native crab *Rhithropanopeus harrisii* (Gould, 1984) – a new component of the benthic communities in the Gulf of Gdansk (southern Baltic Sea). *Oceanologia* 56: 125–139, http://dx.doi.org/10.5697/oc.56-1.125

Hooper DU, Chapin III FS, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawton JH, Lodge DM, Loreau M, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning a consensus of current knowledge. *Ecological Monographs* 75: 3–35, http://dx.doi.org/10.1890/04-0922

Huang K, Boudreau BP, Reed DC (2007) Simulated fiddler- crab sediment mixing. *Journal of Marine Research* 65: 491–522, http://dx.doi.org/10.1357/002224007782689120

Jeschke JM, Bacher S, Blackburn TM, Dick JTA, Essl F, Evans T, Gaertner M, Hulme PE, Kuhn I, Mrugala A, Pergl J, Pyšek P, Rabitsch W, Riccardi A, Richardson DM, Sendek A, Vilà M, Winter M, Kumschick A (2014) Defining the impact of non-native species. *Conservation Biology* 28: 1188–1194, http://dx.doi.org/10.1111/cobi.12299

Kang HK, Poulet SA (2000) Reproductive success in *Calanus helgolandicus* as a function of diet and egg cannibalism. *Marine Ecology Progress Series* 201: 241–250, http://dx.doi.org/10.3354/meps201241

Karlson AM, Gorokhova E, Elmgren R (2015) Do deposit-feeders compete? Isotopic niche analysis of an invasion in a species-poor system. *Scientific Reports* 5: 9715, http://dx.doi.org/10.1038/srep09715

Kauppi L, Norkko A, Norkko J (2015) Large-scale species invasion into a low-diversity system: spatial and temporal distribution of the invasive polychaetes *Marenzelleria* spp. in the Baltic Sea. *Biological Invasions* 17: 2055–2074, http://dx.doi.org/10.1007/s10530-015-0860-0

Keller TA, Powell I, Weissburg J (2003) Role of olfactory appendages in chemically mediated orientation of blue crabs. *Marine Ecology Progress Series* 261: 217–231, http://dx.doi.org/10.3354/meps261217

Kidawa A, Markowska M, Rakusa-Suszczewski S (2004) Chemosensory behaviour in the mud crab, *Rhithropanopeus harrisii tredentatus* from Martwa Wisla Estuary (Gdansk Bay, Baltic Sea). *Crustaceana* 77: 897–908, http://dx.doi.org/10.1163/1568540042781711

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* 16: 199–204, http://dx.doi.org/10.1016/S0169-5347(01)02101-2

Kristensen E, Penha-Lopes G, Delefosse M, Valdemarsen T, Quintana CO, Banta GT (2012) What is bioturbation? The need for a precise definition for fauna in aquatic sciences. *Marine Ecology Progress Series* 446: 285–302, http://dx.doi.org/10.3354/meps09506

Lee PG, Meyers SP (2006) Chemoattraction and feeding simulation in crustaceans. *Aquaculture Nutrition* 2: 157–164, http://dx.doi.org/10.1111/j.1365-2095.1996.tb00055.x

Lehtiniemi M, Ojaveer H, David M, Galil B, Gollasch S, McKenzie C, Minchin D, Occhipinti-Ambrogi A, Olenin S, Pederson J (2015) Dose of truth - monitoring marine non-indigenous species to serve legislative requirements. *Marine Policy* 54: 26–35, http://dx.doi.org/10.1016/j.marpol.2014.12.015

Leppäkoski E, Shiganova T, Alexandrov B (2009) European enclosed and semi-enclosed seas. In: Rilov G, Crooks J (eds) Biological Invasions in Marine Ecosystems: Ecological,

Management, and Geographic Perspectives. *Ecological Studies* 204: 529–547, http://dx.doi.org/10.1007/978-3-540-79236-9_30

Leppäranta M, Myrberg K (2009) Physical oceanography of the Baltic Sea. Geophysical Sciences. Springer-Verlag, Berlin, Heidelberg, 378 pp, http://dx.doi.org/10.1007/978-3-540-79703-6

Marchetti MP, Moyle PB, Levine R (2004) Invasive species profiling? Exploring the characteristics of non-native fishes across invasions stages in California. *Freshwater Biology* 49: 646–661, http://dx.doi.org/10.1111/j.1365-2427.2004.01202.x

Marcus NH, Boero F (1998) Minireveiw: the importance of benthic-pelagic coupling and the forgotten role of life-cycles in coastal aquatic systems. *Limnology and Oceanongraphy* 43: 763–768, http://dx.doi.org/10.4319/lo.1998.43.5.0763

McClelland JW, Valiela I (1998) Linking nitrogen in estuarine producers to land-derived sources. *Limnology and Oceanography* 43: 577–585, http://dx.doi.org/10.4319/lo.1998.43.4.0577

Muggeo VMR (2008) segmented: an R package to fit regression models with broken-line relationships. *R News* 8/1: 20–25

Nordström M, Aarnio K, Bonsdorff E (2009) Temporal variability of a benthic food web: patterns and processes in a low-diversity system. *Marine Ecology Progress Series* 378: 13–26, http://dx.doi.org/10.3354/meps07872

Nordström MC, Lindblad P, Aarnio K, Bonsdorff E (2010) A neighbour is a neighbour? Consumer diversity, trophic function, and spatial variability in benthic foodwebs. *Journal of Experimental Marine Biology and Ecology* 391: 101–111, http://dx.doi.org/10.1016/j.jembe.2010.06.015

Norkko J, Reed DC, Timmermann K, Norkko A, Gustafsson BG, Bonsdorff E, Slomp CP, Carstensen J, Conley DJ (2012) A welcome can of worms? Hypoxia mitigation by an invasive species. *Global Change Biology* 18: 422–434, http://dx.doi.org/10.1111/j.1365-2486.2011.02513.x

Nurkse K, Kotta J, Orav-Kotta H, Pärnoja M (2015) Laboratory analysis of the habitat occupancy of the crab *Rhithropanopeus harrisii* (Gould) in an invaded ecosystem: the north-eastern Baltic Sea. *Estuarine, Coastal and Shelf Science* 154: 152–157, http://dx.doi.org/10.1016/j.ecss.2014.12.046

Ojaveer H, Galil BS, Campbell ML, Carlton JT, Canning-Clode J, Cook EJ, Davidson AD, Hewitt CL, Jelmert A, Marchini A, McKenzie CH, Minchin D, Occhipinti-Ambrogi A, Olenin S, Ruiz G (2015) Classification of non-indigenous species based on their impacts: Considerations for application in marine management. *PLoS Biology* 13(4): e1002130, http://dx.doi.org/10.1371/journal.pbio.1002130

Ojaveer H, Gollasch S, Jaanus A, Kotta J, Laine AO, Minde A, Normant M, Panov VE (2007) Chinese mitten crab *Eriocheir sinensis* in the Baltic Sea – a supply-side invader? *Biological Invasions* 9: 409–418, http://dx.doi.org/10.1007/s10530-006-9047-z

Paavola M, Olenin S, Leppäkoski E (2005) Are invasive species most successful in habitats of low native species richness across European brackish water seas? *Estuarine, Coastal and Shelf Science* 64: 738–750, http://dx.doi.org/10.1016/j.ecss.2005.03.021

Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JE, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* 1: 3–19, http://dx.doi.org/10.1023/A:1010034312781

Paterson RA, Dick JTA, Pritchard DW, Ennid M, Hatcher MJ, Dunn AM (2015) Predicting invasive species impacts: a community module functional response approach reveals context dependencies. *Journal of Animal Ecology* 84: 453–463, http://dx.doi.org/10.1111/1365-2656.12292

Petersen C (2006) Range expansion in the northeast Pacific by an estuary mud crab – a molecular study. *Biological Invasions* 8: 565–576, http://dx.doi.org/10.1007/s10530-005-0160-1

Peterson JP, Fry B (1987) Stable isotopes in ecosystem studies. *Annual Review of Ecology and Systematics* 18: 293–320, http://dx.doi.org/10.1146/annurev.es.18.110187.001453

Pimm SL, Lawton JH (1978) On feeding on more than one trophic level. *Nature* 275: 542–544, http://dx.doi.org/10.1038/275542a0

R Development Core Team (2014) R: A language and environment for statistical computing. The R Foundation for statistical computing, Vienna, Austria 3-900051-07-0 (Available online at http://www.R-project.org/)

Raffaelli D, Bell E, Weithoff G, Matsumoto A, Cruz-Motta JJ, Kershaw P, Parker R, Parry D, Jones M (2003) The ups and downs of benthic ecology: consideration of scale, heterogeneity and surveillance for benthic-pelagic coupling. *Journal of Experimental Marine Biology and Ecology* 285–286: 191–203, http://dx.doi.org/10.1016/S0022-0981(02)00527-0

Reiss J, Birdle JR, Montoy JM, Woodward G (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution* 24: 505–514, http://dx.doi.org/10.1016/j.tree.2009.03.018

Rittschof D (1992) Chemosensation in the daily life of crabs. *American Zoologist* 32: 363–369, http://dx.doi.org/10.1093/icb/32.3.363

Ristvey A, Rebach S (1999) Enhancement of the response of rock crabs, *Cancer irroratus*, to prey odors following feeding experience. *The Biological Bulletin* 197: 361–367, http://dx.doi.dispral/10.2307/1542790

Rolff C (2000) Seasonal variation in δ^{13}C and δ^{15}N of size-fractionated plankton at a coastal station in the northern Baltic proper. *Marine Ecology Progress Series* 203: 47–65, http://dx.doi.org/10.3354/meps203047

Ryan EP (1956) Observations on the life histories and the distribution of the Xanthidae (mud crabs) of Chesapeake Bay. *American Midland Naturalist* 56: 138–162, http://dx.doi.org/10.2307/2422450

Simberloff D, Martin J-L, Genovesi P, Maris V, Wardle DA, Aronson J, Courchamp F, Galil B, García-Berthou E, Pascal M, Pyšek P, Sousa R, Tabacchi E, Vilà M (2013) Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution* 28: 58–66, http://dx.doi.org/10.1016/j.tree.2012.07.013

Solan M, Raffaelli DG, Paterson DM, White PCL, Pierce GJ (2006) Marine biodiversity and ecosystem function: empirical approaches and future challenges. Introduction. *Marine Ecology Progress Series* 311: 175–178, http://dx.doi.org/10.3354/meps311175

Stachowicz JJ, Fried H, Osman RW, Whitlatch RB (2002) Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. *Ecology* 83: 2575–2590, http://dx.doi.org/10.1890/0012-9658(2002)083[2575:BIRAME]2.0.CO;2

Strayer DL (2012) Eight questions about invasions and ecosystem functioning. *Ecology Letters* 15: 1199–1210, http://dx.doi.org/10.1111/j.1461-0248.2012.01817.x

Symstad AJ, Chapin III FS, Wall DH, Gross KL, Huenneke LF, Mittelbach GG, Peters DPC, Tilman D (2003) Long-term and large-scale perspectives on the rela- tionship between biodiversity and ecosystem functioning. *BioScience* 53: 89–98, http://dx.doi.org/10.1641/0006-3568(2003)053[0089:LTALSP]2.0.CO;2

Søreide JE, Nygård H (2012) Challenges using stable isotopes for estimating trophic levels in marine amphipods. *Polar Biology* 35: 447–453, http://dx.doi.org/10.1007/s00300-011-1073-3

Thomsen MS, Wernberg T, Schiel D (2015) Invasions by non-indigenous species. In: Crowe TP, Frid CLJ (eds), Marine Ecosystems: Human Impacts on Biodiversity, Functioning and Services. Cambridge University Press, pp 274–334, http://dx.doi.org/10.1017/cbo9781139794763.010

Toscano BJ, Griffen BD (2012) Predatory crab size diversity and bivalve consumption in oyster reefs. *Marine Ecology Progress Series* 445: 65–74, http://dx.doi.org/10.3354/meps09461

Tran MV (2014) The scent of cannibalism: the olfactory basis of cannibalism in hermit crabs. *Journal of Experimental Marine Biology and Ecology* 457: 8–14, http://dx.doi.org/10.1016/j.jembe.2014.03.019

Turoboyski K (1973) Biology and ecology of the crab *Rhithro-panopeus harrisii* spp. *tridentatus. Marine Biology* 23: 303–313, http://dx.doi.org/10.1007/BF00389338

Törnroos A, Bonsdorff E (2012) Developing the multitrait concept for functional diversity: lessons from a system rich in functions but poor in species. *Ecological Applications* 22: 2221–2236, http://dx.doi.org/10.1890/11-2042.1

Törnroos A, Norström MC, Bonsdorff E (2013) Coastal habitats as surrogates for taxonomic, functional and trophic structures of benthic faunal communities. *PloS ONE* 8(10): e78910, http://dx.doi.org/10.1371/journal.pone.0078910

Törnroos A, Bonsdorff E, Bremner J, Blomqvist M, Josefson AF, Garcia C, Warzocha J (2015) Marine benthic ecological functioning over decreasing taxonomic richness. *Journal of Sea Research* 98: 49–56, http://dx.doi.org/10.1016/j.seares.2014.04.010

Valanko S, Norkko A, Norkko J (2010) Strategies of post-larval dispersal in non-tidal soft-sediment communities. *Journal of Experimental Marine Biology and Ecology* 384: 51–60, http://dx.doi.org/10.1016/j.jembe.2009.12.012

Van Kleunen M, Dawson W, Schlaepfer D, Jeschke JM, Fischer M (2010) Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecology Letters* 13: 947–958, http://dx.doi.org/10.1111/j.1461-0248.2010.01503.x

Velez Z, Hubbard PC, Hardege JD, Barata EN, Canário AVM (2007) The contribution of amino acids to the odour of a prey species in the Senegalese sole (*Solea senegalensis*). *Aquaculture* 265: 336–342, http://dx.doi.org/10.1016/j.aquaculture.2007.02.029

Villéger S, Miranda JR, Hernández DF, Mouillot D (2010) Contrasting changes in taxonomic vs. functional diversity of tropical fish community after habitat degradation. *Ecological Applications* 20: 1512–1522, http://dx.doi.org/10.1890/09-1310.1

Villnäs A, Perus J, Bonsdorff E (2011) Structural and functional shifts in zoobenthos induced by organic enrichment - implications for community recovery potential. *Journal of Sea Research* 65: 8–18, http://dx.doi.org/10.1016/j.seares.2010.06.004

Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E (2007) Let the concept of trait be functional. *Oikos* 116: 882–892, http://dx.doi.org/10.1111/j.0030-1299.2007.15559.x

Vitousek PM (1990) Biological invasions and ecosystem processes: towards an integration of population biology and ecosystem studies. *Oikos* 57: 7–13, http://dx.doi.org/10.2307/3565731

Webb TJ, Tyler EHM, Somerfield PJ (2009) Life history mediates large scale population ecology in marine benthic taxa. *Marine Ecology Progress Series* 396: 293–306, http://dx.doi.org/10.3354/meps08253

Weissburg MJ, Zimmer-Faust RK (1993) Life and death in moving fluids: hydrodynamic effects on chemosensory- mediated pre-dation. *Ecology* 74: 1428–1443, http://dx.doi.org/10.2307/1940072

Werner EE, Gilliam JF (1984) The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15: 393–425, http://dx.doi.org/10.1146/annurev.es.15.110184.002141

Williams AB (1984) Shrimps, lobsters and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institute Press, Washington DC, 550 pp

Zaitsev Y, Öztürk B (eds) (2001) Exotic species in the Aegean, Marmara, Black, Azov and Caspian Seas. Published by Turkish Marine Research Foundation, Istanbul, Turkey, 267 pp

APPENDIX 7:

Inter-annual and spatial variability in the abundance and distribution of a benthic trophic connector species, *Saduria entomon*, in the Baltic Sea

Brian R. MacKenzie[1], Mayya Gogina[2], Michael L. Zettler[2], Jan Warzocha[3]

[1]National Institute for Aquatic Resources, Technical University of Denmark, DK 2800 Kongens Lyngby, Denmark

[2]Leibnitz Institute for Baltic Sea Research (IOW), Rostock-Warnemünde, Germany

[3]National Marine Fisheries Research Institute, Gdynia, Poland

Abstract:

The isopod *Saduria entomon* has a key functional role in Baltic food webs because it is both a predator of other benthic animals and is a prey for higher trophic level species including cod *Gadus morhua*. *S. entomon* is relatively widely distributed and common in large areas of the Baltic Sea. Consequently, it has an important connective role in Baltic food webs because it mediates the flow of carbon and energy from primarily detritivores, scavengers and smaller predators in the benthos back into higher, larger-sized trophic levels where it can contribute to increased production of biomass. Knowledge of the magnitude of variations in its abundance and spatial distribution over time is therefore needed in order to understand and predict how food webs might react when *S. entomon* abundance changes. We have compiled a large database of abundance and distributional data from monitoring and dedicated field studies to estimate the time-space variations at inter-annual and regional scales. The results help define new baselines of abundance and range that can be used in Baltic food web models, and compared with impacts of future climate and nutrient loading changes.

Keywords: *Saduria entomon*, abundance, distribution, variability, Baltic Sea

Poster presented at BONUS Symposium "Science Delivery for Sustainable Use of the Baltic Sea Living Resources, Tallinn, Estonia, Oct. 17-19, 2017:

Inter-annual and spatial variability in the abundance and distribution of a benthic trophic connector species, *Saduria entomon*, in the Baltic Sea

MacKenzie, B. R.[1], Gogina, M.[2], Zettler, M. L.[2], Warzocha, J.[3]

1. DTU Technical University of Denmark
2. Leibniz-Institut für Ostseeforschung Warnemünde
3. MIR Morski Instytut Rybacki Państwowy Instytut Badawczy

Background:

Saduria entomon is a key benthic invertebrate in Baltic food webs. It is both a major predator of other benthic invertebrates and an important prey for numerous fish species, including cod.

Given its important functional role in the foodweb, we wished to quantify time-space variations in its abundance using available sampling data. New studies are needed to better understand the relative role of benthos on cod condition, reproduction and population dynamics.
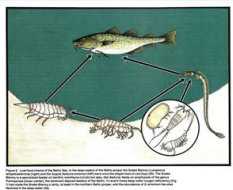
Objectives:

- Compile abundance and distribution data for *S. entomon* in the Baltic Sea and organize data in database
- Conduct statistical analyses to investigate and quantify magnitude of time-space variations across major sub-areas

Methods:

Standardized benthic sampling has been conducted in the Baltic Sea since many decades (e. g., Helcom).
S. entomon abundances have been extracted from existing datasets and compiled into a new database.

Abundances and distributions have been analysed statistically for specific sub-areas, depths and seasons according to data availability.

Results:

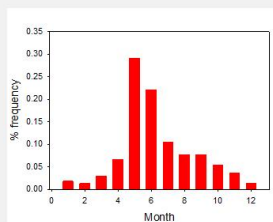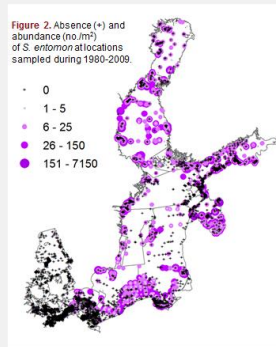A database has been created containing > 28,000 sampling events throughout the Baltic and since the 1950s.

Figure 2. Absence (+) and abundance (no./m²) of *S. entomon* at locations sampled during 1980-2009.

- · 0
- · 1 - 5
- · 6 - 25
- · 26 - 150
- · 151 - 7150

Figure 3. Seasonal distribution of sampling effort for *S. entomon* in ICES Subdivisions 20-32 during 1900 - 2015. N = 24875.
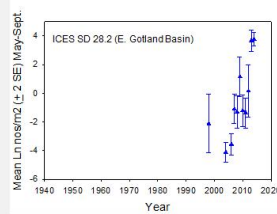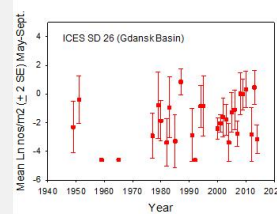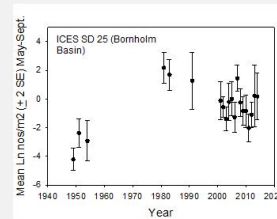

Figure 4. Means (2 SE) of ln nos *S. entomon*/m2 for three sub-areas of the Baltic Sea (ICES SD 25, 25, and 28.2).

Conclusions:

- A large database of *S. entomon* abundance and distribution has been constructed which can be used to quantify variability in a key benthic species and links to other species.
- Some preliminary analyses show large spatial differences and some temporal variations
- Available sampling is concentrated in summer and not able to address seasonal variations. New sampling is required.

Contact for further information:

brm@aqua.dtu.dk