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## Variability of advective connectivity in the Baltic Sea

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### ABSTRACT

Connectivity between different populations of a species is a central parameter in the fields of ecology and evolutionary biology. We here provided decadal, regionally, and depth layer resolved information on connectivity and dispersal patterns for the entire Baltic Sea as a tool for supporting population genetic and ecological studies. The general method to assess dispersal 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 were assessed from Lagrangian particle tracking using ocean circulation model outputs. Generally, for the whole Baltic Sea as well as for all subareas, we observed persistent patterns of dispersal that reflected the basin-like structure of the Baltic Sea, with less transport between the basins. At the same time, dispersal distance and in extension, local retention versus dispersal of particles to other sub-areas, varied considerably over four decades (1970–2010) and among regions within the Baltic Sea, corresponding to a range from high connectivity to partial dispersal barriers. Based on the example of Eastern Baltic cod we then investigated how our dispersal distance datasets can serve as a tool to assess dispersal and the expected connectivity among different populations of a species, as long as some biological information is available. For example, our finding of high dispersal of particles from the Bornholm Basin to the other Eastern Baltic basins could help to explain recent results indicating lack of genetic differentiation of cod across the eastern Baltic Sea. Our results also indicate that the shift in spawning time observed in cod over the past decades and the resulting exposure of eggs and larvae in the water column to a time of the year with a different current regime has likely affected egg and larval export. Finally, our case study also demonstrates how inter-annual variability of ocean current speed and direction at the time of peak reproduction is likely to affect the connectivity among the subareas in the Baltic. To conclude, connectivity datasets from this study are freely available, and can represent a powerful tool to apply in evolutionary and ecological studies of a variety of species in the Baltic Sea.

### 1. Introduction

The connectivity between different populations of a species is a central parameter in the fields of ecology and evolutionary biology. This includes our understanding of meta-population structure, local adaptations and divergence of populations in the context of seascape genetics (Selkoe et al., 2016), and of species distribution ranges and interactions, recruitment, and population dynamics from an ecological perspective (Roughgarden et al., 1988; Gaines and Lafferty, 1995; Gaylord and Gaines, 2000; Grosberg and Cunningham, 2001; Hixon et al., 2002). Not surprisingly, this also has created implications for both resource management (e.g., fish stock delineation) and conservation (e.g., placement of marine protected areas, MPAs). At the same time, understanding the patterns of population connectivity is a complex problem, particularly in the marine setting, where both active movement by adult life stages (Zemeckis et al., 2017) and passive

dispersal of early life stages (e.g., eggs and larvae) with ocean currents (Cowen and Sponaugle, 2009; White et al., 2010a, 2010b) connects populations in the seascape and determines source sink dynamics and local retention.

While marine ecological and population genetic studies have often focused on the active dispersal of species, passive dispersal with ocean currents may be the more relevant factor for most marine species (Selkoe et al., 2016). This includes (1) holoplankton such as many phyto- and zooplankton species (e.g., gelatinous zooplankton), (2) organisms that are sessile or show little mobility but that have planktonic early life stages (e.g., eelgrass, mussels), and (3) most of the mobile species, for which long-distance transport of early life stages still outweighs active movement in the adult stage. The distance and direction of ocean current mediated early life stage dispersal and resulting connectivity patterns thus have considerable influence on the demography and genetic structure of marine species (Paris et al., 2007, Cowen and

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Sponaugle, 2009; White et al., 2010a, 2010b). This is of particular interest in the context of the increasing realization that population structuring is wide-spread in the marine setting (Selkoe et al., 2016; Berg et al., 2015), despite the absence of conspicuous geographical barriers, such as mountains on land, and despite the long planktonic durations of many of the species under (1)–(3) above that could be expected to result in panmixia (Concover et al., 2006; Siegel et al., 2003). In this context, retention in or transport to favorable or unfavorable environments can lead to variation in mortalities and reproduction success (e.g. Sinclair, 1988; Fiksen et al., 2007), and thus affect meta-population dynamics (Kritzer and Sale, 2004).

The quantification of connectivity by passive dispersal in principle depends on both the biological properties of an organism (e.g., egg or larval duration, drift depth, habitat requirements) and the physical properties of the system, i.e., the pattern and dynamics of ocean currents and habitat distribution and characteristics (Trembl et al., 2008; White et al., 2010a, 2010b; Trembl et al., 2015a, 2015b). The understanding of the role of ocean currents in connectivity is increasing, but complicated by the fact that larval dispersal will often be decoupled from straightforward Euclidean distance due to the circuitous and temporally and spatially variable nature of currents (Weersing and Toonen, 2009). In particular the strong potential for seasonal, inter-annual and decadal/long-term variability is often neglected. Oceanographic information that include spatially and temporally resolved information on ocean current patterns over longer time scales would have strong potential to enhance the understanding of spatial population genetic patterns and meta-population dynamics (White et al., 2010a, 2010b). This is particularly relevant as the focus of connectivity studies shifts from short distances and time intervals to macro-regional and long time scales.

The aim of the present study was to provide decadal (1970s, 1980s, 1990s, 2000s), regionally, and depth layer resolved information on connectivity and dispersal patterns for the entire Baltic Sea as a tool for supporting population genetic and ecological studies, and to make this information freely available. We then illustrate based on the concrete example of Eastern Baltic cod how this dataset can provide and tool can be applied to assess dispersal and 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. 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.

## 2. Material & methods

### 2.1. Hydrodynamic modelling

The basis for our analysis is the hydrodynamic Kiel Baltic Sea Ice-Ocean Model (BSIOM; Lehmann and Hinrichsen, 2000; Lehmann et al., 2002). 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; Lehmann et al., 2002; Novotny et al., 2006) were taken as additional boundary condition. The model forced by the Swedish Meteorological and Hydrological Institute (SMHI Norrköping, Sweden) meteorological database (Lars Meuller, pers. comm.) which for the period 1971–2010 covers the whole Baltic drainage basin on a

regular grid of  $1 \times 1^\circ$  with a temporal increment of 3 h. The database consists of synoptic measurements that were interpolated onto the regular grid with a two-dimensional optimum interpolation scheme.

### 2.2. Particle tracking model and calculation of long-term averages of dispersal patterns

Simulated 3D velocities were taken from the above described hydrodynamic model of the Baltic Sea to run a Lagrangian particle tracking model (Hinrichsen et al., 1997). We have performed particle drift and connectivity studies which were not linked to any biological process-based information. Investigations of non-species specific large-scale connectivity patterns were performed for offshore areas of the Baltic Sea. For this purpose, spatially and temporally resolved long-term averages of geographic distances of Lagrangian particles were calculated. These dispersal patterns are based on the long-term wind driven and thermohaline circulation simulated by the BSIOM for a 40 year time period. The release of drifters consisted of particles on locations within the model domain with a horizontal resolution of  $\sim 4.5$  km. 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 focused on the mean flow characteristics in the water column above the halocline. The particles were released every 5 days throughout the whole year and the drift was calculated for a time period of 50 days, with release depths 2.5, 7.5, 12.5, 17.5, 25, 35, 45, 55, 65, 75 and 85 m. Average dispersal distances (mean geographic distances) are available on decadal quarterly time scale basis for specific rectangles ( $50 \text{ km} \times 50 \text{ km}$ ) 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 100 m of the water column.

### 2.3. Stability of mean dispersal distances

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.

We calculated the stability of dispersal distances  $B$  which was 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  $\frac{1}{N} \sum Du$  and  $\frac{1}{N} \sum Dv$  the averaged components of the drift distances, and  $N$  the number of observations at the location under consideration. The vectorial mean of individually simulated dispersal distances 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. The stability of the dispersal distances  $B$  reveals values between 0 and 1 and describes their uncertainty. It is a measure for the ocean circulation variability and hence in potential changes of consistency of connectivity patterns. 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  $50 \text{ km} \times 50 \text{ km}$  rectangles in the Baltic Sea, i.e., the proportion of particles leaving a rectangle within a certain time period.

### 2.4. Statistical analyses of mean dispersal patterns

As a second step, statistical analyses of different mean flow characteristics (mean geographic distance, direction, stability, dispersal

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