BONUS BIO-C3 PROJECT (01/01/2014 - 31/12/2017)
The final publishable summary report, 1 March 2018

Goals and results envisaged at the beginning of the project cycle

The goal of BONUS BIO-C3 was to investigate the **causes and consequences of changes in biodiversity on all its biological scales –** genetic, taxonomic, functional, habitat and ecosystem diversity – in the Baltic Sea system. We wanted to **move away from a static to a dynamic system view** incorporating environmental change as well as the potential for species acclimation and adaptation, and to thus provide an **improved scientific basis for resource management in a changing world**. Essential features of the Baltic are low species diversity, many recent arrivals of non-indigenous species, presence of glacial relict species, and simple food webs that nevertheless sustain goods and services of high economic and societal value. Our specific interest was to assess effects of biodiversity changes on ecosystem function, food web dynamics, productivity, and implications for environmental management in this system. Key objectives were to i) investigate the relative roles of acclimation, adaptation and colonization of native vs. non-indigenous species, ii) advance understanding of functional links between biodiversity, external pressures and food-web interactions and iii) improve our capacity to project future biodiversity.

Work carried out in BIO-C3

Baltic biodiversity is dynamic, responding to various drivers operating at different scales. Using improved knowledge obtained in BIO-C3, and existing large-scale data sets, biodiversity responses in space and time were addressed by hindcasts and projections of abiotic/biotic/anthropogenic drivers including their interactions (climate change, eutrophication, species invasions, fisheries) in spatially explicit models. The identified gradients of human impacts were synthesized into impact assessments to guide management policies including improved operationalization of Good Environmental Status (GES) indicators, design of Marine Protected Areas (MPAs) and fisheries management.

To assess the role of biodiversity in marine ecosystems, BIO-C3 used the Baltic Sea as a natural laboratory. 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, which means that extinctions of resident species or introductions of new species can be expected to have a more dramatic effect compared to species rich and presumably more stable ecosystems.

BIO-C3 aimed 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 utilized 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 were 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.

Main results of BIO-C3

Scientific highlights

Biodiversity changes and their functional implications. - Biodiversity is most often perceived as the (number of) species present in a specific habitat, an environment or an area/region, but also encompasses genetic and functional diversity components. Biodiversity changes to the natural (salinity, oxygen) as well as large scale anthropogenic (eutrophication, sediment dumping, non-indigenous species) and climatic drivers were assessed using traditional biodiversity and quality indices as well as trait-based measures and approaches, through a broad set of statistical and modeling techniques. Using two long-term time series from the Baltic Sea, we evaluated coastal and offshore major phytoplankton taxonomic group biovolume patterns over annual and monthly time-scales and assessed their response to environmental drivers and biotic interactions. Overall, coastal phytoplankton responded more strongly to environmental anomalies than offshore phytoplankton, although the specific environmental driver changed with time scale. A downscaled benthic food-web model has been developed for Baltic sub-regions in order to reconstruct predator-prey interactions during the period of changing levels of eutrophication between 1990 and 2007, suggesting a strong nutrient control of the available food supply to predatory fish and birds in coastal areas with concomitant decline in bivalves and water birds as their predators.

BIO-C3 also focused on the functional properties of biodiversity, i.e. what do organisms do rather than who are they, and on temporal variation (i.e., species turnover). We show that in spite of relatively drastic and rapid changes in species composition, the functional properties are more robust, but do change over longer time scales. This is important background to predict the behavior of ecosystems under the large-scale impacts of e.g. climate change. Another important prerequisite of biodiversity research is the correct identification of the species, especially non-indigenous ones. High-throughput sequencing (HTS) meta-barcoding was applied for the surveillance of plankton communities within the southeastern Baltic Sea. In several cases, non-indigenous species were only identified by meta-barcoding, not by traditional sampling. ***Based on above results, BIO-C3 recommends to stakeholders such as HELCOM, ICES, as well as national and regional environmental bodies to make sure that coordination of sampling programs across trophic levels are in place and that these yield comparable data sets in space and time.*** Accurate assessments of past ecological changes are a prerequisite for predictive analysis. In the Baltic Sea, we have the unique possibility to rely on national and/or regionally sampled and collected monitoring data. **Second,** ***BIO-C3 recommends the inclusion of functional properties into national and regional advice and management action*** (e.g. HELCOM, ICES).

Species and population adaptation - Populations of species may evolve quickly in response to environmental drivers. This relatively new insight in marine ecology is particularly relevant in the Baltic Sea with its steep environmental gradients and ongoing change in salinity (desalination), temperature and other global change associated parameters that are exceeding rates in other world oceans. For two key native zooplankton species, the copepods *Eurytemora affinis* and *Temora longicornis*, a series of common-garden experiments was performed across different locations/populations to determine local tolerance and adaptation potential. Both species displayed pronounced local adaptations across the sampled locations with respect to temperature (*E. affinis*) and salinity (*E. affinis* and *T. longicornis)*, implying evolutionary potential on the one hand, but also prompting the need to conserve populations with their particular response traits rather than species *per se*. As a key example for a NIS, the comb jelly *Mnemiopsis leidyi*, genotypes present in the Baltic in a first invasion wave were replaced by novel ones in the period 2010-2013. In combination with the assessment of ocean currents as drivers of (re-)introduction, this is consistent with secondary spread and re-seeding of genotypes by the prevailing currents while it rules out local reproduction in the Eastern Baltic Sea. Genetic markers (SNPs) were also instructive to assess the level of population mixing and the degree of hybridization between the Western and Eastern Baltic cod stock. A remarkable stability of stock integrity was found with minimal hybridization, possibly reflecting strong selection against hybrids. These findings reinforce that both stocks need to be managed separately, and are likely to be locally adapted to the unique Baltic environment.

Non-indigenous species (NIS) - Several (NIS), such as the round goby, the Harris mud crab *Rhithropanopeus harrisii* and the polychate *Marenzelleria* spp., have altered the biodiversity and food-web structure of the Baltic Sea, introduced new nodes and have the potential to lead to regime shifts. Currently, there are 172 NIS recorded for the Baltic Sea (AquaNIS, http://www.corpi.ku.lt/databases/index.php/aquanis cited 28. February 2018). For most of them (except deliberate releases), we are unable to identify the specific introduction vector, but shipping and natural spread from the North Sea are the two dominating introduction pathways. There are marked subregional differences in the establishment of NIS. Thus, the Baltic Sea cannot be considered as an uniform water body in terms of the established NIS and at least two major regions with differing hydrographic conditions and prevailing introduction pathways can be distinguished: i) Baltic Proper with large gulfs in the NE Baltic Sea, and ii) NW part of the Baltic Sea, incl. the Danish Straits. Our current understanding on ecological impacts of NIS is very fragmentary and we lack critical information on even the most widespread NIS in the Baltic Sea. **Therefore, research on ecological impacts of NIS should be prioritized and the required funding should be secured.**

Current and anticipated food-web changes - Phytoplankton species composition is an important determinant for ecosystem health as these are the producers of essential compounds available for higher trophic level, such as fish. A comparison of essential biomolecules between phytoplankton taxonomic groups explains why a more diverse community composition leads to higher production rates of consumers than mono-specific diets. Microzooplankton, primary consumers in the pelagic food web can to some extent buffer effects of unbalanced stoichiometric ratios for higher trophic levels. For commercially important fish species, results showed that monitoring the growth rate of larvae and evaluation of factors affecting the growth rate should be considered as an important part of the studies related to ecology of larval fish. Further outcomes showed that bottom-up processes, such as prey availability and temperature should be considered among the key drivers for larval and early-juvenile sprat.

As for top-down effects, one focus was the interaction among clupeids and their copepod prey. Predation of the planktivorous fish herring and sprat on key copepod species in the Bornholm Basin showed that both were mainly zooplanktivorous feeding on copepods. The copepod *Pseudocalanus acuspes* evolved a behavioural response to escape peak predation pressure, which occurs mainly at peak spawning periods of sprat. If integrated over the year, the utilization of the copepod production by both clupeids is however comparatively low for the dominant prey species, *indicating an **overall poor trophic coupling between copepods and pelagic planktivorous fishes** in the Bornholm basin.* The grey seal (*Halichoerus grypus*) population in the Baltic Sea has increased considerably during the last decades, causing conflict between seals and commercial fisheries. Estimation of the magnitude and uncertainty in prey consumption revealed that for the most important commercial species (cod, herring and sprat), catches generally exceeded the seal consumption in the entire Baltic Sea but regionally, seal consumption could be more *important.* The varied nature of benthic-pelagic coupling processes and their potential sensitivity to climate, nutrient loading, and fishing was assessed using the Baltic Sea as case study. The magnitude and variability of biological processes, particularly those governed by complex food web feedbacks, were sensitive to all three anthropogenic pressures examined.

Effects and future projection of major environmental drivers - Climate change is predicted to impact the Baltic marine environment in several ways, including warmer temperatures, lower salinity and less sea ice in winter. Climate forcing on species composition is already visible now, and can be well documented in the Baltic owing to its very good long-term data series. For example, profound changes in zooplankton community were recorded at the deep-water stations of the southern Baltic Sea, with significant impacts of hydrological parameters (especially salinity) and climatic forcing on pelagic food web structure and dynamics. Climate projections show that river runoff will increase in future. This will bring more nutrients to the already eutrophicated Baltic Sea. Warmer water will alter biogeochemical cycles in water and sediment. This means that eutrophication can be more severe in future with extending low-oxygen areas and larger cyanobacteria blooms. **To combat eutrophication in a warming world it is even more essential that nutrient load reduction targets are met.** Ocean acidification levels in the Baltic Sea already exceeds values predicted for other ocean areas in the distant future. Effects on commercially important fishes include increased juvenile mortality, with possible negative effects on recruitment. A more in depth transcriptomic analysis of juveniles in OA experiments shows that the fish do not "feel" stress in any way when exposed to OA, which probably makes the situation worse as they cannot counter-regulate the proton excess.

Marine Protected Areas. – An underlying idea behind the designation of Marine Protected Areas (MPAs) is that they will have a positive effect on the entire metapopulation (i.e., including both populations in the MPAs and in the spatially usually more extensive unprotected areas), and thus a net benefit beyond the MPA network *per se*. The theoretical problem is to identify what areas to select as MPAs to obtain networks optimally suited to support this effect. With respect to marine protected areas in the Baltic Sea, BIO-C3 hydrodynamic modeling research revealed that connectivity within the **present HELCOM-MPA/Natura 2000 is generally sufficient, but that some specific improvements can be suggested**. This includes the addition of MPAs along the northwest margin of the Baltic Sea to enhance growth and persistence of target species in both protected and unprotected areas. Adequacy, here measured as local retention, is sufficient for sustaining local populations with larval dispersal for about 15% of the HELCOM-MPAs, while adequacy generally fails for the smaller Natura 2000 areas. Projected reduction in salinity, predicted population fragmentation, low dispersal ability, and the highly structured populations of *Fucus vesiculosus/radicans* may significantly shift the distribution of this canopy-forming alga, and this unique habitat may be lost from a large part of the Baltic Sea. For environmental protection measures to be effective, it is **vital to not only designate specific** (often rather small) sites as **MPAs, but also to be aware of and know several aspects of connectedness** both within and between such areas. Predicted range shifts of unique genotypes may be facilitated by stepping-stone dispersal between suitably connected MPAs, or through assisted translocation to protected refuges.

GES (Good Environmental Status) Indicators - Most indicators currently in use are “state indicators”, which means that they reflect anthropogenic impacts in terms of changes in ecosystem state. This can make it difficult to relate these indicators to a particular pressure (as state changes can result from a complex of anthropogenic pressures) and impedes focused management responses. However, comparing the Baltic to other regional seas, the ratio of pressure indicators specifically addressing a pressure and changes in its magnitude is higher, most focusing on specific target groups (e.g. non-indigenous species, fishes or benthic invertebrates) and anthropogenic activities (e.g. extraction of species). Looking at partitioning of indicators according to their relevance to pressures (either direct or indirect, inferred from the pressure-impact-state matrices), key pressures in the Baltic are well represented. As a case in point, many indicators address nutrient and organic matter enrichment, which reflects eutrophication that is still the most widespread pressure in marine and coastal waters in Europe and the Baltic Sea. Other pressures that are targeted by a few indicators, related to extraction of species (i.e. fishing), non-indigenous species (NIS), physical loss and physical damage to marine habitats. **Pressures that have been identified recently such as marine noise, litter or acidification are represented by few indicators and need further development.**

Synthesis - "The Baltic time Machine" - BIO-C3 scientists initiated and led the concept paper writing initiative *“The Baltic Sea: a time machine for the global future ocean?”* uniting 26 scientists from 8 BONUS projects. A manuscript under the same title was advanced jointly at two writing workshops supported by BONUS clustering funding, and was submitted to the journal “Science Advances” in December 2017. This will **promote the Baltic Sea world-wide as a model** not only for massive environmental degradation, but also for intergovernmental governance and science based management that was able to reverse some of the negative trends.

Dissemination Impact of the research

Throughout the duration of BONUS BIO-C3, we have made strong efforts to pass on the expertise of our project personnel, and to use the scientific output resulting from BIO-C3 to inform stakeholders and policy makers in the Baltic realm and beyond. To do so, we have actively pursued the dissemination of project output on various levels, from the scientific community, to resource managers and politicians, to the public, using a mix of traditional scientific channels, involvement in working groups and advisory councils, to interviews and media channels.

This included e.g., contributions to the implementation of the MSFD on multiple occasions, to the design of the Ballast Water Management Convention, to plans for an integrated non-native species monitoring programme within HELCOM, and to scientific fisheries management advice within ICES. The role of the BONUS BIO-C3 consortium in the science-policy interface was expressed in the strong membership and a total of **402 occasions in which BIO-C3 scientists contributed to stakeholder committees or working group meetings** over the project duration, including those of ICES, HELCOM, EC, MSFD, UN, and OSPAR, and including the presentation of major BIO-C3 results and conclusions at an ad-hoc HELCOM advisory meeting in October 2017. Scientifically, BIO-C3 results have been disseminated in 111 peer-reviewed publications (+ 11 further in review, and numerous in preparation) thus far and hundreds of presentations at scientific conferences and stakeholder events. These efforts included the organization of the successful BONUS theme session "*From genes to ecosystems: spatial heterogeneity and temporal dynamics of the Baltic Sea"* at the ICES Annual Science Conference 2015 in Copenhagen (co-organized with BONUS INSPIRE and BAMBI), bringing together more than 80 scientists from both within and outside the BONUS community, as well as stakeholders and policy makers, and amongst others resulting in an invited guest column in the BONUS in Brief December newsletter on "*Finding bridges between biodiversity research and ecosystem–based management*". A second highlight was the co-organization (with BONUS INSPIRE) of the 1st BONUS symposium "*Science delivery for sustainable use of the Baltic Sea living resources*" from 17-19 October 2017 in Tallinn, Estonia, to share results from BONUS projects with the larger scientific and stakeholder community and to foster science-stakeholder interactions. This event drew 110 scientific (including >70 oral) contributions, and concluded with a half-day stakeholder panel discussion event.

We pursued the **strategy ”dissemination by training”** with a series of successful BIO-C3/BAMBI/INSPIRE/COCOA summer schools in 2015 ("*The Baltic Sea: a model for the global future ocean?*", Glücksburg, Germany, 32 PhD students and postdocs, 13 lecturers) and 2016 (*"Modelling biodiversity for sustainable use of Baltic Sea living resources"* , **Holbæk**, Denmark, 23 students and 10 lecturers) and the BIO-C3 high school teacher workshop "*Bringing Science to the class room: biodiversity in the Baltic realm – function, services and anthropogenic threats"* in Schloss Noer, Germany, from September 9-10 2016 to train teachers as ”multiplicators” passing on knowledge about Baltic biodiversity. Finally, we used blogs, our project website, television, radio, and newspaper appearances, popular science articles, presentations at public outreach events, and a series of short movies on biodiversity in the Baltic realm produced by BIO-C3 and published in 2017, to disseminate the topic ”biodiversity” to the wider public.

The continuity plan of BIO-C3

BIO-C3 continuity is pursued on several levels. Most directly, and ongoing since the end of the official project period, there is a large number of manuscripts on BIO-C3 results in preparation stage, many of them involving scientists from several of the BIO-C3 partners. We are expecting these joint scientific efforts to continue for years. Some of this work is going to be advanced further - including the use of some of the datasets resulting from BIO-C3 - within the ongoing BONUS project BLUEWEBS, in which several BIO-C3 partners are involved. Similarly, via the numerous continuing WG memberships of BIO-C3 scientists, past and new BIO-C3 scientific results will continue to enter the science-policy and science-management arena for years to come. As a consequence, the scientific and science-stakeholder networks created over the duration of BIO-C3 will remain operational.

On a second level, BIO-C3 leaves a **legacy of improved Baltic-scale scientific initiatives** that are now in place and will continue to operate. This includes the improved temporal and spatial coordination of scientific cruises in the open Baltic Sea (8-10 cruises by 4 BIO-C3 partner institutes per year on average), where overlap is avoided and annual coverage optimized. The partners have already jointly planned and harmonized the cruises schedules for 2018 and tentatively for 2019. Out of this network, one issue to pursue further in the future is the collaboration on joint synthesis efforts moving beyond datasets from individual cruises. Further examples are the expansion of the Baltic zooplankton network (http://kodu.ut.ee/~riina82/), which is continuing beyond BIO-C3, and the sample archives created by large-scale international sampling initiatives in the course of BIO-C3, e.g., of the invasive combjelly *Mnemiopsis leidyi* and the non-indigenous species round goby *Neogobius melanostomus* across the Baltic Sea. The latter is curated but still lacking analysis, and is a foundation for future follow up efforts.

On a third level, a feeling that has resonated strongly within the BIO-C3 consortium over the past year has been the **immense potential and interest to pursue joint synthesis efforts** based on the wealth of new information created in BIO-C3 as well as other BONUS projects over the past years. Examples here include the synthesis of the numerous studies on the role of non-indigenous species in Baltic food webs, on structural and functional changes of Baltic ecosystems under climate change and anthropogenic drivers, as well as taking stock of where we stand regarding the use of models in Baltic food web work and of the use of indicators in monitoring and management efforts. This has led to the idea for the BONUS synthesis project XWEBS led by and including both BIO-C3 and external partners, which received a positive evaluation and was invited to negotiations stage by BONUS. We are aiming to also use this platform to funnel BIO-C3 and BONUS project information into future synthesis and dissemination efforts. In parallel to these efforts, we are discussing the potential for a BIO-C3 focused paper about the major project results, conclusions, and recommendations.

Finally, we will continue to disseminate BIO-C3 knowledge to stakeholders on many levels, from interviews and outreach that will result from BIO-C3 publications yet to come, via the various WG memberships of BIO-C3 scientists, to a presentation of BIO-C3 highlights to EU parliament members organized by BONUS in May 2018.

More of BONUS BIO-C3…

The scientific highlight selection and project activities presented above represent but a fraction of the output of BIO-C3. For more information, including access to all of the in-depth scientific deliverable reports provided by our project tasks, an overview and in many cases direct access to BIO-C3 publications and presentations, links to our movies, event reports and lecturer presentations of our summer schools and teacher training camps, links to primary data resulting from our cruises, and much more visit our BIO-C3 homepage www.bio-c3.eu.

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