BONUS BIO-C3

Biodiversity changes: causes, consequences and management implications

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BIO-C3 overview

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

Why is Biodiversity important?

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

Biodiversity and BIO-C3

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

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

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

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

From science to management

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

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I. Executive Summary

The network of marine protected areas (MPAs) in the Baltic Sea, including marine EU Natura 2000 areas constitutes a cornerstone in the effort of the Baltic countries to protect marine biodiversity. Partly overlapping with Natura 2000 is the HELCOM-MPA network, which aims toward an ecologically coherent network based on scientific understanding. However, HELCOM MPAs do not enjoy the extensive legal status as do the Natura 2000 areas. Designation of MPAs is presently based on assessment of the occurrence of species and habitats within the individual potential MPAs and with the exception of birds and marine mammals the designation is typically seen from a national perspective. Further, the criteria for designation of MPAs like the Special Areas of Conservation (SACs) *sensu* the EU Habitats Directive or Special Protected Areas for Birds (SPAs) *sensu* the EC Birds Directive do not relate to the provision of critical ecological processes and supporting food webs and can be seen as reflecting a static state of affairs in terms of biodiversity and bioproductivity. Accordingly, there is a great need for developing tools, which can assess the importance and connectivity of MPAs given current and future ecosystem dynamics. A wider, ecosystem-based approach to monitoring, status assessment and management require operational tools that can encompass the spatial and temporal complexity of the marine ecosystem. Increasingly, it is acknowledged that biophysical and biogeochemical ecosystem modelling approaches are the only feasible options to quantify complex interactions as connectivity across regional and local seas and effects of changes through trophic levels, and form the basis for the state-of-tomorrow MPA management tools.

Task 5.2 aimed at developing tools and methods to quantify the current function of the Baltic MPA network and to assess possible changes given the expected development of drivers (e.g. climate change and nutrient input). The task covers a range of spatio-temporal scales, species and dispersal strategies from blue mussels to waterbirds. The studies include basin-wide studies covering the whole Baltic Sea, high-resolution fine-scale studies of sub-basins and detailed studies of local populations. Several tools were used for the studies. Two studies used biophysical modelling, which is suitable for biological dispersal that is highly influenced by the physical water transport in ocean circulation. Two cases used agent-based modelling driven by 3D hydrodynamic and ecosystem (biogeochemical) modelling, to study the biological dispersal that beside water transport is influenced by biological processes. One case integrated molecular analysis and biophysical modelling to assess genetic connectivity that is highly important to understand the actual dispersal between populations. Finally, a bioenergetics model linked to hydrodynamics and ecosystem (biogeochemical) modelling allowed for quantifying bottom-up driven changes in survival of top-predators (waterbirds).

Knowledge about the large-scale dispersal patterns of for example fish eggs and larvae is essential for designing the optimal network of MPAs and defining ecological relevant management units. Two large-scale connectivity studies used biophysical modelling to provide information on connectivity and dispersal patterns for the entire Baltic Sea. Both studies found that dispersal distance varied considerably among regions within the Baltic Sea. One study focused on decadal (1970s, 1980s, 1990s, 2000s), regional, and depth-layer resolved information on connectivity and dispersal patterns. The results indicated that there are large geographic differences within the Baltic Sea and a general trend towards shorter dispersal distances in the northern part compared to the western and central part. Mean patterns of dispersal rates for four selected subareas in the Baltic Sea, showed relatively high dispersal rates for the western and for the southern and central Baltic Sea. The other large-scale study found that dispersal distance varies considerably among areas and for different dispersal strategies with implications for local recruitment within and connectivity between MPAs in the HELCOM MPA network. The overall conclusion was that many MPAs within the HELCOM MPA network may be too small for significant local recruitment, but that there is good network connectivity, although connectivity may be enhanced in certain areas by adding strategically placed new sites.

In addition to the large-scale general model predictions of Baltic Sea connectivity a number of focus studies were included in task 5.2. The Gulf of Riga is characterised by several internationally important bird protection areas and a series of habitat protection areas was chosen for several case studies. Studies of fine-scale dispersal patterns of blue mussels in Gulf of Riga area showed that source and sink hotspots were only partly included in the existent network of MPAs, and important hotspots were not protected by the MPAs. The study suggests that all MPAs in the area received mussel larvae from other areas (sink) and provided larvae to other areas (source). Local retention was strongly related to size, but even small areas have some degree of local retention. In this case, using blue mussel larvae as a model organism, a MPA size of > 1000 km^2 or a ratio between MPA radius (assuming a circular form) and average dispersal distance > 1.5 was predicted to ensure > 30% local retention. The larvae dispersal strategy was characterised by many larvae being transported relatively short distances (average 34 km) and few long-distances. This is good news for management since it ensures both a high degree of local retention that is thought to be important for sustainable local populations and long-distance dispersal important for genetic diversity.

In the light of the unprecedented loss of mussel populations along the Baltic Sea coasts, it is critical to understand the development and maintenance of connectivity patterns between mussel reef habitats - an essential element of the Baltic MPA network. Although it is a general assumption, that the dispersal potential of the larvae is correlated with the gene flow, some studies show that modelled (larval dispersal) and realized (gene flow) connectivity do not necessarily match. An integrated gene and biophysical modelling connectivity study in Lithuania waters exemplified how changes in the connectivity patterns and impact of an invasive predator can jeopardise the current and projected effectiveness of MPA. The results showed rather consistent present connectivity patterns from both the biophysical model and gene flow analysis, suggesting that mussel reefs in the coastal zone are sinks rather than sources for *Mytilus* larvae. The future increase in larval dispersal distance and decrease in connectivity between reefs, predicted by the climate scenario model, may have several consequences. If there is no efficient larval supply from other nearby reefs, the decrease in local retention and inter-reef connectivity will reduce recruitment and may make the mussel populations on all considered reefs less persistent and resilient.

A downscaled benthic food-web model for the Gulf of Riga was applied in hindcast and forecast mode to study the past and future levels of nutrient control of the available food supply in terms of bivalves to top predators. The projected decline in the biomass of blue mussels was predicted to have a significant impact on the energetics of the Long-tailed Duck in terms of increased foraging effort and mortality. The predicted annual mortality of Long-tailed Ducks in the Gulf at the end of the 21st century in the Baltic Sea Action Plan (BSAP) scenario would lead to a significant decline in the number of Long-tailed Ducks in the whole area as well as in the MPAs. Adding 25% predation by round gobies to the BSAP scenario would lead to further reductions in the carrying capacity of the area for Long-tailed Ducks. The predicted decline following the BSAP scenario will have a serious effect on the importance of the Natura 2000 network of bird protection areas (SPAs) relative to the size of the bio-geographic population, albeit the predicted overall distribution of waterbirds relative to the SPAs will not change markedly (10% less waterbirds in SPAs).

In summary, task 5.2 presents new modelling tools and shows examples and suggestions for their application in operational MPA management to identify optimal MPA network and management units on larger scale complemented with sub-basin studies to identify sink and source hotspots, assess adequacy and connectivity of MPAs. We demonstrated integrated genetic and biophysical modelling that identified present and future challenges to ensure persistent and resilient populations through efficient larvae supply. Finally, we assessed the consequences of reduced nutrient supply for mussel biomass and water birds pointing at the need for tools that can quantify effects through several trophic levels in order to achieve future synergies and compliance between WFD, MSFD and NATURA 2000 plans and ensure biodiversity conservation in the Baltic Sea.

II. Introduction

The network of marine protected areas (MPAs) in the Baltic Sea, including marine EU Natura 2000 areas constitutes a cornerstone in the effort of the Baltic countries to protect marine biodiversity. Partly overlapping with Natura 2000 there is also the HELCOM-MPA network, which aims toward an ecologically coherent network based on scientific understanding. However, HELCOM MPAs do not enjoy the extensive legal status as do the Natura 2000 areas. Designation of MPAs is presently based on assessment of the occurrence of species and habitats within the individual potential MPAs and with the exception of birds and marine mammals the designation is typically seen from a national perspective (HELCOM 2010a). Further, the criteria for designation of MPAs like the Special Areas of Conservation (SACs) *sensu* the EU Habitats Directive or Special Protected Areas for Birds (SPAs) *sensu* the EC Birds Directive do not relate to the provision of critical ecological processes and supporting food webs and can be seen as reflecting a static state of affairs in terms of biodiversity and bioproductivity. However, ecosystem-based environmental management has been the desired approach for the last decade(s), although its realisation in MPA management has been held back by lack of operational management tools that can encompass the spatial and temporal complexity of local marine ecosystems. The only feasible option to understand the connectivity across entire landscapes and the flow of energy through the food web is the use of biophysical and biogeochemical modelling in our endeavour to advance MPA management (e.g. Treml et al. 2015), quantify effects of measures, and align targets for Natura 2000, WFD and MSFD.

The distance and direction of dispersal have considerable influence on the demography and genetic structure of all species populations. In marine benthic ecosystems, connectivity of species during the early life stages is crucial, since exchange during the adult stage may be limited, or in the case of sessile organism impossible. The mixing and exchange of individuals among habitats and populations is of particular importance from an ecological perspective, affecting e.g. species distribution ranges, species interaction, population dynamics, as well as the demographic and genetic structure of populations. Thus, our ability to understand and protect marine populations is linked to our knowledge about connectivity patterns and to our capability to use this knowledge in operational management decisions of MPAs at regional (basin-wide) and local scale (Gaines et al. 2003, Almany et al. 2009). The assessment of the coherence of the Baltic MPA network undertaken in 2010 concluded that the network was still not ecologically coherent, with one of the main problems being a lack of connectivity between several MPAs (HELCOM 2010b).

In the last decades, an important environmental target for the WFD has been to reduce loads of nitrogen and phosphorous to the marine environment, in order to reduce plankton dominance and improve oxygen conditions at the bottom (HELCOM, 2010b). A possible consequence of the expected oilgotrophication is a lower productivity in the marine ecosystem resulting in reduced biomasses of organism that feed on phytoplankton (assuming nutrient-limited growth), e.g. filter feeding mussels and the higher trophic levels as ducks, feeding on mussels. To understand the full consequences of management decisions and to be able to choose cost-efficient measures to improve water quality while maintaining an acceptable level of biodiversity we need tools that can quantify the effect of bottom-up control on top predators.

WP 5.2 applied developed tools in the assessment of the importance of MPA networks for selected species and habitats based on carrying capacity analyses, position of important dispersal corridors and hot-spots for connectivity, analyses of importance of biological diversity for ecosystem functioning, and the expected results of climate changes. Specifically, we studied the patterns of connectivity with models and molecular analysis and developed decision support tools and case studies that based on large- and fine-scale connectivity can support design and management of MPAs in the Baltic Sea. Moreover, we aimed to develop ecological modelling tools that could quantify the effects of the Baltic Sea Action Plan (BSAP) and predicted climate changes on different levels of the food-web and align consequences for populations protected by Natura 2000, MSFD and WDF.

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III. Core Activity

1. Bio-physical modelling tool for assessing decadal, regional, and depth-layer resolved information on connectivity and dispersal patterns for the entire Baltic Sea.

Abstract: This large-scale connectivity studies that cover the entire Baltic Sea area used biophysical modelling to provide decadal (1970s, 1980s, 1990s, 2000s), regional, and depth-layer resolved information on connectivity and dispersal patterns for the entire Baltic Sea. The results indicated that there are large geographic differences within the Baltic Sea and a general trend towards shorter dispersal distances in the northern part compared to the western and central part. Mean patterns of dispersal rates for four selected subareas in the Baltic Sea, showed relatively high dispersal rates for the western and for the southern and central Baltic Sea.

Progress: All work completed and we refer to the detailed report by Hinrichsen 2017 in the appendix. Also Hinrichsen, H.-H. ,von Dewitz, B., Dierking, J. Variability of advective transport-based connectivity in the Baltic Sea. Submitted.

Deviations: No deviations from the workplan

Introduction: Knowledge about connectivity in the Baltic Sea is essential for ecosystem-based management and conservation strategies, e.g. stock-separated management of fisheries. It could also be a basis when considering for example the design of marine protected areas to maintain conservation features or population of exploited fish species. Furthermore, such kind of knowledge is also helpful to assess the importance of MPA networks, positions of important dispersal corridors and connectivity hot-spots in offshore areas could be located. The aim of the present study is to provide decadal (1970s, 1980s, 1990s, 2000s), regional, and depth-layer resolved information on connectivity and dispersal patterns for the entire Baltic Sea.

Methods and Results: The general tool used was bio-physical modelling, which is suitable for biological dispersal that is highly influenced by the physical water transport in ocean circulation. The results are assessed from Lagrangian particle tracking using ocean circulation model outputs. Because of its importance for many biological processes, e.g., fish egg and larval development, and depth layer occupied by many organisms (e.g., phyto- and zooplankton, larval stages of marine fishes) in the Baltic Sea ecosystem, our analysis was focussed on the mean flow characteristics in the water column above the halocline (2.5 and 25 m).

Dispersal distance varied considerably among regions within the Baltic Sea. The sub-basins showed local retention as well as inter-basin connectivity. The novel approach to identify partial dispersal barriers indicated that there may be a few strong barriers that could promote population divergences, and that there may be several areas that are sufficiently demographically independent to justify separate management units. Maps of spatially resolved dispersal distances show that there are large geographic differences within the Baltic Sea and that there is a general trend towards shorter dispersal distances in the northern part compared to the western and central part (Figure 1). Mean patterns of dispersal rates (50 days drift) as well as the mean duration (50% advective loss of particles) for four selected subareas in the Baltic Sea, showed relatively high dispersal rates and consequently relatively low drift durations to reach a 50% dispersal rate were obtained for the western and for the southern and central Baltic Sea (Figure 2). Compared to the relative low dispersal rates during spring and summer (quarter 2 and 3), the relative advective particle losses were observed for the autumn and winter months (quarter 4 and 1). In contrast, for the northern Baltic Sea, winter and spring months revealed the lowest dispersal rates, while the weakest dispersal was obtained for the Gulf of Finland area.

Recommendations: The identification of connectivity of populations between subareas of an ecosystem like the Baltic Sea demonstrates that human coastal communities could be strongly linked and could have an important social and economic aspect: management in one part of an ecosystem affects people who use another part of the ecosystem. Thus, understanding the connectivity in the Baltic Sea is essential for ecosystem-based management and conservation strategies, e.g. stock-separated management of fisheries. It could also be a basis when considering for example the design of marine protected areas to maintain conservation features or population of exploited fish species. Our results are also suitable to assess the importance of MPA networks, positions of important dispersal corridors and connectivity hot-spots in offshore areas could be located.

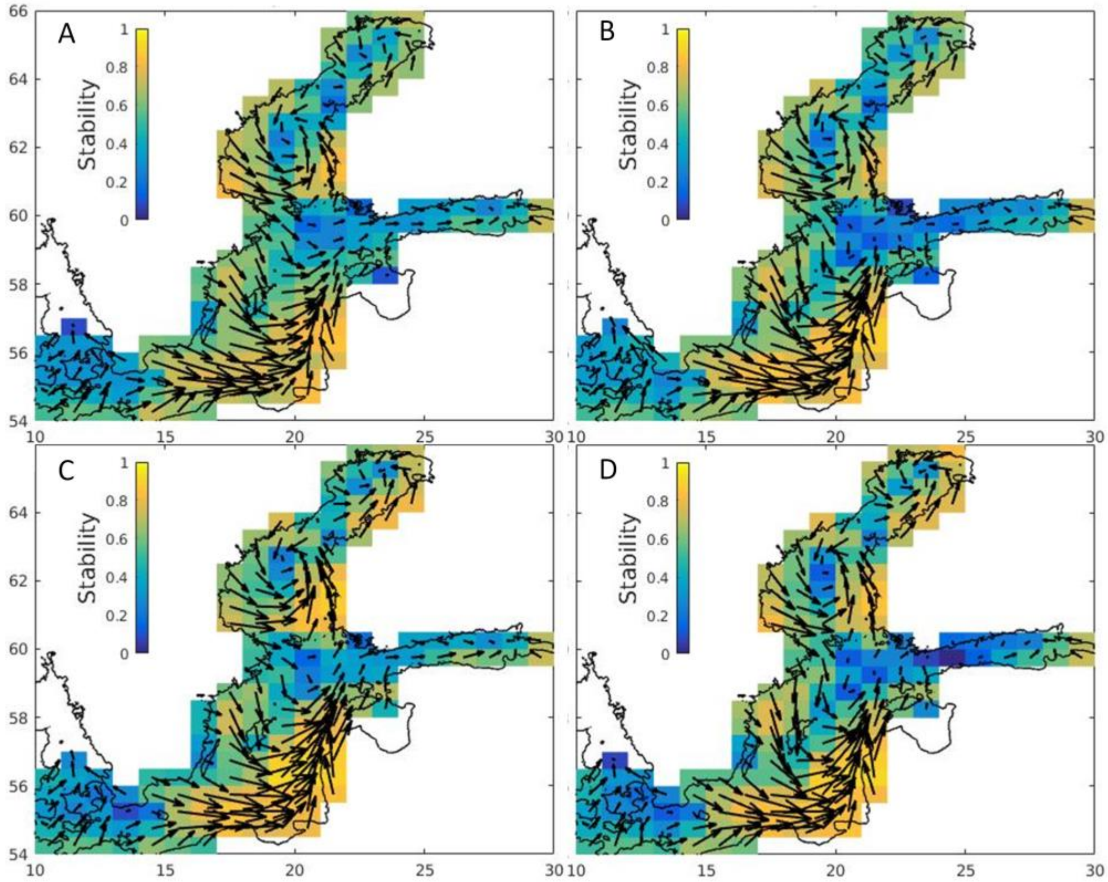

Figure 1. Ocean current based mean geographic distances and stability, 2.5m depth level, 4.quarter decade A) 1971-1980, B) 1981-1990, C) 1991-2000, and D) 2001-2010, drift duration 50 days

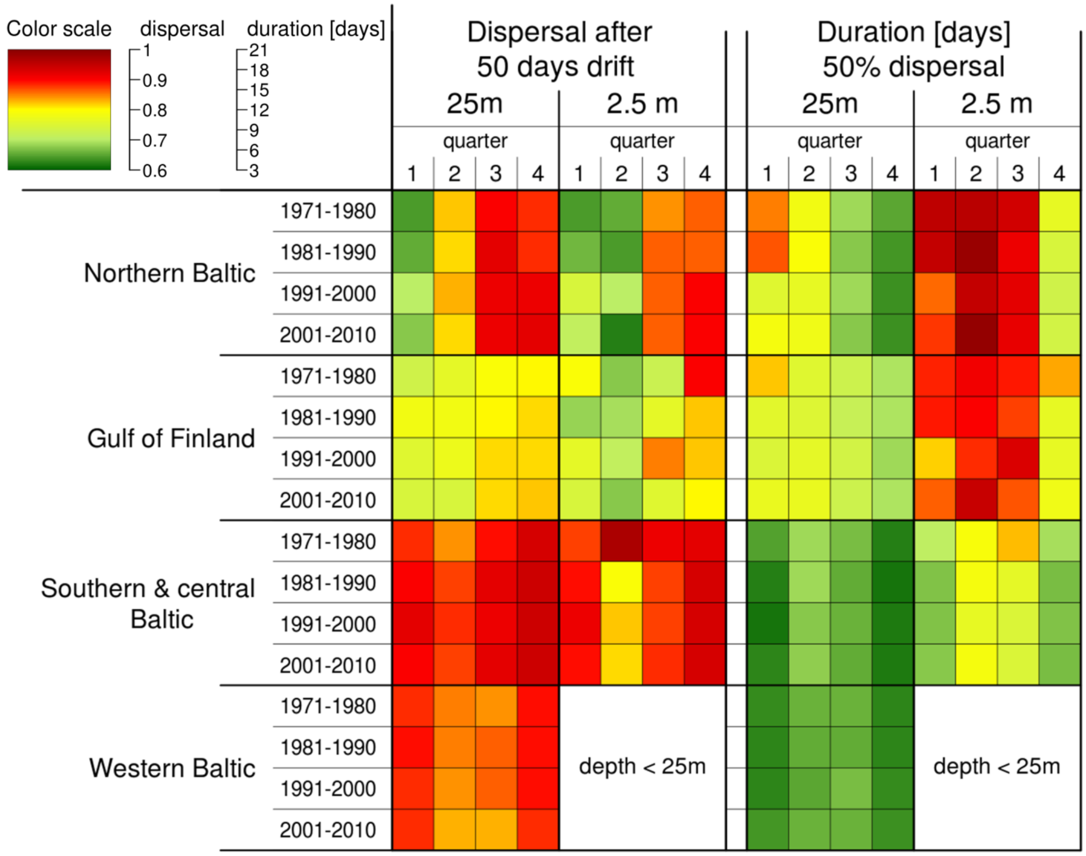

Figure 2. Relative mean dispersal after 50 days drift (left panel), and mean duration of drift until 50% dispersal (right panel) in the different subareas of the Baltic Sea

2. Basin-wide connectivity - identifying optimal networks and management units.

Abstract: A bio-physical model was used to simulate dispersal distance and connectivity in the whole HELCOM area. Dispersal distance varies considerably among areas and for different dispersal strategies with implications for local recruitment within and connectivity between MPAs in the HELCOM MPA network. Many MPAs seem too small for significant local recruitment. A novel framework to identify optimal MPA networks with regard to connectivity suggests that the HELCOM MPA network is reasonably well connected, although some gaps are identified. A new approach to identify partial dispersal barriers indicate that there may be a few strong barriers that impede gene flow and facilitate local adaptations, and that there may be several areas that are sufficiently demographically independent to justify separate management units. The HELCOM MPAs are fairly well distributed among such management units, although units along the Swedish coast is less well represented.

Progress: All work completed and we refer to the detailed report by Jonsson et al. (2017) in the Appendix.

Deviations: No deviations from work plan.

Introduction: Dispersal and connectivity are today recognized as key factors for local population dynamics and population persistence, with implications for the design of ecologically coherent MPAs. On ecological time scales dispersal reduces the risk of local extinctions and on evolutionary time scales the realized gene flow affects genetic diversity and evolution of local adaptations. Understanding dispersal and the source-sink dynamics of metapopulations are important for conservation and restoration of marine populations, and an important conservation criterion when selecting marine protected areas (MPAs). In this study the aim was to assess dispersal and connectivity in relation to the HELCOM MPA network, and to identify dispersal barriers in a geographically explicit way that may suggest management units

Methods and Results: The present study uses biophysical modelling to estimate dispersal and connectivity in the seascape of the Baltic Sea including the whole HELCOM area. The biophysical model combines a hydrodynamic model of the ocean circulation with Lagrangian particle tracking simulations where biological traits like spawning time, PLD, and vertical behaviour were implemented. From a large number of dispersal trajectories we constructed connectivity matrices specifying dispersal probabilities within the HELCOM area. Based on the connectivity matrices we have mapped dispersal distance and direction and identified optimal MPA networks using a novel method based on eigenvalue perturbation theory. In addition, we employed a new method to identify partial dispersal barriers in the Baltic seascape that may indicate separate management or evolutionary significant units. Maps of spatially resolved dispersal distance for a range of generic dispersal strategies show that there are large geographic differences in the Baltic seascape, which may affect the extent of local recruitment in HELCOM MPAs. Based on connectivity we identified optimal MPA networks with respect to maximum metapopulation growth rates. Interestingly, the optimal MPA networks, with some exceptions, largely overlap with the present HELCOM MPA network indicating sufficient connectivity within an ecological coherence framework (Fig. 3). The identification of dispersal barriers and possible management units indicates that the HELCOM MPA network is reasonable well represented in most units (Fig. 4).

Recommendations: Especially for the long-distance dispersal strategies many MPAs seem too small to allow significant local recruitment. Based on the comparison between optimal networks and the present HELCOM MPAs there seems to be some gaps in connectivity, e.g. along the Swedish coast in the Gulf of Bothnia and Bothnian Bay, as well as along the Swedish coast between Stockholm and Öland. Here there may be potential for an extension of the present network. The analysis of partial dispersal barriers may indicate demographic independence and the presence of unique local adaptations and thus suggest management units. A comparison shows that HELCOM MPAs are fairly well distributed between many of these suggested management units. There are some exceptions where MPAs are scarcer, mainly along the Swedish coast in the Gulf of Bothnia and Bothnian Bay, as well as along the Swedish coast between Stockholm and Öland.

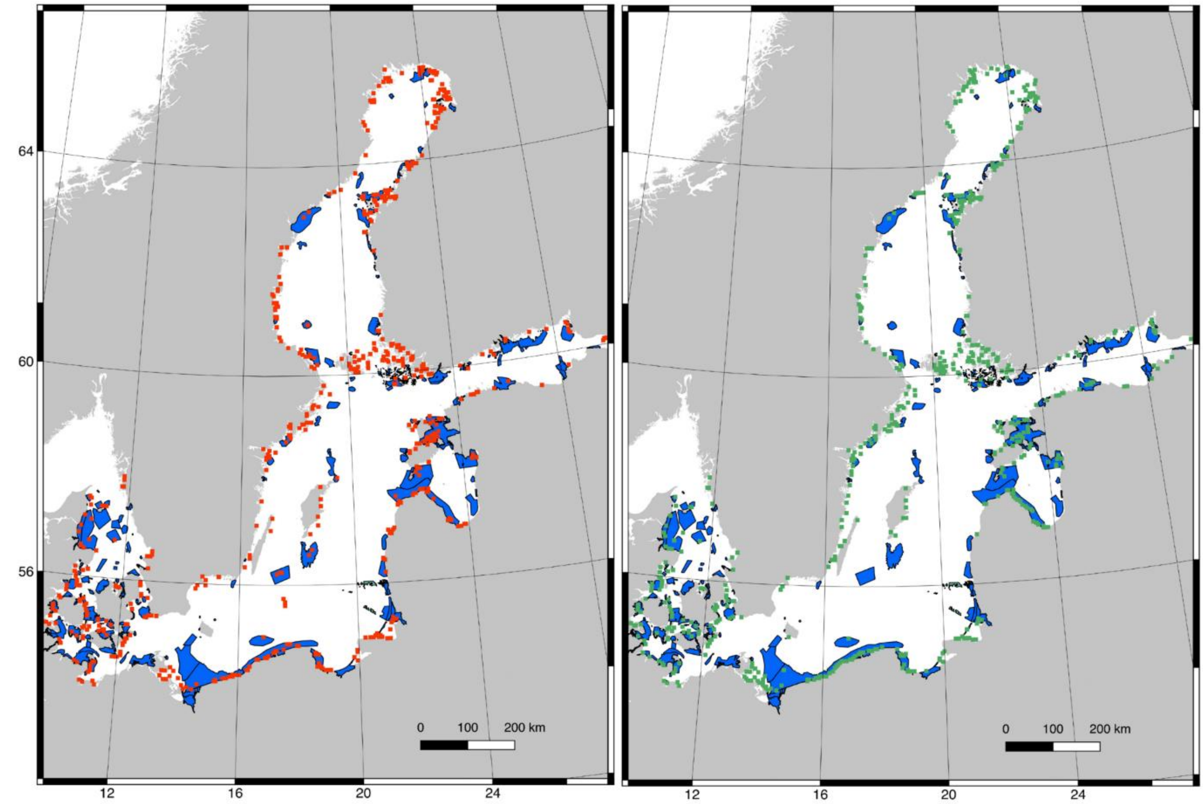

Figure 3. Left panel: Identification of the optimal MPA network (red squares) using the EPT framework for dispersal strategy B (Table 1). Right panel: Identification of a multi-species consensus network (green squares based on the EPT framework and the four dispersal strategies in Table 1. Also shown is the present HELCOM MPA network as blue polygons.

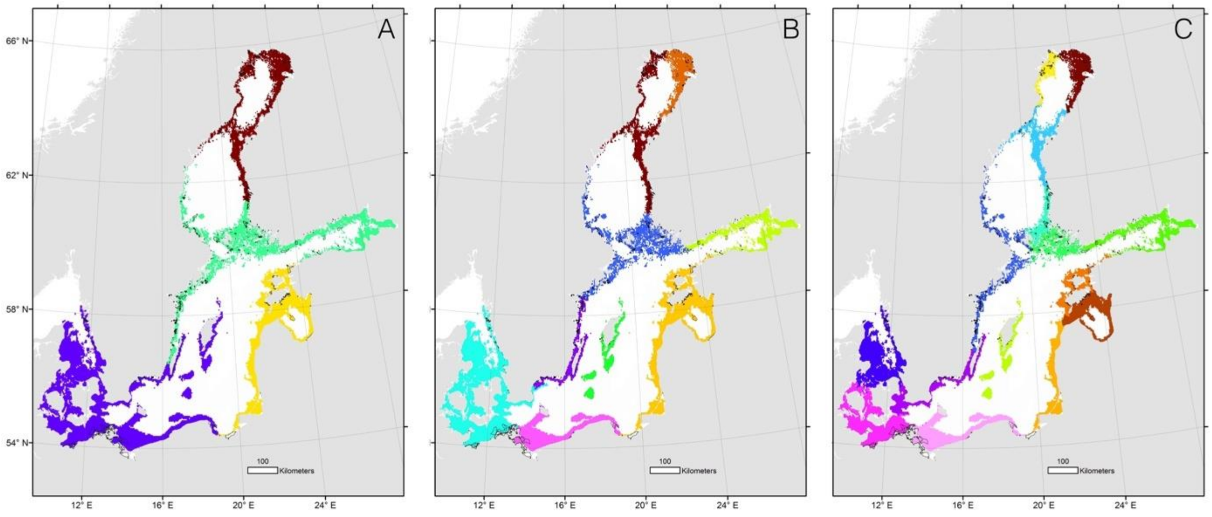

Figure 4. Identification of dispersal barriers for a dispersal strategy similar to the blue mussel Mytilus spp. and a habitat specified by the depth interval 0-30 m. (A) Low allowed dispersal between areas

producing 4 clusters. (B) Medium allowed dispersal between areas producing 9 clusters. (C) High allowed dispersal between areas producing 15 clusters.

3. Local connectivity between MPAs in the Gulf of Riga area. Source and sink hotspots.

Abstract: A fine-scale agent-based model (MIKE ABM-lab) linked with hydrodynamic- and ecosystem modelling was used to identify connectivity sink and source hotspots as well as to describe connectivity between MPAs in the Gulf of Riga area. Source and sink hotspots were only partly included in the existent network of MPAs, and important hotspots were not protected by the MPAs. The study suggests that all MPAs in the area received larvae from other areas (sink) and also provided larvae to other areas (source). Knowledge about the patterns of larvae distribution between in sub-basins and between MPAs is important to be able to protect important source areas, especially for those populations that serve as food for mussel eating birds.

Progress: All work completed and we refer to the detailed report by Middelboe *et al.* (2017a) in the Appendix.

Deviations: No deviations from work plan.

Introduction: The spatial design of protected areas can help optimize dynamic interactions between benthic populations for recovery, larval production and connectivity. However, MPA designs based on larval dispersal information are complicated due to the challenge to track larvae directly in the field and a lack of quantitative methods to assess the interactions and use them in operational management (Krueck *et al.* 2017). Owing to the lack of ability to track larvae in the field biophysical modelling was used to study connectivity patterns. Although alignments of field observations with biophysical models are still rare (e.g., Sponaugle *et al.* 2012), simulating dispersal patterns provides the only feasible option to project connectivity for multiple species across entire seascapes (Treml *et al.* 2015) and advance associated MPA management. In this study we aimed to define source and sink hotspots for *Mytilus* larvae in the Gulf of Riga area and specifically study how the present network of MPAs is located in relation to hotspots and how the connectivity is between local MPAs in the area.

Methods and Results: Small-scale connectivity was modelled using agent-based modelling (MIKE ABM lab) linked with the output of 3D hydrodynamic and ecosystem modelling (MIKE 3 Ecolab). In the ABM model, larvae transport by currents or passive drift is calculated using a combination of advection and dispersion, the former determined by the current velocity predicted by the hydrodynamic model, and the latter calculated using a random walk method and representing the movement of agents in response to currents not resolved by the hydrodynamic model, at a scale smaller than the applied model resolution. While a wide array of other environmental conditions other than the ones mentioned above affects the dispersal, survival, and settlement of mussel larvae, from a modelling perspective, it is necessary to make a range of simplifying assumptions in regard to describing the governing forces that control distribution patterns of mussel larvae.

In each of the model years, mussel larvae dispersal simulations were analysed individually relative to spawning and settlement success and degree of local recruitment. The importance of “sources” was calculated as the number of larvae spawned in a subarea relative to all spawned larvae. The relative importance of sinks was calculated as the number of larvae settled relative to the total amount of settled larvae. Total importance for connectivity was expressed as the sum of importance as source and sink. The same approach was used to calculate connectivity between MPAs, using MPAs instead of the subareas, the total number of larvae settled as the basis for assessing the importance as source and a relative measure of the MPA importance as sink.

The average relative importance of the areas as spawning (source) and settlement (sink) areas was spatially variable in the study area (for details see Middelboe *et al.* 2017). The source and sink hotspot areas are only partly located in MPAs, the main part being in bird protection areas (SPAs, Figure 5) that are not designated to protect the benthic habitats. A large connectivity hotspot not included in MPAs is the area off the south-east coast of the island Saarema. The matrix of connectivity between MPAs revealed the importance of the different areas as source and sink for each other and the degree of local retention of the areas (Table 1). The local retention varied between 5 and 60% and the importance of MPAs as source between 7 and 45%.

Recommendations: Hotspot analysis is useful together with information on pressures as decision support to protect important source areas and thereby ensure efficient larvae supply to maintain the mussel populations in the Gulf of Riga area, and thus ensure food availability for the wintering ducks that occur in large numbers in the area, which is of internationally significance. Furthermore, in case of significant disturbance to local populations, the degree of local retention and specific knowledge about source population is essential as basis for restauration decisions.

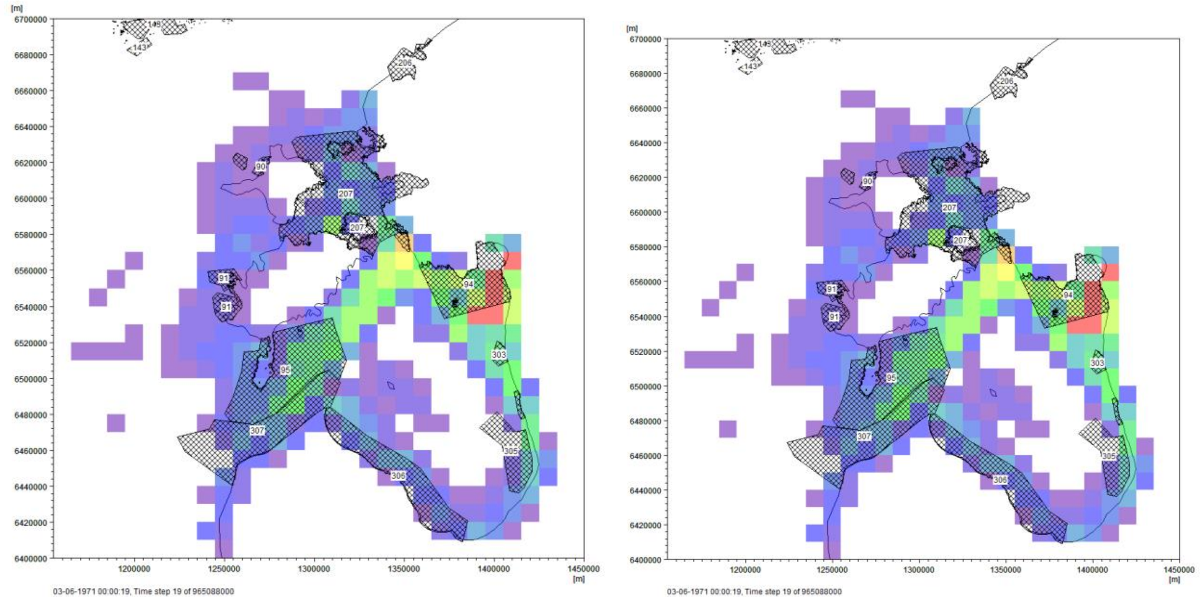

Figure 5 Importance of areas as sink expressed as the proportion of settled larvae (left) and importance of areas as source expressed as larvae spawned as a proportion of all spawned larvae (right). The average of the years 1995 to 2007 is shown. Hatched areas are marine protected areas, each identified by their ID.

Table 1. The relative importance of MPAs in the Gulf of Riga area as sink and source for the MPA network, based on modelled connectivity of Mytilus larvae. A relative measure of the importance of the MPAs as sink from other MPAs (no and IDs shown), degree of local retention and the % or larvae from the MPA settling in other MPAs as a measure of the importance as source (no and IDs shown) are shown.

ID	Sink (-)	Sink Number of MPAs (ID	Local retention	Source (%)	Source Number of MPAs (ID)
90	<0.1	1 (207)	6%	14%	2(94,**207**)
91	0.2	1 (207)	12%	15%	4(**94,95**,207,307)
94	7.3	6 (90.91,95,207,303,304,305)	46%	7%	5(207,303,304,305,307)
95	10.2	4 (91, 207,306,307)	44%	11%	2(306,307)
207	2.9	3 (90,91,94)	40%	12%	4(90,91,**94**,95)
303	1.0	3 (94,304,305)	5%	38%	4(**94**,304,**305**,306)
304	0.6	3 (94,303,305)	5%	45%	4(94,303,**305**,306)
305	13.1	4 (94,303,304,306)	17%	21%	4(94,303,304,**306**)
306	4.4	5 (95,303,304,305.307)	60%	25%	3(**95**,305,**307**)
307	5.4	4 (91,94,95,306)	29%	29%	2(**95**,306)

4. Assessing MPA adequacy and connectivity. Dispersal distances, local retention and network connectivity based on large and fine-scale connectivity models

Abstract: Quantitative assessments of MPA functionality is often difficult due to lack of quantitative methods. Here we study the larvae movement using large (basin-wide) and fine-scale (Gulf of Riga area) connectivity modelling to calculate dispersal distances of larvae spawned in MPAs, the degrees of local retention and assess the optimal MPA network. The study shows that methods based on connectivity modelling can support MPA decisions and management on large and fine scale with operational management tools.

Progress: All work completed and results included in a manuscript in progress, see Middelboe *et al.* (2017b) in the Appendix**.**

Deviations: No deviations from work plan.

Introduction: Marine species with pelagic larval stages are often regarded as open on even large scales, which has fundamental consequences for the design of marine protected areas (MPAs). The long-term persistence of a population within an MPA requires either (1) that the MPA is large enough to allow significant local recruitment, e.g. through local retention of larvae, or (2) that MPAs are connected by larval dispersal thereby replenishing one another (network persistence). Design of MPAs should thus carefully consider larval dispersal and connectivity between habitats within a network of MPAs (Gaines *et al.* 2003; Almany *et al.* 2009).

In the present study we aim to assess important aspects of adequacy and ecological coherence of the HELCOM MPA network, which covers more than 53000 km^2 of protected habitats in the Baltic Sea and the Kattegat (HELCOM 2010a). Specifically, we use biophysical modelling to assess the expected proportion of self-recruitment and how this depends on the size and location of MPAs. We also compare the performance of different spatial resolution of modelling with a test case in the Gulf of Riga where habitat information is also included. Finally, we assess the connectivity within the HELCOM MPA network with a new theoretical framework in order to find the optimal extension to enhance the connectivity within the present MPA network.

Methods and Results: Large-scale biophysical modelling. The dispersal of organisms (eggs, spores, larvae or rafting algae) was modelled on the scale of the whole HELCOM area with a Lagrangian particle-tracking model driven off-line with flow fields from a regional-scale ocean circulation model. Simulations of dispersal were carried out for 4 different dispersal strategies, which represent some of the key species in the Baltic Sea: *Fucus* spp., *Idotea* spp., *Mytilus* spp., and the flounder (*Platichthys flesus*). However, the dispersal traits of many Baltic organisms can approximately be represented by these four strategies. Based on the resulting connectivity matrices we calculated the mean dispersal distance and direction for each of the 28442 model grid cells. Local retention that may lead to local recruitment was calculated for each of 151 HELCOM MPAs as the proportion of virtual larvae released and also settled within the model grid cells overlapping with the boundaries of each MPA.

The small-scale dispersal of mussel (*Mytilus edulis*) larvae was modelled on the scale of the Gulf of Riga area with a coupled Eulerian-Lagrangian framework that allows for an accurate representation of hydraulics and water quality within a spatially complex system over time, and which simultaneously describes (i.e. models) entities such as the dispersal and settlement of larvae on an individual level.

Each years of mussel larvae dispersal simulations was analysed individually to determine dispersal distances and local recruitment. For each virtual larvae the distance between spawning and settlement was calculated and it was noted if spawning and settlement occurred in MPAs in the area. Local retention was calculated for each MPA as the number of larvae settling in the same MPA as it was spawned in relation to total number of spawned. Large-scale and fine-scale analysis showed remarkably similar results. Local retention was strongly related to size, but even small areas have some degree of local retention (Figure 6). In this case, using *Mytilus* larvae as model organisms a size of > 1000 km^2 or a ratio of MPA radius: average dispersal distance > 1.5 was predicted to ensure 30% local retention. The larvae dispersal strategy with many larvae being transported relatively short distances (average 34 km) and few long-distances ensures both local retention important for sustainable local populations and long-distance dispersal important for genetic diversity.

Using the eigenvalue perturbation framework, we identified the optimal extension of the HELCOM MPA network with respect to connectivity. In the demonstration shown in Figure 7 we show an extension of 1400 km^2 or about 3% of the present network. The main features of the proposed extension are added MPAs in the Bothnian Bay, the Swedish Baltic coast, and in the Archipelago Sea. The optimal extension also shows that proposed sites are often clustered promoting local retention.

Recommendations: Relationships between MPA size and dispersal distance of the organism in focus for protection can be used to estimate the adequacy of MPAs to ensure sufficient levels of local retention. The distribution of dispersal distances can also be used to evaluate the length of genetic connectivity. The overall conclusion from this and the accompanying report “Basin-wide connectivity - identifying optimal MPA network and management units” is that many MPAs within the HELCOM MPA network may be too small for significant local recruitment, but that there is good network connectivity, although connectivity may be enhanced in certain areas by adding strategically placed new sites. The study shows that tools based on large- and fine-scale modelling are useful as decision support as they provide operational management tools**.**

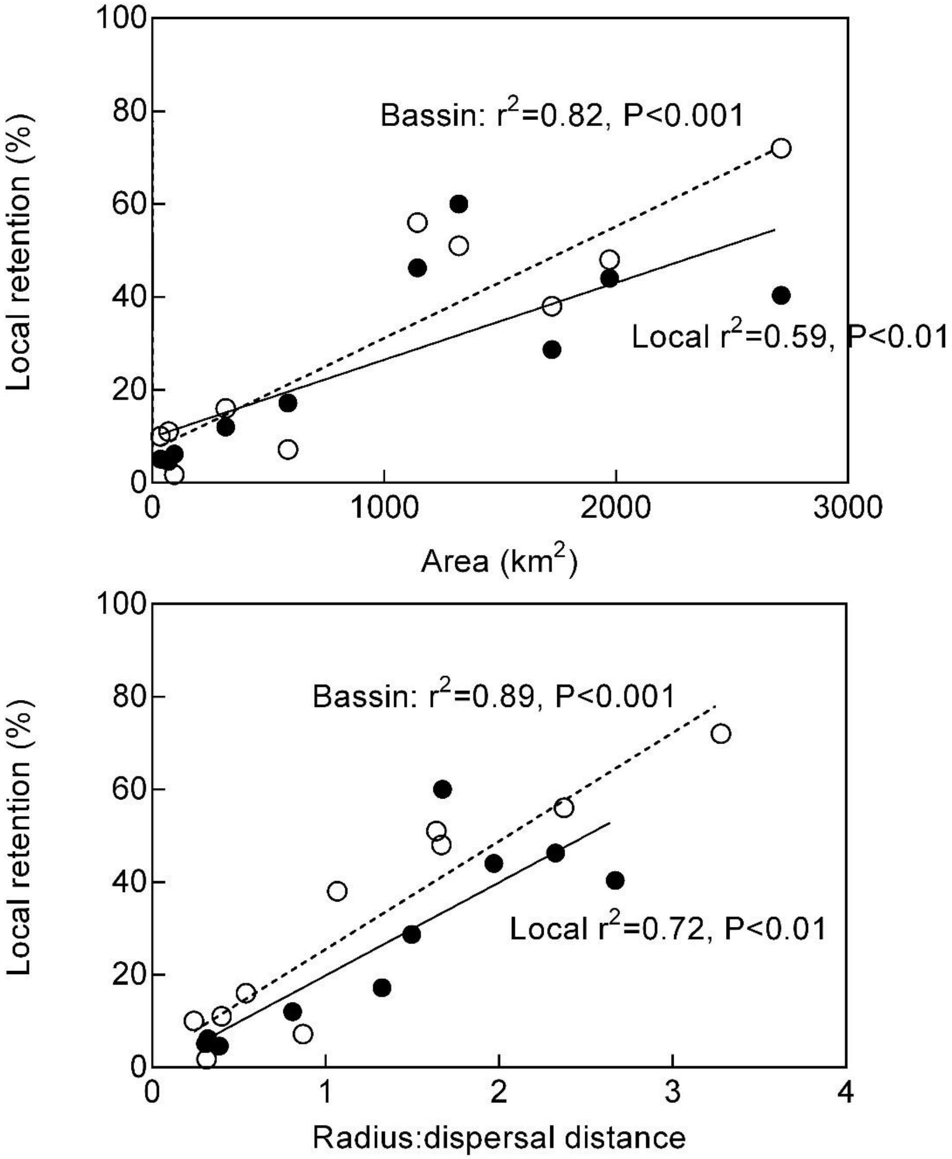

Figure 6. Local retention as a function of MPA area (upper) and radius: dispersal distance ratio calculated using the basin-wide (open circles) and local-scale mode (filled).

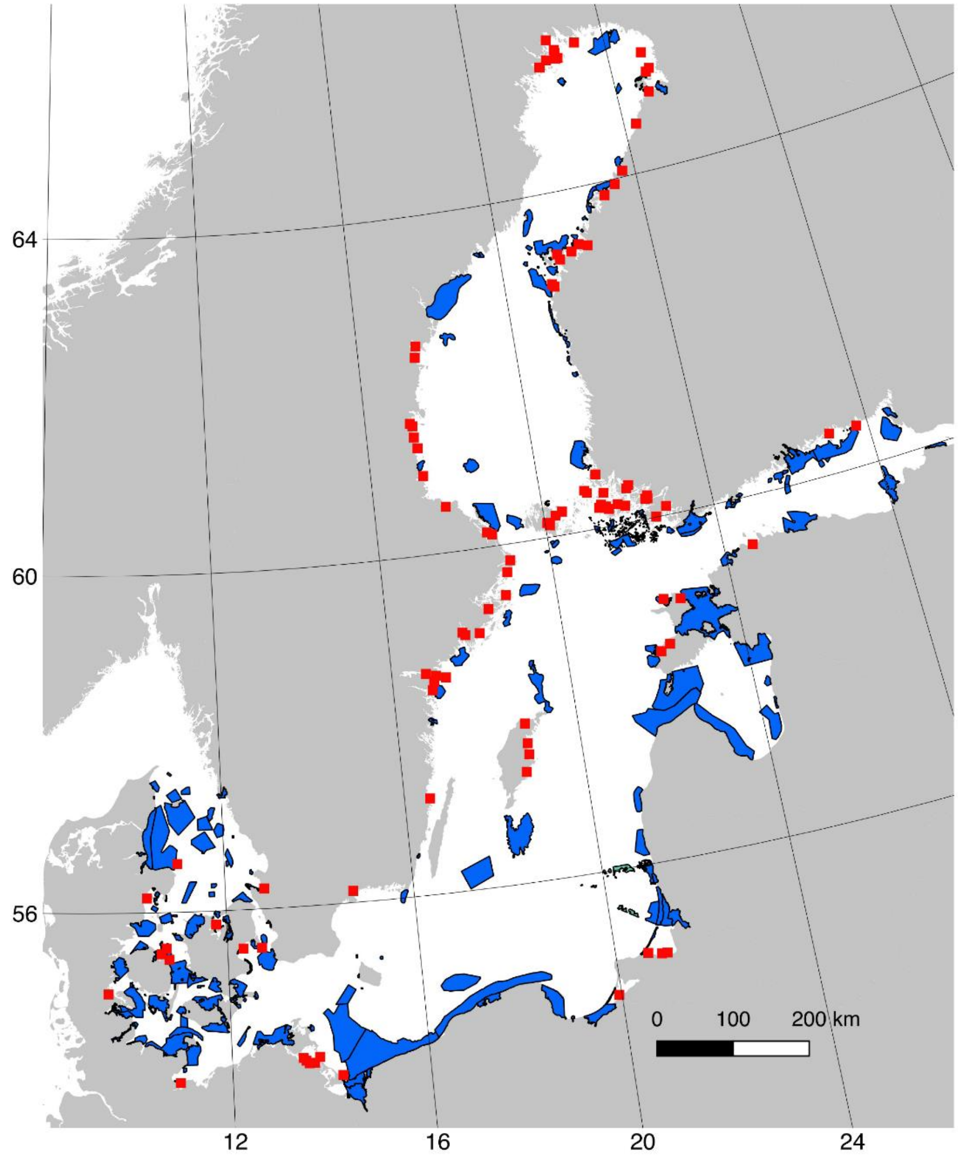

Figure 7. Optimal extension (red squares) of the present HELCOM MPA network (blue polygons) based on a multi-species strategy (strategies A-D in Table 1).

5. Genetic population structure and connectivity of Lithuanian blue mussel, and its possible changes due to emerging/increasing pressures (e.g. invasive round goby).

Abstract: The national and regional Marine Protected Area (MPA) networks designed earlier, did not take into account all the diversifying, intensifying and emerging pressures. Thus, protection of these valuable habitats and species may be compromised and allocation of current MPAs might need re-consideration to account for the rapidly changing environmental settings and potential implications for

habitat connectivity. In this regional case study, we exemplify how changes in the connectivity patterns and unprecedented impact of an invasive predator can jeopardise the current and projected effectiveness of MPAs, by applying tiered connectivity assessment based on gene flow analysis and hydrodynamic modelling, including climate projections for two emission scenarios. We also provide considerations for improved adaptive management and conservation strategies as well as outlook for the further research and monitoring programmes.

Progress: Completed, manuscript submitted for publication to the “Ecology and Evolution” journal.

Deviations: None

Introduction: In the context of the overall lowered biodiversity in the Baltic Sea, reef habitats dominated by ecosystem engineer species like mussels (*Mytilus* spp.) and macrophytes are local hotspots of structural and functional diversity and subjects for marine conservation policies. These habitats, characterised by elevated species richness and relatively high secondary production, provide feeding grounds for important bird species, shelter for small fish and fish fry, spawning substrates for important commercial fish species (e.g. Baltic herring). Moreover, dense mussel beds in the coastal areas are capable of removing large amounts of organic particles from the water column, thus contributing to the benthic-pelagic coupling process and serving as a biological filter. Along with other components of the Baltic Sea ecosystem, reef habitats undergo gradual alterations associated with the increasing anthropogenic impacts and climate change. In addition to that, mussel reefs in the eastern Baltic are currently facing unprecedented predation pressure by the invasive round goby *Neogobius melanostomus.* With the massive loss of mussel cover on the coastal reefs caused by round goby predation, volumes and complexity of microhabitats available for macrofauna have noticeably reduced, affecting local biodiversity, standing biomass and secondary production, and subsequently - reduced food availability for higher trophic levels with inescapable effects on the entire coastal food web.

In the light of this unprecedented loss of mussel populations along the Baltic Sea coasts, it is critically important to understand the development and maintenance of connectivity patterns between mussel reef habitats - an essential element of the Baltic MPA network. There are different approaches to analyse the patterns of connectivity in marine ecosystems. Population genetics and larval dispersal potential of the sedentary benthic species are the most common ones for deriving direct and indirect measures of connectivity. Although it is generally assumed that dispersal potential of the larvae is correlated with the gene flow, some studies show that modelled (larval dispersal) and realized (gene flow) connectivities do not necessarily match (Foster et al. 2012). Therefore in this study we adopted a complementary connectivity assessment approach, integrating genetic and biophysic connectivity assessment, for robust inferences on population persistence and sustainability of the current MPAs.

Methods and Results: The study was conducted in the Lithuanian Exclusive Economic Zone (EEZ), south-eastern Baltic Sea. The stony reefs considered in this study (Figure 8, Table 2) comprise of the mix of boulders, cobbles, pebbles and small patches of sandy sediment, where boulders are dominant and usually cover more than 40 % of the seabed. Prior to the round goby invasion, almost entirely overgrown boulders by perennial vegetation, blue mussels and barnacles were the most valuable coastal reef habitats with highest biodiversity and animal biomasses exceeding 6 kg m-2. For molecular analyses (genetic connectivity assessment), adult mussels (2-3 cm length) were collected by SCUBA divers or by dredge during different sampling occasions in 2013. Genomic DNA was extracted from foot muscle. Seven fluorescently labelled microsatellite loci were amplified in PCR reactions. The level of population differentiation and population structure were assessed. Contemporary migration rates were estimated using a Bayesian method, implemented in BAYESASS 1.3

The present connectivity structure among three mussel reefs off the Lithuanian coast was also estimated with a biophysical model of larval dispersal. The biophysical model combined flow fields from an ocean circulation model with a Lagrangian particle-tracking model simulating transport of individual larvae from spawning to settling locations. We also explored if connectivity patterns are expected to change in the future due to climate change effects on the water circulation in the Baltic Sea. Projections of future ocean velocity fields were modelled with the three-dimensional circulation model RCO-SCOBI (the Swedish Coastal and Ocean Biogeochemical model coupled to the Rossby Centre Ocean circulation model), which was forced by regionalized atmospheric data from the global climate model ECHAM5 and the A1B and A2 emission scenarios for the atmospheric forcing up to the end of the century (2070-2099).

The results revealed rather consistent present connectivity patterns both from the biophysical model and gene flow analysis, suggesting that mussel reefs in the coastal zone are sinks rather the sources for *Mytilus* larvae (Figure 9). The future increase in larval dispersal distance and decrease in connectivity between reefs, predicted by the climate scenario model, may have several consequences. If there is no efficient larval supply from other nearby reefs (e.g. those northward to Reef 3, in the Latvian coastal zone and southward to Reef 1 in Russian EEZ), the decrease in local retention and inter-reef connectivity will reduce recruitment and may make the mussel populations on all considered reefs less persistent and resilient.

Recommendations: The lower local retention and reduced inter-reef connectivity, especially from offshore to coastal reefs, predicted by the climate-scenario model may also call for larger MPAs, stronger protection of offshore reefs, and perhaps focusing more on Reef 3, which is expected to maintain highest local retention. The current results are particularly alarming in the light of the continuing round goby impact on mussel reefs along the SE Baltic coasts. Loss of self-sustainable coastal populations and decrease of larval supply from southerly reefs can make the recovery of coastal mussel reefs impossible in the longer-term perspective. The absence of ongoing national monitoring at these habitats as well as absence of rapid response to biological invasions and mitigation plans impede adequate protection regime. The MPA status of the vulnerable reef habitats plays a controversial role here, restricting options for active response measures to the round goby expansion and largely serving as a ‘no-take zone’ for the thriving invasive species population.

For improved governance of MPAs and marine ecosystems in general, we suggest considering an adaptive ecosystem-based management approach, allowing for pliable response to both continuous ecosystem dynamics and emerging environmental challenges. In the context of the current study, adaptive management would imply re-consideration of the current SE Baltic MPAs taking into account the future change scenarios and development of mitigation strategies for emerging and prospective risks, cascading from different pressures.

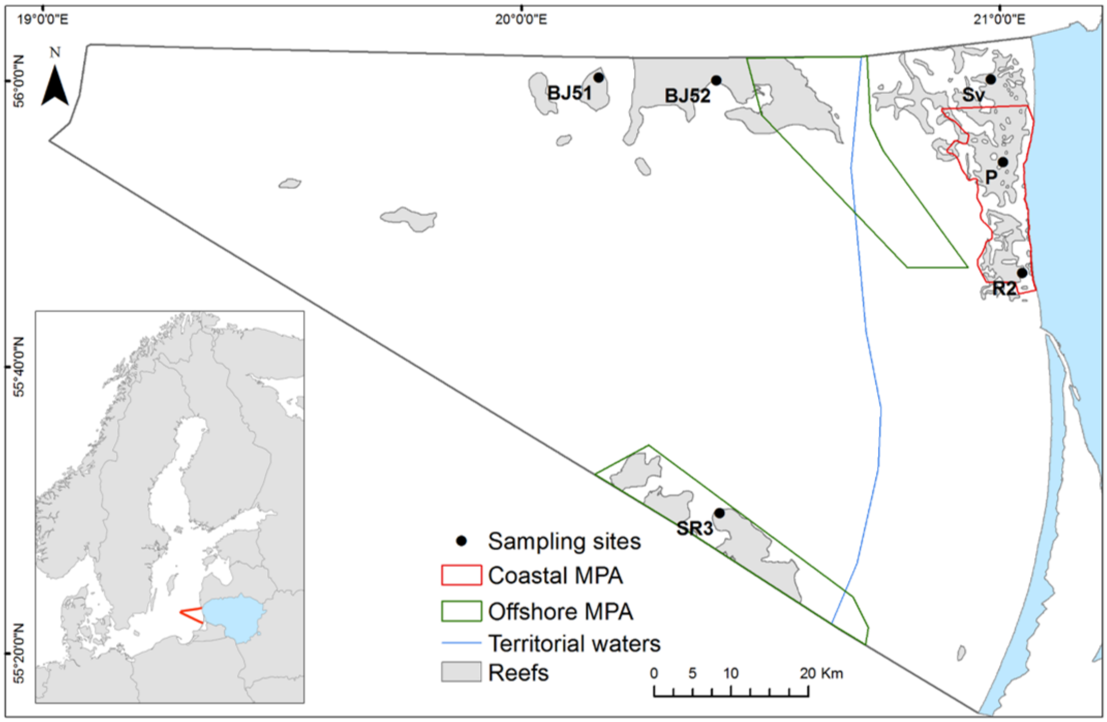

Figure 8: Mussel reefs and mussel sampling sites within and outside MPAs in the Lithuanian EEZ, SE Baltic Sea. Inset shows location of the study region.

Table2.: Mussel sampling sites information. Sampling locations are visualized in Figure 1.

Reef (*Sampling location*)	**MPA**	**Depth, m**	**Sample size, n**	**Prominent environmental pressures**
Reef 1 (SR3)	offshore	45	36	Proximity to D6 oil platform (Russian EEZ), proximity to intensive demersal trawling areas
Reef 2 (*BJ51*)	none	42	22	Relatively undisturbed, planned windparks' construction
Reef 2	offshore	30	33	Low densities of round gobies

(*BJ52*)				
Reef 3 (*Sv*)	none	10	26	Proximity to the Butinge oil terminal, high densities of round gobies
Reef 3 (*P*)	coastal	8	23	High densities of round goby, regular beach nourishment by sand
Reef 3 (R2)	coastal	10	27	Curonian Lagoon plume area, high densities of round gobies

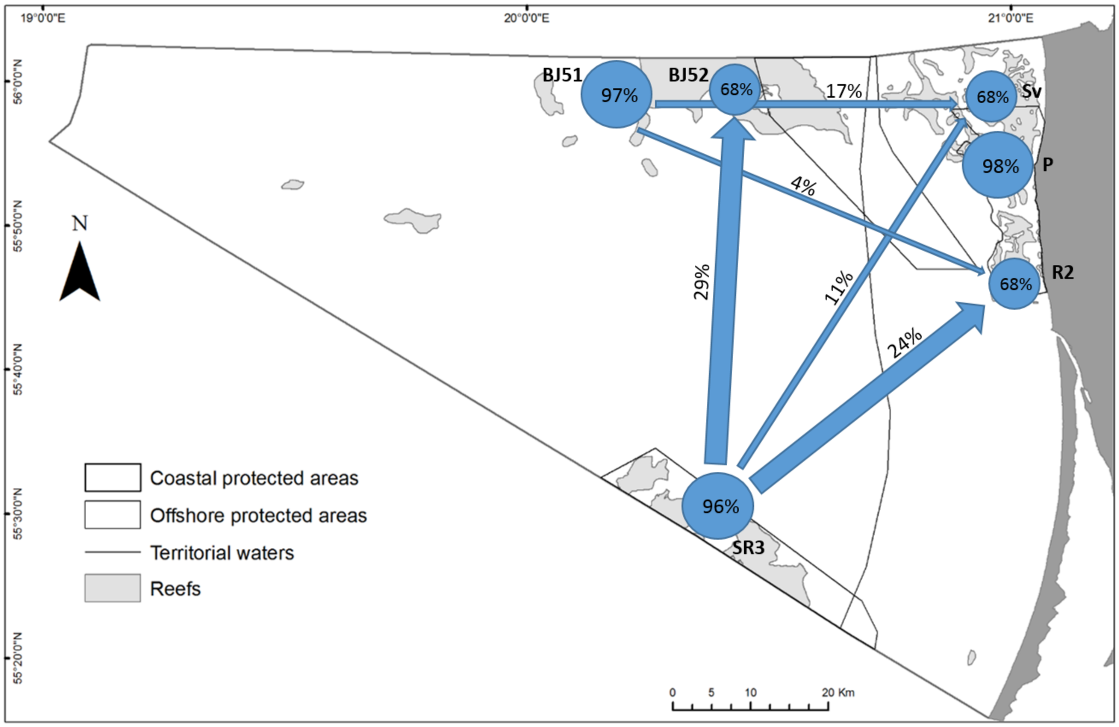

Figure 9 Recent migration rates between the analysed mussel populations estimated using BAYESASS. The numbers within the circles denote the proportion of nonmigrants within populations. Arrows indicate predominant direction of gene flow (migration rates >0.03); numbers on arrows represent proportion of migrants between populations. The populations are labelled as indicated in Table 1

6. Predicted future changes in biodiversity drivers and carrying capacity of MPAs in the Gulf of Riga.

Ramūnas Žydelis & Henrik Skov - DHI

Abstract: DHI's downscaled benthic 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 available food

supply in terms of bivalves to top predators. The impact of reduced eutrophication and associated ecosystem changes on the network of marine Natura 2000 areas in the Gulf were analysed using one climate scenario (A1B_1) and two eutrophication scenarios from Ecosupport (a reference scenario and a scenario with the implementation of the BSAP). The model data covered the period between 2008 and 2100. The impact was assessed by analysing trends in benthic carrying capacity and spatial heterogeneity in the biomass and distribution of two species of bivalves (*Mytilus edulis, Macoma baltica*) and foraging dynamics and mortality of two species of non-breeding molluscovorous waterbirds (Long-tailed Duck *Clangula hyemalis,* Velvet Scoter *Melanitta fusca*) in relation to the currently designated network of EU Special Protection Areas (SPAs) in Latvia and Estonia. Spatio-temporal declines in the biomass of the two bivalve species in the SPAs indicate that they most likely are governed by long-term effects through improved eutrophication control augmented by the implementation of the Baltic Sea Action Plan. The decline in *Mytilus* biomass was predicted to have a significant impact on the energetics of the Long-tailed Duck in terms of increased foraging effort and mortality. The predicted annual mortality of Long-tailed Ducks in the GoR at the end of the 21st century was predicted to be 21,000 in the Reference scenario and 60,000 following the BSAP scenario – the latter would lead to a significant decline in the number of Long-tailed Ducks in the Gulf and the SPAs. Adding 25% predation by round goby *Neogobius melanostomus* to the BSAP scenario would lead to further reductions in the carrying capacity and further increased mortality of Long-tailed Ducks to a level of 164,000 per year. The predicted decline in *Mytilus* biomass and in the abundance of the Long-tailed Ducks following the BSAP scenario will have a serious effect on the importance of the NATURA 2000 network of SPAs relative to the size of the bio-geographic population, albeit the predicted overall distribution of waterbirds relative to the SPAs will not change markedly (10% less waterbirds in SPAs).

Progress: Analyses completed.

Deviations: None.

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). Reconstruction of past ecosystem changes in the Gulf (WP 4.2) revealed a nutrient-driven localised decline in productivity affecting the entire benthic food web. One of the main aims of the model has been to estimate past and future changes in predator-prey interactions caused by climate changes and strong eutrophication mitigation measures implemented under the BSAP. The model complex includes a seaduck energetics module, which estimates the condition, survival and mortality of two seaduck species, which function as key predators on bivalves in the region; Long-tailed Duck *Clangula hyemalis* and Velvet Scoter *Melanitta fusca*. Long-tailed Ducks mainly prey on *Mytilus* while Velvet Scoters mainly prey on *Macoma*. One of the key applications of the model complex has been to assess potential impacts of climate changes and eutrophication control on the quality of the marine protected areas network in the Gulf of Riga. The current marine Natura 2000 network in the Gulf of Riga is large and covers 15,000 km^2 or 37% of the modelled surface area of the Gulf including the Irbe Strait and parts of the Eastern Gotland Basin (Figure 10, Table 3). The network is composed of 50% Special Protection Areas pursuant to the EC Bird Directive

(SPAs), 23% Special areas of Conservation pursuant to the EU Habitats Directive (SACs) and 27% combined SPAs and SACs. Of the 77% of the network designated as SPAs five areas rich in non-breeding waterbirds including the two modelled species comprise the major part of the area of MPAs or 58.8%. The five SPAs are " Irbes saurums" and "Rigas lica rietumu piekraste" in Latvia as well as "Kura kurgu", "Pärnu lahe" and "Väinamere" in Estonia.

Table 3. Surface area of Natura 2000 areas in the Gulf of Riga designated as SPAs and SACs and combined SPAs and SACs

Site type	Area (km^2)	% of network	% of model area
SPA	7,610.60	49.92	18.51
SAC	3,486.19	22.86	8.48
SPA and SAC	4,150.13	27.22	10.09
TOTAL	**15,246.93**	**100.00**	**37.08**

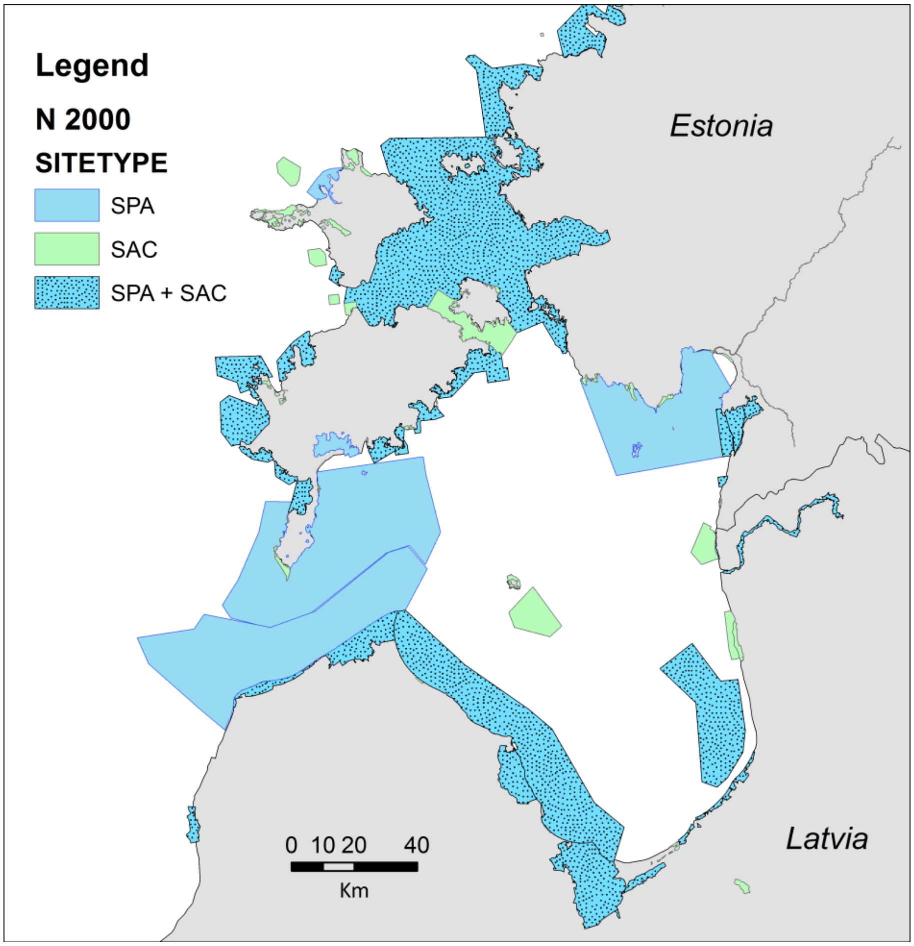

Figure 10. The network of Natura 2000 areas in the Gulf of Riga.

Methods and Results: A high-resolution food-web model complex (Figure 11) was developed to study the dynamics of the small-scale spatial structure of the biomasses of two bivalve species (*Macoma baltica* and *Mytilus edulis*) and related trophic interactions in the Gulf of Riga and Irbe Strait between 1990 and 2007 (Rasmussen *et al.* 2015). The model complex consists of three interlinked components; an ecosystem model based on a coupled local biophysical and ecosystem model (MIKE 3 FM & ECOLAB), a bivalve population model and a seaduck energetics module. The ecosystem model describes the pelagic and benthic ecosystem with benthic macrophytes, mussels, 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 Chl-a and biomass of bivalves (g DW soft tissue/m^2) were extracted and tested for spatio-temporal trends. 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 than least-squares estimators are, because it is much less sensitive to outliers. It is calculated by determining the slope between every pairwise combination and then finding the median value. The Median Trend test was applied for the entire 18-year time series characterised by a steep decline in concentrations of nitrogen between 1990 and 2007 (Skov 2017).

The seaduck energetics module was developed using an individual-based model describing the relationships between wintering Long-tailed Ducks and Velvet Scoters and their food resources with the aim of assessing possible impacts of change in mussel biomass caused by lower nutrient concentrations. The module was run for the years 1977, 1987, 1995, 2001, 2020, 2040, 2060, 2080 and 2099. The seaduck energetics module relates individual behaviours such as feeding activity, rate of food intake or interference to environmental factors and food availability and provides detailed insight into aspects which constrain species fitness and numbers of birds using mussel resources. The module also accounts for already existing human pressures such as shipping traffic. The module is an adjusted version of the individual-based model on Common Eider developed in relation to the impacts assessment for the Fixed Link across the Fehmarn Belt between Germany and Denmark (FEBI 2013). The module was developed using a specialised software platform MORPH (Stillman 2008).

The assessment showed similar (declining) standardised trends in the BSAP scenario for SPAs and the entire GoR area for *Mytilus*, whereas the mean biomass of *Macoma* was predicted to remain stable for the entire GoR but decline in the SPAs (Figure 12). The declining trends in *Mytilus* biomass were stronger in the BSAP scenario as compared to the reference scenario and with a steep slope setting in earlier (2008 versus 2050) in the BSAP scenario. For *Macoma*, on the other hand similar trends were predicted between BSAP and reference scenarios. Accordingly, the long-term spatio-temporal declines in the biomass of the two bivalve species in the SPAs are most likely an effect of eutrophication measures implemented before 2008 (the date for the reference scenario) with improved eutrophication control and strong declines in nutrient concentrations and phytoplankton productivity after 2008 augmenting the decline in the biomass of *Mytilus*. The decline in the biomass of bivalves mainly affected the carrying capacity in relation to waterbirds with respect to *Mytilus*, which had significant impact on the energetics of the Long-tailed Duck in terms of increased foraging effort and mortality (Figure 13, Figure 14). The predicted annual mortality of Long-tailed Ducks in the GoR at the end of the 21st century was predicted to be 21,000 in the reference scenario and 60,000 following the BSAP scenario – the latter would lead to a significant decline in the number of Long-tailed Ducks in the Gulf and the SPAs. Adding 25% predation by round goby Neogobius melanostomus to the BSAP scenario would lead to further reductions in the carrying capacity and further increased mortality of Long-tailed Ducks to a level of 164,000 per year.

The predicted decline in *Mytilus* biomass and in the abundance of the Long-tailed Ducks following the BSAP scenario would have a serious effect on the importance of the NATURA 2000 network of SPAs as the decline would cause the proportion of the bio-geographic population hosted by the SPAs to reach below a level which is in line with the conservation targets for the SPAs. This impact will be amplified by round goby predation of bivalves. The decline in the biomass of *Macoma* was not predicted to reach a level inducing strong mortality of Velvet Scoters within this century. It should be noted that despite the profound changes in the benthic carrying capacity, the predicted overall distribution of waterbirds relative to the SPAs will not change markedly as 60% of waterbirds were predicted to occur in SPAs at the beginning of the century and this percentage is expected to decline to about 50% at the end of the century. The decline will mainly take place in the Gulf itself where the reduction in benthic carrying capacity is predicted to be strongest (Skov & Rasmussen 2017). Hence, the waterbirds will be displaced towards the SPAs in the western part of the area in the Irbe Strait and along the Estonian and Latvian coast (Figure 15, Figure 16, Figure 17).

Recommendations: The model predictions indicated a severe knock-on effect of improved water quality management and reductions in nutrient (nitrate) concentrations driven by WFD goals, on the carrying capacity of the NATURA 2000 areas in the GoR, counteracting bird population goals for the protected areas. The range of predicted scenarios strongly suggests that with the implementation of the BSAP and the continued abundance of round gobies major challenges will be ahead in order to achieve synergies between targets for water quality and biodiversity conservation. The model predictions have been verified by significant recent declines in observed abundance of the two studied seaduck species in the GoR (Skov *et al.* 2011). Obviously, local ecosystem models like this one for the Gulf of Riga may provide useful decision support tools in order to achieve future synergies and compliance between the WFD, the MSFD and the NATURA 2000 plans and goals for water quality and biodiversity conservation in many coastal areas of the Baltic Sea.

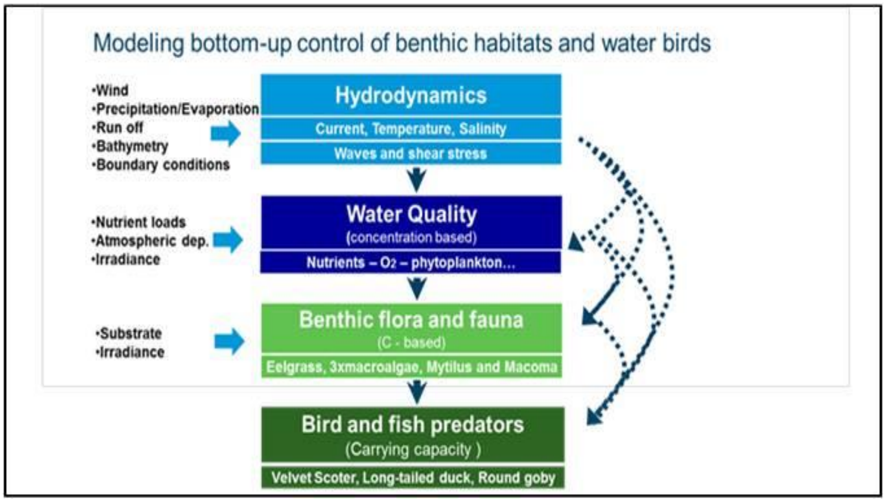

Figure 11. Overview of ecosystem model framework.

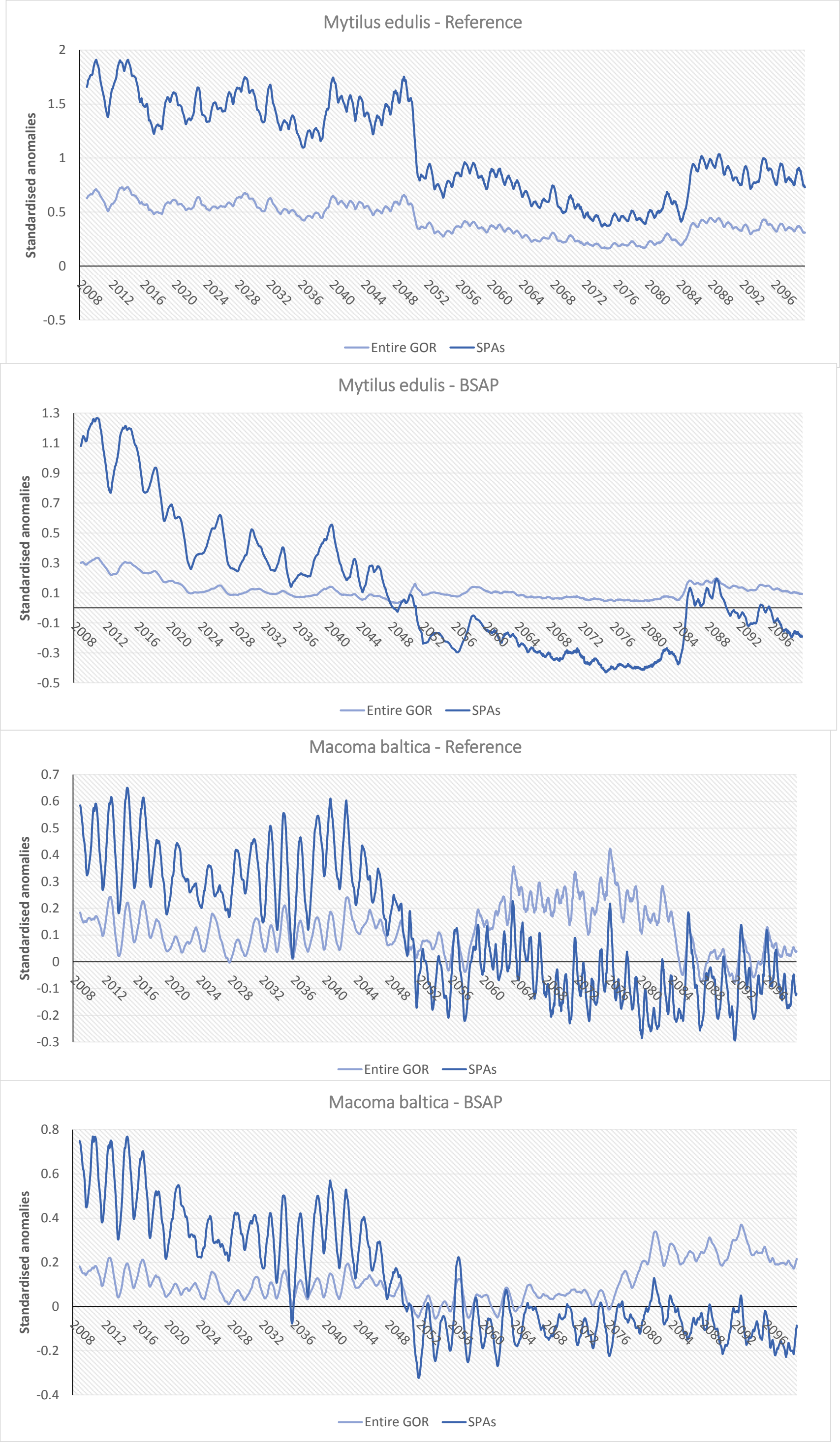

Figure 12. Comparison of trends in biomass of Macoma baltica and Mytilus edulis between the SPAs and the entire Gulf of Riga during the period 2008-2100 – both the BSAP and the reference scenarios. Biomass values (g AFDW/m^2) have been transformed to standardised anomalies. Declining trends are predicted to be stronger in SPAs as compared to the whole area. Declining trends in Mytilus are predicted to be amplified during the BSAP scenario.

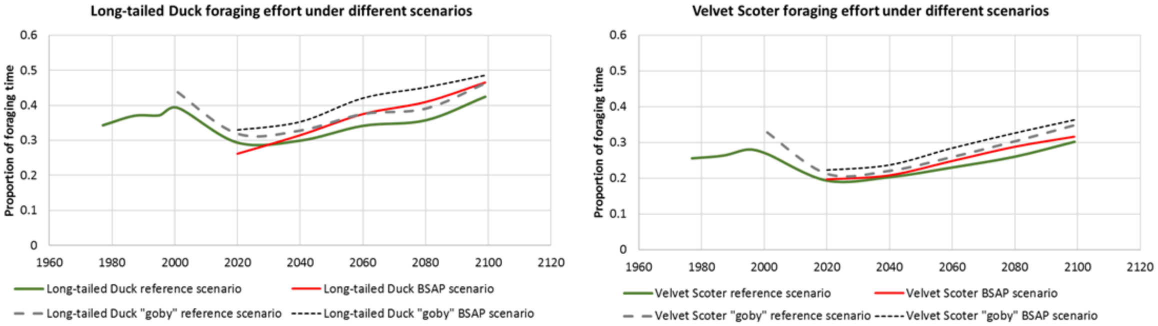

Figure 13. Comparison of foraging effort of Long-tailed Duck and Velvet Scoter under different scenarios. The waterbirds are predicted to spend more time foraging and hence be under more stress during the BSAP scenario with continued presence of round goby.

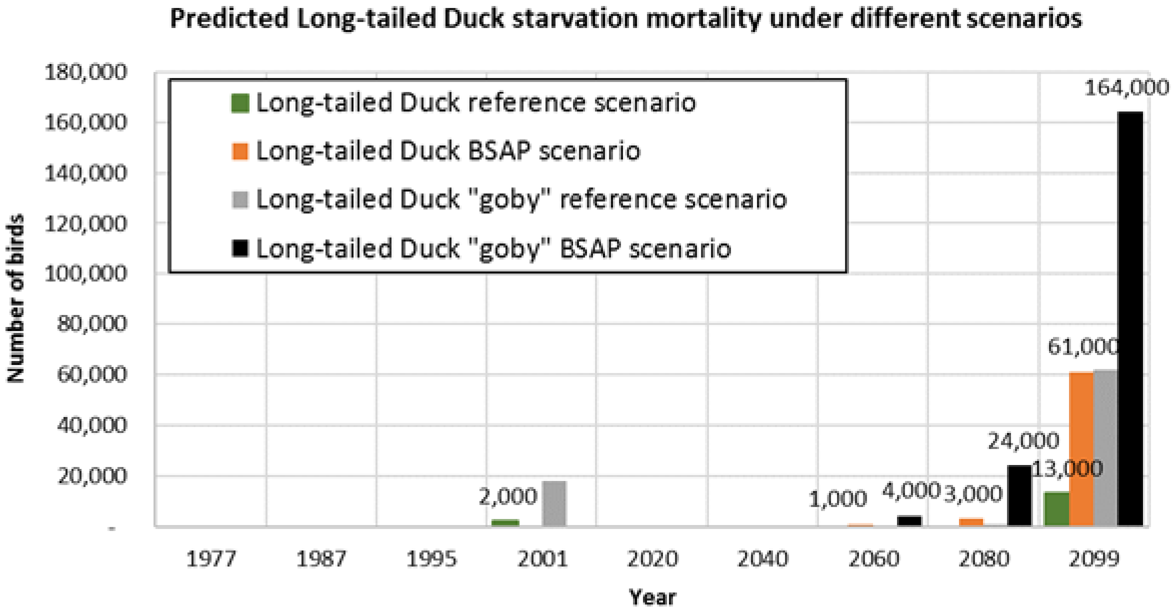

Figure 14. Predicted mortality of Long-tailed Ducks due to starvation under different scenarios. "Reference scenario" – business as usual and condition of the Baltic Sea continues under the current state of nutrient input. "BSAP scenario" – if Baltic Sea Action Plan reducing nutrient input into the Baltic Sea is implemented. "Goby reference scenario" – "reference scenario" with additional predation by round gobies assuming that fish reduce bivalve biomass by 25% at depths below 15 meters. "Goby BSAP scenario" – "BSAP scenario" with additional predation by round gobies assuming that fish reduce bivalve biomass by 25% at depths below 15 meters.

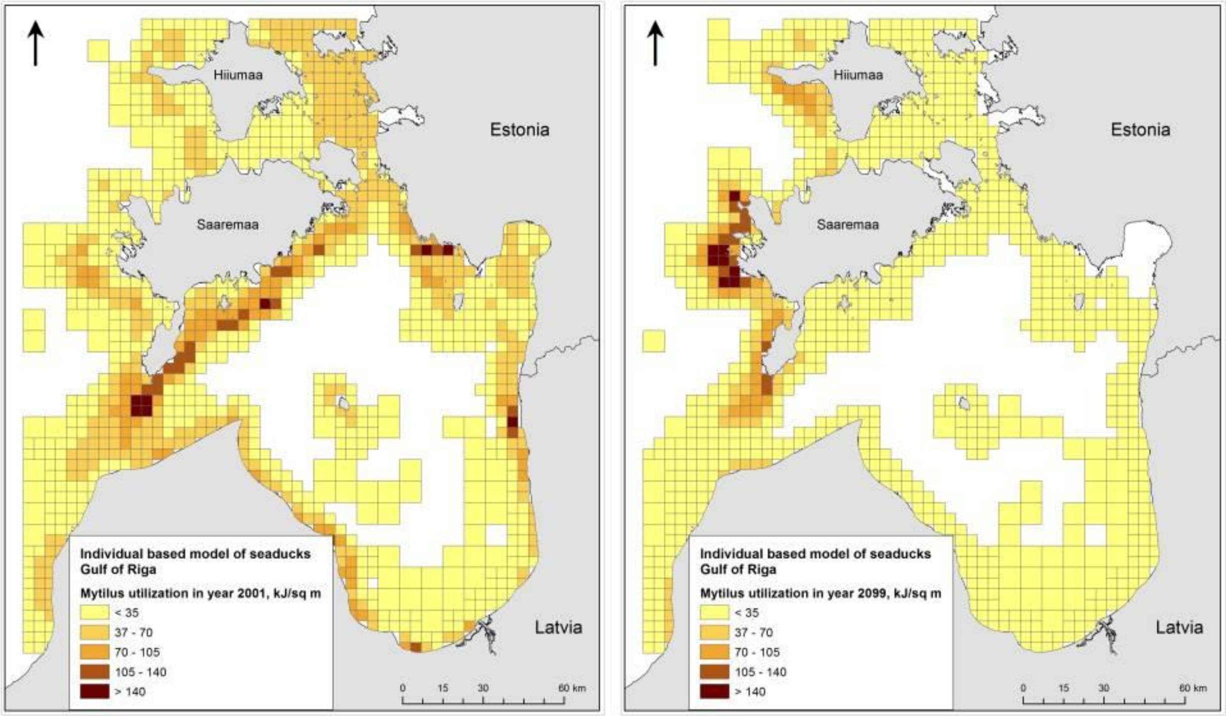

Figure 15. Predicted utilization of filter-feeding bivalves (Mytilus and Mya) by seaducks in the Gulf of Riga in 2001 (left map) and 2099 (right map).

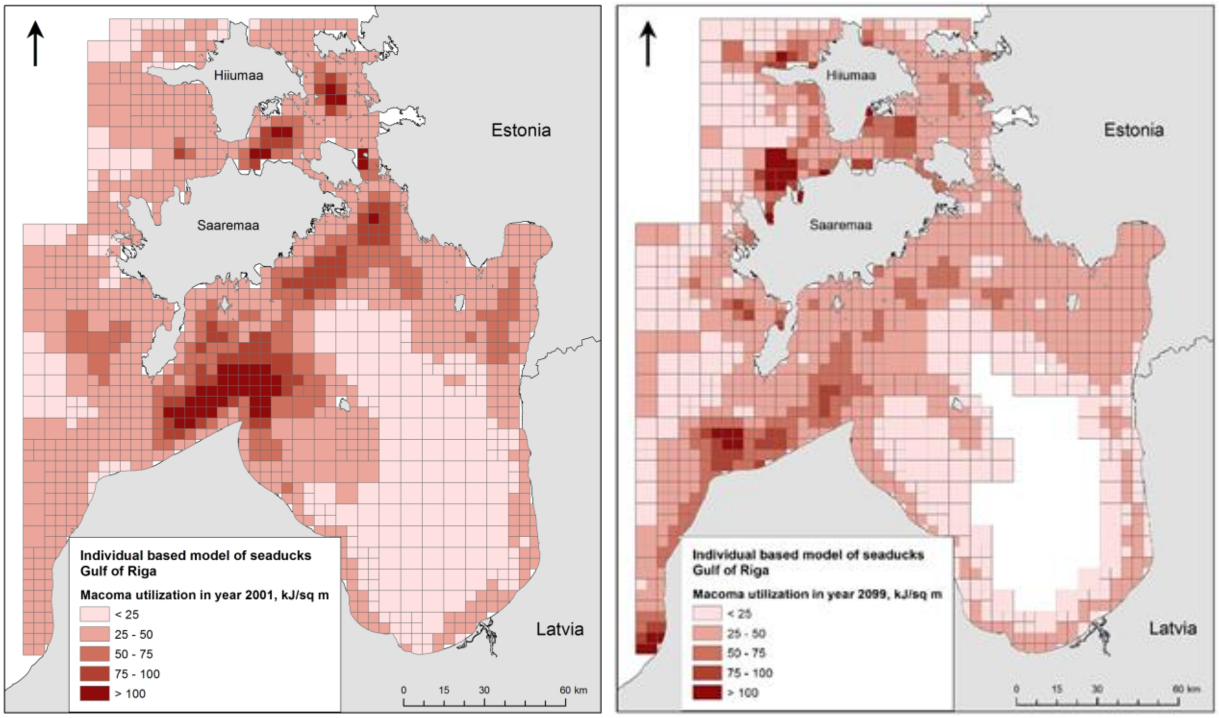

Figure 16. Predicted utilization of deposit-feeding bivalves (Macoma) by seaducks in the Gulf of Riga in 2001 (left map) and 2099 (right map).

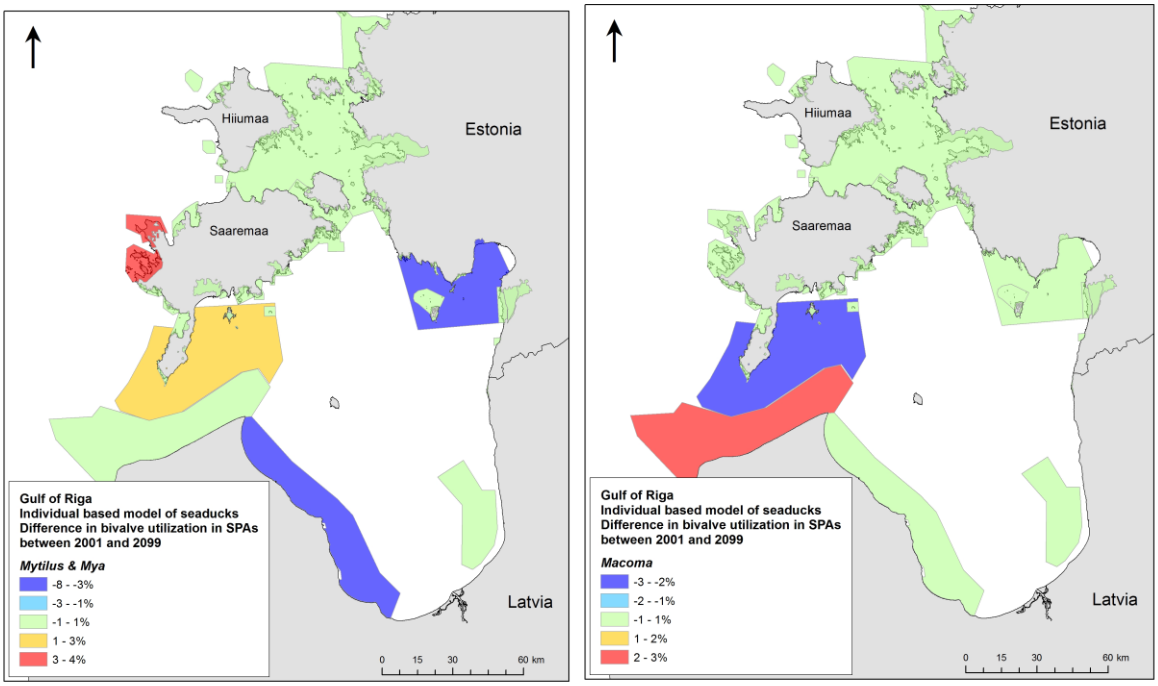

Figure 17. Predicted % change in bivalve utilization by seaducks in the Gulf of Riga between 2001 and 2099. Separate maps presented for filter-feeding bivalves Mytilus & Mya (left map) and deposit-feeding bivalves Macoma (right map).

Appendices

Bio-physical modelling tool for assessing decadally, regionally, and depth layer resolved information on connectivity and dispersal patterns for the entire Baltic Sea.

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INTRODUCTION

The distance and direction of dispersal have considerable influence on the demography and genetic structure of marine species. In marine ecosystems, connectivity of species early life stages via ocean current transport is of particular interest, since exchange during the (often sedentary) adult stage may be limited or – in the case of sessile organism – impossible. Moreover, retention in or transport to favorable or unfavorable environments can lead to variation in mortalities, and eventually, reproduction success. The mixing and exchange of individuals among habitats and populations is of particular importance from an ecological perspective, affecting e.g. species distribution ranges, species interaction, population dynamics, as well as the demographic and genetic structure of populations. In an evolutionary context, it is also essential for the understanding of factors underlying population divergence and local adaptation.

The aim of the present study is to provide decadally (1970s, 1980s, 1990s, 2000s), regionally, and depth layer resolved information on connectivity and dispersal patterns for the entire Baltic Sea. This dataset provides a framework in which to assess the expected connectivity among different populations of a species, as long as some biological information (e.g., spawning or bloom area and time, depth layer occupied, larval duration or life span of short-lived organisms) is available. As such, it can help researchers in the Baltic Sea to generate informed hypotheses regarding connectivity among population of interest, and can serve as an example for similar data resources elsewhere. Knowledge about connectivity in the Baltic Sea could be essential for ecosystem-based management and conservation strategies, e.g. stock-separated management of fisheries. It could also be a basis when considering for example the design of marine protected areas to maintain conservation features or population of exploited fish species. Furthermore, such kind of knowledge might also be helpful to assess the importance of MPA networks, positions of important dispersal corridors and connectivity hot spots in offshore areas could be located.

The general tool used was biophysical modelling, which is suitable for biological dispersal that is highly influenced by the physical water transport in ocean circulation. The results are assessed from Lagrangian particle tracking using ocean circulation model outputs.

MATERIAL & METHODS

The basis for our analysis is the hydrodynamic Kiel Baltic Sea Ice-Ocean Model. The horizontal resolution of the coupled sea ice–ocean model is at present 2.5 km, and in the vertical 60 levels are specified, which enables the upper 100 m to be resolved into levels of 3 m thickness. The model domain comprises the Baltic Sea, Kattegat and Skagerrak. At the western boundary, a simplified North Sea is connected to the model domain to provide characteristic North Sea water masses. Here, sea level variations in the North Sea/Skagerrak calculated from the BSI (Baltic Sea Index) were taken as additional boundary condition. The model forced by the Swedish Meteorological and Hydrological Institute (SMHI Norrköping, Sweden) meteorological database which for the period 1971 - 2010 covers the whole Baltic drainage basin on a regular grid of 1 x 1° with a temporal increment of 3 hours. The database consists of synoptic measurements that were interpolated onto the regular grid with a two-dimensional optimum interpolation scheme.

Simulated 3D velocities were taken from the above described hydrodynamic model of the Baltic Sea to run a Lagrangian particle tracking model. We have performed particle drift and connectivity studies, which could not be linked to any biological process-based information. Investigations of non-species specific large-scale connectivity patterns have been performed for offshore areas. For this purpose, spatially and temporally resolved long-term averages of geographic distances of Lagrangian particles were calculated for the whole Baltic Sea. These dispersal patterns are based on the long-term wind driven and thermohaline circulation calculated by using a coupled sea ice-ocean model of the Baltic Sea for a 40-year period. The release of drifters consisted of particles within the model domain with a horizontal resolution of ~ 4.5 km. The particles were released every 5 days throughout the whole year and the drift was calculated for a period of 50 days, with release depths 2.5, 7.5, 12.5, 17.5, 25, 35, 45, 55, 65, 75 and 85m. Average dispersal distances (mean geographic distances) are available on decadal quarterly time scale basis for specific rectangles (50 km x 50 km) in the Baltic Sea. The mean geographic distances cover temporal windows ranging from 5 to 50 days resolved at 5 days intervals and are available for the upper 100m of the water column.

However, averaged dispersal distances provide no information about their variability. Thus, for a more complete representation regarding the variance of dispersal we have calculated the stability of the non-species specific dispersal distances (mean geographic distances) as well as the dispersal rates between subareas.

The stability which is defined as the ratio of the averaged vectorial drift distance and the averaged arithmetic drift distance

$$B = \frac{(\overline{Du}^{\,2} + \overline{Dv}^{\,2})^{\,0.5}}{\frac{1}{N}\sum_{i=1}^{N}(Du_i^2 + Dv_i^2)^{\,0.5}}$$

With $\frac{1}{N}\Sigma Du$ and $\frac{1}{N}\Sigma Dv$ the averaged components of the drift distances, and N the number of observations at the location under consideration. The vectorial mean is obtained by taking the vectorial values of individually observed dispersal distance vectors, and the arithmetic mean dispersal distance is calculated by averaging the distances without regard to the direction. Secondly, as a measure for the strength of the dispersal patterns, we have calculated the relative advective loss of particles (dispersal) for each of the 50 km x 50 km rectangles in the Baltic Sea.

As a second step, statistical analyses of different mean flow characteristics (mean geographic distance, stability, dispersal rates) for different subareas of the Baltic Sea were performed. The geographical ranges of these subareas are given in Table 1. A schematic flow of the present drift modelling study to provide temporally, regionally, and depth layer resolved information on connectivity and dispersal patterns for the entire Baltic Sea is illustrated in Fig. 1.

RESULTS

Horizontal distribution patterns of mean geographic distances, stabilities and dispersal: Because of its importance for many biological processes, e.g., fish egg and larval development, and depth layer occupied by many organisms (e.g., phyto- and zooplankton, larval stages of marine fishes) in the Baltic Sea ecosystem, our analysis was focussed on the mean flow characteristics in the water column above the halocline (2.5 and 25 m).

Sea surface level: Generally, from the model for many subareas of the Baltic Sea a clear evidence of persistent dispersal patterns exists which comprise mostly the basin-like structure of the Baltic Sea with less transport between the basins. Fig. 2 displays the mean geographic distances as well as their stabilities for 25 days drift simulations taking into account the fourth quarter of the decades from 1971-2010 if particles were released at the 2.5m level. Generally, the mean geographic distances suggest a stable cyclonic circulation cell in the eastern Gotland Basin with recirculation towards the west in the northern part which extended in the south to the Bornholm Basin and the Gdansk Deep. However, the latter appears to be less stable than the pattern in the eastern part of the Gotland Basin. Similar but less stable cyclonic circulation pattern existed in the Bothnian Sea, while in the Bothnian Bay and the Gulf of Finland no stable cyclonic circulation patterns predominated. Furthermore, although strong current fluctuations in the western Baltic exist, in some areas the long-term mean geographic distances reached stabilities up to 60%. Baltic Sea wide averages of geographic distances as well as their stabilities were obtained for the decades 1991-2000 and 2001-2010. During the fourth quarter of the decades, for most of the Baltic Sea strong relative advective losses of particles (80-100%) for the 50 km x 50 km rectangles in the Baltic Sea were obtained (Fig. S1), suggesting at the sea surface the existence of strong connectivity between neighbouring areas.

Mean values for the second quarters of the decades indicate less intensive circulation patterns with relatively low, less stable geographic mean distances (Fig. 3). However, a cyclonic circulation pattern was established in the central Baltic Sea in the decade (1981-1990) and continued until 2001-2010. The mean geographic distances as well as their stability increased significantly. Throughout the investigation period (1971-2010) the dispersal rates in the majority of the Baltic Sea area remained at high levels > 80%, but for example in the northern most part of the Baltic Sea (Bottenwiek) and in the eastern part of the Gulf of Finland the dispersal rates were much lower (Fig. S2). For most of the Baltic Sea area (except the most northern part) strong advective losses of particles were obtained, suggesting at the sea surface the existence of strong connectivity between neighbouring areas.

In summary, mean geographic distances, their stabilities as well as dispersal rates decrease with depth (not shown), but for all decades and for all depths the fourth quarters show the most intense advective transports.

Statistical parameter of mean geographic distances, stabilities and dispersal: Considering the mean geographic distances related to its stability for the surface level for the different subareas, particles generally travelled within ~ 300 km of their release areas after 50 days drift duration. The highest mean geographic distance was obtained for the subarea central Baltic Sea followed by the one for the most northern subarea. Lower distances were observed for the western Baltic Sea and the Gulf of Finland area. For all subareas the mean geographic distances are highly positively correlated to the stability of the ocean currents ($0.78 < r > 0.88$), indicating that longest transport routes of particles can only be caused by stable ocean currents. For the subareas 2 and 4, stabilities up to 0.9 were observed, while for the western Baltic Sea and the Gulf of Finland much lower stabilities up to 0.7 resulted. For the latter, more variable ocean current patterns could be expected.

Mean patterns of dispersal rates in dependency on a 50 days drift duration as well as the mean duration for 50% advective loss of particles (dispersal) for each of the 50 km x 50 km rectangles are displayed for four selected subareas in the Baltic Sea (Fig. 4; Table 1). Generally, for both depth levels, relatively high dispersal rates and consequently relatively low drift durations to reach a 50% dispersal rate were obtained for the western and for the southern and central Baltic Sea. Compared to the relative low dispersal rates during spring and summer (quarter 2 and 3), the relative advective particle losses were observed for the autumn and winter months (quarter 4 and 1). In contrast, for the northern Baltic Sea, winter and spring months revealed the lowest dispersal rates, while the weakest dispersal was obtained for the Gulf of Finland area.

Mean geographical distances, their stabilities as well as the relative dispersal patterns (loss of particles) are available on decadal quarterly time scale basis for each of the specific rectangles (50 km x 50 km) in the Baltic Sea. The average dispersal distances cover temporal windows ranging from 5 to 50 days resolved at 5 days intervals and they are available for the upper 90m of the water column. The data needed to e.g. produce horizontal distribution maps, will be made available online.

DISCUSSION

We used a bio-physical model to simulate decadally (1970s, 1980s, 1990s, 2000s), regionally, and depth layer resolved ocean-current based dispersal distances and connectivity patterns in the whole Baltic Sea area as framework for population genetic studies. This dataset provides a framework in which to assess the expected connectivity among different populations of a species, as long as some biological information (e.g., spawning or bloom area and time, depth layer occupied, larval duration or life span of short lived organisms) is available. Dispersal distance varied considerably among regions within the Baltic Sea. The sub-basins showed local retention as well as inter-basin connectivity. The novel approach to identify partial dispersal barriers indicated that there may be a few strong barriers that could promote population divergences, and that there may be several areas that are sufficiently demographically independent to justify separate management units. Maps of spatially resolved dispersal distances show that there are large geographic differences within the Baltic Sea and that there is a general trend towards shorter dispersal distances in the northern part compared to the western and central part. This might be due to a reduced momentum flux caused by the relatively high spatial extension of sea ice, especially in winter and spring. Secondly, dispersal distances are also dependent on the pelagic larval duration, as well as the depth interval in which propagules are drifting. As such, the new information provided here can help researchers in the Baltic Sea to generate informed hypotheses regarding connectivity among population of interest, and can serve as an example for similar data resources elsewhere.

The general results obtained from this specific physical oceanographic study suggest that dispersal has the potential to be considered from the perspective of organisms for calculating population connectivity. The available datasets can therefore help to interpret observed patterns in population structure and/or demographics and recruitment dynamics of different species in the Baltic Sea. They can also be used to generate informed hypotheses, e.g., regarding expected patterns of isolation by distance or source-sink dynamics, in future studies, including on newly established non indigenous species, based on the frequency and strength of particle dispersal. In the Baltic Sea, there are examples of a surprising degree of population differentiation, often related to the strong environmental gradients in the Baltic Sea. At the

same time, for other organisms, population structure is lacking. In both cases, the extent of connectivity is highly relevant when assessing the specific drivers of either divergence or homogeneity.
Connectivity studies could be one leg of multidisciplinary studies to understand connectivity at different scale for broadcast spawning marine species in the Baltic Sea which are subject to commercial exploitation. The results obtained from our drift model study suggest that at smaller scales there were high levels of connectivity, but that there was generally low connectivity at larger scales, hence some areas were highly connected and others highly isolated and thus dependent on self-reproduction to sustain local populations. Secondly, extraction of species specific dispersal and connectivity scenarios from the data sets available online then allow the analysis of more specific questions. The combination of dispersal and connectivity information provided here, environmental datasets (e.g., on species specific drivers such as salinity level) and studies using genetic markers to assess (meta-)population structure and population divergence, offers high potential to lead to new insights regarding the respective roles of isolation and environmental selection..

The identification of connectivity of populations between subareas of an ecosystem like the Baltic Sea demonstrates that human coastal communities could be strongly linked and could have an important social and economic aspect: management in one part of an ecosystem affects people who use another part of the ecosystem. Thus, understanding the connectivity in the Baltic Sea is essential for ecosystem-based management and conservation strategies, e.g. stock-separated management of fisheries. It could also be a basis when considering for example the design of marine protected areas to maintain conservation features or population of exploited fish species. Our results are also suitable to assess the importance of MPA networks, positions of important dispersal corridors and connectivity hot-spots in offshore areas could be located.

Acknowledgement

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TABLES

Table 1: Geographical ranges of selected subareas of the Baltic Sea

Area	Latitude	Longitude
1) Western Baltic	< 55.5 N	10-15 E
	55.5-57 N	10-14 E
2) Southern and Central Baltic	55.5-60.5 N	14-22 E
3) Gulf of Finland	58-60.5 N	22- 30 E
4) Northern Baltic	> 60.5	

FIGURE CAPTIONS

Fig. 1 Schematic flow of particle tracking for calculation of dispersal patterns and connectivity

Fig. 2 Ocean current based mean geographic distances and stability, 2.5m depth level, 4.quarter decade A) 1971-1980, B) 1981-1990, C) 1991-2000, and D) 2001-2010, drift duration 50 days

Fig. 3 Ocean current based mean geographic distances and stability, 2.5m depth level, 2.quarter decade A) 1971-1980, B) 1981-1990, C) 1991-2000, and D) 2001-2010, drift duration 50 day

Fig. 4 Relative mean dispersal after 50 days drift (left panel), and mean duration of drift until 50% dispersal (right panel) in the different subareas of the Baltic Sea

FIGURES:

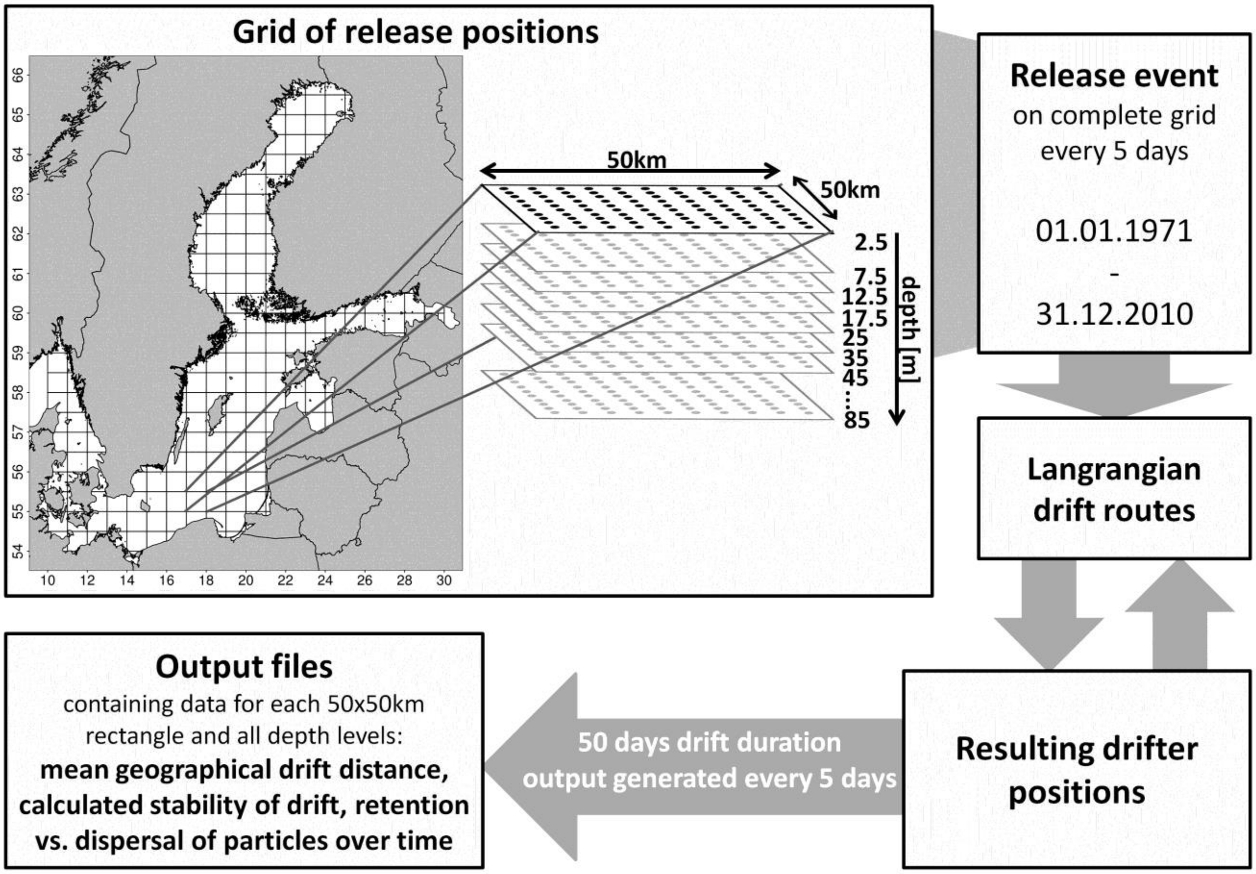

Fig. 1

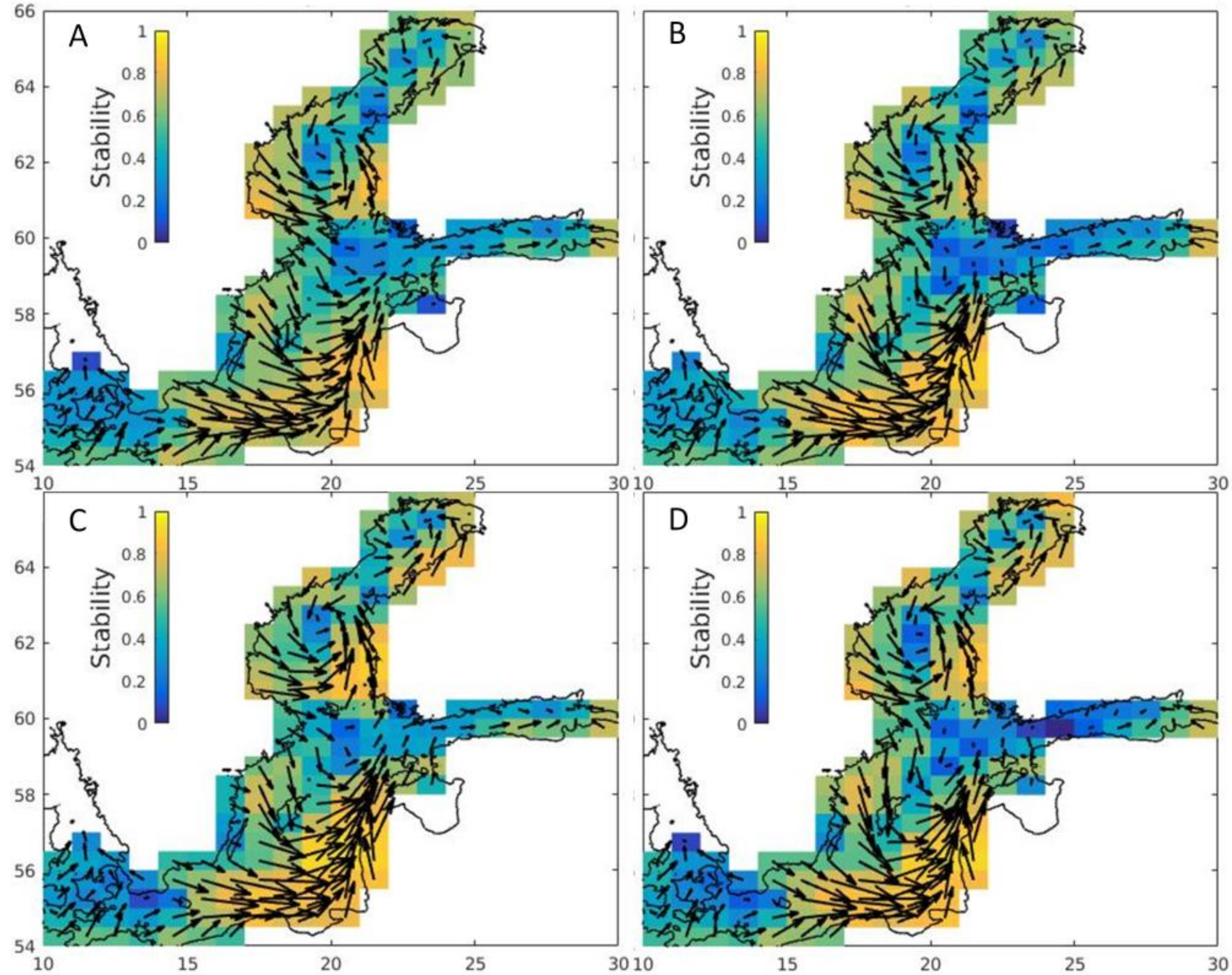

Fig.2

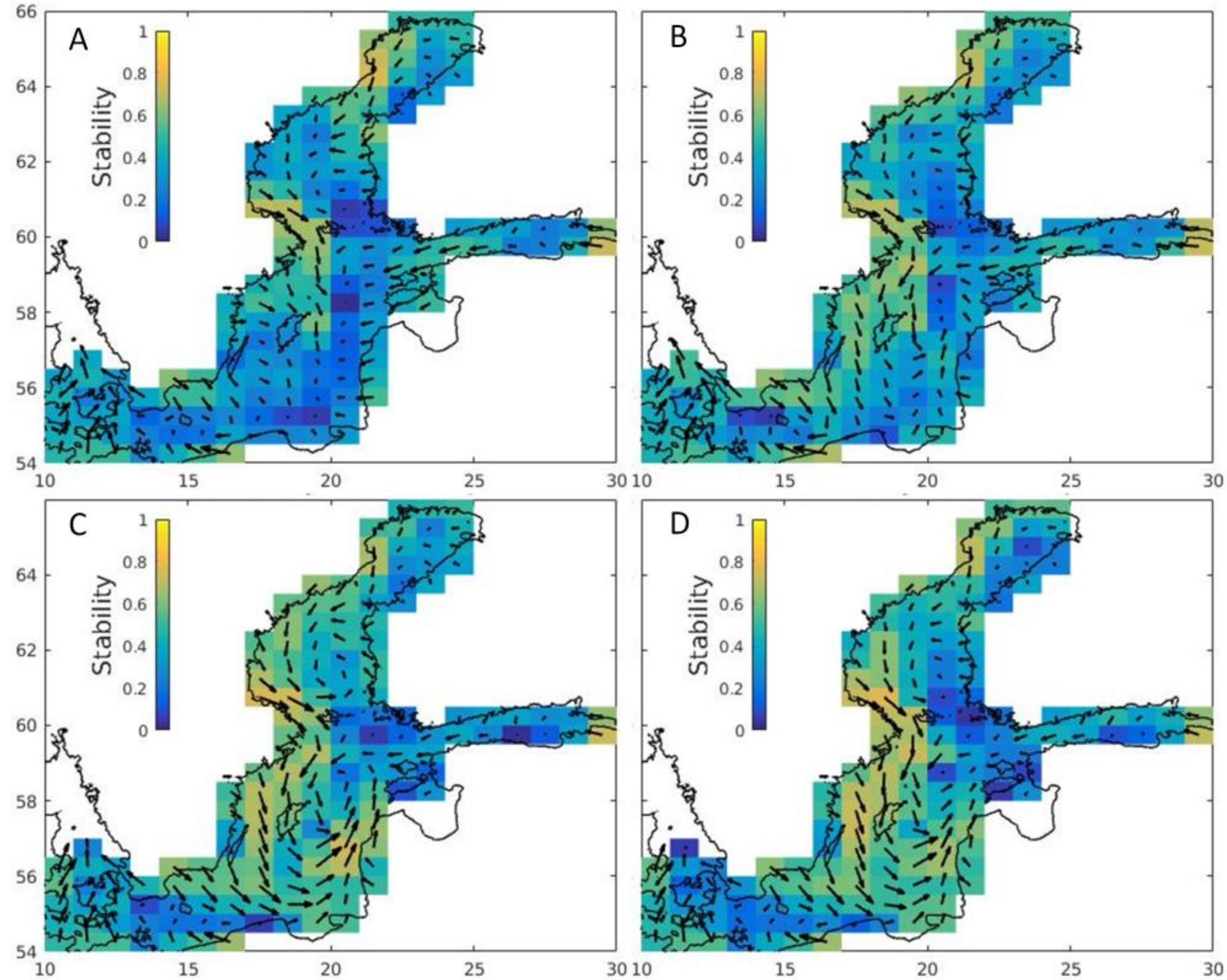

Fig.3

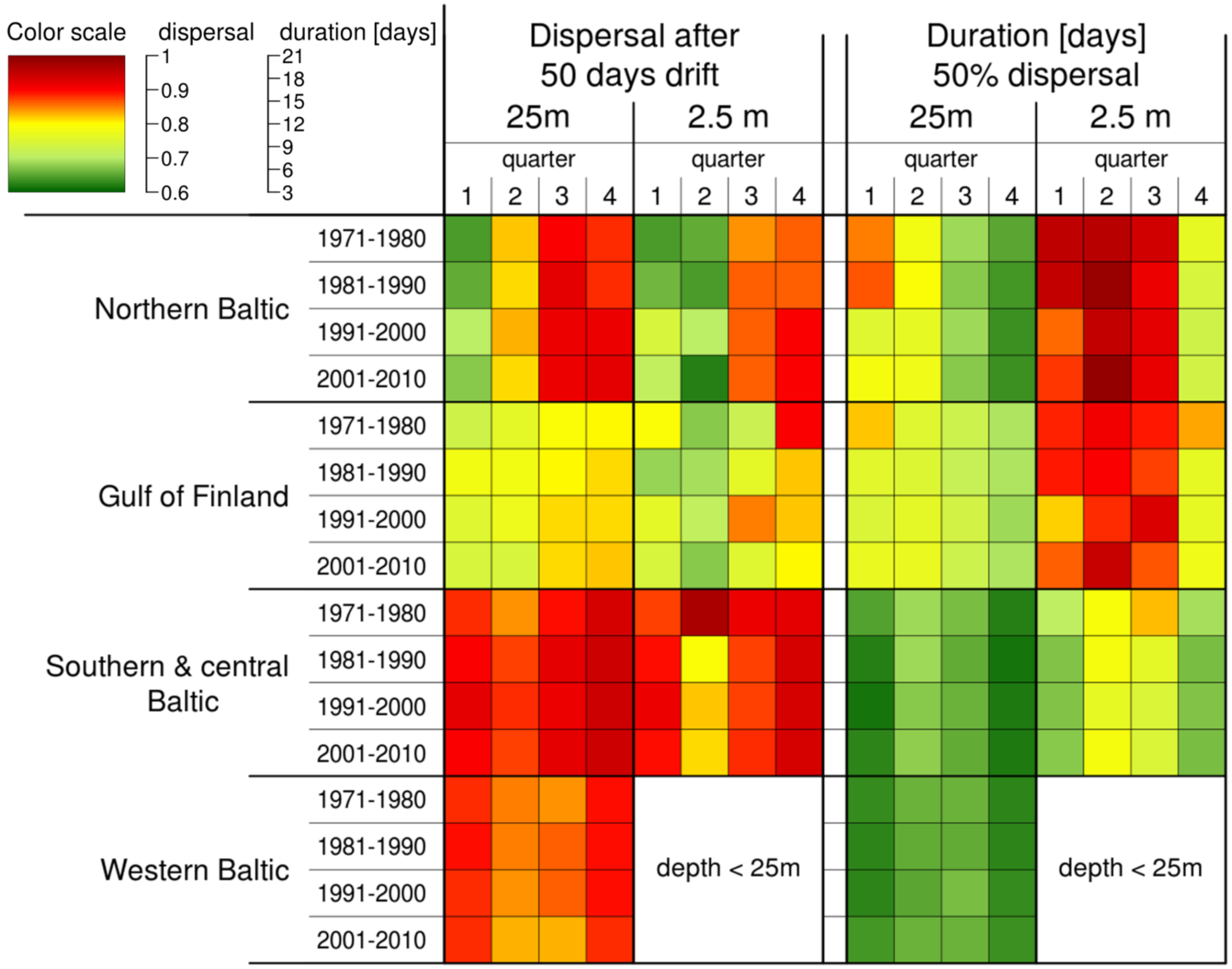
Color scale
dispersal
duration [days]
1
0.9
0.8
0.7
0.6
21
18
15
12
9
6
3
Dispersal after 50 days drift
Duration [days] 50% dispersal
25m
2.5 m
25m
2.5 m
quarter
quarter
quarter
quarter
1
2
3
4
Northern Baltic
Gulf of Finland
Southern & central Baltic
Western Baltic
1971-1980
1981-1990
1991-2000
2001-2010
depth < 25m
depth < 25m

Fig. 4

Basin-wide connectivity - identifying optimal MPA network and management units

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Source and sink hotspots. Local connectivity patterns between MPAs in Gulf of Riga area.

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Assessing MPA adequacy and connectivity. Dispersal distances, local retention and network connectivity based on large and fine-scale connectivity models

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Connectivity profiles of temperate reef habitats for guiding adaptive conservation strategies in the context of changing marine ecosystem

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