INSPIRE

BONUS ECOSYSTEM: Verbundprojekt INSPIRE: Integration räumlicher Verbreitungsprozesse in Ökosystemmodelle zur nachhaltigen Nutzung von Fischbeständen; Vorhaben: Hochauflösende Modellierung der Entwicklung und Verteilung von Fischbeständen

Abschlußbericht

1.02.2014 bis 31.01.2018

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Das diesem Bericht zugrunde liegende Vorhaben wird mit Mitteln des Bundesministeriums für Bildung, Wissenschaft, Forschung und Technologie unter dem Förderkennzeichen 03F0681C gefördert. Die Verantwortung für den Inhalt liegt bei dem Autor.

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1. Kurzdarstellung

1.1 Aufgabenstellung

INSPIRE zielte auf die substanzielle Erweiterung unseres Kenntnisstandes über die nachhaltige Nutzung kommerzieller Fischarten in der Ostsee. Die Nutzarten Hering, Sprotte, Dorsch und Flunder sind zugleich wichtige ökologische Schlüsselarten. Durch INSPIRE wurden wesentliche Kenntnislücken in den folgenden Bereichen geschlossen: a) Verbreitungsmechanismen unterschiedlicher Lebensstadien der Fischarten, b) Einfluss von Klimaänderungen und Fischerei auf die Struktur und Funktion des Ökosystems und c) Wahrnehmung dieser Stressoren in analytischen Verfahren zur Bestandsstärke der genannten Zielarten. Die grundlegenden Fragestellungen von INSPIRE waren: 1. Welche Habitatscharakteristika (pelagisch und benthisch) bedingen die räumliche Verteilung von Dorsch, Hering, Sprotte und Flunder? 2. In welchem Ausmaß beeinflussen Fischereidruck und Interaktion zwischen den Arten (z. B. Prädation) die lokale und regionale Verteilung der Nutzfische? 3. Welche Faktoren bestimmen Habitatskonnektivität und Migration der Fischarten/Populationen? 4. Inwiefern beeinflussen Populationsstrukturen die Ergebnisse der Bestandsschätzungen? GEOMAR leistete Beiträge zum AP 1 (Räumliche Verteilung): Kartierung von räumlichen Verteilungen der Fischarten auf Basis existierender Daten, neuen Messungen und statistischen Methoden; AP2 (Passive Verdriftung, aktive Migration und Habitatskonnektivität): Drift früher Lebensstadien von den Laichgebieten zu den Kinderstuben, Migration adulter Individuen sowie die Bedeutung von kleinskaligen Bewegungen für die Arteninteraktion; AP3 (Skalierung von Individuen zu Populationen): Skalierung der Bewegung von einzelnen Individuen bis zur räumlichen Verteilung von Populationen, Quantifizierung des Einflusses von regionalen ökologischen Risiken auf die großskalige Produktivität und räumlichen Verteilungen.

Die wesentlichen Beiträge GEOMARs zu INSPIRE waren komplexe hochauflösende hydrodynamische Modellrechnungen der gesamten Ostsee, Driftmodellierung mit einem Langrangen Driftmodell (IBM-Individual Base Model) und die Analyse der hydrodynamischen Bedingungen und Variabilitäten in der gesamten Ostsee auf saisonaler, zwischenjährlicher und dekadischer Zeitskala. Für die Entwicklung und Verteilung der Fischarten sind die Sauerstoffbedingungen in der Ostsee von großer Bedeutung. Das Kieler Ostseemodell ist in der Lage, Sauerstoffbedingungen einschließlich hypoxischer und anoxischer Bereiche realistisch zu modellieren. Die hydrodynamischen Modellergebnisse flossen direkt in die nachgeschaltete Driftmodellierung zur räumlicher Verteilung bzw. Verdriftung von juvenilen Dorschen und Flundern ein.

1.2 Voraussetzungen, unter denen das Vorhaben durchgeführt wurde

Für die Durchführung des Vorhabens war das Kieler Ostseemodellsystem Voraussetzung. Das Modellsystem besteht aus dem gekoppelten Meereis-Ozeanmodell der Ostsee (BSIOM, Lehmann & Hinrichsen 2002, Lehmann et al. 2014) und einem nachgeschalteten Lagrangen Driftmodell (Hinrichsen et al. 1997; Lehtiniemi et al. 2012). Das Modellsystem wurde an der CAU (Christian Albrechts Universität Kiel) auf dem NEC-SX-ACE Hochleistungsrechner gerechnet. Die Analysen und Visualisierung wurden auf lokalen Rechnern des GEOMAR erstellt. Die Basis für die im Rahmen von INSPIRE erstellten Untersuchungen waren Modellläufe über den Zeitbereich von 1979-2017.

1.3 Planung und Ablauf des Vorhabens

Die Arbeiten wurden gemäß dem im Projekt verankerten Zeitplan durchgeführt. Der Zeitplan wurde eingehalten.

1.4 Wissenschaftlicher und technischer Ausgangszustand

Die Basis für die Arbeiten im Teilprojekt war das gekoppelte Meereis-Ozeanmodellsystem der Ostsee. Das Modellsystem wurde in den vergangenen Jahren konsequent für wissenschaftliche Untersuchungen genutzt und weiterentwickelt. Das Modellsystem ist führend im Bereich der Ostseeforschung.

1.5 Zusammenarbeit mit anderen Stellen

Im Rahmen von INSPIRE fand eine intensive Zusammenarbeit mit insgesamt 11 Teilprojektpartnern statt (University of Tartu, Estland; Danmarks Tekniske Universite, Dänemark; Morski Instytut Rybacki-Panstwowy Instytut, Polen; Stockholm University, Schweden; Swedish University of Agricultural Sciences Schweden; Institute of Food Safety, Animal Health and Environment, Lettland; Thünen Institute of Baltic Sea Fisheries, Federal Research Institute for Rural Areas, Foresty and Fisheries, Deutschland; University of Hamburg, Deutschland; Natural Resources Institute, Finnland; Lund University, Schweden; Uppsala University, Schweden)

2. Durchgeführte Arbeiten und Ergebnisse

2.1 Zusammenfassung der Ergebnisse

Im Berichtszeitraum wurden Beiträge zu Task 1.2 (Kartierung von räumlichen Verteilungen der Fischarten auf Basis existierender Daten, neuen Messungen und statistischen Methoden), Task 2.1 (Drift früher Lebensstadien von den Laichgebieten zu den Kinderstuben, Migration adulter Individuen) sowie Task 3.1 (Skalierung individueller Bewegungen zu räumlichen Populationsdichten) geleistet.

Für die Periode 1979-2017 wurden die Strömungs-, Temperatur-, Salzgehalts- und Sauerstoffverhältnisse mit dem Kieler Ostseemodell berechnet. Der wesentliche Prozess, der die Sauerstoffbedingungen in den tiefen Becken der Ostsee bestimmt, sind sogenannte Salzwassereinbrüche. Die Variation der Sauerstoffbedingungen hat entscheidenden Einfluss auf die Reproduktionsvolumen oder Habitate von Dorsch und Flunder (Hinrichsen et al. 2016). Hierzu wurden die atmosphärischen Bedingungen, die zu Salzwassereinbrüchen bzw. großen Volumenschwankungen führen, detailliert untersucht (Lehmann, et. al. 2017). Weiterhin dienten die Modelldaten als Basis für eine nachgeschaltete Driftmodellierung, mit der die Verdriftung von Fischeiern und Larven für die gesamte Ostsee berechnet werden konnte. Durch die Modellierung ist ein hochauflösender 4-dimensionaler Datensatz für die gesamte Ostsee einschließlich Skagerrak und Kattegat für Temperatur, Salzgehalt, Sauerstoff, Oberflächenauslenkungen und Strömungen entstanden. Der Datensatz diente als Basis für die nachgeschaltete Driftmodellierung und lieferte zusätzlich hydrodynamische Daten zu den historischen und aktuellen Beobachtungsdaten. Modelldaten wurden verschiedenen INSPIRE-Partnern zur Verfügung gestellt. Aus dem Datensatz konnten Änderungen der chemisch-physikalischen Bedingungen bestimmt werden, die Habitatsstrukturen oder Reproduktionsvolumina beeinflussen. Mit dem nachgeschalteten Lagrangen Driftmodell konnte die Verdriftung von Fischeiern und Larven unter unterschiedlichen atmosphärischen Bedingungen berechnet werden.

2.2 Ergebnisse zu den Arbeitsschwerpunkten bezüglich des Projektarbeitsplans

AP1. Räumliche Verteilungen:

Für die Zirkulationsmodellrechnungen werden konsistente Atmosphärendaten benötigt. Für INSPIRE wurden aus den ERA-Interim Reanalyse-Daten für den Zeitbereich 1979-2013, später für die Folgejahre 2014 bis 2017 Modell-Antriebsdaten für den nordeuropäischen Raum extrahiert und für das Ostseemodell aufbereitet. Im Dezember 2014 fand ein großer Salzeinbruch in die Ostsee statt. Salzwassereinbrüche transportieren salz- und sauerstoffreiches Wasser über die Schwellen (Darß und Drodgen) in die Ostsee und verändern in den tiefen Becken die Salzgehalts- und Sauerstoffbedingungen nachhaltig. Die veränderlichen Bedingungen von Temperatur, Salzgehalt und Sauerstoff in der gesamten Ostsee konnten mit dem Kieler Ostseemodell realistisch simuliert werden. Der entstandene 4-dimensionale Modelldatensatz wurde neben Prozessstudien zu Salzwassereinbrüchen (Lehman et al. 2017; Höflich et al. 2018) auch für die Berechnung von Habitaten und zur Driftmodellierung genutzt (Hüssy et al. 2015; Hinrichsen et al. 2016; Hinrichsen et al. 2017). Monatsmittel der hydrodynamischen Modellergebnisse wurden anderen Projektpartnern zur Verfügung gestellt (Orio et al. 2017; Frelat et al. 2018).

AP2. Passive Verdriftung, aktive Migration und Habitatskonnektivität

In diesem Arbeitsschwerpunkt wurde die Drift früher Lebensstadien von den Laichgebieten zu den Kinderstuben, die Migration adulter Individuen sowie die Bedeutung von kleinskaligen Bewegungen für die Arteninteraktion untersucht. Mittels hydrodynamischer und Driftmodellierung wurde die Verdriftung von Dorscheiern und -Larven untersucht. Eier und Larven sind hierbei passive Drifter, die durch das simulierte 4-dimensionale hydrodynamische Feld driften. Die Drifter registrieren während der Drift die Umgebungsvariablen Temperatur, Salzgehalt und Sauerstoff, so dass unter vorgegebenen Randwerten die Drift enden kann und die Partikel aus dem System entfernt werden. Die Ergebnisse der Driftmodellierung erlauben, Untersuchungen zur Konnektivität und zur Eignung von Habitaten sowie die Überlebenswahrscheinlichkeiten von Eiern und Larven zu berechnen (Hüssy et al. 2015; Hinrichsen et al. 2016; Hinrichsen et al. 2017).

AP3. Skalierung von Individuen zu Populationen

In diesem Arbeitspaket ging es um die Skalierung der Bewegung von einzelnen Individuen bis zur räumlichen Verteilung von Populationen, Quantifizierung des Einflusses von regionalen ökologischen Risiken auf die großskalige Produktivität und räumlichen Verteilungen. Die Ergebnisse aus der Driftmodellierung tragen auch zum AP3 bei. Zum ersten Mal wurde eine Driftstudie durchgeführt, in der Dorscheier in typischen Dorschlaichgebieten eingesetzt wurden. Mit dem Erreichen des Larvenstadiums wurde die Drift gestoppt (Hinrichsen et al. 2016). In einem Folgeexperiment dienten die Endpunkte der Dorscheierdrift als Startpunkte für eine nachgeschaltete Larvendrift. Die Larven wurden bis zu dem Stadium verfolgt, an dem sie zum Bodenleben übergehen (ca. 90 Tage). Wenn die Drift in geeigneten Habitaten endete, wurden die Partikel als Jungfische registriert. Im Falle dass kein geeignetes Habitat erreicht wurde, wurden die Partikel aus dem System entfernt. Die Studie zeigte, dass ein Teil der Larven/Jungfische aus dem östlichen Ostseebestand durch Drift in den westlichen Bestand gelangen und damit dem westlichen Bestand zugeordnet werden (Hinrichsen et al. 2017).

Publikationen und Vorträge die in Bezug zum durchgeführten Vorhaben stehen

Frelat, R., Orio, A., Casini, M., Lehmann, A., Merigot, B., Otto, S., Sguotti, C., Möllmann, C. 2018. A three-dimensional view on biodiversity changes: spatial, temporal , and functional perspectives on fish communities in the Baltic Sea. ICES Journal of Marine Science, doi:10.1093/icesjms/fsy027.

Hinrichsen, H.-H., Lehmann, A., Petereit, C., Nissling, A., Ustups, D., Bergström, U., Hüssy, K. 2016: Spawning areas of eastern Baltic cod revisited: Using hydrodynamic modelling to reveal spawning habitat suitability, egg survival probability and connectivity patterns. Progress in Oceanography, 143, 13-25.

Hinrichsen, H.-H., von Dewitz, B., Lehmann, A., Bergström, U. and Hüssy, K. 2017. Spatio-temporal dynamics of cod nursery areas in the Baltic Sea. Progress in Oceanography 155: 28-40.

Höflich, K., Lehmann, A., Myrberg, K.: Disentangling the role of atmopsheric and oceanic conditions in the occurrence of major Baltic inflows: The importance of haline stratification in the Belt Sea. EGU General Assembly, Vienna, Austria, 17-22 April 2016.

Höflich, K., Lehmann, A., Myrberg, K.: On the role of the haline conditions in the Belt Sea in the formation of highly saline barotropic inflows to the Baltic Sea. 1st Baltic Earth Conference "Multiple drivers for the Earth system changes in the Baltic Sea region", Nida, Lithuania, 13-17 June 2016.

Höflich, K., Lehmann, A., Myrberg, K. Towards an improved mechanistic understanding of major saltwater inflows into the Baltic Sea. 11th Baltic Sea Science Congress, Rostock, Germany, 12-16 June 2017.

Höflich, K., Lehmann, A., Myrberg, K. Towards an improved mechanistic understanding of major saltwater inflows into the Baltic Sea. In preparation.

Hüssy, K., H.-H. Hinrichsen; M. Eero; H. Mosegaard; J. Hemmer-Hansen; A. Lehmann; L. S. Lundgaard. 2015. Spatio-temporal trends in stock mixing of eastern and western Baltic cod in the Arkona Basin and the implications for recruitment. ICES Journal of Marine Science, 73: 293-303.

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Lehmann, A., Höflich K., Post, P., Myrberg, K.: Pathways of deep cyclones associated with large volume changes (LVCs) and major Baltic inflows (MBIs). 1st Baltic Earth

Conference "Multiple drivers for the Earth system changes in the Baltic Sea region", Nida, Lithuania, 13-17 June 2016.

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Lehmann, A., Hinrichsen, H.-H., Höflich, K. 2017. Climate variability of hydrographic conditions of the Baltic Sea and their impact on cod nursery areas. 11Th Baltic Sea Sciences Congress, 12-16 June, 2017, Rostock Germany.

Lehmann, A., Hinrichsen, H.-H., Höflich, K. 2017. Climate variability of hydrographic conditions of the Baltic Sea and their impact on cod nursery areas. BONUS Symposium: Science delivery for sustainable use of the Baltic Sea living resources. Tallinn, Estonoa, 17-19 October 2017.

Orio, A., Bergström, U., Casini, M., Erlandsson, M., Eschbaum, R., Hüssy, K., Lehmann, A., Lozys, L., Ustups, D. and Florin, A-B. 2017. Characterizing and predicting the distribution of Baltic Sea flounder (*Platichthys flesus*) during the spawning season. Journal of Sea Research, 126: 46-55.

Ojaveer, H., Neuenfeldt, S., Horbowy, J., Blenckner, T., Casini, M., Kornilovs, G., Polte, P., Möllmann, C., Aro, E., Lehmann, A., Nilsson, A., Nissling, A. Integrating Spatial Processes Into ecosystem models for sustainable utilization of fish REsources (INSPIRE), ICES Annual Science Conference, 15-19 September 2014, A Curuna, Spain

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Lehmann, A., Hinrichsen, H-H., Krauss, W. 2002. Effects of remote and local atmospheric forcing on circulation and upwelling in the Baltic Sea. Tellus 54A:299-316.

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Lehtiniemi, M., Lehmann, A., Javidpour, J., Myrberg, K. 2012. Spreading and physico-biological reproduction limitations of invasive American comb jelly *Mnemiopsis leidy*i in the Baltic Sea. Biol. Invasions 14:341-354.

Anhang

Erfolgskontrollbericht

1. Beitrag des Ergebnisses zu den förderpolitischen Zielen des Förderprogramms

Die hochauflösende hydrodynamische Modellierung zur Entwicklung und Verteilung von Fischbeständen war Teil des BONUS-Verbundprojekts INSPIRE (Integration räumlicher Verbreitungsprozesse in Ökosystemmodelle zur nachhaltigen Nutzung von Fischbeständen). Das INSPIRE Konsortium bestand aus 12 Arbeitsgruppen aus 7 Ostseeanrainerländern (University of Tartu (UT-EMI), Danmarks Tekniske Universitet (DTU-Aqua), Morski Instytut Rybacki-Panstwowy Instytut Badawczy (MIR-PIB), Stockholm University (SU), Swedish University of Agricultural Sciences (SLU), Institute of Food Safety, Animal Health and Environment (BIOR) Thünen Institute of Baltic Sea Fisheries, Federal Research Institute for Rural Areas, Forestry and Fisheries (TI-OF), University of Hamburg (UHAM), Natural Resources Institute Finland (LUKE), Helmholtz Centre for Ocean Research Kiel (GEOMAR), Lund University (LU), Uppsala University (UU). INSPIRE hatte zum Ziel, den Kenntnisstand über die nachhaltige Nutzung kommerzieller Fischarten in der Ostsee (Hering, Sprotte, Dorsch und Flunder) substanziell zu erweitern und hierbei speziell die Verbreitungsmechanismen unterschiedlicher Lebensstadien, Einfluss von Klimaänderungen und Fischerei auf die Struktur und Funktion des Ökosystems und die Wahrnehmung dieser Stressoren in analytischen Verfahren zur Bestandsstärke zu untersuchen. Die Ergebnisse der hochauflösenden hydrodynamischen Modellierung lieferte einen substantiellen Beitrag zum Erreichen der INSPIRE-Ziele.

2. Wissenschaftliche und technische Ergebnisse des Vorhabens

Das Projekt hat zu neuen Erkenntnissen über die Verdriftung von Fischeiern und -Larven im Ostseeraum geführt. Weiterhin ist es gelungen, in der Kombination von hydrodynamischer Modellierung und Driftmodellierung ein Modellsystem zu entwickeln, mit dem Verbreitungsmechanismen von frühen Lebensstadien verschiedener Fischarten, Habitiatscharakteristiken Konnektivät und Migration untersucht werden kann. Dies ist vor allem auch durch die intensive Kooperation mit den Partnern des INSPIRE-Projekts gelungen (s. Publikationsliste des Schlußberichtes).

3. Verwertbarkeit der Ergebnisse

Die erzielten Ergebnisse werden bzw. wurden publiziert. Die Modellergebnisse wurden zentral auf Datenspeichern des GEOMAR gespeichert und sind Basis weiterer Untersuchungen bzw. Publikationen. Die gewonnenen Erkenntnisse und die während der Projektlaufzeit entstandenen Partnerschaften mit nationalen und internationalen Institutionen und Wissenschaftlern bilden eine wichtige und wertvolle Grundlage für zukünftige Projekte im Bereich der Klima- und Ostseeforschung. Die Methodik ist außerdem auf andere Meere und Seegebiete übertragbar.

4. Arbeiten, die zu keiner Lösung geführt haben

-keine-

5. Einhaltung der Ausgaben- und Zeitplanung

Ausgaben- und Zeitplanung wurden eingehalten.

BONUS INSPIRE PROJECT (01. February 2014 – 31. January 2018)
The final publishable summary report
Date 31. March 2018

1 Project outline of goals and results envisaged at the beginning of the project cycle

Understanding the changes in spatial distributions of cod, herring, sprat and flounder, and disentangling the role of natural drivers and various human induced impacts constituted the challenging topic for the research in BONUS INSPIRE. The project set out to fill in the most persistent gaps in knowledge of the spatial ecology of the major commercial fish and thereby supported the effectiveness of the relevant policies and ecosystem-based management of the Baltic Sea.
BONUS INSPIRE substantially advanced our knowledge on the four major commercial fish species in the Baltic Sea. These fish form more than 95% of the commercial catches and represent key elements of the Baltic Sea ecosystems. To accomplish the main goals, BONUS INSPIRE addressed the following questions:

What physical, chemical and biological (prey and predators) parameters characterise the spatial distributions of cod, herring, sprat and flounder?
To what extent do fishing and species interaction affect the local and basin-scale distribution of exploited stocks?
What drives spatial connectivity and migrations of different fish populations?
How does population structure and separation of natural populations impact stock assessment outcomes?

2 Work carried out in the project

Substantial amount of data was collected in order to generate new knowledge regarding fishes hereabouts at different times and causes for these occurences. This constituted the main part of fieldworks in the project. Thus, we performed extensive gillnet and beach seine surveys to monitor the distributions of the main life stages of cod and flounder over the whole Balic Sea. Acoustic and experimental trawling surveys were performed to obtain additional information on distribution and abundance of juvenile and adult herring and sprat together with collection of their stomachs for dietary analysis. The distribution of sprat eggs and larvae in the open Baltic Sea was surveyed to identify the reproduction areas of sprat. To reveal the spatial distributions of pelagic and demersal spawning flounder in various parts of the Baltic Sea, vital parameters of the egg and spermatozoa were investigated.

To gain an understanding of the past, various types of historical data (e.g., zooplankton, fish tagging, fish larval abundance, fish stomach content data, acoustic/international trawl survey data) was standardised and assembled together with the newly collected data. Data and information obtained from different modern techniques (genetics, morphometrics & otolith chemistry) were also assembled to develop tools for separating flounder ecotypes and enabling allocation of catch by these ecotypes.

Besides collecting data, we used models to evaluate drift patterns of cod, herring and flounder eggs, and to analyse stock mixing between different areas. The drift of fish eggs and larvae was then scaled to temporally and spatially resolved distribution and settlement probability maps. We also developed a mathematical model that couples key fish populations to a complex suite of trophic, environmental and geomorphological factors. By using advanced spatial statistics, annual and seasonal maps of fish distribution in demersal and pelagic habitats from 1978 onwards was established. A basic spatially explicit multispecies length-based model was developed, which integrates population dynamics, foraging behaviour and predator (cod) growth. Analytical stock assessments of cod, sprat and herring stocks were run by several relevant assessment units, based on

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different combinations of management areas and incorporation of biological/ecological knowledge of the species. A variety of assessment models and methods for estimation of management reference points have been tested and applied for flounder.

3 Main results achieved during the project

The experience gained during the gillnet and beach seine surveys to monitor the distribution and habitat preferences of the main life stages of cod and flounder survey was used to produce guidelines for future sampling. The dual response of the gillnet survey results to salinity and water depth suggested the existence of two distinct flounder ecotypes, demersal and pelagic spawning, with the abundance of the two respective ecotypes related to different biotic and abiotic factors (see also below).

A hydrodynamic model combined with a Lagrangian particle tracking technique was utilised to provide long-term knowledge of environmentally-related survival probability and drift of eastern Baltic cod eggs and larvae. Eggs initially released as drifters in the westernmost spawning grounds were more affected by sedimentation than those released in the eastern spawning grounds. For all spawning areas temperature dependent mortality was only evident after severe winters. Egg buoyancy in relation to topographic features like bottom sills and strong bottom slopes could appear as a barrier for transport of Baltic cod eggs and could potentially limit the connectivity of Baltic cod early life stages between the different basins in the central and eastern Baltic Sea.

Connectivity of pelagic, early life stages via transport by ocean currents is of particular interest, as it may affect survival chances of offspring, recruitment success and mixing of stocks across management units. Based on drift model studies, the transport of larvae showed a high intra- and inter-annual variability, but also some general, consistent patterns of retention within and dispersion to different management areas. Good agreement of drifter end-positions, representing potential juvenile settlement areas with actual catches of juveniles from bottom trawl surveys, suggests that the drift simulations provide reasonable estimates of early life stage connectivity between cod populations in the investigated areas. High exchange rates of drifters between management areas suggest that cod populations are demographically correlated.

For the first time, a drift study has been performed in which fertilized cod eggs have been released in historically important Baltic cod spawning grounds. These eggs drifted at levels of neutral buoyancy until they entered the first feeding state. The end-positions of this drift study were the starting positions for the subsequent drift study, where first feeding stage larvae drifted until they reached the age of settlement. The study has shown that particles representing eastern Baltic cod juveniles settled to a relatively large extent in the western Baltic cod management area and may significantly contribute to western Baltic cod recruitment. Therefore, it could be suggested that larval and juvenile transport could contribute to recruitment in the western Baltic Sea.

The spatial resolution of mixing of Eastern and Western Baltic cod suggests immigration occurring north of Bornholm and propagating throughout the Arkona Basin. The immigration cannot be attributed to spawning migration, as no seasonal trend in stock mixing was observed. Thus, the immigration of Eastern cod does therefore not seem to contribute significantly to Western Baltic cod's recruitment.

The cod tagging data indicate that only a small fraction of the tagged population is conducting trans-basin migrations with the net displacement being largely independent of the time. This means that adult migrations probably do not contribute to whole Baltic scale re-distributions of cod. Furthermore, it implies that regional stock recovery might not lead to recovery of cod in the whole Baltic Sea, but rather to regional regulation of stock size due to density-dependent processes.

The spatial extent of flounder eggs and larvae represented as modelled particles is primarily determined by oxygen and salinity conditions. The reproduction habitat most suitable was determined for the Gdansk Deep, followed by the Bornholm Basin. Relatively low habitat suitability was obtained for the Arkona Basin and the

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Gotland Basin. Eggs initially released in the Arkona Basin and Bornholm Basin were strongly affected by sedimentation compared with those released in the Gdansk Deep and Gotland Basin. Highest relative survival of eggs occurred in the Gdansk Deep and in the Bornholm Basin. Relatively low survival rates in the Gotland Basin were attributable to oxygen-dependent mortality while oxygen content had almost no impact on survival in the Arkona Basin. For all spawning areas mortality caused by lethally low temperatures was only evident after severe winters. Buoyancy of eggs and larvae in relation to topographic features appear as a barrier for their transport and potentially limits the connectivity of early life stages between the different spawning areas.

Information about species interactions at a spatial scale comparable to the perceptive abilities of the involved species is crucial for the establishment of predictive, food consumption models at the population level. Nevertheless, such information is sparse due to methodological constraints. Cod predation took place in the Bornholm Basin during late winter primarily at dusk and dawn during ascent and descent of sprat associated with school dissolution and formation. Cod resided close to the bottom outside these temporal predation windows. Sprat schools were located at the same depth or deeper than cod during daylight hours, whereas dispersed sprat at night were situated higher in the water column. These vertical dynamics could be explained by fitness optimization using bioenergetics and trade-offs between temperature, oxygen saturation of the water, and predation risk. The study thus forms the first step to providing a mechanistic background for the aggregate functional response of cod at basin scale and beyond.

At a high stock size, adult cod is distributed over large area, whereas at low stock sizes the population contracts into the most favorable areas in terms of abiotic conditions, supporting thereby the existence of density-dependent habitat selection. Analyses of vertical distribution revealed a clear day/night pattern, proving the existence of an overall migration of adult cod to the pelagic habitat during night-time. Temporal drop in the occurrence of cod in the distribution area of sprat and herring, and in the occurrence of large cod in the distribution area of small cod was observed. A decline in prey occurrence in the areas occupied by cod evidences that lower feeding opportunities of cod on fish prey occurred during the past 20 years. A strong link between extent of hypoxic areas and cod condition was also evidenced, likely operating through habitat contraction, decline in benthic prey and direct effects on cod physiology. This new knowledge help understanding the decline in cod condition.

Predator–prey interactions are a primary structuring force in marine foodwebs and they play an important role in the dynamics of both marine fish populations and their prey. Study in the feeding of two dominant zooplanktivorous clupeids – herring and sprat – evidenced that the fullness of fishes' stomachs increased with the increasing proportions of prey in the zooplankton community. The share of empty stomachs was lower for sprat, and among smaller fish in both species. Our results point to high interspecific competition, where sprat seems to be more successful than herring in finding and consuming prey, and therefore may have an advantage over herring when the zooplankton community is dominated by small-sized taxa.

Sprat tended to aggregate in deeper waters in spring season while moving towards coastal waters and aggregating at 30-70m depth during feeding. The main factors determining aggregation and distribution pattern of sprat in spring were previous winter's severity and water temperature in 50-100 m depth layer during the autumn months (September-October). In last two decades, sprat distribution has shifted northward coinciding with an increase in winter temperatures and population size. The investigated area of Eastern Central Baltic is supposedly important for the reproduction of sprat as the proportion of sprat spawning stock biomass significantly increases in years of rich year-class formation. A hypothesis is put forward that Gotland Deep basin is the centre of distribution of sprat stock in the Baltic Sea.

For most herring populations in the Baltic Sea frequenting coastal zones and inner coastal waters for spawning and larval retention, this means that important drivers and stressors of recruitment dynamics are acting on the scale of regional basins or estuaries. Generally, reproductive success and year class strength of Baltic herring

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populations is strongly determined by the survival of early life stages such as eggs and larvae in local nursery areas. However, the explicit mechanisms by which local stressors might affect overall recruitment are currently not well understood. It appeared that in the very shallow part of the Gulf of Riga, high summer temperatures, which likely exceed the physiological optimum, may negatively affect larval survival. Therefore, the observed simultaneously high growth and mortality rates primarily resulted from a rapidly increasing and high water temperature that masked potential food-web effects. The investigation suggests that the projected climate warming may have significant effect on early life history stages of the dominating marine fish species inhabiting shallow estuaries.

An ontogenetic loop in habitat use during larval ontogeny indicated an active habitat selection and revealed a key role of shallow littoral waters for larval herring retention in the Western Baltic Sea. Elemental fingerprinting in herring earstones revealed a distinct chemical separation between juvenile herring caught in the vicinity of the Island of Ruegen in the south-western Baltic Sea and other potential nursery areas. This novel information will increase our understanding of the contribution of particular coastal nursery areas to overall western Baltic herring productivity.

The eastern Baltic cod stock was assessed with two models, in which natural mortality in recent years was allowed to increase. It was shown that the assessment models with natural mortality (M) related to growth perform much better than the standard assessment models in which M is assumed constant. In addition, a stock similar to eastern cod with natural mortality increasing in recent years was generated. It appeared that the assessment of such stock using constant natural mortality performs similarly badly as recent assessments by the International Council for the Exploration of the Sea (ICES) in terms of model diagnostics. The obtained results strongly suggest that natural mortality of cod in recent years markedly increased.

Herring and sprat were assessed according to former assessment units (AUs), used up to 1990s. Such assessments reflect better both biological characteristics of stocks and spatial overlap of clupeids with predator (cod), than the standard assessment performed presently by ICES. Assessments of herring show similar trends in biomass development in AUs as well as in fishing mortality. In general, assessments of sprat also show similar trends in stock biomass and fishing mortality developments in the considered AUs. The sum of biomasses by AUs is close to ICES estimates of sprat biomass in the Baltic Sea. However, differences in intensity of exploitation of the stocks by AUs might be substantial (fishing mortality being higher in the north-eastern areas) and spatial management could be suggested. Such management would require assessment and data by former AUs.

Egg and spermatozoa characteristics, genetics, morphometrics and earstone microchemistry were applied to develop tools for separating demersal and pelagic spawning flounder and enable allocation of catch to different spawning types of flounder in different management areas. Although it was possible to correctly classify 74% of flounder based on morphometry, it required use of 18 morphological characteristics' landmarks and hence was quite time consuming. Results from the otolith chemistry revealed that further studies are needed before the findings can be used for stock separation.

Important elements of flounder fishery are discards. They could not be directly included into the assessments as time series of reliable discards estimates are very short. The general conclusion was that inclusion of discards increase estimates of biomass in similar rate as discards rate but has little effect on estimates of fishing mortality. Trends in biomass estimates with modelled discards included were similar to trends in biomass estimates without discards.

Potential early warning indicators for the Eastern Baltic cod stock development were examined. Indicators characterising the recruitment environment could be suggested for early warning, such as depth at 11 psu isohaline. The rescaled Baltic International Trawl Survey (BITS) index may also be considered an early warning indicator of cod stock size.

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Altogether 15 species-based (herring, sprat, cod and flounder) spatially explicit indicators were identified and elaborated. These address the following three EU Marine Strategy Framework Directive descriptors: D1 Biodiversity, D3 Exploited fish stocks and D4 Food-webs. In addition, composite indicator to evaluate status of the cod and herring stocks at the pan-Baltic scale was developed, by applying the recently developed Baltic Health Index framework. We also presented the indicator-testing framework, which can be used to identify responses of food-web indicators to manageable pressures while accounting for the biotic interactions in food-webs linking such indicators. The outcomes, essentially D3 indicators on spawning stock biomass and fishing mortality, were discussed in the light of potential precautionary reference and Good Environmental Status (GES). Several indicators need further work not only to develop reference points and targets, which will ultimately result in achievement of GES, but also consider spatial scales for indicator aggregations.

Several spatially-explicit novel research results emerged, which will make valuable contribution for advaning the ecosystem-based managemnt in the Baltic Sea. The highlights include: i) recent abundant presence of sprat in the NE Baltic Sea is likely facilitated by superior competitive feeding to herring; ii) the commercial extinction of the previously abundant autumn spawning herring in the early 1980s was likely due to too high fishing mortality; iii) spatial distribution and size composition of sprat and herring affect the individual performance in salmon and cod, suggesting the need for spatial management of sprat; iv) the presently implemented area closures of cod fisheries in Gdansk Deep and Gotland Basin are likely to be largely ineffective in enhancing the cod stock; and v) the two subpopulations of flounder seem to use different areas following settlement (but see also above).

BONUS INSPIRE was conducted in close collaboration with ICES and the Baltic Sea Advisory Commission, which ensured immediate delivery of new research results to the main stakeholders of the project. We were, for example, organising and co-convening Theme Session ‘From genes to ecosystems: spatial heterogeneity and temporal dynamics of the Baltic Sea’ at ICES Annual Science Conference in 2015, jointly with BONUS BIO-C3 and BAMBI projects. Together with these two projects, we also contributed to the BONUS 2015 summer school “The Baltic Sea: a model for the global future ocean?” and organised the BONUS 2016 summer school “Modelling Biodiversity for Sustainable Use of Baltic Sea Living Resources”. BONUS INSPIRE scientists performed multiple national and international advisory roles on fisheries and marine ecosystem management. Our BONUS symposium on ’Science delivery for sustainable use of the Baltic Sea living resources’ (jointly with BONUS BIO-C3), which also accommodated stakeholder panel discussion had nearly 150 participants with in total of over 100 scientific presentations given. We already published 49 peer-reviewed papers, produced 18 additional manuscripts, defended 2 PhD thesis, and participated in 370 stakeholder committee meetings and 34 media events. We contributed to several international collaborations, such as global networks on ‘Indicators of the Seas’ and ‘Oceans Past Initiative’, and participated in developing the Baltic Health Index.

4 The continuity plan of the project

Several important actions will be performed in relation to continuity of the project. We will continue our involvement in ICES and HELCOM work to ensure that all the created knowledge will be considered in the advisory process for fisheries and marine ecosystems management. We will also finalise 18 unfinished manuscripts and ensure their submission to peer-reviewed scientific journals. Several BONUS INSPIRE scientists are part of the recently accepted BONUS project on ‘Taking stock of Baltic Sea food webs: synthesis for sustainable use of ecosystem goods and services’ (XWEBS). This will facilitate further utilisation and synthesis of INSPIRE results into a broader context of the Baltic Sea ecosystems structure and functioning. The project website will be kept up and running for at least additional 2 years with continuous update of appropriate information (e.g., publications, collaborative projects).

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The work initiated in BONUS INSPIRE has already resulted in several successful new project applications, such as Morphometric and fitness variation in *Platichthys flesus*, Tagging Baltic Cod (TABACOD) and H2020 project on Paradigm for Novel Dynamic Oceanic Resource Assessments (PANDORA).

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