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Assessing the demographic connectivity of common cockles in a shallow estuary as a basis for fisheries management and stock protection efforts

Flemming Thorbjørn Hansen^{1,3,*}, Anders Chr. Erichsen², Camille Saurel¹,
Pedro Seabra Freitas¹

¹Section for Coastal Ecology, DTU AQUA, Technical University of Denmark, 2800 Kgs. Lyngby, Denmark

²Environmental Solutions, DHI A/S, Agern Allé 5, 2970 Hørsholm, Denmark

³Present address: Environmental Solutions, DHI A/S, Agern Allé 5, 2970 Hørsholm, Denmark

ABSTRACT: Common cockle *Cerastoderma edule* populations in the Danish Limfjorden constitute an important ecosystem component and a valuable resource for fishermen and industries, providing a large proportion of cockle landings in both Denmark and the European Union. However, processes driving cockle recruitment and mortality are not well understood, and prevent sustainable fisheries management and species protection efforts. We report a thorough study of processes that are the main drivers of population recruitment, namely larval dispersal and settlement. Outputs from biophysical modelling of cockle larval dispersal, connectivity analysis and derived graph theory metrics were used to analyse potential demographic connectivity or isolation between known cockle populations and other parts of Limfjorden. The results show that the most productive and commercially important cockle beds are almost exclusively dependent on larval imports from unexploited spawning biomass elsewhere rather than on self-recruitment, allowing for exploitation levels that would be unsustainable otherwise. Other parts of Limfjorden are relatively isolated, relying mostly on self-recruitment. The results also show that in some areas where predicted larval settlement potentials are highest, the absence of a cockle population indicates that other factors, likely environmental, are more important. This study provides an example of contrasting population dynamics and connectivity, suggesting that the vulnerability of cockle populations to exploitation or natural mortality may be highly variable and interlinked. Ignoring processes affecting larval dispersal may jeopardise cockle populations and fisheries in Limfjorden. This study highlights the importance of understanding processes of marine connectivity for the protection of bivalve populations and sustainable fisheries management.

KEY WORDS: Larval dispersal · Connectivity · Agent-based modelling · Cockles · *Cerastoderma edule* · Limfjorden

1. INTRODUCTION

The spatial distribution of most benthic populations in marine systems is connected via dispersal of pelagic life stages (e.g. Grantham et al. 2003, Josefson & Hansen 2004, Cowen et al. 2006, Trembl et al. 2008, Cowen & Sponaugle 2009, Josefson 2016). Such dispersal is driven by ocean currents. The dis-

persal pathways that link habitats and populations drive recruitment dynamics and gene transfer (which supports population resilience), and affect the ability of populations to recover (Balbar & Metaxas 2019). Despite the general consensus regarding the importance of the dispersal of pelagic life stages for shaping benthic populations and communities, studies on this topic are only rarely considered in marine popu-

*Corresponding author: flth@dhigroup.com

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lation protection (Balbar & Metaxas 2019, Darnaude et al. 2022) or as a basis for sustainable management of fisheries (Berger et al. 2021).

In general, the dispersal of pelagic larvae of benthic organisms depends on the temporal and spatial variability of the speed and direction of ocean currents and of the pelagic larval duration (PLD). Different species have different PLDs, ranging from a few hours to several weeks or even months (Bradbury et al. 2008, Hilário et al. 2015); subsequently, the potential distances of larval dispersal may vary considerably among species. However, PLD itself does not necessarily scale to dispersal distance, particularly in systems dominated by oscillating or complex current directions and vertical velocity gradients (e.g. Gomes et al. 2016, Nolasco et al. 2022). In addition, species may exhibit vertical migration behaviour (e.g. tidal or counter tidal) synchronised to promote or inhibit dispersal distances (Hill 1991). Within species, PLD varies, as larval development is typically affected by water temperature, with increasing temperature reducing the length of the PLD and vice versa (e.g. Filgueira et al. 2015, Lawlor & Arellano 2020). Similarly, reproductive development and onset of spawning in bivalves are strongly influenced and often triggered by temperature (Bayne et al. 1976, Philippart et al. 2003, Bernard et al. 2011, Zippay & Helmuth 2012); thus, shifts in spawning season may affect larval dispersal in areas with distinct seasonal circulation patterns (e.g. Lett et al. 2010).

Breeding population distribution and densities of benthic species, along with specific reproductive output, onset and duration of spawning events, larval mortality, larval behaviour during drift and the PLD, potentially affect the dispersal and settlement patterns of pelagic life stages. While this is the case for common cockles (e.g. Dare et al. 2004, Robins et al. 2013, Coscia et al. 2020, Vera et al. 2022), the implications for cockle recruitment are not yet fully understood. Predation-induced mortality from filter-feeding adult cockles and other bivalves, known as larviphagy (Dare et al. 2004, Troost et al. 2008, Malham et al. 2012), may result in low larval settlement of cockles in years with high predation pressure and vice versa. Other studies have found higher successful spatfall following warm winters (Dare et al. 2004), although its impact on recruitment was not addressed. In cockles, environmental drivers dominate settlement, survival and recruitment processes (Dankers 1993), often with no clear relationship between the size of reproductive adult stocks and numbers of recruits (Andresen et al. 2014). Thus, a high larval production (~ 1 million eggs female⁻¹,

Dare et al. 2004) does not necessarily translate into high settlement or recruitment success.

While annual cockle stock recruitment may be complex and difficult to predict, potential cockle larval dispersal and settlement patterns can be predicted if ocean currents, the PLD of cockle larvae and the distribution of cockle beds are known. Larval dispersal is typically studied with biophysical modelling, which combines hydrodynamic models simulating the direction and speed of ocean currents, and agent-based modelling (ABM), which simulates the Lagrangian drift trajectories and settling of individual larvae. Outputs from this type of biophysical modelling are widely used as a basis for analysing the connectivity within and between subpopulations of marine organisms (Cowen et al. 2003, Treml et al. 2015, Truelove et al. 2017, Coscia et al. 2020). In this context, we use the term demographic connectivity to specifically refer to the relative contribution to population growth rates of dispersal versus local recruitment (Lowe & Allendorf 2010), operating on an intra-annual and ecological time scale, as opposed to evolutionary connectivity, operating on multigenerational and long-term time scales (Lowe & Allendorf 2010, Hawkins et al. 2016, Marandel et al. 2018).

During the last 2 decades, a growing number of studies have successfully linked the outcome of biophysical models with empirical data, emphasizing the importance of marine connectivity in both an evolutionary and a demographic context. For example, a recent meta-study on coral reef fish found clear relationships between connectivity metrics derived from biophysical modelling, biodiversity indices and species abundances (Fontoura et al. 2022). Numerous other studies have found links between empirical population genetic gradients and dispersal barriers inferred from biophysical modelling (e.g. Mertens et al. 2018 and references therein).

Common cockles *Cerastoderma edule* are widely distributed throughout the northeastern Atlantic Ocean, including the North Sea, where the species inhabits shallow coastal areas with fine-grained sandy or muddy sediments (Tyler-Walters & Hiscock 2021). Cockles are buried in the upper 5 cm and may reach densities up to 10 000 ind. m⁻² (Tyler-Walters & Hiscock 2021). While the common cockle is an important ecosystem component serving as a food source for breeding and migrating water birds (e.g. Bakker et al. 2021) and a significant ecosystem engineer (e.g. Ciutat et al. 2007, Donadi et al. 2013), it also supports extensive commercial fisheries in intertidal areas in the UK, Ireland, Netherlands, France, Spain and Portugal (data from Eurostat 2013–2020).

The Danish strait, Limfjorden, currently supports large subtidal cockle populations subject to intensive fishing. In some years, it is the most valuable individual bivalve fishery in Denmark constituting ca. 1/3 of the total cockle landings in Europe (Eurostat), with annual landings between ca. 5000 and >10 000 t (data from Danish Fisheries Agency for 2013–2022). This fishery is heavily reliant on a single small fishing area, Kås Bredning, for regular and large landings, accounting for 65 % of total annual landings from Limfjorden (range 43–82 %, 2017–2022). Other basins within the fjord system are fished less frequently due to large variations in cockle abundances, suggesting that cockle populations in these areas are less resilient and subject to variations in recruitment and mortality. Other subpopulations of cockles are located within protected Natura 2000 areas where fisheries are prohibited. Variations in these cockle subpopulations, either from recruitment failure or natural and fishing mortality, may disrupt larval dispersal pathways and potentially compromise the whole of Limfjorden cockle fisheries, risking significant economic and social impacts on fishermen and industry stakeholders. This suggests a fragility in the exploitation of cockle populations that needs to be addressed by reliable stock estimates, but also by understanding the local reproductive and recruitment dynamics of cockles, to sustainably manage and exploit the resource.

The aim of the present study was to investigate the demographic connectivity of cockle populations in Limfjorden and how important fishing grounds may be replenished. Since the distribution of cockles in Limfjorden is widely spread, with densities varying

highly between sites and years, the study also aims at addressing the general patterns of the potential larval dispersal and connectivity in the whole of Limfjorden. Such information can guide decisions regarding the sustainable management of cockle exploitation and/or the protection of strongly or weakly connected spawning stocks in relevant areas of Limfjorden.

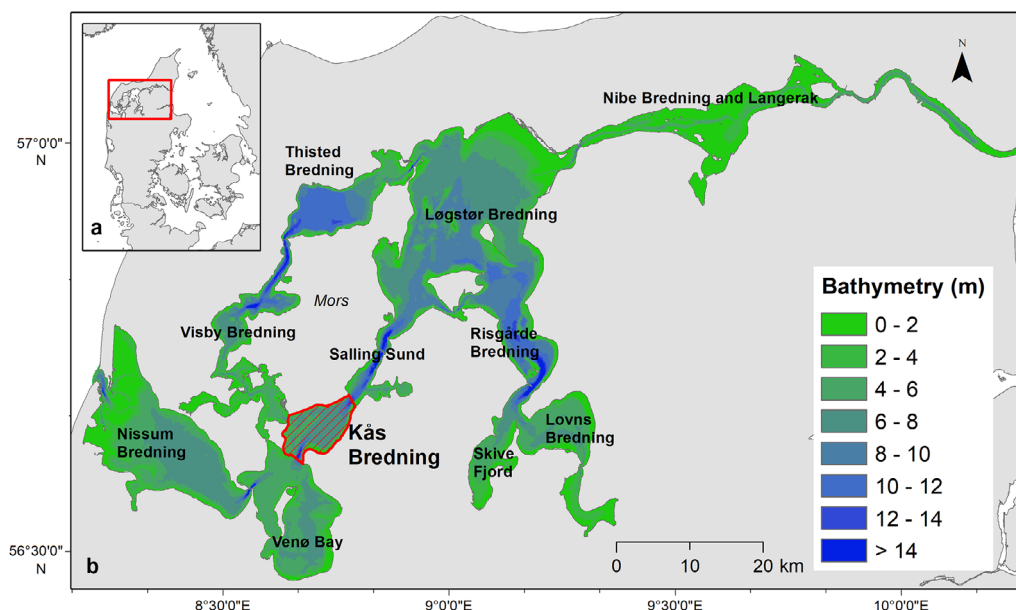
2. MATERIALS AND METHODS

2.1. Overview

We use an ABM approach for simulating the larval dispersal driven by simulated ocean currents, predicted by a hydrodynamic model, also referred to as Lagrangian ocean modelling (van Sebille et al. 2018). Results from larval dispersal simulations, i.e. of start and end positions of individual simulated agents, are further analysed to understand the connectivity within and between both known subpopulations of cockles and other potential cockle habitats in Limfjorden. All data processing and analysis of the model output from the ABM were done in R 4.1.0 (R Core Team 2021).

We discriminate between 3 types of geographical references in Limfjorden: sub-basins, major cockle beds and administrative units. Sub-basins refer to distinct geographical sections named according to Fig. 1. Major cockle beds refer to areas with known high cockle densities (see Fig. 3, for details see Section 2.2). Administrative units refer to mussel fisheries management units (Section S1.5 in Supple-

Fig. 1. (a) Location and (b) bathymetry of Limfjorden. Red hatched area indicates the outline of Kås Bredning (administrative unit), where the most important commercial cockle stocks are located. Names refer to sections of Limfjorden referred to as sub-basins in the text



ment 1 at www.int-res.com/articles/suppl/m731p293_supp/). In the following sections, the term larvae is used when referring to simulated agents.

2.2. Study area

Limfjorden is a shallow enclosed strait of ca. 180 km in length located in the northern part of the Jutland peninsula connecting the North Sea to the west with the Kattegat to the east (Fig. 1), covering an area of ca. 1575 km² with an average depth of 4.8 m and a maximum depth of 24 m. The salinity in Limfjorden varies from 19 to 34 PSU. Currents are driven by changes in water levels between the North Sea in the west and Kattegat in the east, wind forcings and the topology of the estuary. Freshwater from local rivers, especially in the southern and central part of Limfjorden, also affects currents, salinity and stratification.

Water level at the western entrance is driven by tides and wind, and the water exchange with the North Sea is on average 4000 m³ s⁻¹ (and up to 8000–10 000 m³ s⁻¹). Due to the presence of narrow straits and the resulting flow resistance, only a minor part of the water entering the system flows eastwards into the adjacent sub-basins, resulting in residual currents (Section S1.1 in Supplement 1) with a flux of approximately 300 to 400 m³ s⁻¹. Inside the different sub-basins, wind affects local currents, resulting in some

inter-annual variability. Seabed substrates consist mainly of mixed sandy and muddy substrates recognised as suitable habitats for common cockles and other bivalves, except for inner parts of the system subject to temporary seasonal anoxic conditions and low salinities (Jørgensen 1980, Dolmer et al. 1999). Surveys during 2018 and 2019 showed that cockles are patchily distributed throughout Limfjorden and in highly variable densities (see Fig. 3) (Freitas et al. 2019, 2020, 2021). Kås Bredning, where most of the commercial cockle fisheries occurs, in the western part of Limfjorden covers ca. 52 km² (Fig. 1), where ca. 13.4 km² comprises fishing grounds, and on average only ca. 3.9 km² are fished in any given year.

2.3. Hydrodynamic model

Data on ocean currents originate from a hydrodynamic model, MIKE 3 FM (DHI 2017a), set up and calibrated for Limfjorden, specifically for addressing the local hydrodynamic conditions and processes (Erichsen & Birkeland 2019). The computational mesh has a horizontal resolution ranging from less than 100 m in the narrow passages and inlets to up to ca. 500 m in the central parts of the main basins (Fig. 2) and a vertical resolution of 20 layers. The hydrodynamic setup includes open boundaries to the west connecting to the North Sea and to the east connecting to Kattegat.

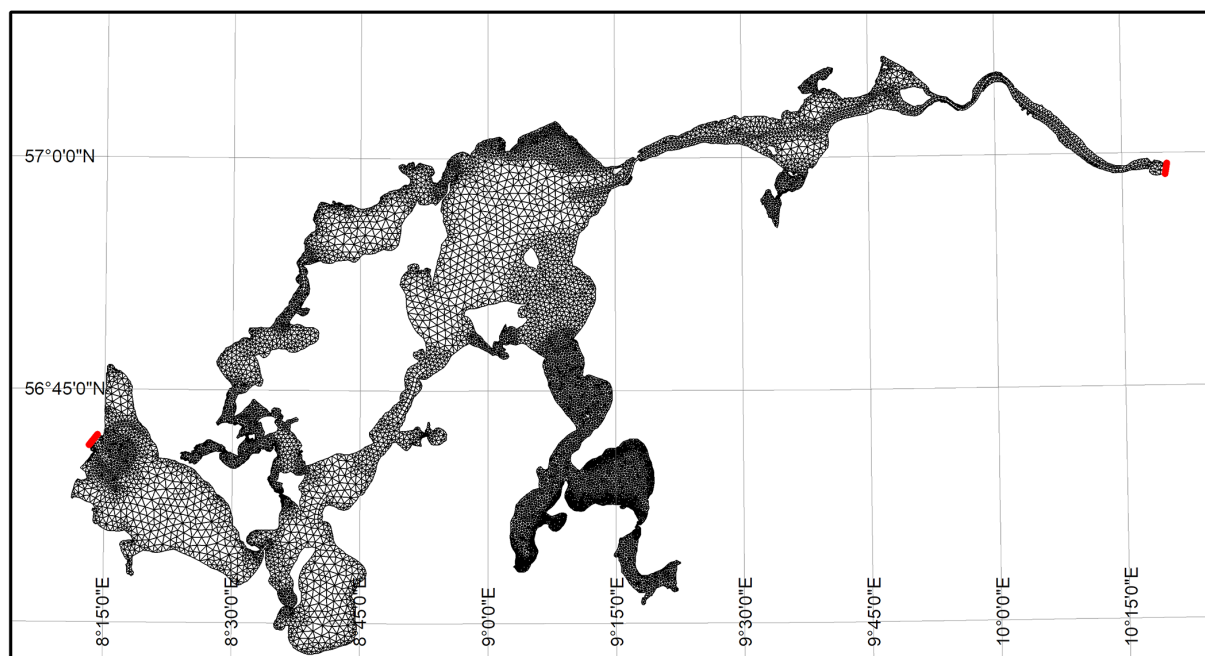


Fig. 2. Computational mesh used in the MIKE 3 FM hydrodynamic model for Limfjorden. Open model boundaries to the North Sea (west) and to Kattegat (east) are indicated in red

The hydrodynamic model was originally developed to support nationwide biogeochemical modelling of Danish marine waters for the Danish Environmental Protection Agency, and has been evaluated by an international evaluation committee (see Implement Consulting Group 2017). Model validation is reported in Erichsen & Birkeland (2019). The temporal resolution of simulated ocean currents was a 1 h time step. Hydrodynamic results for the 7 yr period 2010 to 2016 were used for the larval dispersal model. More details on the hydrodynamic model are available in Section S1.1 in Supplement 1.

2.4. Agent-based model

For larval dispersal modelling of cockle larvae, we used the ABM environment ABM Lab (DHI 2017b). ABM Lab is part of an open equation solver, ECO Lab, for building and executing both Lagrangian (particle tracking and ABM) and Eulerian (concentration based) modelling either executed online parallel to the MIKE 3 FM hydrodynamic modelling (DHI 2017a) or executed offline using stored hydrodynamic model results from MIKE 3 FM (e.g. Heinänen et al. 2018) or from other hydrodynamic models (e.g. Jansen et al. 2021). The drift of each agent is calculated based on current speed and direction of the element in the computational grid within which the agent is located without interpolation of current velocities between neighbouring grid cells.

The PLD for cockles has been reported as ranging from ca. 2–3 up to 5–6 wk (Lebour 1938, Creek 1960, Jonsson et al. 1991, Dare et al. 2004, Malham et al. 2012). We used a PLD of 35 d, similar to the PLD used by Coscia et al. (2020), for simulating larval dispersal of cockles in the Irish Sea. The primary spawning period was assumed to occur from 1 May to 30 June, based on a review on cockle spawning onset and duration for different latitudes (Mahony et al. 2020). Agents were released at the seabed in the centroids of a 1×1 km grid covering the extent of Limfjorden comprising 1538 release locations. One agent was released in each release location every 6 h for the 2 mo spawning period. In total, 381 424 agents were released per year. To account for hydrodynamic processes unresolved by the spatial discretisation of the hydrodynamic model, we used a constant horizontal dispersion coefficient of $1 \text{ m}^2 \text{ s}^{-1}$ (Rossi et al. 2014, Brennan et al. 2019) and a vertical coefficient of $0.01 \text{ m}^2 \text{ s}^{-1}$ (Visser 1997). The simulations were run for an additional 35 d for all agents to settle after the end of the spawning period. The hydrodynamic

model includes flooding and drying of cells in the computational grid, during oscillating water levels, and all agents stranded on dry cells during the simulations were discarded from further analysis. The total area of cells affected by flooding and drying constituted between 1.7 and 5.1% of the model domain per year. Stranded agents are primarily artefacts resulting from an inadequate grid resolution or time step at the very local scale rather than representing a true biological process. The number of discarded agents constituted on average 14% of the agents released per year, of which the majority of ca. 75% were located in the eastern parts of Limfjorden.

2.5. Connectivity matrices

Connectivity analysis was done by dividing Limfjorden into a grid of 2×2 km (Fig. 3), where all pairwise connections (= start and end positions of agents) between grid cells were counted and stored in a connectivity matrix for each year. Only grid cells in the 2×2 km connectivity grid that coincide with at least 1 release point for agent releases in the agent-based model were included in the connectivity analysis. The connectivity matrices for individual years and for the whole 7 yr period (sum of all pairwise connections) were converted to connectivity probability matrices. One set of matrices represented the probability of agents being exported from one grid cell to any of the other grid cells (or the same grid cell, here referred to as local retention [LR]). Another set of matrices represented the probability of agents being imported to each grid cell from any of the other grid cells (or the same grid cell, here referred to as self-recruitment [SR]). The terms LR and SR used here are consistent with Lett et al. (2015). Probability values for each element in the connectivity probability matrices representing export and LR were calculated relative to the initial release of agents in that element excluding agents stranded on dry cells but including agents exported out of the model domain across the open boundaries. Thus, the sum of calculated export plus LR probabilities of all connections for each grid cell in some cases is significantly less than 1, especially in areas close to either of the open boundaries where export of agents occurs. Probability values for each element in the connectivity probability matrices representing import and SR were calculated relative to the number of agents settled in each grid.

The 2 different types of connectivity matrices describe connectivity from different perspectives (Lett et al. 2015, Ospina-Alvarez et al. 2020). Probabilities

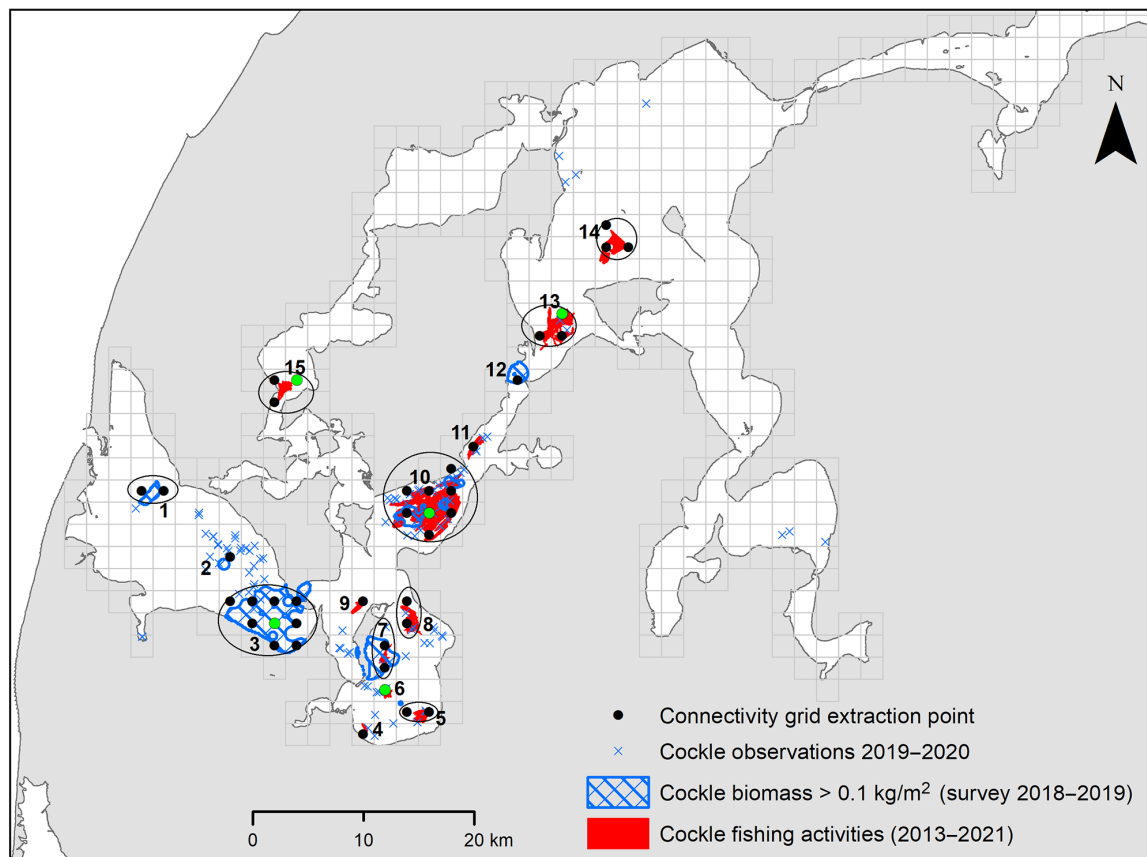


Fig. 3. Location of existing major cockle beds from fishing activities (BlackBox data recorded from 2013 to 2021, red colour), and interpolated (using inverse distance weighting) cockle biomass $> 0.1 \text{ kg m}^{-2}$ (survey data from 2018 to 2019, cross-hatched blue colour). Non-quantitative observations from 2019 to 2020 are indicated by blue x-markers. The $2 \times 2 \text{ km}$ grid applied for connectivity analysis shown in grey outline (part of the grid in the eastern part of Limfjorden is not included in this figure). Dots: extraction points for existing major cockle beds in the connectivity matrix. Green dots: locations for extraction of connectivity probability maps included in the main manuscript, Fig. 4 and Section S1.2 in Supplement 1 (www.int-res.com/articles/suppl/m731p293_supp/). Numbers: major cockle bed IDs for reference in the text; and for major cockle beds comprising > 1 extraction point, extraction points are encircled

of larval export (including LR) are proportionally independent of the size of the spawning population, i.e. the relative distribution of exports to other sites remains the same independent of number of eggs spawned, and can provide valuable information for management to identify cockle beds, which may potentially serve as an important larval suppliers to other sites. In contrast, probabilities of larval import (and SR) are dependent on the size of the spawning populations in different beds where larvae originate. Thus, while the import connectivity probabilities may provide managers with an indication of the reliance cockle beds may have on SR relative to imports from other sites, the relative proportion of imports and SR based on realised connectivity may look different. Both connectivity matrices can be combined with data on cockle spawning biomasses to provide estimates on realised connectivity (e.g.

Watson et al. 2010). Here, we exclusively address potential connectivity.

2.6. Connectivity probability maps

Connectivity probability maps were extracted for grid cells representing the 15 known major cockle beds representing agent export (including LR) and agent import (including SR) (see Fig. 4, Section S1.2 in Supplement 1). Data on major cockle beds were extracted from processed BlackBox data and survey data. The BlackBox (BlackBox R2, Anchor Lab) is a continuous GPS positioning and vessel activity registration system installed on board all bivalve fishing vessels, providing data at 10 s intervals (Nielsen et al. 2021). BlackBox data were combined with data on cockle landings from 2013

to 2021 (DTU Aqua unpubl. data). Survey data on cockle biomass ($>0.1 \text{ kg m}^{-2}$) were identified from previous surveys in 2018 and 2019 (DTU Aqua unpubl. data). A connectivity matrix describing the pairwise connectivity probabilities between the 15 major cockle beds was extracted from 40 representative $2 \times 2 \text{ km}$ subareas in the connectivity grid (dots in Fig. 3).

2.7. Cluster analysis

To identify the general patterns of potential connectivity of cockles in the whole of Limfjorden and the location and strength of possible dispersal barriers, cluster analysis was applied using the clustering algorithm Infomap (Rosvall & Bergstrom 2008) available in the R package igraph (Csárdi & Nepusz 2006). The Infomap algorithm is based on information theory principles and has been used previously in marine connectivity studies (Rossi et al. 2014, Huserbråten et al. 2018, Pastor et al. 2021, 2022). The Infomap algorithm solely determines the number of clusters and their individual size and extent, and does not require any user-set thresholds.

Cluster analyses were done using the connectivity matrix representing the connections as absolute numbers of connections for individual years and for all years pooled together and both for the non-transposed and the transposed matrices. The former results in clusters representing groups of $2 \times 2 \text{ km}$ grid cells that export agents to each other, and the latter represents groups of grid cells that import agents from each other. The 2 methods produce a somewhat different but supplementary delineation of clusters. The use of transposed graphs was recently proposed by Moutsinas et al. (2021) for detecting graph structures in trophic networks.

To facilitate the interpretation, cluster analysis results are graphically represented including information on the strength (dispersal probabilities) of the within- and between- cluster connectivity. For the non-transposed matrices, probabilities representing the export of agents between clusters are calculated relative to the total number of agents with a start position within each cluster. For the transposed matrices, probabilities representing the import between clusters are calculated relative to the total number of agents with an end position within each cluster. Only clusters based on a minimum of four $2 \times 2 \text{ km}$ grid cells are included. Likewise, only connections between clusters with a minimum of eight $2 \times 2 \text{ km}$ grids cells are included.

2.8. Graph theory metrics

In addition to the dispersal probability maps and cluster analysis results, we extracted the graph theory metrics referred to as strength and transitivity (Montoya & Solé 2002, Csárdi & Nepusz 2006, Costa et al. 2017). Strength is also referred to as weighted degree and describes the weighted number of connections (referred to as edges in graphs) in and out of each grid cell (referred to as nodes in graphs), weighted by the connectivity of each connection as in the corresponding connectivity matrices. We extracted the in-strength and out-strength of each grid cell, where grid cells with high values of in-strength represent major potential sink areas, and grid cells with high values of out-strength represent major potential source areas. The transitivity is a graph metric that is defined as the total realised number of triangular connections in the neighbourhood of a given node (or grid cell in the connectivity grid) that the node is connected to, relative to the total possible number of triangular connections in the same neighbourhood. If an area (grid cell) in Limfjorden is connected to a number of other grid cells, the transitivity is a measure for how tight this neighbourhood network is. Transitivity attains values between 0 and 1, where the value represents the relative proportion of realised triangular networks in the neighbourhood of the node.

2.9. Sensitivity analyses

Several standard sensitivity analyses were carried out to test robustness of results regarding alternative PLDs (21, 25, 30, 40, 50 d), alternative spawning period (1 April–31 May) and alternative horizontal ($10 \text{ m}^2 \text{ s}^{-1}$) and vertical ($0.001 \text{ m}^2 \text{ s}^{-1}$) dispersion coefficients. Results evaluated included larval import probability maps for selected major cockle beds and cluster analysis results. Evaluations were done by visual inspection.

3. RESULTS

3.1. Connectivity of existing major cockle beds

For visualisation of the dispersal dynamics of cockle larvae, examples of connectivity probability maps (export and import) were extracted for selected $2 \times 2 \text{ km}$ grid cells representing individual major cockle beds (Fig. 4). Connectivity between each pair

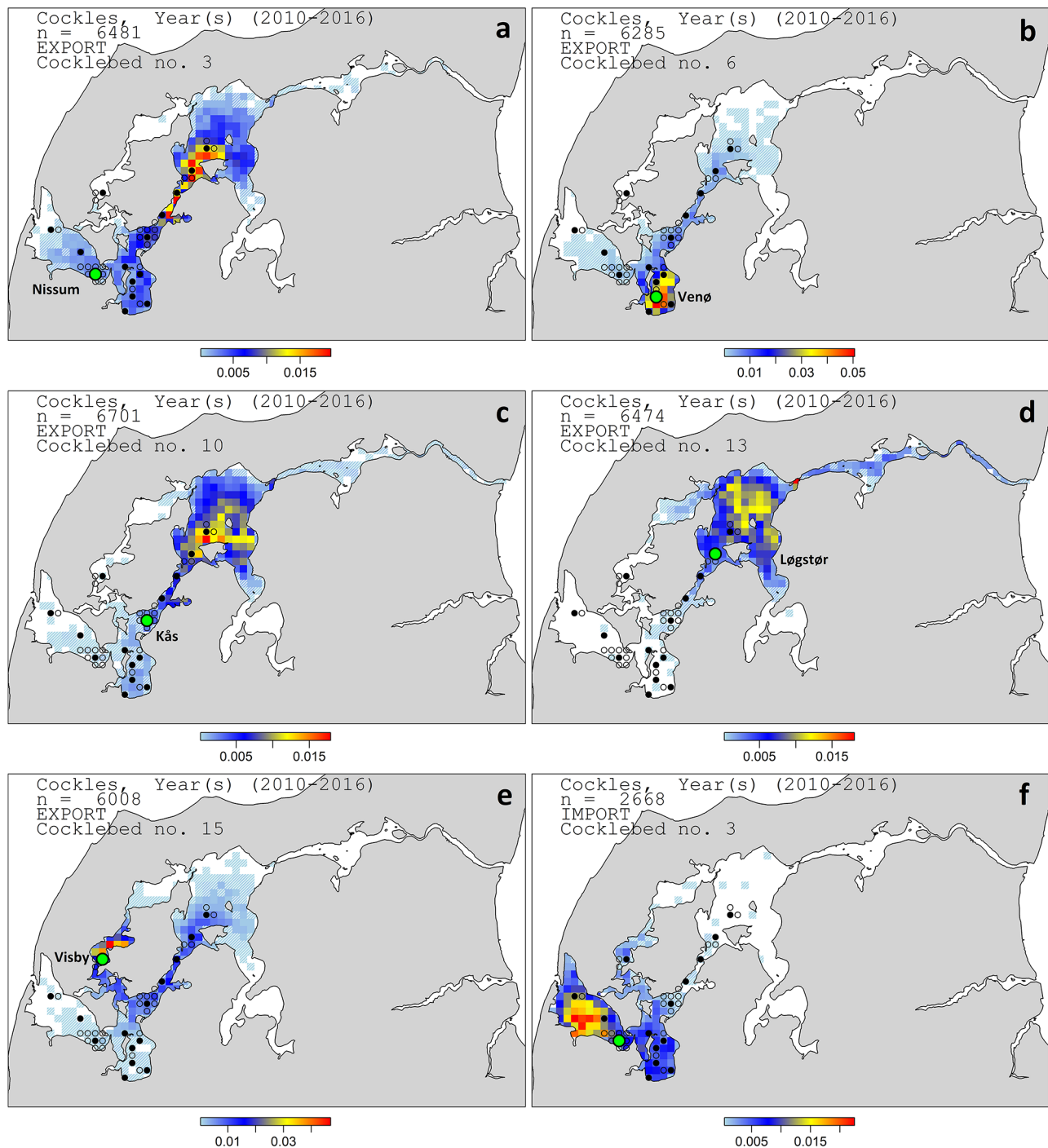


Fig. 4. (a–e) Export and (f–j) import connectivity probability maps for selected positions in the connectivity grid (enlarged green dot) representing existing major cockle beds in Limfjorden (nos. 3, 6, 10, 13 and 15, Fig. 3) based on cockle larval dispersal simulation for 7 yr, 2010 to 2016. For export connectivity probability maps, colour legends represent dispersal probabilities calculated relative to the initial release of larvae in the agent-based model including larvae exported out of the domain across the open boundaries but excluding agents stranded on dry cells (see Section 2.4). For import connectivity probability maps, colour legends represent dispersal probabilities calculated relative to the total number of larvae settled in each grid. n refers to the total number of larvae included in the analysis. Black dots (filled and hollow) refer to connectivity grid (2 x 2 km) cells which coincide with high cockle densities from the 2018 to 2019 survey and/or from cockle fisheries data (Black-Box data) from 2013 to 2021 (see Section 2.6). Filled dots represent 2 x 2 km grid cells for extraction of export and import connectivity probability maps selected to represent each of the 15 cockle beds referred to in Fig. 3

(Fig. 4 continued on next page)

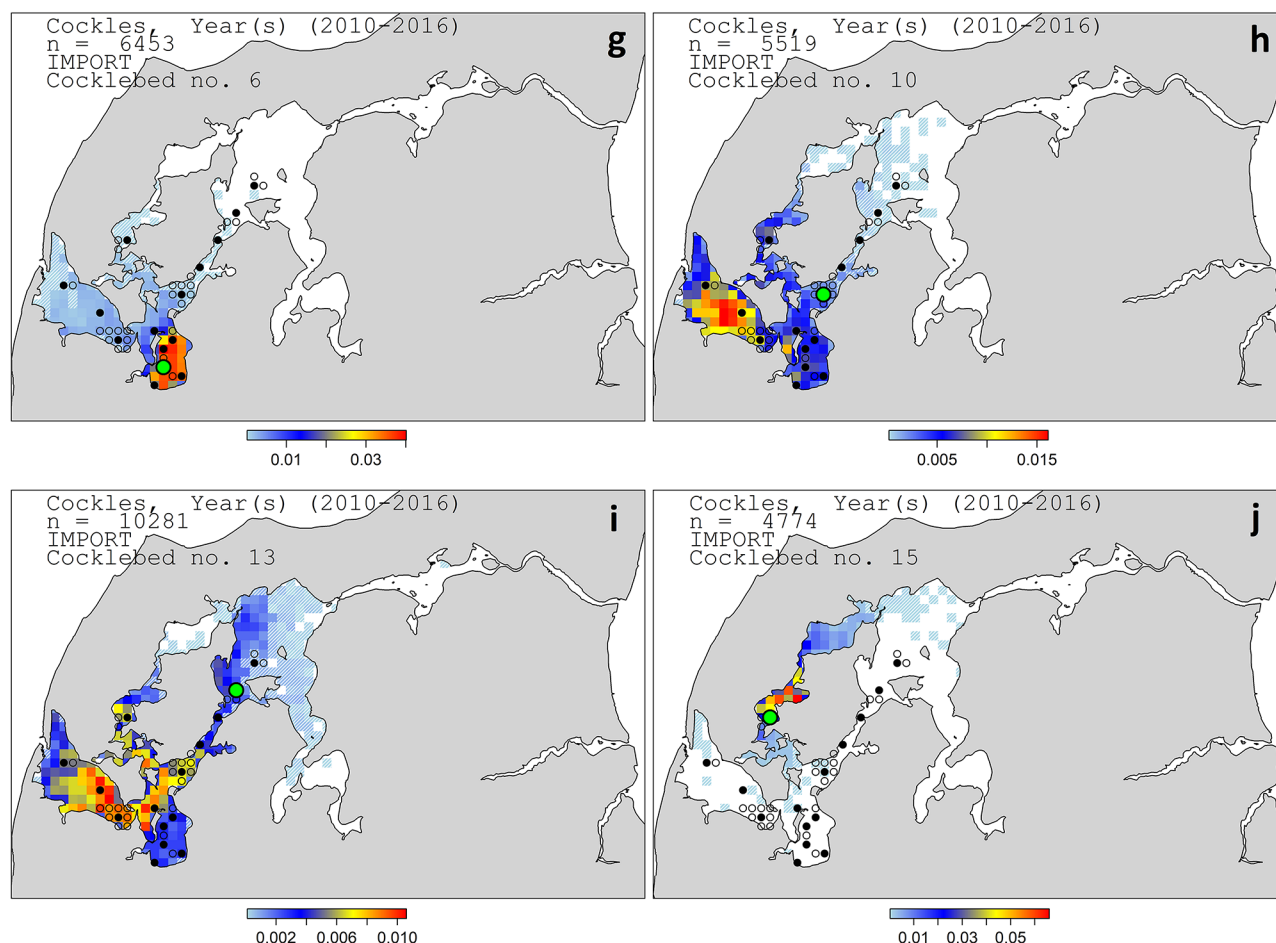


Fig. 4 (continued)

of 2×2 km grid cells constituting the 15 major cockle beds has been summarised systematically in connectivity probability matrices (values in %) representing the export (plus LR) and import (plus SR), highlighting major cockle beds that are particularly well connected and those which are not (see Tables 3 & 4). The clear asymmetry of strengths of connectivity (colours) on either side of the diagonal of both matrices is a result of the dominant west-to-east dispersal of larvae along the central axis of Limfjorden, with limited connectivity in the other direction, except for cockle bed 15 (in Visby Bredning), where anticlockwise dispersal dominates around the island of Mors.

Diagonal values in the export and import connectivity matrices represent the LR and SR, respectively, of the individual 2×2 km grid cells that each of the major cockle beds are composed of. Individual grid cells representing major cockle beds located in relatively isolated parts of Limfjorden (beds 4–8 in Venø Bay and bed 15 in Visby Bredning) have a high proportion of both LR and SR. In Venø Bay, LR and SR

constitute up to 4.2% (mean 2.3, SD 1.3) of the original larval release and up to 3.7% (mean 2.7, SD 1.0) of the larval settlement, respectively. In Visby, the corresponding values are 3.3% (mean 1.9, SD 1.3) and 4.2% (mean 2.7, SD 1.4). In Venø Bay, some major cockle beds are distributed within the bay (beds 4–8), and due to the circulation patterns, results show that 20.1% of larvae released eventually settle in one of the other major cockle beds located here (Table 1).

The main donor areas for major cockle bed 10 in the most important fishing area, sub-basin Kås Bredning, are major cockle beds in the neighbouring 3 sub-basins: beds 2 and 3 (Nissum Bredning), beds 4 to 8 (Venø Bay), and bed 15 (Visby Bredning). Of the 18.5% of larvae settled in major cockle bed 10, Kås Bredning, 16.7% originates from major cockle beds in other sub-basins (Table 1), with 9.7, 4.6 and 2.0% from each of these 3 sub-basins, respectively. In comparison, only 0.2% of the larvae settled in bed 10 originates from beds 13 and 14 (Løgstør Bredning)

Table 1. Summary of export and import connectivity probabilities between major cockle beds in Limfjorden (Fig. 3), which are grouped into sub-basins (Fig. 1). Export represents fractions of larvae in major cockle beds in each sub-basin that settle in major cockle beds in other sub-basins or in cockle beds in the same sub-basin (=local retention). Import represents fractions of larvae that settle in major cockle beds in each sub-basin that are released from cockle beds in other sub-basins or from cockle beds in the same sub-basin (=self-recruitment)

Sub-basin	Cockle bed no.	Export		Import	
		Export to other major cockle beds (%)	Local retention (%)	Import from other major cockle beds (%)	Self-recruitment (%)
Nissum Bredning	1–3	17.3	3.4	4.8	11.8
Venø Bay	4–9	8.1	20.1	5.7	23.5
Kås Bredning	10	8.0	1.4	16.7	1.8
Sallingsund	11–12	5.9	0.7	18.6	0.5
Løgstør Bredning	13–14	0.5	2.9	17.1	1.9
Visby Bredning	15	13.7	4.9	0.1	7.8

and beds 11 and 12 (Sallingsund). SR in bed 10 constitutes ca. 1.8% of the total number of larvae settled here. Thus, the most important fishing area is largely relying on recruitment via larval import from other sub-basins, transported by the dominant west-to-east circulation pattern. The most important major cockle beds serving as donor areas for known major cockle beds in Limfjorden (1–15, Fig. 3) are beds 2 and 3 (in Nissum Bredning), beds 4 to 8 (in Venø Bay) and bed 15 (Visby Bredning), where ca. 20.7, 28.2 and 18.6%, respectively, of all larvae released will settle in another (or the same) major cockle bed (Table 1).

While SR in major cockle beds located in the narrow sections along the central axis of the dominating west-to-east current is low (i.e. Kås Bredning, Sallingsund and Løgstør Bredning), constituting less than 2% of the total number of larvae settled there, major cockle beds in more isolated parts of Limfjorden have a relatively high SR, with beds 4 to 8 (Venø Bay) being the most confined sub-basin with an SR of approximately 20.1% of the larvae released.

Examples of year-to-year variations in connectivity probabilities from selected locations within existing major cockle beds are shown in Section S1.3 in Supplement 1. Results indicate that year-to-year variations are limited.

3.2. Cluster analysis and identification of dispersal barriers

Cluster analyses were done (Fig. 5) using connectivity matrices representing the 7 yr period 2010 to 2016 for the non-transposed (export) and the transposed (import) matrices. Note that the proportions of LR and SR for individual clusters are higher than those for individual 2 × 2 km grid cells (see Tables 3

& 4), as both LR and SR are calculated relative to the sum of agent release and the sum of agent settlement within the extent of each cluster. Results show that most of Limfjorden, particularly along the central axis, is relatively well connected, with the western (Nissum Bredning) and central (Kås Bredning and Løgstør Bredning) parts being connected predominantly unidirectionally from west to east but with only limited exchange of larvae from east to west (Fig. 5). More isolated areas are represented by smaller clusters (Venø Bay, Lovns Bredning and Skive Fjord) with dispersal barriers located at narrow inlets connecting these areas with the larger clusters of the central Limfjorden. However, given the relatively long PLD of cockles, these barriers still allow for some exchange of larvae, particularly from confined areas, with unidirectional dispersal towards the central basins (i.e. Kås Bredning and Løgstør Bredning) being dominant. The cluster comprising the northwestern strait of the island of Mors (Visby Bredning and Thisted Bredning) is dominated by a strong dispersal barrier, towards the east. However, due to the long PLD, larvae from areas within this cluster may reach the central parts of Limfjorden (e.g. Løgstør Bredning) via Kås Bredning and Sallingsund following an anticlockwise dispersal around the island of Mors. The easternmost parts of Limfjorden (Nibe Bredning and Langerak) are highly affected by the significant export of larvae out of Limfjorden to Kattegat. Cluster analysis results for individual years (Section S1.4 in Supplement 1) show similar results for all years with some deviation, especially the limited variation of the exact location of the unidirectional dispersal barrier between the western (Nissum Bredning) and eastern (Løgstør Bredning) parts of Limfjorden. However, the overall patterns of clusters for all years are comparable.

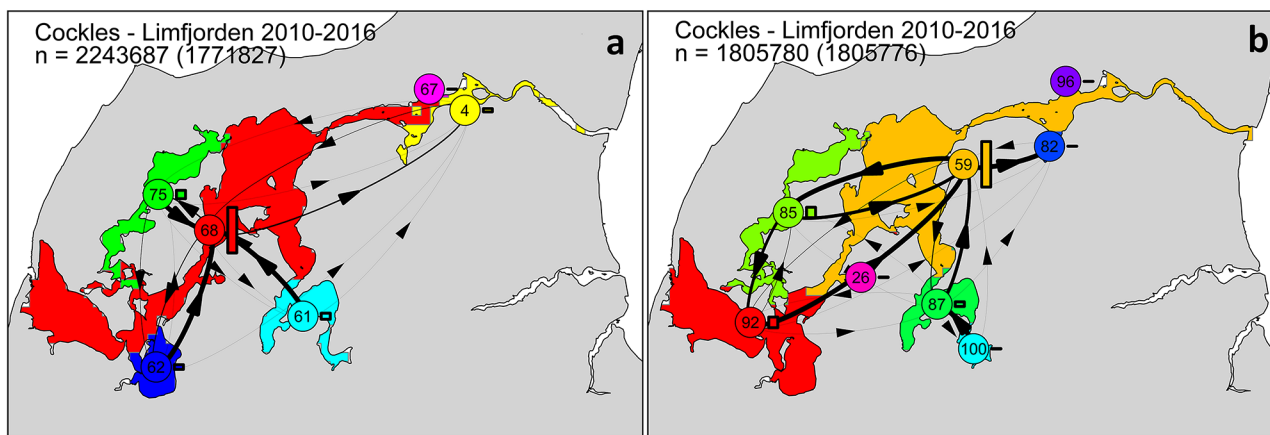


Fig. 5. Results from cluster analysis of the (a) non-transposed (export) and (b) transposed (import) connectivity matrices of the simulated agent trajectories for 7 yr, 2010 to 2016, dividing Limfjorden into clusters represented by a unique colour. (a) Values in the cluster centroids (circles) indicate the level of local retention as the fraction (in %) of larvae with an initial position in each cluster that settles within the same cluster. Similarly, arrows represent exchanges (export) of larvae between clusters, with thickness reflecting the relative proportion of the exchange (export) of larvae relative to the total number of larvae with a start position within each cluster. (b) Values in the cluster centroids (circles) indicate the level of self-recruitment within each cluster as the fraction (in %) of larvae that settles within each cluster that has a start position in the same cluster. Similarly, arrows represent exchanges (import) of larvae between clusters, with thickness reflecting the relative proportion of the exchange (import) of larvae relative to the total number of larvae with an end position within each cluster. Bars beside each cluster centroid in both maps indicate the relative number of larvae that define each cluster, and bar heights are normalised relative to the cluster based on the highest number of larvae. An upper threshold for arrow thickness was set to 10 %

3.3. Graph metrics

Source areas (out-strength, Fig. 6a) represent the proportion of released larvae that settle in another, or the same, 2×2 km grid cell. Since larvae are evenly released in the entire Limfjorden, source areas are not representing any biologically relevant entity of the system, except the proportion of larvae that are lost or exported out of the model domain across open boundaries towards the North Sea and Kattegat. Results show that in the easternmost parts of Limfjorden (east of Løgstør Bredning), more than 90 % of the larvae released here are exported to the Kattegat. In

the westernmost part of Limfjorden (Nissum Bredning), larvae are only lost to the North Sea from areas close to the boundary.

The primary sink areas (in-strength, Fig. 6) are in the central parts of Limfjorden (central and southern Løgstør Bredning, northern Sallingsund and the strait of the island of Mors). The western parts, including the entire Nissum Bredning, and the most isolated area to the southeast, Skive Fjord, both receive very few larvae and can be regarded as having relatively low potential import of larvae spawned elsewhere. Areas close to the North Sea model boundary may, however, receive larvae from the

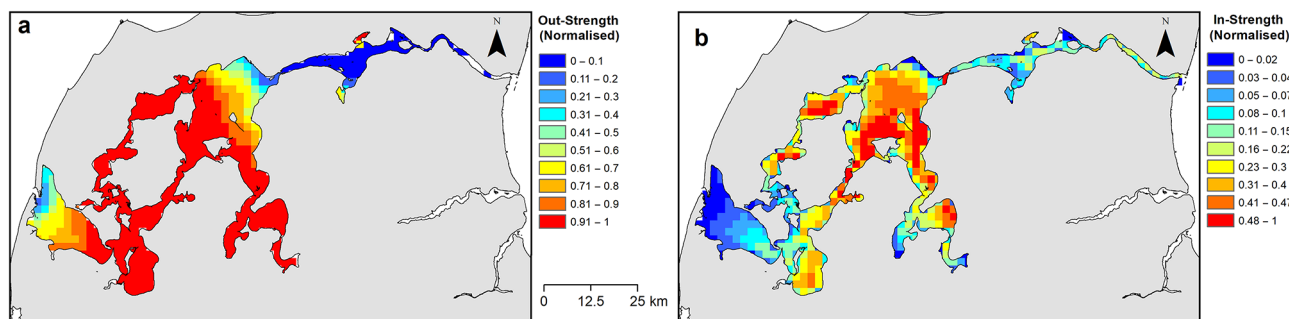


Fig. 6. (a) Source areas also referred to as out-strength, which is the weighted number of connections (edges) out of each cell (node) normalised relative to the maximum value. (b) Sink areas also referred to as in-strength, which is the weighted number of connections (edges) into each cell (node) normalised relative to the maximum value. Legend values for out-strength and in-strength are classified using linears and quantiles, respectively

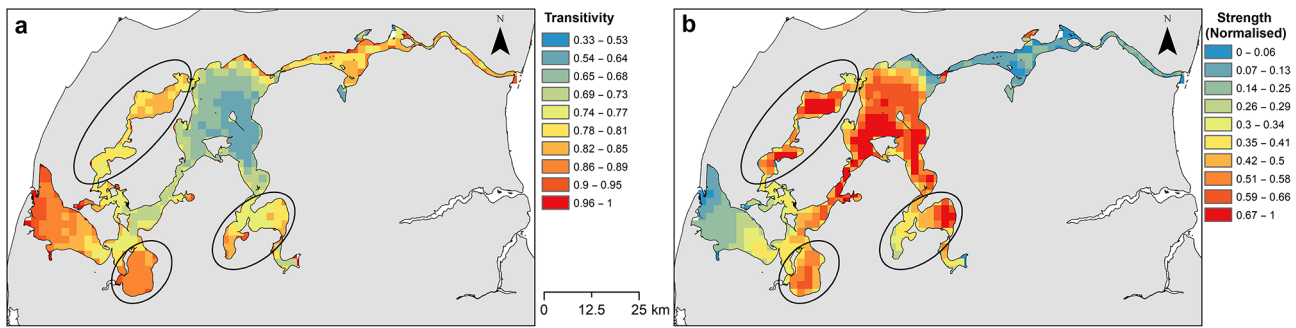


Fig. 7. (a) Transitivity of all 2×2 km grid cell in Limfjorden based on the connectivity matrix for 2010 to 2016. (b) In-strength and out-strength, i.e. the weighted total number of connections in and out of each 2×2 km grid cell in Limfjorden. Encircled areas are areas with both high transitivity and high in-degree and out-degree. Colour legends are classified using quantiles. Values in both maps are normalised relative to the maximum value in each map

North Sea, but to what extent would have to be addressed in a separate study.

The calculated transitivity for Limfjorden (Fig. 7a) shows the lowest values in the central parts of Limfjorden (including Løgstør Bredning and Sallingsund). These areas are where the total numbers of in- and out-strength are highest (Fig. 7b). Although these areas only have 50 % of the possible triangular connections in their neighbourhood, they still have a very large number of connections. Nissum Bredning, on the other hand, has the highest mean transitivity, 87 % (SD 5.9 %), of the possible triangular connections in their neighbourhood, but there is only a relatively low number of total connections. More confined areas (encircled areas, Fig. 7) have both a high transitivity and a high number of connections and are consistently identified as individual clusters in the cluster analysis presented earlier, both for individual years and for the entire 7 yr period.

3.4. Connectivity between sub-basins

Export (including LR) and import (including SR) connectivity probabilities between sub-basins in Limfjorden are presented as a summary (Table 2) of the connectivity matrices with subdivisions into administrative units (Sections S1.5 & S1.6 in Supplement 1). The full connectivity matrix for the whole of Limfjorden (all 2×2 km grid cells) is included in Supplement 2 at www.int-res.com/articles/suppl/m731p293_suppl/. For the western and central parts of Limfjorden, the connectivity patterns in the connectivity matrices are similar to the patterns discussed previously in Section 3.1, considering the connectivity between major cockle beds (Tables 3 & 4). For the main fishing area, Kås Bredning, SR in the sub-basin constitutes 3.9 % of larvae settled here, and LR constitutes 2.8 % of lar-

Table 2. Summary of export and import connectivity probabilities between sub-basins in Limfjorden. Export represents fractions of larvae in one sub-basin that settle in other sub-basins or in the same sub-basin (~local retention). Import represents fractions of larvae that settle in one sub-basin that are released from other sub-basins or from the same sub-basin (~self-recruitment). Sub-basin names refer to Fig. 1. The exact outline of individual sub-basins and the outline of administrative (adm.) units and associated IDs are included in Section S1.5 in Supplement 1

Sub-basin	Adm. unit ID	Export		Import	
		Export to other adm. units (%)	Local retention (%)	Import from other adm. units (%)	Self-recruitment (%)
Nissum Bredning	1.2.3.4.10.29.216	62.4	11.1	15.6	84.4
Venø Bay	5.6.7.8	51.7	46.2	34.6	65.4
Kås Bredning	9	96.1	2.8	96.1	3.9
Sallingsund	11.12.13	79.8	18.6	88.9	11.1
Løgstør Bredning	14.15.16.33.34.35.36.37.38.39	19.9	60.6	49.5	50.5
Visby Bredning	23.24.25.26	64.3	33.8	36.6	63.4
Thisted Bredning	27.28.30.32	26.5	71.8	27.6	72.4
Skive Fjord and Risgårde Bredning	17.18.19.22	56.2	39.4	34.4	65.6
Lovns Bredning	20.21	28.3	70.5	14.4	85.8
Nibe Bredning and Langerak	40.41.42	0.4	2.0	93.6	6.4

vae released. Similar low SR and LR are found in the eastern part of Limfjorden (Nibe Bredning, 6.4 and 2.0%, respectively), with slightly higher SR in the central parts (including Sallingsund, 11.1 and 18.6%, respectively). In the westernmost parts (Nissum Bredning), LR is only 11% of larvae released here, but SR is 84% of the larvae settled here, indicating that import of larvae from other parts of Limfjorden is limited. SR in the most isolated sub-basins to the north (Thisted Bredning) and to the southeast (Lovns Bredning) constitutes 72.4 and 85.8%, respectively, of the larvae settled here. Similarly, LR constitutes 71.8 and 70.5%, respectively, of the larvae released here. For the southeastern parts of Limfjorden (i.e. the sub-basins of Skive Fjord and Lovns Bredning), almost 40% of the cockle larvae (Fig. 5) are exclusively exported to the larger central sub-basin (Løgstør Bredning), while larvae are received primarily from within these sub-basins themselves via larval exchange (import and export) or SR (ca. 87%, Fig. 5). A similar pattern is evident for the strait to the north of the island of Mors (Visby Bredning and Thisted Bredning), although with a clear net transport towards the west. In the most eastern parts of Limfjorden (Nibe Bredning and Langerak), larvae are exported to the Kattegat across the open model boundary, with only a very limited number (0.4%) of larvae exported towards the west.

3.5. Sensitivity analysis

Results from the sensitivity analyses are included and discussed in Sections S1.7–S1.14 in Supplement 1. In general, model results showed a slight increase in the areal extent of donor areas of individual cockle beds with increasing PLD but were disproportional to the relative change in PLD. The core donor areas (yellow and red colours in Fig. 4, Section S1.13 in Supplement 1) showed a limited spatial displacement with increasing PLD but with a tendency of the core donor area to become less pronounced. Changes in PLD from 30 to 50 d did not affect the number and the outline of individual clusters; only LR and SR were reduced with increasing PLD. Changing the spawning period only had marginal effect. Differences between years showed limited variability with the overall patterns of the cluster analysis results, with dispersal probability maps being comparable. Increase in horizontal dispersion resulted in an increase in the number of clusters in the most isolated parts of Limfjorden.

4. DISCUSSION

4.1. Findings

In this study, we investigated the potential demographic connectivity of common cockles in Limfjorden in general and specifically between the highly productive and commercially important cockle fishing area Kås Bredning and other parts of Limfjorden. Patterns in demographic connectivity may explain some of the temporal and spatial variability in cockle stock densities and demography observed in Limfjorden (Freitas et al. 2019, 2020, 2021), and the analyses identified cockle beds that serve as main suppliers of cockle larvae to cockle beds in other parts of the system. Some cockle beds were found to be more isolated and more reliant on SR. The results also show that in the central part of the fjord system, where predicted larval settling is highest, the absence of a cockle population indicates other factors, potentially environmental ones, are more important. These are discussed below (this section) and may include local variability in seabed substrates and sediment conditions, food availability, inter- and intraspecific competition for space and predation by adult cockles and other filter feeders on pelagic larvae.

The most important fishing area, Kås Bredning, where the largest proportion of cockle landings occurs, relies heavily (and possibly solely) on external larval supply from multiple cockle populations elsewhere in the fjord system. This can explain why Kås Bredning sustains a relatively stable recruitment of cockles, producing regular and large cockle landings every year. One of the donor areas is the largest known contiguous and currently unexploited population of cockles in the western part of the fjord system (Nissum Bredning) and is located within a protected Natura 2000 area. Historically, limited shellfish fisheries (e.g. mussels and flat oysters) have been permitted in parts of Natura 2000 areas in Limfjorden. Findings in this study, however, indicate that cockle fisheries in Nissum Bredning may potentially affect cockle larval supply to the currently exploited fishing areas east of Nissum Bredning, in particular Kås Bredning. The most potentially vulnerable cockle populations are found in the more confined parts of the fjord system, including the northwestern strait of the island of Mors (Visby Bredning) and the relatively isolated parts to the southeast (Skive and Lovns Bredning). Annual recruitment here is probably almost exclusively based on SR and thus potentially vulnerable to changes in population size within individual sub-

red: 0.01–0.1%; white: <0.01%

[illegible]

basins, either resulting from natural mortality or over-exploitation.

While demographic connectivity patterns found between existing subpopulations of cockles are supported by observations from survey data and cockle landings, other demographic connectivity predictions are not supported by empirical data. For instance, the large central basin (Løgstør Bredning) was identified as a primary sink area, subject to a potentially high input of larvae from multiple other parts of Limfjorden (including most of the existing major cockle beds) as well as larvae potentially originating from SR. Still, large and dense cockle populations have only been observed in the southern parts of Løgstør Bredning and not in the central and northern parts, where predicted settling is highest and comparably optimal. A hypothesis is that one or more environmental and/or ecological factors may limit the recruitment of cockles in these areas. Several factors may potentially affect the recruitment of cockles, including various environmental factors like oxygen and sediment conditions (Dare et al. 2004), predation (de Montaudouin & Bachelet 1996), food availability (de Montaudouin & Bachelet 1996), disease (Malham et al. 2012, review), adult cockle abundance (André & Rosenberg 1991, Beukema & Dekker 2018) and fisheries (Ens et al. 2004, Beukema & Dekker 2018 and references therein).

Løgstør Bredning has the largest reported biomass of blue mussels *Mytilus edulis* recorded in the period 2012 to 2021 (stock assessment reports, e.g. Nielsen et al. 2018), which are competitors for food and space, via deteriorated sediment conditions and via larval predation (Donadi et al. 2013, Meyer et al. 2021). Recorded biomasses of blue mussels in prime cockle fishing areas in Limfjorden are relatively lower than those in the central and northern parts of Løgstør Bredning (DTU Aqua unpubl. data). However, while interspecific competition and/or larval predation from e.g. mussels may theoretically explain some of these discrepancies, observations by the authors of high cockle densities found next to dense blue mussel populations (e.g. Kås Bredning and southwestern Løgstør Bredning) suggest that other factors may be more important. Environmental conditions originating from hydrodynamic and biogeochemical model simulations and monitoring data show that current speed, oxygen conditions and food in terms of chl *a* are slightly more favourable in these prime cockle areas compared to conditions in the central and northern parts of Løgstør Bredning (data extracted from Erichsen & Birkeland 2019, 2020; survey data from the Surface Water Monitoring Data-

base, ODA, <https://odaforalle.au.dk/>). Observations by the authors during monitoring campaigns and mussel bottom-culture activities also suggest that sediment conditions in Løgstør Bredning are variable with patchily unconsolidated mud that deviates from the locations with high cockle densities, despite identical seabed sediment classification (EMODNET 2022).

One or more of these dissimilarities in environmental conditions, interspecific competition and/or larval predation may explain the discrepancy between the existing distribution of high-density populations of cockles and the locations of the primary sink areas for cockle larvae in Løgstør Bredning predicted from biophysical modelling in this study. This decoupling between larval settlement and recruitment has been found for cockles at other study sites (e.g. Dankers 1993, Andresen et al. 2014), and findings in this study indicate the occurrences of this decoupling and the causal relationships of the underlying processes may be highly site dependent. These findings also emphasise that the analysis of potential connectivity based on biophysical modelling alone without data on the present distribution of the species studied and/or habitat quality may lead to biased conclusions on sink–source dynamics and ultimately misguidance of management practices, particularly when recruitment processes are not well understood.

4.2. Challenges

Pastor et al. (2021) studied the potential connectivity of blue mussels in Limfjorden using a combination of larval dispersal modelling and population genetic analysis. The modelling approaches were similar to the present study, although less systematic in terms of spatial coverage of larval release points, and not including the westernmost parts of Limfjorden, e.g. Nissum Bredning. A PLD of 21 d was used for mussels, while we used 35 d for cockles. Despite the shorter PLD, the authors concluded that Limfjorden is a well-connected system supported by the genetic results showing no genetic deviations between sampling sites. This conclusion seems reasonable considering the relatively high abundance of blue mussels throughout Limfjorden (including numerous bottom cultures and line cultivation sites) and/or when considering a multigenerational or evolutionary context. For cockles, however, the current knowledge on distribution and abundance indicates many more patchy occurrences with high spatial and temporal variability, and large areas where cockles are almost

absent (like central and northern parts of Løgstør Bredning). Thus, demographic connectivity processes may be more important for cockles than for mussels in a system like Limfjorden, despite a relative longer PLD.

The different conclusions between the 2 studies highlight one of the most challenging topics in marine connectivity studies. As for most other larval dispersal and marine connectivity studies, criteria for when a connection between sites can be considered strong or weak are not trivial (e.g. Treml et al. 2012, Jacobi et al. 2012) and remain unresolved. Factors such as fecundity, larval mortality and recruitment success are important in addition to larval dispersal and connectivity. A relatively low demographic connectivity inferred from a biophysical model may not necessarily imply that populations are not connected in a demographic context and vice versa (Treml et al. 2012). For species with high reproductive outputs (like cockles and blue mussels) and high population densities, even low calculated dispersal probability may be sufficient to supply a minimum of larval settlement to support a large recruitment, resulting in larval dispersal and settlement only having a secondary importance relative to environmental and ecological factors. Thus, the identification of criteria or thresholds to discriminate between strong and weak connectivity that is biologically relevant is required for a better interpretation of outcomes from connectivity studies (Cowen et al. 2006). For cockles, as for other marine species, such criteria or thresholds need to be addressed in future research on demographic connectivity (e.g. aiming at examining statistical correlations between observations of abundances and annual recruitment successes) and on environmental and ecological explanatory variables (e.g. from both monitoring data and hydrodynamic and biogeochemical model outputs) and larval dispersal and connectivity metrics, as presented here.

While criteria for connectivity thresholds are indeed a key challenge for evaluating the outcome of marine connectivity analyses, uncertainties associated with model assumptions and model parameterisations are other crucial factors to address. In our study, the hydrodynamic data set is in high spatial resolution and well calibrated; however, any refinement and downscaling of the computational grid and/or time step may potentially affect the outcome of the biophysical model and hence the derived connectivity metrics. Reviews of previous studies suggest that such refinement tends to increase LR (Swearer et al. 2019). This is supported by the sensitivity analysis in our study showing a decrease in lar-

val dispersal with an increase in the horizontal dispersion factor, where horizontal dispersal is included to reflect dispersal processes not resolved in the computational grid of the hydrodynamic model. Uncertainties also relate to biological parameters including the PLD and the designated spawning period. Sensitivity analysis, however, indicated connectivity metrics in terms of the spatial dispersal probability and cluster analyses were relatively insensitive, except for PLD of 25 d or less. Finally, stranded agents in the biophysical model were discarded from the connectivity analysis, and this may potentially introduce a bias to the results presented here. In parts of Limfjorden where existing dense cockle beds are found, discarded agents comprise an average of 3.6% of the total number of released agents each year. The potential implication for the results presented here is assumed to be marginal.

4.3. Implication for cockle fisheries management

The use of larval dispersal modelling and connectivity analysis has previously been proposed as a tool to support marine management. Uses may include optimal selection and planning of marine protected areas (e.g. Shanks et al. 2003, Ross et al. 2017, Jonsson et al. 2020), marine spatial planning (e.g. Jonsson et al. 2021), optimisation of coastal ecosystem services (e.g. Ospina-Alvarez et al. 2020), identification and delineation of exemptions areas within the Ballast Water Management Convention (Baetens et al. 2018, Hansen & Christensen 2018) and optimisation of monitoring networks for marine invasive species (Lindegren et al. 2022). Many of these studies, like the study presented here, rely on estimates of potential connectivity rather than realised connectivity (Watson et al. 2010), and the implication for recruitment and population development are often not addressed directly. Although predictions of recruitment and population growth are often complex and limited by available data and knowledge of individual drivers, the use of meta-population concepts and modelling, together with reasonable assumptions of demographic rates, can provide a useful insight to the population dynamics that can be expected or predicted within and between subpopulations of marine organisms. Here, meta-populations refer to subpopulations that belong to an interconnected network where demographic rates (offspring, mortality, etc.) and dispersal rates (larval sources and sinks) together drive population recruitment, densities and growth rates at a subpopulation level. These types

of analyses are essential for evaluating different resource management strategies, such as population catch quotas and no-harvest areas (Puckett et al. 2014, Theuerkauf et al. 2021). For the management of the cockle fishery in Limfjorden, the study presented here provides a baseline for such future assessment, where analysis of potential connectivity in combination with data from annual stock assessment and fisheries surveillance can support the prediction of future stock development under different management strategies and scenarios. This includes the impacts from opening of non-fished areas, which may provide significant larval supplies to other areas, or closure of fished areas that may be heavily reliant on SR.

Larval dispersal modelling and connectivity analyses as presented here are valuable tools for gaining insight into the potential causalities of some of the underlying processes driving population distribution and dynamics of cockles in a system like Limfjorden. However, empirical data are required for validation if we want to take this type of study a step further. These could include multiannual monitoring and stock assessment of cockles and other competitive species and their demography; larval surveys (e.g. Paris & Cowen 2004); elemental fingerprinting of larval shells (Nolasco et al. 2018); genetic relatedness (Couvray & Coupé 2018); and monitoring and modelling (calibrated and validated) of key environmental drivers such as temperature, oxygen concentrations, food availability, currents and sediment conditions.

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