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TITLE:
Larval connectivity of Northern Shrimp (Pandalus borealis) in the northwest Atlantic.

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ABSTRACT

Northern Shrimp (Pandalus borealis) represents one of the most important fisheries in the northwestern Atlantic Ocean, but few studies have considered connectivity among different management units (i.e., stocks). Using a biophysical model, we investigated potential larval dispersal among North Atlantic Fisheries Organization (NAFO) divisions and its interannual variability during the long pelagic larval phase of *P. borealis* (~3 months). Overall, we found a largely stable, stream-like larval connectivity system driven by the main currents that flow over both the Greenland and Canadian continental shelves, with a relatively low but consistent exchange of larvae between Greenland and Canada across the Baffin Island continental shelf. We observed highest potential settlement densities on the northwestern Greenland and Newfoundland shelves, representing retention areas that correspond to highest abundances of adult shrimp. Intermittent and variable larval exchanges of lower magnitude also occurred between populations less obviously associated with the major circulation features. Our study improves understanding of Northern Shrimp stock-recruitment relationships at the metapopulation level, which could help determine the appropriate spatial scale to improve management strategies.

KEY WORDS

biophysical modelling, larval dispersal, metapopulation, shrimp, Pandalus, Northwest Atlantic
INTRODUCTION

Northern Shrimp (*Pandalus borealis*) represents one of the most important fisheries in the Northwestern Atlantic Ocean (3rd highest value in Canada in 2018, DFO 2019a) and the most important fishery in Greenland. The species spans the continental shelf from the west coast of Greenland to Northeastern Canada (i.e., Newfoundland, Labrador, and Baffin Island) and into the Gulf of St. Lawrence. In the past 15 years, Northern Shrimp stocks declined dramatically in some areas (e.g., Newfoundland shelf, South Greenland), while some others remained relatively stable (Labrador, Baffin Bay) or declined and increased again in abundance (e.g., West Greenland) (Burmeister and Riget 2019; DFO 2019b, 2019c). Despite recent improvements in knowledge of population dynamics (Jorde et al. 2015; Le Corre et al. 2019), significant uncertainty remains in understanding the large-scale patterns of change and linkages among Northern Shrimp populations throughout our focal area in the northwest Atlantic (Figure 1), and how these linkages may affect the stock-recruitment relationship for management units.

Genetic analysis (Jorde et al., 2015) documented a genetically homogeneous metapopulation of Northern Shrimp in the northwest Atlantic, which is ecologically structured primarily by temperature and larval dispersal patterns. Despite potential long geographic distances among populations, the long pelagic larval phase of *P. borealis* (2-3 months) may allow large-scale stock-recruitment demographic coupling among management units that comprise the metapopulation (Le Corre et al. 2019). Local and large-scale (i.e., connectivity network) processes might therefore drive shrimp population dynamics, emphasizing the crucial importance of demographic connections through larval dispersal (e.g., source, sink) among geographically separated populations of bentho-pelagic species for understanding population density, persistence and regulation (Cowen and Sponaugle 2009). For example, previous modeling studies reported high connectivity among Northern Shrimp populations among southern and northern stocks from western Greenland, but weak connectivity to stocks in the Northwestern Atlantic.
Ocean (Hvid Ribergaard et al. 2004; Jorde et al. 2015). Modeling studies by Le Corre et al. (2019) suggested high larval connectivity among management units on the Newfoundland and Labrador shelves but no study has assessed the importance of populations in the Canadian Arctic as potential sources of recruits. In the context of source-sink dynamics, understanding the role of each stock in providing larvae, larval dispersal by currents, and spatiotemporal variability in connectivity and oceanography could improve understanding of Northern Shrimp metapopulation dynamics.

The complexity of regional ocean circulation and its spatiotemporal variability complicate the evaluation of the role of environmental conditions on shrimp larval dispersal. Whereas adult stocks are mainly benthic and located on the continental shelves under specific and relatively stable conditions in our study area (e.g., 1-6 °C bottom temperature, 150-600 m depth, DFO 2017), Northern Shrimp pelagic larvae experience a broad range of environmental conditions in surface waters (e.g., temperature, ocean circulation), which could influence connectivity patterns among stocks. More specifically, stronger surface currents at the shelf edge (e.g., offshore branch of the Labrador Current) could result in large-scale dispersal potential, whereas weaker coastal currents (e.g., Baffin Island Current, West Greenland Current) could result in higher larval retention. In addition to potential variability in the vagaries of currents, spatiotemporal variability in environmental conditions (e.g., water temperature, salinity) may also strongly influence larval dispersal (Cowen and Sponaugle 2009). Large-scale phenomena, such as the North Atlantic Oscillation (NAO), also contribute to interannual variability in the circulation regime of the Northwest Atlantic Subpolar Gyre, which weakens or strengthens depending on NAO atmospheric conditions. Such interannual variability necessitates studies of contrasting years across the NAO index range, because NAO-related changes in ocean circulation could influence larval dispersal patterns (Han et al. 2014; Wang et al. 2016; Le Corre et al. 2019).
Northern Shrimp tolerate a relatively broad range of environmental conditions (e.g., temperature), and their early-life development rate strongly depends on environmental conditions (Storm and Pedersen 2003; Ouellet and Chabot 2005). Lower water temperature prolongs larval stage duration, potentially extending larval dispersal among areas. Because the first three larval stages (stages I to III) inhabit the upper and most spatially variable layer of the water column (Ouellet and Allard 2006), Northern Shrimp larvae might experience considerably colder waters in Baffin Bay than in areas further south. Sea surface temperature gradients observed in our study area range from -2 to 16 °C during the larval period (i.e., spring and summer), potentially producing substantial variation in development rates of shrimp larvae from different spawning aggregations. Similarly, spatial variation in water temperature may also impact the timing of egg hatching. In this context, consideration of water temperature effects on egg and larval development in different areas of the Northwestern Atlantic Ocean should provide a realistic assessment and better understanding of larval dispersal patterns.

The application of a coupled biophysical particle-tracking model can facilitate the study of Northern Shrimp larval dispersal patterns under a broad range of environmental conditions in such a large-scale and complex system (Cowen and Sponaugle 2009; North et al. 2009; Treml et al. 2012). Such models suitably represent hydrographic and biological processes, and offer the possibility of manipulating various factors of interest. More specifically, they allow experimental evaluation of the impact of key biological variables (e.g., larval vertical swimming behaviour, pelagic larval duration) under variable oceanographic conditions. In addition to exploring the impact of biological parameters on larval dispersal, tracking larvae under different ocean circulation scenarios related to variable atmospheric drivers enables assessment of interannual variability of larval connectivity patterns.

Building on the work of Le Corre et al. (Le Corre et al. 2019), we used a biological particle-tracking model (Paris et al. 2013) driven by North Atlantic hindcasts of ocean circulation (Brickman et al. 2016; Wang et
al. 2016) to simulate larval dispersal of Northern Shrimp in the Northwestern Atlantic Ocean. Using empirical data on concentrations of *P. borealis* adult populations on the Greenland and northeastern Canadian continental shelves, we assess potential larval dispersal and settlement patterns among management units, and their inter-annual variability under a broad range of NAO conditions. From these projections, we determined the role of each population in terms of self-settlement and larval supply to other geographic divisions, and defined the degree to which different populations contribute to the metapopulation (e.g., occasional, preeminent) and their role (e.g., source, sink) within Northern Shrimp source-sink dynamics. Because water temperature strongly influences pelagic larval duration (PLD), we also evaluated the sensitivity of larval connectivity patterns (e.g., larval settlement patterns and scale of larval dispersal) to PLD through different larval development scenarios based on water temperatures observed in the study area. Overall, we aim to provide information on the relative stability of the main large-scale connectivity processes at the Northwest Atlantic scale. Identifying the main sources and sinks of larvae associated with population interdependence within the metapopulation offers key ecological elements to improve our understanding of stock-recruitment relationships in the region, and thereby help improve management strategies.
MATERIAL AND METHODS

Study region and ocean circulation model

Our study area extended from Newfoundland Grand Banks in the south (approx. 43 °N) to Baffin Bay in the North (72 °N), and from Hudson Strait in the West (-70 °E) to southwest Greenland in the east (-42 °E); this region encompasses the highest shrimp abundances in the Northwest Atlantic (Figure 1). The Labrador Sea Subpolar Gyre dominates large-scale ocean circulation in the region. The West Greenland Current (WGC), the Baffin Island Current (BIC), and the Labrador Current (LC) represent the prevailing features in the region, with current velocities up to 0.7 m s⁻¹ (Figure 2). The WGC carries waters north from the Nordic Seas to West Greenland. South of Davis Strait, the WGC bifurcates to the west to join the LC, which carries cold water from the Arctic to the South. The BIC carries waters from the Canadian Arctic archipelagos and joins the LC near Hudson Strait. Moreover, some weaker branches of those currents or connected currents (e.g., inner branch of the LC, Hudson Strait Current) can strongly influence larval dispersal on the Canadian and Greenland shelves (Le Corre et al. 2019). Interannual (i.e., decadal and NAO) and seasonal variations in environmental conditions (i.e., wind and temperature) influence the principal currents in the region (Han et al. 2014; Wang et al. 2016).

We used ocean current simulations from a North-Atlantic ice-ocean model based on Nucleus for European Modelling of the Ocean (NEMO) (Brickman et al. 2016; Wang et al. 2016) forced by wind, heat flux, and freshwater inputs for the region. Horizontal resolution was 5-7 km, whereas vertical resolution followed a gradient from 1 m at the surface to 200 m at 1250 m depth, which provided adequate resolution for shelf-scale processes (e.g., fronts, eddies, North et al. 2009). In order to address computational storage problems related to the large scale of the ice-ocean model, we used 5-day averages of the current velocity component fields and water temperature offline in a particle-tracking model. To limit the computing time, we selected 4 years with different annual North Atlantic Oscillation
indices (station-based, 1999: 2.25, 2009: 0.72, 2010: -5.96, 2012: -0.25) (National Center for Atmospheric Research Staff 2019) to represent a broad range of ocean circulation conditions. Previous studies validated the ice-ocean model with observational data, thus supporting its suitability as a tool for the study of interannual variability of larval dispersal (Brickman et al. 2016; Wang et al. 2016).

**Particle-tracking model**

We used the Connectivity Modeling System (Paris et al. 2013), an open access spatially explicit individual-based model that couples several biophysical operational modules into a Lagrangian stochastic particle-tracking model, to assess shrimp larval dispersal from hatching to settlement. We used the CMS basic configuration associated with the vertical migration module, the stochastic horizontal diffusivity component (random walk - diffusivity coefficient Kh=64 m2 s-1, based on Okubo 1971), and the module that prevents larvae from settling at the coast (Paris et al. 2013). The model moved shrimp larvae forward every six hours using a fourth order Runge-Kutta method of advection based on linear interpolation over time of consecutive horizontal oceanographic circulation data. We also moved larvae vertically every six hours following a diel and ontogenic migration pattern (see below) from Le Corre et al. (2019), based on in-situ and lab experiments (Bergström 2000; Ouellet and Allard 2006). Vertical current velocities were negligible relative to horizontal velocities and larval vertical migration behaviour and were therefore not considered in larval dispersal. We ran all dispersal experiments independently and recorded larval trajectories daily.

**Northern Shrimp populations**

*Release sites* - Based on data availability in 14 Northwest Atlantic Fisheries Organization divisions (NAFO divisions, and on the Convention on Cooperation in the Northwest Atlantic Fisheries, June 2017; note that we created area 0C for the purpose of this study) (Figure 1), we estimated Northern Shrimp population densities using scientific trawl-survey data from 2005 to 2012 collected by Fisheries and
Oceans Canada (Newfoundland and Labrador - fall survey, divisions 2HJ3KLNO), the Northern Shrimp Research Foundation (Canadian Arctic region, divisions 0ABC2G), and the Greenland Institute of Natural Resources (West Greenland summer survey, divisions 1ABCDEF). Using a Geographic Information System (QGIS version 3.6 2019), we divided the area in 50 x 50 km cells, and estimated the mean Northern Shrimp density (kg km\(^{-2}\), all ages considered) within each cell. We then selected the centroids of cells (based on sampling locations) with averaged shrimp densities greater than 100 kg km\(^{-2}\) as release sites for all the experiments (n = 288 sites) (Figure 1). Simulations released 100 larvae per day from each site for 30 days (for a total of 864,000 larvae released per year), regardless of the density of adults in each cell.

**Release period** - Previous studies reported that water temperature influences timing of Northern Shrimp egg hatching (Pedersen et al. 2002; Ouellet and Chabot 2005; Ouellet et al. 2007; Koeller et al. 2009). With knowledge of the gradient in surface temperature in the study area from April to June, the ratio of ovigerous vs. non-ovigerous shrimp collected by Canadian fisheries observer data (from 1996 to 2015 – not shown), as well as observations in Greenland waters (Hvid Ribergaard et al. 2004), we created five groups with different larval release periods (Supplement S1). For divisions with the earliest release period (i.e., 1EF, 3L), we released 100 larvae every day for 30 days from April 1\(^{st}\) to 30\(^{th}\), in contrast to larval releases from May 11\(^{th}\) to June 9\(^{th}\) in divisions with later larval release (i.e., 0ABC, 1A) (i.e., 864,000 larvae released in total).

**Larval development and swimming behaviour** – Previous studies on *P. borealis* demonstrated that dispersal occurred principally during the first five planktonic larval stages (Pedersen et al. 2002; Ouellet and Chabot 2005; Ouellet and Allard 2006; Ouellet et al. 2007; Rasmussen and Aschan 2011). The swimming capacity of Northern Shrimp larvae increases through changes in ontogenic and diel vertical swimming behaviours (Bergström 2000; Ouellet et al. 2007). Our simulations restricted the first three
larval stages to the upper part of the water column, but allowed a larger migratory depth range in stages 4 and 5 (Ouellet and Allard 2006; Le Corre et al. 2019) (Supplement S2). In order to comply with the stage-duration structure of the larval vertical migration module of CMS, we defined the duration of each of the 5 stages based on limited laboratory studies within the range of modeled water temperatures within the study area (Storm and Pedersen 2003; Ouellet and Chabot 2005). We generated three developmental scenarios, with constant stage duration of 14, 17 (default scenario), and 20 days (Supplement S2), to capture the potential effect of water temperature on larval dispersal through larval development (i.e., larval stage duration), and assessed the sensitivity of the results to pelagic developmental duration. These predetermined scenarios resulted in total pelagic developmental durations of 70, 85, and 100 days, respectively, consistent with previous studies with similar environmental conditions (Astthorsson and GislaÁson 1991; Pedersen et al. 2002; Ouellet and Chabot 2005; Rasmussen and Aschan 2011). Based on those three scenarios, and the average temperature encountered by larvae during an 85-day period (Supplement S2), we explored a fourth scenario with 14-day stage duration (larvae released from 1DEF3L, average water temperature >1 °C), 17-day (1ABC2HJ3K, -1 °C ≤ T ≤ 1 °C, release from), or 20-day (0ABC2G,T < -1°C).

Across the different experiments, individuals could settle any time during a 20-day competency period following their larval development phase if located where depth was less than 1000 m (i.e., 26 potential destination divisions, bathymetry based on the General Bathymetric Chart of the Oceans (GEBCO 2014, 30 arc seconds grid)) (Figure 1) given that scientific surveys report few adult shrimps below this depth. Biophysical models that track particles over several weeks for particle tracking add uncertainties; we therefore based connectivity metric analyses (except travelled distances) on potential settlement locations encountered during the entire 20-day competency period (Le Corre et al. 2019).

Analyses
Spatial patterns – For each larval dispersal experiment, we used 1-degree cells to summarize larval positions during the 20-day competency period (i.e., 17,280,000 larval positions per experiment), and counted all larval positions located within suitable habitats (i.e., NAFO divisions from 0 to 1000 m depth) as successful potential settlers. We then compared the spatial distributions of potential settlement densities (settlers·km\(^{-2}\)) among experiments (e.g., years, PLD) using Pearson's correlation statistics for corresponding cells.

Settlement success and dispersal distances – For each division where we released larvae, we calculated the number of larvae that reached a suitable habitat (i.e., settlement success and export rate), including self-recruitment within the release division. We also estimated the average path distance (± standard deviation) travelled by successful settlers released from each NAFO division during their larval developmental phase, with distance travelled as a cumulative total from larval release to the time when they reached competency. We also tracked the temperature encountered by larvae during the dispersal phase and calculated the average for each release division.

Connectivity matrix – Connectivity estimates in the present study represent “potential connectivity”, defined by Watson et al. (2012) as the likelihood of larval transport from source to sink areas. We assessed connectivity among NAFO divisions and regions using connectivity matrices and diagrams because international stock assessments (NAFO) commonly use these divisions. For each experiment, we recorded source and position of successful settlers (i.e., destination divisions) during the 20-day competency period, and calculated the percentage of larval positions between all source-destination combinations (14 sources and 26 destinations). We also totalled the number of links observed between different divisions to assess the extent of the network.

Connectivity diagram – Based on the connectivity matrix, we generated connectivity diagrams representing larval fluxes among areas and their yearly variability, where node size was related to the number of larvae released in each NAFO division, and edge (i.e., arrow) width and colour depended on
the number of larvae transported between NAFO divisions and yearly variability of the link, respectively.

For clarity, we only display links that represented more than 0.1% of the total number of potential settler positions. A circular arrow represents self-settlement around each NAFO node and indicates larval overall settlement success beside each release node. We established the average connectivity diagram by averaging the connectivity matrix over 4 years for each combination of NAFO nodes. All the analyses were made using Matlab release 2016b (The MathWorks, Inc).
RESULTS

Ocean Circulation

Ocean circulation simulations effectively represented the West Greenland Current (WGC), the Labrador Current (LC), and the Baffin Island Current (BIC), as well as the on-shelf related currents as the dominant features in the region during every year of the study (Figure 2). The WGC resulted in higher average current velocities (Figure 2 and Supplement S1) in southern Greenland (e.g., 0.20±0.13 m s\(^{-1}\) in division 1F), gradually decreasing along the Greenland shelf to minimum velocities in division 1A (0.06±0.04 m s\(^{-1}\)). The LC resulted in higher overall current velocities on the Canadian shelf than on the Greenland shelf. The highest average current velocities occurred along the Labrador coast (0.31±0.16 m s\(^{-1}\) in 2H), whereas lower velocities characterized the northern (i.e., 0.13±0.07 m s\(^{-1}\) in 0A) and southern divisions (i.e., 0.14±0.07 m s\(^{-1}\) in 3K) (Figure 3). Relatively low yearly variability characterized these dominant circulation features, except for the BIC and the Hudson Strait Current. Relatively high yearly variability of current velocity also occurred in areas north of Davis Strait. Generally higher seasonal variability in current velocities occurred at the beginning and/or end of the larval dispersal period (i.e., Spring and late Summer/Fall) in both surface and deep layers of transects 1 and 3 (Figure 3, right panel), but we observed no clear NAO-related pattern among years.

When averaged over the entire potential larval dispersal period (April to early-October), highest average surface water modeled temperatures (>4.9 °C) occurred in southern Greenland (divisions 1DEF) and southern Newfoundland (division 3L), in contrast to lowest values (<0.3 °C) in northern Greenland (division 1A) and northeastern Canada (division 0ABC2G) (Supplement S1). Those results largely agree with large-scale oceanographic patterns based on observations in the region (Colbourne et al. 2017). Seasonal variation in surface and deep water temperature during the larval dispersal period was generally consistent among years (Figure 4, right panel), despite much warmer surface temperatures in
Canadian Arctic and Labrador coasts in 2012. Less pronounced seasonal warming of deep water (i.e., April to October) in Canadian waters than in Greenland during the study period (Figure 4, right panel) led to higher average deep layer water temperatures in Greenland (5.2 °C) than in Canadian waters (≤1.3 °C) (Figure 4). The initiation of spring warming of surface waters occurred first in Greenland waters (early-April) consistently, followed by Newfoundland, Labrador, and Canadian Arctic waters, respectively (Figure 4, right panel).

Larval dispersal - Yearly variations

Settlement densities – Based on the default 17-day stage duration scenario (i.e., 85-day PLD), highest yearly average settlement densities occurred near Disko Island (divisions 1AB) and the Newfoundland shelf and Grand Banks (divisions 2J3KL) (Figure 5), and similar settlement patterns were consistently observed every year (results not shown). Overall highest settlement success rates in 2010 (85.3%, NAO -), contrasted lowest rates in 1999 (78.3%, NAO +), and intermediate rates in 2009 and 2012 (Figure 6). For the default 17-day stage duration scenario, we observed relatively low overall variability of settlement densities among years (Pearson’s R ≤ 0.92 between 1999-2010, 2009-2012, and 2010-2012) (Figure 6); 2010 (NAO -) differed most from the other years (0.85 ≤ Pearson’s R ≤ 0.93), whereas 1999 and 2009 were most similar (Pearson’s R = 0.96). On the northern Labrador shelf (divisions 2GH), higher potential settlement occurred in 1999 (+9% of average settlement in 2G, +12% in 2H) and 2012 (+17% in 2G, +7% in 2H) (Figure 8, right y-axis).

Distance travelled - Distance travelled by successful settlers depended strongly on their origin and on current velocities during larval development (Figure 7). Larvae released from locations with consistently weaker currents (e.g., divisions 1AB) travelled approximately 500 km in 85 days (i.e., 17-day stage duration), whereas larvae released from locations with higher current velocities (e.g., division 0B2GHJ3KL) travelled distances in excess of 1,000 km in 85 days. Larvae released in southwestern
Greenland (division 1CDEF) travelled between 500 and 1,000 km, and varied more from year to year than larvae released from northern Greenland. Most unsuccessful settlers released from southern divisions (2J3KL) travelled over 1,500 km in 85 days, with negligible settlement success rates for larvae that travelled beyond 2,000 km (results not shown). Overall, patterns in distance travelled by larvae from each release area were highly consistent among years.

**Connectivity** – Simulated shrimp larval dispersal patterns across the region were consistent with the main oceanic features in the region (i.e., Labrador gyre), along with substantial retention in northwest Greenland, Hudson Strait, and Newfoundland shelves. Using the default larval development scenario (i.e., 17-day stage duration, 85-day PLD), the number of links representing potential larval exchange among 26 NAFO divisions (14 NAFO release divisions) fluctuated between 174 (2010) and 149 connections (2012), with 126 occurring every year and a total of 189 different links over the 4 years (Figure 8). Connectivity between links varied little between years (Figures 8 and 9), but more substantially for links with lower average larval exchange rates (i.e., warm colour links, Figure 9).

Irrespective of the year, high self-settlement (retention) occurred in 1A (>10% of overall settlement) with >80% of larvae as self-settlers (Figures 5 and 8). Substantial self-settlement also occurred in the Hudson Strait area (division 0C), despite occasional minor influx of larvae from northern Canada and Greenland (Figure 8). Despite some self-settlement, most larvae settling in 3KL divisions originated from the Arctic and Labrador shelf (i.e., mainly from OB2GJH for 3K, and 2GHJ3K for 3L), the latter location mostly exporting larvae to southern locations. Most of the settlement on the Labrador shelf (divisions 2GHJ) was supplied from various source areas in northern Canada and Greenland (Figure 9), with a higher influx of larvae arriving from Canadian Arctic divisions 0B to 2GH in 1999 and 2012 (Figure 8).

Larval exchange from Greenland to Canada was relatively low during all year (Figure 8), but even lower exchange occurred between 1BC and 0B in 2010 (NAO- year). Furthermore, with the exception of 2012,
A considerable number of settlers were delivered to the Gulf of St. Lawrence (from Labrador 2GHJ) and southern Newfoundland (from Newfoundland 3KL) every year (Figures 5 and 8).

**Larval dispersal - Impact of pelagic larval duration and space-related PLD**

The three developmental scenarios (i.e., 14, 17, and 20-day stage duration corresponding to 70, 85, and 100-day PLD, respectively) yielded differences in settlement density patterns (Figure 10), despite highly correlated overall spatial density patterns (Pearson’s R > 0.94). As expected, the middle duration scenario (i.e., 17-day stage duration) produced similar settlement success and density pattern to the average scenario all over the study area. The experiment implying shorter developmental periods (i.e., 14-day stage duration) consistently increased overall settlement success (82.9% on average over 4 years) and settlement density in most areas (especially division 3K and 1CD), except for northernmost Greenland, Newfoundland Grand Banks, and Gulf of St. Lawrence (division 1AB, 3P, 4RS) where settlement rates decreased compared to the middle duration scenario. In contrast, the 20-day development scenario yielded lower overall settlement success (79%), and lower than average settlement rates in most areas, except locations at the extremes of the study area (i.e., north Greenland, Grand Banks, Gulf of St. Lawrence). Under the 14-day developmental scenario, successful settlers travelled shorter mean distances (774 km on average over 4 years) than larvae in the 17-day (917 km), and 20-day scenarios (1062 km in 2012) (Figure 7). Compared to the 17-day PLD scenario, larval connectivity matrices decreased or increased the number of connections between divisions for 14-day or 20-day larval stage durations, respectively (Figure 11). Longer (shorter) larval stage duration promoted more larval exchanges between locations further (closer) apart compared to the 17-day scenario, and increased (decreased) spreading of larvae across the region. Larval dispersal simulations incorporating different larval stage durations (i.e., 14, 17, and 20-day) in relation to water temperatures encountered by larvae (i.e., T > 1 °C, 1°C > T > -1°C, and T < -1 °C, respectively; see Methods for more
details) revealed reduced settlement density in divisions 0ABC, 1AB, and 2GHJ, but higher densities in 1CD, 3KL, compared to the yearly averaged 17-day scenario (Figure 11-d). This scenario produced the same number of links among divisions as with the 17-day scenario, despite minor changes in the connectivity matrix.
DISCUSSION

Our study aimed to improve understanding of larval dispersal during the long pelagic larval duration of Northern Shrimp; these extended larval durations constrain in situ tracking and thus require modeling approaches. A previous study that focused on Newfoundland and Labrador shelves demonstrated the potential importance of dispersal (i.e., several hundreds of kilometres) of pelagic larvae among management areas of the Labrador and Newfoundland shelf (Le Corre et al. 2019), but lacked the necessary data to consider the supply of larvae from northern areas (Canadian Arctic and Greenland). Our larger scale study of Northern Shrimp at the scale of the northwest Atlantic revealed a stream-like larval connectivity system that mostly followed onshelf currents consistently throughout the study years (i.e., WGC, LC), despite variation in atmospheric forcing reflected in the ice-ocean model. Larval dispersal from south to north on the western Greenland shelf and from north to south on the Canadian shelves resulted in high connectivity in Northern Shrimp populations, but with limited exchange between the Greenland and Canadian shelves. The areas of highest potential settlement occurred in northern Greenland and the Newfoundland shelves, where generally weaker currents occurred. The role of larval stage duration on larval settlement patterns was also quite striking, especially within such a large area with considerable temperature gradients.

Larval connectivity patterns

We identified two consistent stream-like systems on the Greenland and Canadian shelves, with relatively limited larval exchange between them. On the Greenland shelf, the West Greenland Current transported larvae from sites located in the south (divisions 1DEF) to the northernmost sites, where we identified a high larval retention area near Disko Island (divisions 1AB). The bifurcation of the WGC at the Davis Strait exchanged some larvae between the Greenland (divisions 1BC) and Canadian shelves (OB). On the Canadian shelf, the inner branch of the Labrador Current and Baffin Island Current primarily...
drove the north to south stream-like larval connectivity from northern source areas (divisions 0BC2GHJ) to southern sink areas (divisions 3KL), which allowed larvae to remain on the continental shelf. The transport of larvae by the offshore branch of the LC appeared limited because of its location off the shelf edge and our release of larvae between the mainland and the shelf edge. The stream-like pattern resulted in consistently high settlement rates in the major sink areas, characterized by generally weaker and more complex ocean circulation. In contrast, lower settlement occurred in locations with strong, directionally consistent currents (divisions 2GHJ). The retention areas (divisions 0C1AB3KL) could play an important role for the long-term persistence of Northern Shrimp in the region by acting as resilient populations in the system that receive larval recruits on a regular basis (Fogarty and Botsford 2007; Cowen and Sponaugle 2009). In such a metapopulation context with a high level of connectivity, some of these retention areas could also act as steady sources of larvae to downstream areas. We identified a key stepping-stone role for the south of Baffin Bay shelf area (division 0B) for shrimp populations over just a few generations (Jorde et al. 2015; Buonomo et al. 2017). This area provided as an important source of larvae for the Newfoundland and Labrador shelves, and also received non-negligible larval input from Greenland. In such an asymmetrical stream-like connectivity network, the Northern Shrimp populations in division 0B likely play a predominant role in larval (associated gene) flow between the Greenland and Canadian shelves, an interpretation consistent with the relatively low genetic differentiation reported by Jorde et al. (2015).

Variability of larval dispersal related to ocean circulation

The larval connectivity links that transported the most larvae (i.e., stream like connectivity) were consistent among years, but some appreciable secondary connections between areas varied from year to year. Such variability suggests that more isolated populations (e.g., 0A, 3P, northeast of the GOSL) might receive intermittent rather than consistent larval supply over years, in contrast to more consistent
supply to locations with the highest adult shrimp abundances. As previously reported by Brickman et al. (2016), higher seasonal variability occurred in onshelf and coastal currents, particularly above the banks (i.e., intensity and direction), in contrast to lower variability in shelf-break currents (e.g., LC on the shelf edge), associated with large-scale ocean circulation patterns. The overall stability of the main ocean circulation pattern resulted in comparable connectivity patterns over years, but the onshelf seasonal variation in ocean circulation likely contributed to among year variation in settlement patterns and success, travelled distances, or number of secondary connections within the system.

We did not fully explore yearly variability in ocean circulation because of the extent and complexity of the system (Wang et al. 2016), but we did not detect any clear relationship or consistency between any connectivity metrics, surface current velocities, and the NAO index. However, lower than average surface current velocities observed in most areas on the Newfoundland and Labrador shelves in 2012 (average NAO) (Figure 3, plot f1 and h1) resulted in overall shorter travel trajectories, whereas larvae released on the Greenland shelf travelled a lower average distance in 2010 (NAO-). In 1999 (NAO+), our modeling indicated higher potential settlement rates in northern Labrador (divisions 2GH), higher larval exchange between northwest Greenland and the Canadian Arctic Labrador shelf, and lower larval export toward the Gulf of St. Lawrence. This variation in ocean circulation on the Labrador shelf, as well as the higher overall settlement success observed in 2010 (NAO-), as previously reported by Le Corre et al. (Le Corre et al. 2019) on the Newfoundland and Labrador shelves using a different model might reflect lower current speed (Figure 3) over shallower areas (i.e., shelves) related to different atmospheric forcing and NAO conditions. Even if we could identify some year to year variation in connectivity patterns, we only studied four years spanning different NAO conditions. This analysis provided valuable insight into interannual variability in ocean circulation within the system, but was insufficient to thoroughly test any relationship between NAO and connectivity patterns.
Role of PLD and temperature

Changing larval stage duration noticeably impacted several connectivity metrics, but not the overall pattern, which remained similar under all conditions explored in our simulations. According to settlement density pattern similarities, variation in larval stage duration had less impact than yearly variability, but settlement patterns remained highly comparable. As expected, shorter PLD (i.e., 14-day stage duration) decreased distance travelled by larvae and number of links with potential settlement areas, resulting in more limited larval dispersal and associated variability, and increased larval retention and settlement success. In the 14-day stage duration scenario, the stream-like connectivity pattern on the Greenland and Canadian shelves still drove most larval exchange along the shelves, but lower distances travelled favoured onshelf retention and limited connections across the Davis Strait. Conversely, longer larval stage experiments increased the extent of larval dispersal and lowered retention, but the main connectivity links persisted. When we considered the gradient in water temperature in the region (PLD scenario #4), we found increased larval exchange and decreased number of settlers for larvae released in colder areas whereas numbers of settlers increased and dispersal decline for larvae released in warmer locations. For example, a longer larval stage duration for larvae originating from the Canadian Arctic associated with the strong inshore branch of the LC, transferred potential settlers from the Labrador shelf (i.e., divisions 2GHJ) to the Newfoundland shelf (i.e., divisions 3KL). Nonetheless, scenario #4 must be interpreted with caution on the Greenland shelf as some larvae may have been released in warmer southern locations, but travelled to colder northern locations without altering stage duration.

Beyond spatial variability in water temperature among regions, we also identified variation in average water temperature across years in some locations (e.g., transect 2 and 3 in 2012), but our connectivity models did not consider such temporal variability. In this example, increased surface water temperature
(>+3°C on average in mid-July 2012)(Figure 4, transects 1 and 2) would have shortened some larval development stages by several days, which might have altered the overall larval connectivity pattern by the same order of magnitude as a 3-day reduction in larval stage duration. Even when we altered stage duration and PLD, similar larval connectivity patterns (e.g., source and sink areas) resulted in comparable larval exchange among areas, irrespective of stage duration. Our study underscores the importance of improving knowledge of such benthic-pelagic species with slow larval development rates under cold water conditions (T<2°C, Ouellet et al. 2017) in order to better assess pelagic larval duration variability and associated potential larval dispersal in temperate, sub-Arctic and Arctic regions by using individual-based models that explicitly consider water temperature during larval dispersal.

Comparison to other model and limitations

Our study improves understanding of Northern Shrimp large-scale larval connectivity in the northwest Atlantic, but we recognize key limitations to our study. Despite successful validation of the ice-ocean model for the region (Brickman et al. 2016; Wang et al. 2016), our approach may not have represented some small-scale oceanographic features (e.g., cross-shelf currents) than we might have achieved with a higher temporal or spatial model resolution (Le Corre et al. 2019). Interestingly, our study using a large-scale ice-ocean model resulted in greater (+15% in average) water transport and slightly different ocean circulation across the Labrador shelf than the model used by Le Corre et al. (Le Corre et al. 2019). Though inevitable, such differences among ocean circulation models are difficult to explain given complex interactions of various factors such as model resolution, forcing data, and boundary conditions (Hufnagl et al. 2017). The dominant larval connectivity patterns and scale of larval dispersal were comparable to other studies in similar environments (Hvid Ribergaard et al. 2004; Shanks 2009; Jorde et al. 2015; Le Corre et al. 2019), even with longer distances travelled by larvae (+210 km travelled distances in average for larvae released in 2GJH3K), and potential larval connectivity between
geographic divisions that were further apart in this study compared to Le Corre et al. (Le Corre et al. 2019). Higher settlement success rates (i.e., larvae remaining on shelves) in this study compared to Le Corre et al. (Le Corre et al. 2019) largely reflect different experimental designs (e.g., more release sites located onshore of the shelves, different suitable settlement areas), and slightly different onshelf circulation between models, which resulted in lower export of shrimp larvae to unsuitable areas beyond the continental shelf. Our study did not consider larval input from the eastern boundary of the study area (e.g., Iceland, Eastern Greenland), but such larval supply must be minimal and/or sporadic given the high genetic differentiation among those areas (Jorde et al. 2015). We also did not consider the Flemish Cap population as a larval source because of its marginal role in terms of larval supply to the continental shelf (Jorde et al. 2015). Nonetheless minimal exchange of larvae occurred between the Newfoundland and Labrador shelves and division 3M, which corroborates suggestions of oceanographic isolation of Flemish Cap shrimp populations from continental shelf populations (Jorde et al. 2015; Le Corre et al. 2019). Overall, the large-scale larval connectivity patterns observed in this study were qualitatively consistent with results from other biophysical models, despite some expected divergence at finer scales (Hufnagl et al. 2017).

Beyond fine-scale physical uncertainties, our semi-quantitative approach considered the most important Northern Shrimp populations over the area, but excluded various biological and environmental factors affecting pre- and post-settlement processes (e.g., predation/mortality), and we based settlement habitats simply on depth (0-1000 m) in the study region. However, locations of highest adult shrimp density coincided with the modelled high settlement areas, despite unanticipated high settlement over the Newfoundland Grand Banks. Those discrepancies between model projections and DFO survey observations occurred principally in shallow areas (0-100 m) with relatively high density and diversity of groundfish (e.g., Grand Banks) that presumably increase predation rates and limit persistence of juvenile shrimp over time (Parsons 2005). We acknowledge that modelled potential settlement patterns and
other connectivity metrics require in situ verification (Brosset et al. 2019), or genomic confirmation (e.g., next generation sequencing), but our study increases understanding of the larval component of potential connectivity over remote and data poor regions.

Population dynamics and management

Our study revealed an overall stability of larval dispersal patterns of a bentho-pelagic species at the scale of the Northwest Atlantic Ocean, despite inter-annual variability of the ocean circulation and the relatively long pelagic larval duration of this species. Those findings emphasize the importance of steady retention areas for species with long pelagic durations, as larvae accumulate in those oceanographic convergence zones by simple advection in open water. However, as mentioned above, we observed some changes in potential settlement density in specific areas during given years (e.g., Gulf of St. Lawrence and southern Newfoundland shelf in 2010), and more variability of connectivity processes would likely emerge at a smaller spatial scale (Le Corre et al. 2019). Such deviations from average settlement patterns (i.e., fluctuating connectivity) may play an important role for long-term metapopulation dynamics, because more isolated populations could be highly influenced by the higher larval supply occurring during those specific years. Given anticipated Northern Shrimp habitat shifts northward in response to climate change in the region (Ouellet et al. 2017), the larval retention area, the structure of the connectivity network, and its associated variability identified in our study, Northern Shrimp may be able to access a large range of potential habitats over a relatively short time frame, potentially facilitating adaptation to a changing environment (Lett et al. 2010). Our study confirmed that larval connectivity should then be considered as a stochastic feature, in association with variable larval production and post-settlement survival, to improve our understanding of bentho-pelagic population persistence and distribution (Cowen and Sponaugle 2009; Le Corre et al. 2015).
In light of the potential contribution of each population/division in the context of this study (i.e., fixed release sites and number of larvae, no mortality or post settlement process), we were able to determine the contribution of each population in terms of potential larval supply to the system. Those findings allowed us to distinguish among populations consistently supplying vast (e.g., division 0B), more targeted areas (e.g., division 1B or 2G), or experiencing large larval export to unsuitable areas (e.g., 3L). Those findings could help to adapt fisheries or marine reserve management strategies for benthopelagic species with respect to the role of the population within the connectivity network (Fogarty and Botsford 2007). For example, to favour the persistence or help replenish a given sink population (e.g. division 3K, DFO 2019b), it would be more beneficial from a larval connectivity perspective to maintain a maximum larval supply from upstream populations, whereas adult abundance in some areas (e.g., shelf edge in division 3K) would have little impact on the potential settlement rate in this area. In the context of a more self-sustaining population (e.g., division 1A), any loss of adult abundance should be examined carefully to ensure a sufficient level of larval supply in order to maintain the population at a sustainable level. Managers and policy makers would then likely benefit of the consideration of larval connectivity into decision-making procedures (e.g., spatially structured stock assessment models) (Fogarty and Botsford 2007; Cadrin et al. 2019), even if excluding the effect of smaller-scale processes (e.g., habitat, post-settlement survival).

Concluding remarks

Larval connectivity models for Northwest Atlantic Northern Shrimp populations confirm consistent interactions among fisheries management areas at a broad spatial scale (i.e., international), and spatial and temporal variability in the exchange of larvae among populations (i.e., divisions). Within the context of declining stocks and changing environments, fisheries managers should pay particular attention to populations that represent important larval sources (e.g., 01B, 2GH) or to establishing strategic links.
between distant populations (e.g., OB) that facilitate metapopulation persistence (Cowen and Sponaugle
2009). Our study offers useful information on larval connectivity patterns, which complement other
crucial processes (e.g., trophic interactions, environmental conditions) within spatially structured
models (Fogarty and Botsford 2007; Garavelli et al. 2018; Cadrin et al. 2019). Such approaches would
improve understanding of Northern Shrimp population dynamics, and provide a basis to improve
Northern Shrimp management strategies in the Northwest Atlantic (Fogarty and Botsford 2007).
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Figure 1: Map of Northern Shrimp (*Pandalus borealis*) biomass densities (all ages considered) in North Atlantic Fisheries Organization (NAFO) divisions from 0 m to 1000 m depth. Green dots indicate the locations of the 288 release sites located in 50 km x 50 km cells with shrimp density over 100 kg km\(^{-2}\) (Map created under QGIS 3.6, bathymetry based on GEBCO 2014, see Methods for details).
Figure 2: Map of the main surface oceanographic features and currents in the Northwest Atlantic study area. Based on the simulations from the hydrodynamic model, the map includes the average surface current direction and speed (0-30 m), size of the directional arrows and background colour denote current velocity. The main oceanographic features displayed on the map are: Baffin Island Currents (BIC), Davis Strait (DS), Flemish Cap (FC), the Great Banks (GB), the Gulf of St. Lawrence (GSL), Hudson Strait (HS), the inshore branch of the Labrador Current (LCi), the offshore branch of the Labrador Current (LCo), and the Western Greenland Current (WGC). Represented mainland features are: Baffin Island (BAF), Greenland (GL), Labrador (LAB), and Newfoundland (NL). The map also shows the 200 m and 1000 m isobaths, and the location of the 4 transects (and associated number) presented in Figure 3 and 4. This map and related ones (Figures 5, 6, 9, and 10) were created using the M_Map mapping package (version 1.4) under Matlab release 2016b.
Figure 3: Variability of the hydrodynamic model current velocities along 4 transects located on the Northwest Atlantic continental shelf. Transect locations are shown in Figure 2. Left panels (a, c, e, g): Time-averaged current velocities (in m s\(^{-1}\)) from 0 to 380 m depth over the study period (April–October) across transects 1 (a), 2 (c), 3 (e), and 4 (g); Green boxes denote the surface and deep subsampling layers where we calculated the average current velocity values (and standard deviation) displayed on the graph. Subdivided right panels (b, d, f, h) display bar plot representing the yearly anomaly (one colour per year – see the legend) against the average (5-day intervals) current velocity (m s\(^{-1}\)) within the surface (upper graph) and deep (lower panel) layers of each of the 4 transects during the study period (April to October). The black line on each subplot represents the yearly averaged seasonal variability in current velocity (m s\(^{-1}\)) during the same period.
Figure 4: Variability of the hydrodynamic model water temperature along 4 transects located on the Northwest Atlantic continental shelf. Transect locations are shown in Figure 2. Left panels (a, c, e, g): Time averaged water temperature (in °C), from 0 to 380 m depth over the study period (April–October) across transects 1 (a), 2 (c), 3 (e), and 4 (g); Green boxes denote the surface and deep subsampling layers where we calculated average water temperature values (and standard deviation) displayed on the graph. Subdivided right panels (b, d, f, h) display seasonal variability (April to October – 5-day intervals) in water temperature for each year of the study (one colour per year – see the legend) within the surface (upper subplot) and deep (lower subplot) layers of each of the 4 transects.
Figure 5: Yearly averaged spatial distribution of settlement density during the competency period. The potential settlement density (number of potential settlers per km²) from simulations in the same experimental configuration (17-day stage duration) was averaged over 4 years. We only considered settlers potentially reaching suitable habitats (i.e., NAFO division from 0 m to 1000 m).
Figure 6: Settlement anomalies over years. Spatial anomalies (red: higher settlement, blue: lower settlement) of potential settlement density during the competency period (settlers km$^{-2}$) for the 4 studied years (a: 1999, b: 2009, c: 2010, and d: 2012). Settlement was compared in each cell to the yearly averaged settlement density (see figure 5). Each subplot shows the overall settlement success rate (i.e., percentage of larvae that reached a suitable habitat) for each year.
Figure 7: Distribution of settlers after larval dispersal and distance travelled from larval release sites when they reached competency (85 days) under various experimental conditions. The four (4) configurations of larval stage duration were 14-day (a), 17-day (b), 20-day (c), and variable from 14 to 20-day (d). For each NAFO division, we represented the number of released (left y axis - x10⁴ to obtain the actual number) larvae in a bar plot, and characterized the percentage of unsuccessful larvae (light gray), successful settlers (gray), and self-settlers (dark gray) with different fill colours. For each release area, we calculated the mean distance travelled (right y axis - kilometres, mean ± standard deviation) by larvae before reaching competency over the 4 years of the study.
Figure 8: Connectivity matrix representing the exchange of larvae (successful settlers) between the different NAFO divisions for each year of the study (a: 1999, b: 2009, c: 2010, d: 2012) under the same experimental configuration (17-day stage duration). The colour of the cell corresponds to the relative frequency of larvae released from a NAFO division (upper x-axis) that arrived at the “receiving” division (left y-axis) based on a 20-day competency period. White cells denote absence of connection. We calculated the overall settlement variability per receiving division (right y-axis) on the basis of the percentage of the 4 year averaged settlement density. For each year, we show the total number of links between NAFO divisions (upper-right corner). The presentation sequence of the NAFO divisions follows the main circulation pattern of the Northwest Atlantic Subpolar Gyre.
Figure 9: Connectivity diagrams representing the destination of larvae averaged over 4 years from each NAFO division examined (under the 17-day stage duration configuration – 20-day competency period). For clarity purpose, we divided the region into 4 larval release areas (subplot a: Greenland, b: Canadian Arctic, c: Labrador, and d: Newfoundland), displaying only links that represent more than 0.1% of the total number of settlers. The node size (i.e., larval release division - in red) relates to the number of larvae released in each NAFO division, and edge (i.e., arrow) width and colour depend on the number of larvae transported between NAFO divisions and yearly variability of the link, respectively. A circular arrow around each release division (red nodes) represents self settlement; larval overall settlement success is shown beside each release node. Each node is randomly positioned in its division.
Figure 10: Yearly averaged spatial distribution of settlement density during the competency period, and settlement anomalies over different stage duration configurations. The average potential settlement density (number of potential settlers per square kilometre at the surface) was averaged from simulations in each stage duration configuration over the 4 years (a). We considered only settlers potentially reaching suitable habitats (i.e., NAFO division from 0 to 1000 m). Spatial settlement anomalies (red: higher settlement, blue: lower settlement) of the potential settlement density during the competency period (settlers km\(^{-2}\)) are shown for the 3 stage durations (b: 14-day, c: 17-day, d: 20-day stage duration). We compared settlement in each cell to the average settlement density (a). The overall settlement success rate (i.e., percentage of larvae that reached a suitable habitat) for each year configuration is displayed above each subplot.
Figure 11: Connectivity matrix representing the average exchange of larvae (successful settlers) over 4 years between the different NAFO divisions under the same experimental configuration (17-day stage duration), and corresponding settlement anomalies over different stage duration configurations. For subplot (a), the colour of the cell corresponds to the 4-year averaged relative frequency of larvae released from a NAFO division (upper x-axis) that arrived at the “receiving” division (y-axis) based on a 17-day stage duration, and 20-day competency period. Absence of connection is represented in white. The settlement anomalies (red: higher settlement, blue: lower settlement) compare settlement connectivity patterns in various
stage duration configurations (b: 14-day, c: 17-day, and d: stage duration depending on the release division) to the average connectivity pattern assuming a 17-day stage duration configuration (subplot (a)). For the variable stage duration configuration (d), we assigned each division a larval stage duration based on water temperature encountered during larval dispersal (bottom x-axis); we expected no difference to the average connectivity matrix (a) for release divisions assigned a 17-day stage duration configuration. Each configuration shows the total number of links between NAFO divisions (upper-right corner). The presentation sequence of the NAFO divisions follows the main circulation pattern of the Northwest Atlantic subpolar Gyre. See Methods for further explanations.