



## SYMPOSIUM

# Larval Dispersal Modeling Suggests Limited Ecological Connectivity Between Fjords on the West Antarctic Peninsula

Amanda F. Ziegler <sup>1</sup> Lisa Hahn-Woernle, Brian Powell, and Craig R. Smith

Department of Oceanography, University of Hawai'i at Mānoa, Honolulu, HI 96822, USA

From the symposium “New Frontiers in Antarctic Marine Biology” presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2020 at Austin, Texas.

<sup>1</sup>E-mail: ziegler8@hawaii.edu

**Synopsis** Larval dispersal is a key process for community assembly and population maintenance in the marine environment, yet it is extremely difficult to measure at ecologically relevant spatio-temporal scales. We used a high-resolution hydrodynamic model and particle-tracking model to explore the dispersal of simulated larvae in a hydrographically complex region of fjords on the West Antarctic Peninsula. Modeled larvae represented two end members of dispersal potential observed in Antarctic benthos resulting from differing developmental periods and swimming behavior. For simulations of low dispersing larvae (pre-competency period = 8 days, settlement period = 15 days, swimming downward) self-recruitment within fjords was important, with no larval settlement occurring in adjacent fjords <50 km apart. For simulations of highly dispersing organisms (pre-competency period = 35–120 days, settlement period = 30–115 days, no swimming behavior), dispersal between fjords occurred when larvae were in the water column for at least 35 days, but settlement was rarely successful even for larvae spending up to 150 days in the plankton. The lack of ecological connectivity between fjords within a single spawning event suggests that these fjords harbor ecologically distinct populations in which self-recruitment may maintain populations, and genetic connectivity between fjords is likely achieved through stepping-stone dispersal. Export of larvae from natal fjord populations to the broader shelf region (>100 km distance) occurred within surface layers (<100 m depth) and was enhanced by episodic katabatic wind events that may be common in glaciomarine fjords worldwide.

## Introduction

The biogeography of Antarctic benthic organisms is governed by a suite of evolutionary and ecological processes, including larval dispersal (Arntz et al. 1994; Clarke 2008; Clarke et al. 2009; Thatje 2012). The potential for long-distance dispersal generally increases as the pelagic larval duration (PLD) increases (Palumbi 2003b; Shanks et al. 2003; Siegel et al. 2003; Cowen and Sponaugle 2009; Shanks 2009), and can be evolutionarily advantageous because it may increase local genetic variation and provide opportunities for exploitation of new habitats (Strathmann 1974; Palmer and Strathmann 1981; Strathmann 1985; Hill, 1991; Pechenik 1999; Krug 2001). The capacity for long-ranging dispersal differs across the highly variable life histories of Antarctic benthic fauna, including planktotrophy (Thorson

1950; Mileikovsky 1971; Jablonski and Lutz 1983; Bosch and Pearse 1990; Starr et al. 1990; Pearse et al. 1991; Clarke 1992; Pearse 1994; Poulin and Féral 1996; Stanwell-Smith and Peck 1998; Stanwell-Smith et al. 1999; Peck et al. 2005). Planktotrophic larvae generally have a longer PLD than lecithotrophic larvae, suggesting that they are capable of longer distance dispersal. In the absence of other life-history data, this relationship has been used extensively to predict dispersal capabilities (Selkoe and Toonen 2011) but uncertainty in PLD estimates can lead to vast under- or over-estimation of dispersal distance and population connectivity (Cowen et al. 2007; Cowen and Sponaugle 2009; Shanks 2009; Young et al. 2012). Several recent studies report surprising degrees of isolation and population genetic structure for organisms with seemingly

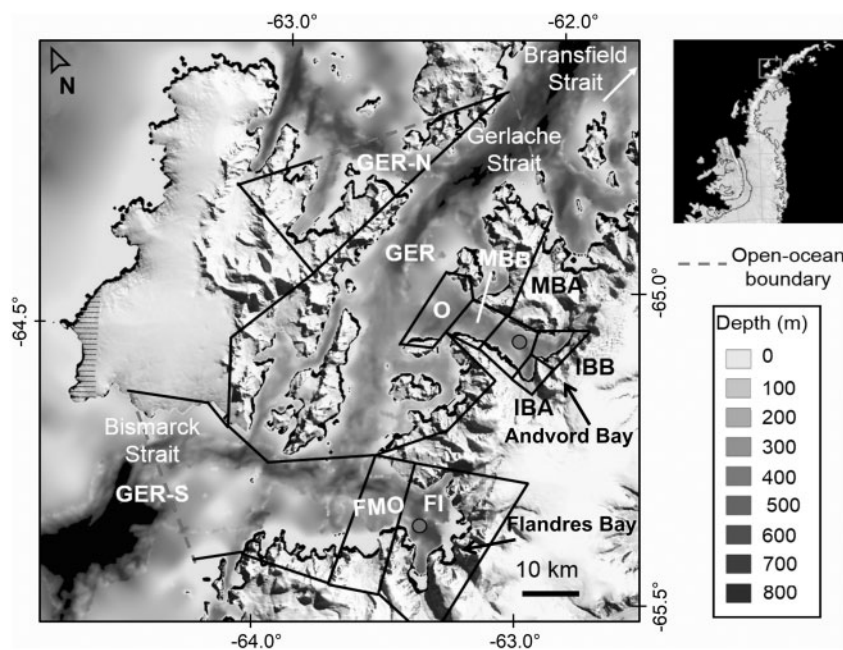
high dispersal potential (Swearer et al. 2002; Sköld et al. 2003; Paris et al. 2007; Siegel et al. 2008; Cunningham et al. 2009; Weersing and Toonen 2009; Hoffman et al. 2011; Ledoux et al. 2012; Damerau et al. 2014; Riesgo et al. 2015; Almany et al. 2017). Inference of dispersal distance or connectivity requires knowledge of not only the PLD, but also larval behaviors (Bingham and Young 1991; Palumbi 1994; Paris et al. 2007; Woodson and McManus 2007; Schlag and North 2012), and ocean circulation (Mullineau and Mills 1997; Palumbi 2003a; Thornhill et al. 2008; Xu et al. 2018).

Genetic measures of connectivity assess processes operating over evolutionary timescales (Hedrick and Miller 1992; Sunnucks 2000; Vignal et al. 2002; Selkoe and Toonen 2006; Holsinger and Weir 2009; Bryan-Brown et al. 2017) and may not be ecologically informative because the methods cannot detect population structure when exchange between populations is >10 migrants per generation (Slatkin 1995; Crandall et al. 2019). Ecologically relevant connectivity (i.e., sufficient exchange between populations to affect population dynamics) occurs on much shorter temporal scales (Cowen and Sponaugle 2009). For example, exchange of only a few individuals per generation may be sufficient to maintain genetically homogeneous populations that are in fact ecologically distinct (Wright 1950; Slatkin 1993). The study of ecological connectivity considers populations as sources or sinks and quantifies the dynamics that link metapopulations, such as larval import/export (Levin 1974, 1976; Wilson 1992; Marquet et al. 1993; Mouquet and Loreau 2003; Leibold et al. 2004; Mouquet et al. 2006). For organisms with limited life-history or population data (e.g., Antarctic benthos), models can be useful tools to estimate quantify these dispersal processes. Computational advances now enable ecologists to couple high-resolution regional hydrodynamic models to larval behavior models to track large numbers of simulated larvae (Bidegain et al. 2013; Döös et al. 2013; Paris et al. 2013; van Sebille et al. 2018), and thus to predict realistic dispersal patterns in otherwise difficult-to-study regions (Kettle and Haines 2006; North et al. 2011; Watson et al. 2011; Young et al. 2012; Piñones et al. 2013; Hilario et al. 2015). Historically, Antarctic dispersal studies have used genetic techniques to assess connectivity across the Antarctic Circumpolar Current and the effect of isolation on evolution (Damerau et al. 2012; Hunter and Halanych 2008; Riesgo et al. 2015; Thornhill et al. 2008; Wilson et al. 2007; Wilson et al. 2009). Few studies have utilized Lagrangian models or a combination of genetic and modeling techniques to

investigate connectivity on ecologically relevant spatial and temporal scales (Brasier et al. 2017; Matschiner et al. 2009; Piñones et al. 2013).

The West Antarctic Peninsula (WAP) consists of an extensive network of fjords, islands and deep channels with complex hydrography and circulation (Hofmann et al. 1996; Smith et al. 1999; Klinck et al. 2004; Savidge and Amft 2009), making it an excellent location for studying the impact of small-scale circulation features on dispersal. Fjords may create barriers to dispersal because larvae must be entrained within waters shallower than fjord sill depths for export (Bouchet and Taviani 1992; Buhl-Mortensen and Heisster 1993) and the estuarine circulation characteristic of many fjords may cause population-to species-level differentiation in planktonic dispersers (Bilton et al. 2002; Cunningham et al. 2009; Wright 1943). Along the Danco Coast of the WAP, the confluence of two water masses (Bransfield Strait Water and Circumpolar Deep Water) occurs in the vicinity of two glaciomarine fjords; Andvord and Flandres Bays (Hofmann et al. 1996; Cook et al. 2016). Water masses differ between these fjords separated by <50 km (Lundesgaard et al. 2020) suggesting that they may have different larval sources, leading to distinct benthic community compositions (Grange and Smith 2013). Fjord waters in Andvord Bay are typically quiescent with sluggish currents (< 5 cm/s) flowing into the fjord at depths deeper than 300 m and out of the fjord shallower than 300 m with limited connection to the outer shelf waters in the bordering Gerlache and Bismarck Straits where flows routinely reach ~40 cm/s (Lundesgaard et al. 2020). The greatest exchange between fjord and shelf waters has been observed in response to episodic, short-term (hours to days) katabatic wind events (Lundesgaard et al. 2019). Katabatic winds are a feature of glaciomarine fjords globally, and in Greenland and Norwegian fjords, these winds dramatically affect the surface circulation (Svendsen and Thompson 1978; Sutherland et al. 2014; Spall et al. 2017) while along-shore winds outside of the fjord can affect the strength of buoyancy-driven vertical mixing within the fjord (Carroll et al. 2015). The influence of katabatic winds and fjord circulation on the transport and dispersal of larvae has not yet been investigated in the Antarctic.

This study aims to assess the dispersal potential of benthic megafauna from two glaciomarine fjords, Andvord and Flandres Bays, by coupling a high-resolution hydrodynamic model with a particle-tracking model. We focus on understanding patterns of larval exchange and settlement between the fjords during the summer (December–April) and consider



**Fig. 1** The model domain encompassing Andvord and Flandres Bays as well as the surrounding Gerlache, Bransfield, and Bismarck Straits. Bathymetry (depth in meters) is shown by shading. Black lines indicate model boundaries used to tabulate particle settlement and locations and are referred to as: Inner Basin A (IBA), Inner Basin B (IBB), Middle Basin A (MBA), Middle Basin B (MBB), Outer Basin (O) in Andvord Bay, Central Gerlache Strait (GER), Northern Gerlache Strait (GER-N), Southern Gerlache Strait (GER-S), and Mouth (FMO) and Inner Basin (FI) in Flandres Bay. Filled circles give the particle release locations in MBA and FI and dashed lines indicate the three open-ocean boundaries of the model domain.

the physical processes that may affect larval export from the study region.

## Methods

### Hydrodynamic and particle-tracking models

We modeled larval dispersal within a domain along the WAP encompassing two glaciomarine fjords, Andvord and Flandres Bays, as well as the surrounding Gerlache and Bismarck Straits (Fig. 1) from December 1, 2015 to April 28, 2016. We used the Lagrangian TRANSPORT model, LTRANS (Schlag and North 2012; North et al. 2006; North et al. 2011) to model the dispersal of simulated larvae (particles). LTRANS relies on predictions from the Regional Ocean Modeling System (ROMS, Haidvogel et al. 2008; Shchepetkin and McWilliams 2009) to produce the hydrodynamics experienced by the particles. The full hydrodynamic model description and sensitivity analysis is presented elsewhere (Hahn-Woernle et al. 2020). In short, we utilized 3-hourly advection and diffusion predictions from ROMS that were generated over 25 terrain-following depth layers with a 350-m horizontal resolution (Hahn-Woernle et al. 2020) that accurately resolves mesoscale circulation features. Topography for the model domain was combined from Global Multiresolution Topography

Synthesis (Ryan et al. 2009), General Bathymetric Chart of the Oceans, and high-resolution multibeam data available from the Marine Geoscience Data System (MGDS; <http://www.marine-geo.org>). Tides were provided by the TPX08 global model (Egbert et al. 1994; Egbert and Erofeeva 2002). The atmospheric forcing was based on the Regional Atmospheric Climate Model (RACMO, Reijmer et al. 2005; Van Wessem et al. 2014) and further calibrated to observations from Automatic Weather Stations (AWS) (Hahn-Woernle et al. 2020). Water properties at boundaries were constrained by observations of temperature and salinity from CTD profiles from 1999 to 2017. The hydrodynamic model begins November 1, 2015 with a 30-day spin-up period and simulates the circulation for the summer months December–April.

We constructed four dispersal scenarios based on published characteristics of Antarctic benthic megafauna including PLD, pre-competency period, fecundity and behavior (Table 1). The scenarios, referred to as AndHigh, FlaHigh, AndLow, and FlaLow, are detailed in Table 2. In short, AndLow and FlaLow represent larvae with low dispersal potential, modeled after the larvae of the common Antarctic tunicate *Cnemidocarpa verrucosa*. These larvae have a short pre-competency period of 8 days, followed by

**Table 1** Life-history traits from published literature for Antarctic benthic megafauna with high and low dispersal potential. Larval mode indicates whether the species produces feeding (planktotrophic, “P”) or non-feeding (lecithotrophic, “L”) larvae. “Larval release time” is the annual spawning period or an estimate based on reports of gravid females. “Pre-competency period” represents the minimum time in days required for larvae to reach settlement competency in the water column. “The pelagic larval duration (PLD)” is the maximum time in days larvae can spend in the water column to reach competency and settle. Fecundity is the number of eggs produced per female per spawning event. *Cnemidocarpa verrucosa* is a tunicate. All high dispersal species are echinoderms. \* indicates species documented in Andvord and/or Flandres Bays.

Organism	Larval mode	Larval release time	Pre-competency period	Pelagic larval duration	Fecundity	References
Low dispersal potential						
<i>Cnemidocarpa verrucosa</i> *	L	June–July/Oct.–Nov.	8–16 days	~8 days	Unreported	16, 13
Porifera *	L	Unreported	Hours	12 h to 2 weeks	Unreported	7, 8, 10
High dispersal potential						
<i>Promachorcinus kergulensis</i>	L	Oct.–Nov.	60–90 days	Unreported	29,000	9
<i>Sterechinus neumayeri</i> *	P	Nov.–Dec.	115 days	Unreported	12,700	1, 5, 15
<i>Porania antarctica</i> *	P	Nov.–Jan.	65–78 days	Unreported	35,000	2, 3
Asteroidea sp.	P / L	Unreported	150–180/60–90 days	Unreported	Unreported	3
<i>Lophaster gaini</i> *	L	Feb.–Mar.	Unreported	Unreported	3000–5000	12
<i>Psilaster charcoti</i> *	L	Nov.–Dec.	Unreported	Unreported	10,000	3, 4
<i>Odontaster</i> spp.*	P	Sept.–Nov.	167 days	Unreported	Unreported	11, 12, 14
<i>Acodontaster</i> spp.	L	Nov.–May	91–100 days	Unreported	Unreported	3, 9, 16
<i>Protelpidia murrayi</i> / <i>Peniagone vignoni</i>	L	Unreported	60–90 days	Unreported	1498–9986	6

References: [1] Bosch et al. 1987; [2] Bosch 1989; [3] Bosch and Pearse, 1990; [4] Galley, 2004; [5] Galley 2005; [6] Galley et al. 2008; [7] Leys and Ereskovsky, 2006; [8] Maldonado, 2006; [9] McClintock and Pearse, 1987; [10] McClintock et al. 2005; [11] Pearse and Bosch, 1986; [12] Pearse et al. 1991; [13] Sahade et al. 2004; [14] Stanwell-Smith and Clarke, 1998; [15] Stanwell-Smith and Peck, 1998; [16] Strathmann et al. 2006.

**Table 2** Modeling scenario details

Pre-competency period and pelagic larval durations (PLD) are given in days.

Scenario	Release location	Release depth (m)	Particles released	Pre-competency period	Pelagic larval duration (PLD)	Start date	End date
AndLow	Andvord (MBA) –64.85946, –62.57267	456	10,000	8	23	12/1/2015	12/23/2016
FlaLow	Flandres (FI) –65.07292, –63.16805	546	10,000	8	23	12/1/2015	12/23/2016
AndHigh	Andvord (MBA) –64.85946, –62.57267	456	10,000	35, 60, 90, 120	150	12/1/2015 - 12/15/2015	4/28/2016
FlaHigh	Flandres (FI) –65.07292, –63.16805	546	10,000	35, 60, 90, 120	150	12/1/2015 - 12/15/2015	4/28/2016

a settlement period of 15 days during which larvae swim toward the seafloor at 1 mm/s (Sahade et al. 2004; Strathmann et al. 2006). In general, results of AndLow and FlaLow simulations are also representative of WAP sponges (Porifera). Particles in these scenarios were released from MBA in Andvord Bay (AndLow) and FI in Flandres Bay (FlaLow) on December 1. AndHigh and FlaHigh simulations represent larvae with high dispersal potential based on

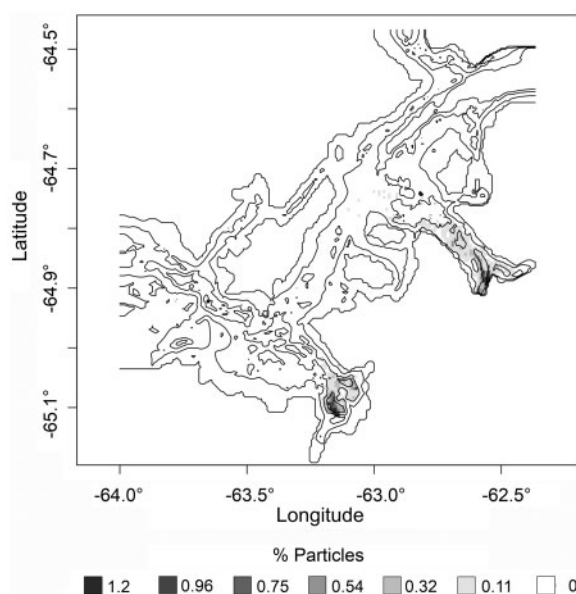
Echinoderm larvae, mostly asteroids (Table 1) with pre-competency periods of 35–120 days, no directed swimming behavior (i.e., passive particles) and a PLD of 150 days (Bosch et al. 1987; McClintock and Pearse 1987; Bosch 1989; Bosch and Pearse 1990; Pearse and McClintock 1990; Galley et al. 2005, 2008; Grange 2005). Though there are some reports of Antarctic Echinoderms with PLDs longer than 150 days (Bosch and Pearse 1990; Pearse et al.

1991; Stanwell-Smith and Clarke 1998), this is the maximum duration we could model. Particles were released from MBA in Andvord Bay (AndHigh) and FI in Flandres Bay (FlaHigh) every day at midnight for the first 15 days of December generating 15 different simulations to assess the effect of release date (Table 2). In all simulations, 10,000 particles were released  $\sim 50$  mab to avoid unrealistic dispersal prior to competency due to the reflective seafloor boundary. We are confident that 10,000 particles reasonably captured the statistical variability of dispersal pathways in our study as the variance of larval dispersal distances changed little when particle number was doubled from 5,000 to 10,000 (Supplementary Figure 1). The open-ocean boundaries in the model domain were non-reflective and particles projected to cross these boundaries stopped at the boundary for the remainder of the simulation and were interpreted to have left the domain. Particles that contacted the seafloor after the pre-competency period was reached stopped moving and had successfully settled. Results from our model simulations represent the dispersal of larvae from an individual during a single austral summer (December 1–April 28) spawning event in the absence of mortality. We consider the influences of population-level fecundity, mortality, and dispersal patterns on overall connectivity in our study region in the “Discussion” section.

### Statistical analyses

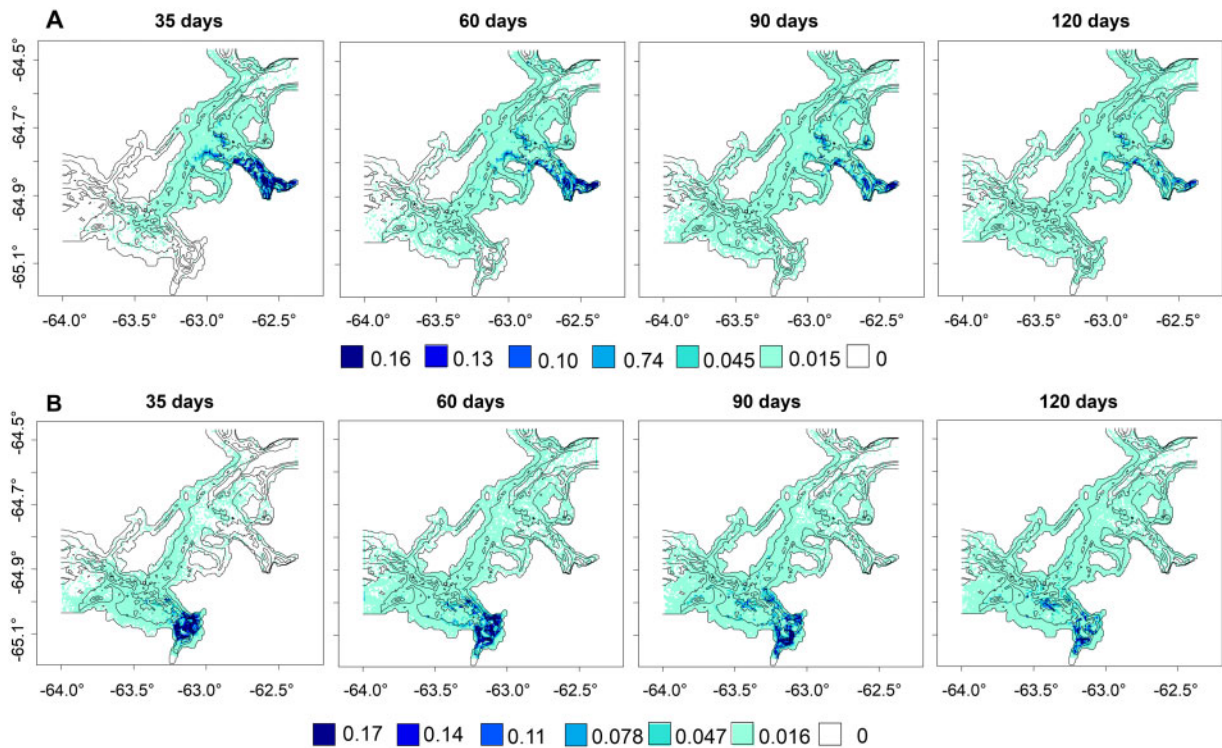
At the end of each model simulation, the percentage of particles settled in the model domain and those that crossed open-ocean boundaries were tabulated. A  $0.005^\circ \times 0.01^\circ$  grid was applied to the particle distributions using the “mapplot” package in R (Gerritsen 2018) to generate heatmaps of settled particle distributions (Figs 2, 3, and 4). For AndHigh and FlaHigh scenarios, these heatmaps represent pooled distributions from all 15 simulations (i.e., a total of 150,000 larvae each). The mean dispersal distance of larvae for each simulation was calculated as the mean cumulative distance particles had traveled by the end of the simulation. For AndHigh and FlaHigh scenarios, this was calculated for each pre-competency period. The dispersal distance we calculated is an overestimate of the linear distance a particle traveled from release to settlement but provides an overall measure of movement for comparison.

We also investigated the influence of currents and katabatic wind events on larval movements. Wind speeds were measured from an AWS atop Useful Island in the Gerlache Strait ( $64.725^\circ$  S,  $62.816^\circ$

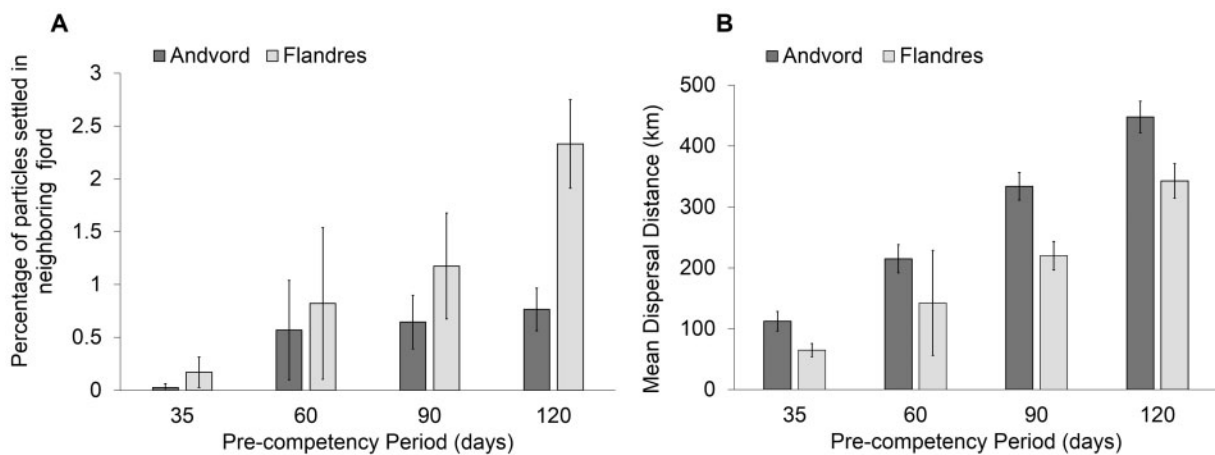


**Fig. 2** Settled particle distributions after 23-day simulations of 10,000 larvae released from Andvord Bay (AndLow) and Flandres Bay (FlaLow). Shading corresponds to the settled particle percentage per  $0.005^\circ \times 0.01^\circ$  grid cell. Bathymetric contours represent 0, 200, 400, 600, and 800 m isobaths.

W) during December 2015–April 2016 and the direction rotated  $60^\circ$  counter-clockwise such that positive wind speeds correspond to the down-fjord direction out of Andvord Bay (Lundegaard et al. 2020). Original, 10-min wind speeds of the along-fjord wind component were down-sampled to generate a 3-hourly time series using the “decimate” function in R (Ligges et al. 2015). We use wind speed observations rather than modeled winds because while the general pattern of these winds is reproduced well by the model, we want to compare dispersal patterns to known times of strong water exchange caused by katabatic winds (Lundegaard et al. 2019). Current velocity was determined from 3-hourly output of ROMS predicted velocity components within the surface and bottom depth layer of the model domain at particle release locations. Time-series of current velocities and the along-fjord component of wind speeds were correlated with the timing of the maximum distance each particle traveled in a single 3-h period during simulations of AndHigh and FlaHigh scenarios using Spearman correlation (correlation coefficient reported as “rho”). Cross-correlation was conducted to investigate correlation and lag between time series and significance was determined as lags exceeding the 5% critical values. Finally, the dominant frequencies of variability in these time series were determined via spectral analysis using the “pspectrum” function in R (Barbour et al. 2019).



**Fig. 3** Settled particle distributions at the end of April for all 15 high-dispersal simulations of 10,000 larvae each released from (A) Andvord Bay (AndHigh) and (B) Flandres Bay (FlaHigh). Panels represent precompetency periods of 35, 60, 90, and 120 days. Blue shades indicate the percentage of particles per  $0.005^\circ \times 0.01^\circ$  grid cell and bathymetric contours indicate the 0, 200, 400, 600, and 800 m isobaths.



**Fig. 4** (A) The percentage of particles (+SD) settled within the neighboring fjord when released from Andvord Bay (dark bars, AndHigh) and Flandres Bay (light bars, FlaHigh) for 35, 60, 90, and 120-day precompetency periods. (B) Mean dispersal distance (km, +SD) for particles from all 15 simulations of AndHigh (dark bars) and FlaHigh (light bars) scenarios across different pre-competency periods.

## Results

### Low-dispersal-potential simulations: AndLow and FlaLow

In the AndLow simulation, particles settled in  $<1$  day after competency was reached, on average, indicating that many particles remained near the

seafloor during initial dispersal. However, some particles were mixed upward more than 300 m reaching a minimum depth of 118 m. The mean dispersal distance of these simulated larvae was  $23.88 \pm 5.41$  km; however, no particles exited the model domain during the 23 days. In fact, only 0.22% of particles exited Andvord Bay and settled within the Gerlache Strait

(GER), leaving more than 99% of particles settled within Andvord Bay, predominantly in basins <8 km from the release location (Fig. 2). In the FlaLow simulation, particles remained closer to the seafloor with a maximum vertical displacement of 256 m. No particles exited Flandres Bay and the mean dispersal distance was  $10.64 \pm 2.04$  km, roughly half that of the AndLow simulation. 1.02% of particles left the inner basin (FI) where they were released to settle at the fjord mouth (FMO), which is 6 km from the release point. For comparison, 10.3% of particles in the AndLow simulation settled in basin MBB, a similar lateral distance from the release point indicating that retention within the inner basins of Flandres Bay was greater than in Andvord Bay. Retentive features could be seen in the particle distributions in the inner basins of Flandres Bay throughout the simulation. For AndLow and FlaLow simulations, no particles settled in the adjacent fjord (Fig. 2).

#### High-dispersal-potential simulations: AndHigh and FlaHigh

In all 15 simulations of the AndHigh scenario, a retentive feature was observed in MBB which recirculated particles toward MBA, increasing the retention time of particles within the fjord (Supplementary Fig. 2, right). Particles first exited Andvord Bay via the southwest edge of the fjord mouth into the Gerlache Strait at a depth of ~240 m (236.16–240.97 m) 8.6 days ( $\pm 2$  days) after release. On average, it took 9.47 days ( $\pm 1.97$  days) for particles to first enter the surface layer (<35 m depth), and 33.5 days ( $\pm 6$  days) for the first particle to reach the inner basins of Flandres Bay (FI). After 1 day of settlement (i.e., on Day 36) 24% of particles had settled, predominantly within Andvord Bay (21.31%), indicating that many particles had remained close to the seafloor during dispersal. By Day 60, almost 75% of particles had settled within Andvord Bay with an additional 16.8% settled in the Gerlache Strait; however, no particles had settled within Flandres Bay though there were particles present in the fjord by this time. By Day 90, nearly all particles (>98%) had settled and no additional particles had reached Flandres Bay. By the end of the 150-day simulations, all particles had settled (except those which had exited the model domain via open-ocean boundaries), and on average 0.03% settled in Flandres Bay. Patterns of initial movements were similar for simulations of 60, 90, and 120-day pre-competency periods. The percentage of particles settling in the adjacent fjord increased with increasing

pre-competency period but remained low reaching a maximum of only 1.58% for all simulations (Fig. 3A).

There were no clear patterns in particle settlement across release dates, though particle releases on December 5, 8, 9, and 11th resulted in the earliest arrival of particles into Gerlache Strait (GER) i.e., after 6.125–6.875 days. Particles first exited the model domain via the central Gerlache Strait boundary (GER) after 35.5 days ( $\pm 2.88$  days), the northern Gerlache Strait boundary (GER-N) after 36.2 days ( $\pm 2.4$  days), and via the southern Gerlache Strait boundary (GER-S) after 51.2 days ( $\pm 8.9$  days). Overall, 19.49–39.18% of all high-dispersal particles exited the model domain over the course of the simulations depending on the pre-competency period. Up to 30% of particles exited the domain across the central Gerlache Strait boundary (GER) alone.

In simulations of the FlaHigh scenario, particles were entrained in retentive circulation features within the inner basins of Flandres Bay after initial release (Supplementary Fig. 2, left) and eventually moved into the mouth of Flandres Bay (FMO) where they became more dispersed. On average, it took 14.69 days ( $\pm 4.18$  days) for particles to first enter the surface layer (<35 m). Particles entered the bordering Central Gerlache Strait (GER-S) within 12.25 days ( $\pm 2.5$  days). Approximately 22 days later ( $\pm 3.7$  days), the first particles entered Andvord Bay, and moved to the inner basins within 42.65 days ( $\pm 6$  days) after release. Particles first exited the model domain via the southern Gerlache Strait boundary after 34.65 days ( $\pm 4.9$  days) and it took 48.875 ( $\pm 4.7$  days) and 55.6 days ( $\pm 6.7$  days), for particles to exit the domain via the two Gerlache Strait boundaries, GER and GER-N, respectively. These transport times are comparable to simulations of particles released from Andvord Bay (AndHigh). The greatest export of particles (13%) occurred across the southern Gerlache Strait boundary (GER-S) for simulations of larvae with a 120-day pre-competency period and varied from 7.1% to 19.9% in total across all boundaries. Settlement in Andvord Bay was low; on average, 0.17%, 0.82%, 1.18%, and 2.33% of particles from Flandres Bay settled within Andvord Bay for pre-competency periods of 35, 60, 90, and 120 days, respectively (Fig. 3B). For particles with a pre-competency period of 35 days, only 5 of the 15 simulations experienced successful transport from FI into IBA. For the FI to IBA connection to be present in all 15 simulations, a pre-competency period of >90 days was required. For all pre-competency periods investigated, particles

released on December 8th entered the Gerlache Strait fastest (in 9 days), and the percentage of particles settled within Andvord Bay was highest in this simulation. A greater proportion of particles successfully settled in the adjacent fjord when released from Flandres Bay than from Andvord Bay for all pre-competency periods (Fig. 4A). However, more than four times as many particles settled in FI during FlaHigh simulations compared to those settling in MBA during AndHigh simulations (22% versus 4.82%, respectively) even when pre-competency period was long (120 days). Overall, the mean dispersal distance increased with increasing pre-competency period, but the dispersal distances of particles in FlaHigh simulations were lower than those in AndHigh simulations for all pre-competency periods ( $64.95 \pm 10.8$  km to  $411.1 \pm 21.6$  km versus  $112.2 \pm 16$  km to  $507.2 \pm 13$  km) (Fig. 4B). For reference, the furthest linear distance between settlement locations or open-ocean boundaries was  $\sim 100$  km.

#### Surface winds and currents

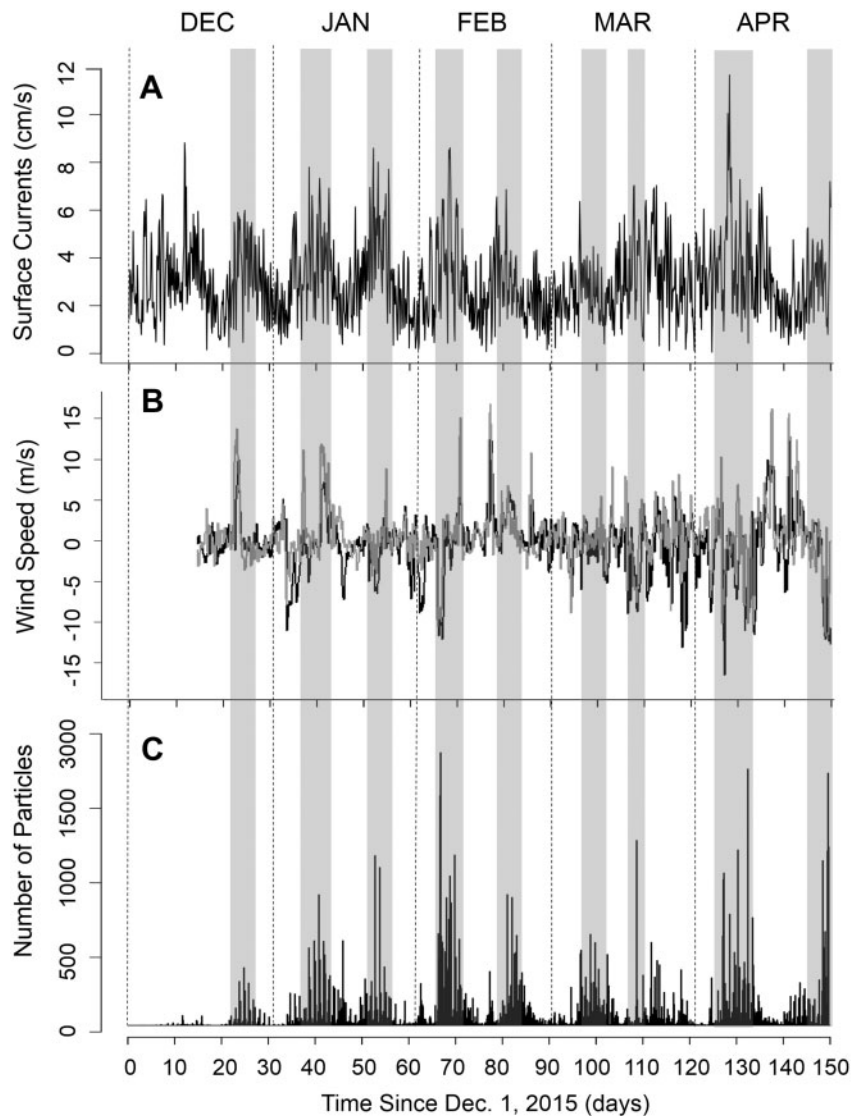
The time of maximum horizontal and vertical transport of each particle during a single 3-h period in the 15 simulations of AndHigh and FlaHigh was determined and histograms of these data were generated. The histogram for AndHigh simulations was multi-modal with slight periodic signals and peaks at  $\sim 68$ , 130, and 150 days (Fig. 5). A similar distribution for FlaHigh simulations had peaks at 127, 132, and 149 days (Fig. 6). Correlation analyses between the AndHigh distribution and down-fjord wind speeds revealed a very weak positive correlation ( $\rho = 0.098$ ). Cross-correlation analysis indicated that increased down-fjord winds during the preceding 9 h significantly affected particle transport, and this effect could persist for nearly 6 days. Spectral analysis revealed that the dominant periodicities of the horizontal transport distribution matched those of the  $O_1$  and  $K_1$  tidal constituents with frequencies of  $\sim 24$  h as well as dominant 15–20-day periodicities of surface wind speeds (Supplementary Fig. 3). These tidal periodicities have been measured from oceanographic moorings in the Gerlache Strait previously (Lundesgaard et al. 2020). Similar periodicities of  $\sim 24$  h and 15–20 days were also present in the distribution of particle exit times across open-ocean boundaries in the central Gerlache Strait. Particles released around December 5–11, 2015 were exported from the fjords more rapidly in both AndHigh and FlaHigh scenarios. Although AWS wind speed data is not available prior to December 15, 2015, shipboard measurements in Andvord Bay revealed a very strong

down-fjord katabatic wind event around December 10 with wind speeds  $>25$  m/s. Lundesgaard et al. (2019) simulated this event and found that it could export the upper 35 m of water from the fjord into the Gerlache Strait. The average surface current velocity around December 8, 2015 in Andvord Bay (MBA) was 3.7 cm/s, more than twice the full time series average. Therefore, it is likely that wind events of similar and even reduced magnitude could transport particles that are near the surface. Direct comparison of particle transport times and observed down-fjord wind events within Flandres Bay was not possible during this study. However, peak times of horizontal particle transport also matched the timing of dominant tidal frequencies and surface current velocities in FI (Fig. 6). The highest surface current velocity in Flandres Bay occurred on Day 128 of the model, reaching  $>9$  cm/s and remaining above 3 cm/s for 24-h, corresponding to one of the peaks in the horizontal transport distribution. Overall, there was a stronger correlation between maximum horizontal transport times and surface current velocities for particles released from Flandres Bay than from Andvord Bay ( $\rho = 0.202$  and 0.154, respectively). Cross-correlation analyses indicated that this positive correlation is significant for up to about 3 days following elevated surface currents in AndHigh simulations but up to 6 days in FlaHigh simulations. Surface wind speeds and current velocities were very weakly correlated with the times of maximum vertical transport of particles for both AndHigh and FlaHigh (Supplementary Figs 4 and 5). Peak times of maximum particle advection (both horizontally and vertically) generally match times of maximum particle export across open-ocean boundaries (Supplementary Fig. 6).

## Discussion

We simulated the dispersal of benthic megafaunal larvae with varying degrees of dispersal potential during austral summer within two glaciomarine fjords along the West Antarctic Peninsula. Our results are based upon a numerical model that simulates the circulation of this region and we assume that this model provides a realistic representation of the regional hydrodynamics as demonstrated by Hahn-Woernle et al. (2020). We note that sea ice can influence circulation dynamics in this region as early as late March that is not captured by this model. For larvae with low dispersal potential, we found very limited dispersal ( $<24$  km) and no exchange between neighboring fjords within the 23-day simulations indicating that there is a limited

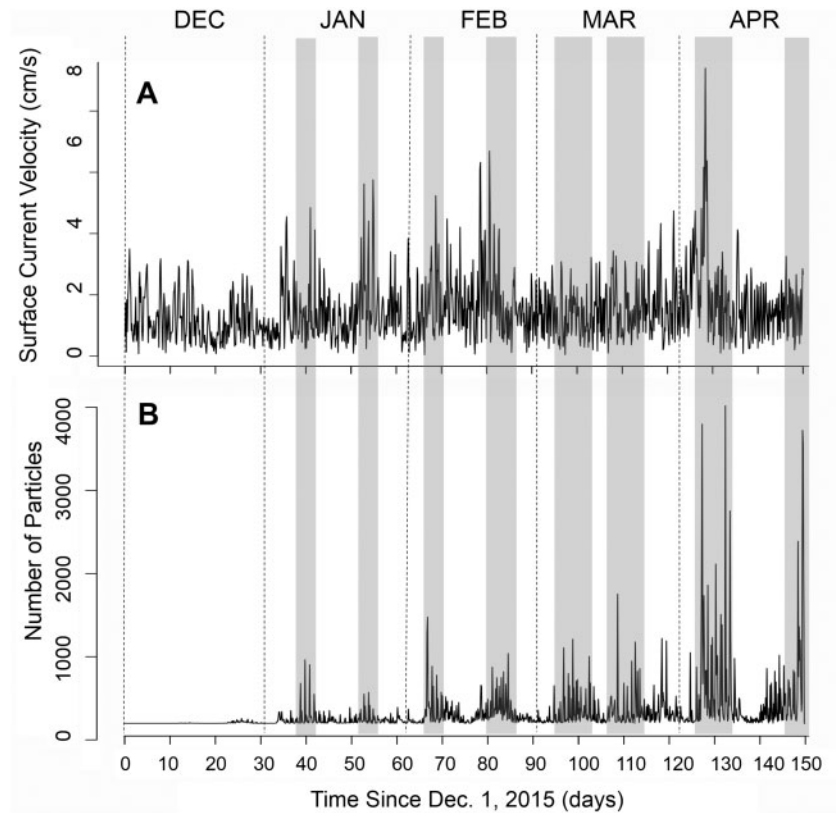




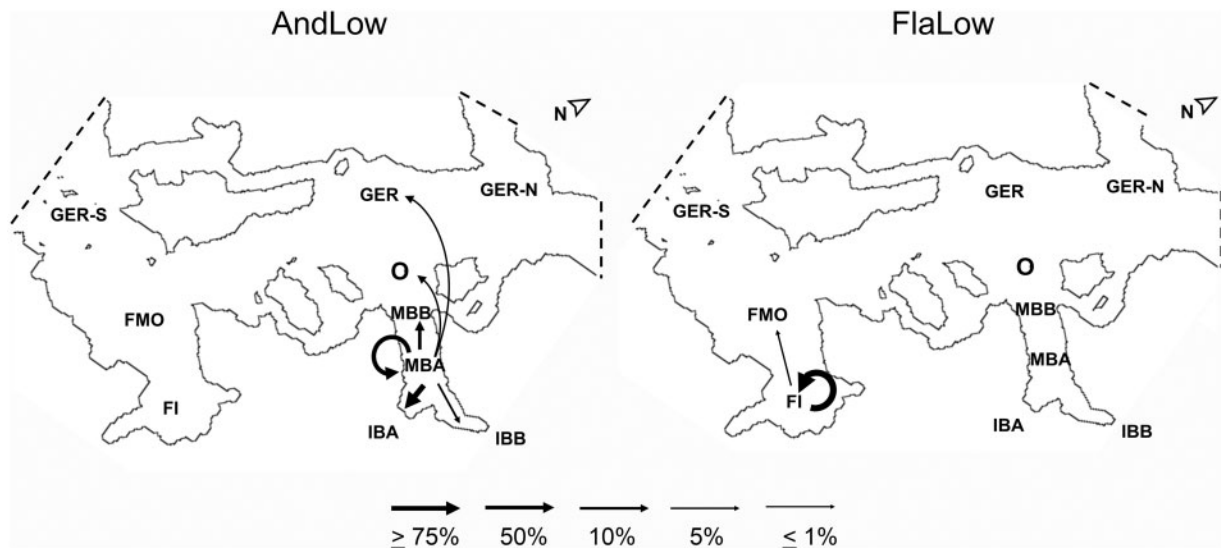
**Fig. 5** (A) Surface current velocity (cm/s) measured at MBA, (B) along-fjord surface wind speed (m/s) measured at an AWS in Gerlache Strait (light line) and predicted by the model (black line) and (C) the time of maximum horizontal transport for 15 simulations of the AndHigh scenario. Peaks of the transport distribution are highlighted in gray. All data were sampled every 3 h and dotted lines delineate calendar months that are labeled at the top for reference. Note that negative wind speeds are oriented up-fjord, while positive speeds are down-fjord.

pathway for connectivity between populations in these fjords (Fig. 7). These simulations are representative of tunicate and sponge larvae with extremely short pelagic stages (e.g., 1 h to 2 weeks) and weak swimming behavior (Sahade et al. 2004; Lambert 2005; Leys and Ereskovsky 2006; Maldonado 2006; Strathmann et al. 2006; Ben-Shlomo et al. 2010). The proportion of self-recruitment (i.e., settlement in the fjord basin from which they were released) was high, reaching up to 22%, and we conclude that this is likely an important process for maintaining abundant populations of low dispersing organisms especially within the middle and inner basins (MBA, IBA, IBB, FI). Photographic surveys have documented

adult populations of several tunicate species in Andvord and Flandres Bays (Grange and Smith 2013; Ziegler et al. 2017) though the abundances and dominant species vary. Tunicate species turnover between fjords is unlikely to be caused by food competition alone as these locations experience similar levels of annual productivity (M. Vernet, pers. comm.) and is instead likely aided by dispersal-limitation. Our results indicate the potential for differences in population genetic structure of low dispersing organisms between Andvord and Flandres Bays. Other studies have found genetic structure in tunicate populations along the Chilean coast over very small (<10 km) spatial scales (Giles



**Fig. 6** (A) Surface current velocity (cm/s) at FI, (B) time of maximum horizontal transport for 15 simulations of the FlaHigh scenario. Modes of the transport distribution are highlighted in gray. All data were sampled every 3 h and dotted lines delineate calendar months that are labeled at the top for reference.



**Fig. 7** Conceptual connectivity diagrams illustrating settlement between regions for low dispersal simulations (AndLow and FlaLow). Lines connect release points (MBA and FI) to regions in which particles settled successfully and are weighted by the percentage of settled particles. Regions with no lines reaching them did not experience settlement during the simulations. Dashed lines represent open-ocean boundaries.

et al. 2018), but the only population genetic studies of tunicates in the Antarctic have focused on connectivity across the Antarctic Circumpolar Current

and Polar Front (e.g., Demarchi et al. 2010). Some tunicates, including *Callitris verrucosa*, have been observed releasing larvae during the winter (Sahade

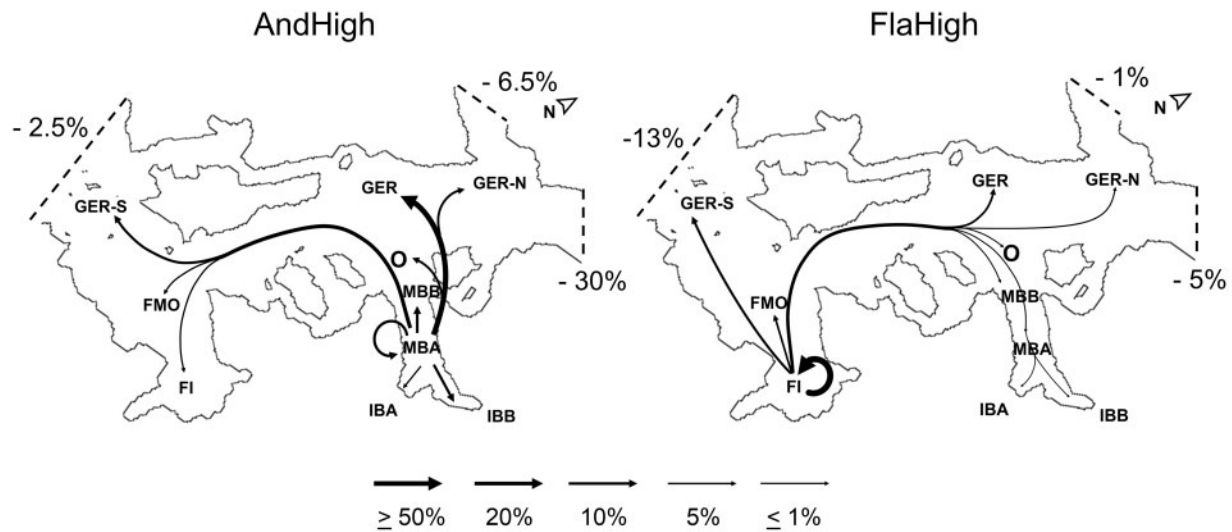
et al. 2004), but it is unlikely that larval dispersal distances would be greater for this species during winter when the presence of sea ice decouples water flow from atmospheric forcing (Lundesgaard et al. 2020). Therefore, we expect increased retention of low-dispersing larvae released during winter resulting in even shorter dispersal distances and increased self-recruitment (Swearer et al. 2002). Based on our results, we conclude that Andvord and Flandres Bays are not significant sources of low-dispersing larvae (e.g., tunicates, sponges) to neighboring fjords within our study region or to the greater West Antarctic Peninsula Shelf (Fig. 7).

Isolated populations maintained by self-recruitment are particularly sensitive to changes in local conditions and stochastic events (Hastings and Botsford 2006). In glaciomarine fjords, stochastic events impacting the benthos may result from turbidity events, glacial sedimentation, and ice scour in shallower regions (<200 m). The populations with the greatest proportion of self-recruitment in our study (i.e., MBA, IBB, IBA, and FI) occur in locations where sediment accumulation rates within the fjords are relatively high and expected to increase with future climate warming (Koppes et al. 2015; Eidam et al. 2019). Increased sedimentation will dilute the organic carbon food source to benthos and could more rapidly bury sessile forms and settling larvae, thereby increasing larval mortality and reducing essential self-recruitment. Additionally, it is expected that warming temperatures could increase meltwater input to the fjords (Dierssen et al. 2002) that can affect vertical mixing and the strength of estuarine circulation within the fjord (Jenkins 2011; Sciascia et al. 2013; Carroll et al. 2015; Straneo and Cenedese 2015; Cape et al. 2019). These processes also affect biogeochemistry and productivity (Dierssen et al. 2002), and could indirectly increase the export of larvae from fjords by entraining larvae into surface layers that are then more likely to be exported by katabatic wind events.

In this study, we simulated larvae originating from only two within-fjord locations, while additional larval sources from stepping-stone populations are likely to exist in suitable habitat in other locations inside the fjord and in the Gerlache Strait (e.g., sedimented basins, fjord walls, dropstones) (Grange and Smith 2013; Ziegler et al. 2017). To fully evaluate the role of stepping-stones for connectivity of populations with low-dispersing larvae, additional sampling and modeling studies are needed.

We also simulated the dispersal of larvae with high dispersal potential that were released from Andvord and Flandres Bays over a 15-day period

in December. Long pre-competency periods increased both the mean dispersal distance and the influence of oceanographic conditions on larval settlement distributions. We found that settlement in the adjacent fjord increased with increasing pre-competency period. While connectivity between Andvord and Flandres Bays occurred during all 150-day simulations, <3% of all particles settled within the adjacent fjord and self-recruitment was high suggesting that populations within these fjords are ecologically isolated (Fig. 8). This supports the hypothesis that some components of the benthic community are recruitment-limited (e.g., dropstone fauna, Ziegler et al. 2017) and that dispersal processes contribute to the species turnover observed between fjords, even for organisms with seemingly high dispersal potential (Grange and Smith 2013). Although there is evidence of demersal swimming behavior in some echinoderms (Chia et al. 1984), this has not been documented for Antarctic species and was not included in our model parameterization. However, we expect that organisms with such behavior would experience greater isolation and reduced exchange between fjords. Increased dispersal may be achieved during periods of katabatic winds. We found that lateral and vertical transport of larvae increased during katabatic wind events and this may have indirectly increased the percentage of larvae exported to the broader WAP shelf. Thus, katabatic winds may be an important mechanism for providing dispersal pathways between the fjord populations we investigated and regions on the northern WAP shelf. Once larvae are exported from the fjords, the northeasterly flow of the Gerlache Strait and Antarctic Circumpolar Current west of Anvers Island could carry them rapidly toward the north. There is evidence of population genetic structure in a brittle star (*Ophionotus victoriae*) with otherwise high dispersal capabilities that mirrors this proposed trajectory (Hunter and Halanych 2008). Overall, we conclude that populations of organisms with a high dispersal potential (e.g., some asteroids and other echinoderms) in Andvord and Flandres Bays do not exchange significant amounts of larvae but may be significant sources of larvae to the broader WAP shelf, especially to northern WAP regions. For larvae with greater swimming capacities than investigated in our study, exchange between Andvord and Flandres Bays may still be low if swimming entrains larvae into surface layers that are more easily exported by katabatic winds and subsequently transported in the dominant northeasterly currents of the Gerlache Strait. Katabatic winds also affect retentive features in fjords. For example, in Wilhelmina Bay, a



**Fig. 8** Conceptual connectivity diagrams illustrating settlement between regions for high dispersal simulations (AndHigh and FlaHigh). Lines connect release points (MBA and FI) to regions in which particles settled successfully and are weighted by the percentage of settled particles. Regions with no lines reaching them did not experience settlement during the simulations. Percentages of particles exiting the domain across each open-ocean boundary (dashed lines) are provided.

fjord just to the north of Andvord Bay, katabatic winds have been linked with aggregations of Antarctic krill inside the fjord that are a key prey species for higher trophic levels in the WAP (Nowacek et al. 2011). Therefore, the influence of these episodic winds may be complex and should be investigated further.

Dispersal models are limited by the parameterization of life-history traits including fecundity, larval behavior, development type and timing, and mortality. Direct observation of larval behavior has only been conducted for a few Antarctic species (e.g. *Cnemidocarpa verrucosa*) and is much easier for short-lived, low-dispersing organisms. Thus, little is known about the development and behavior of most organisms producing high-dispersing larvae. In dispersal models, the fecundity dictates the number of larvae simulated by the model, and larger numbers better capture the statistical variability of larval trajectories. However, models are computationally restricted to numbers of larvae that may not be representative of a full population nor the full spawning capacity of an individual over an entire reproductive season. Our study modeled an individual fecundity of 10,000 that is appropriate for Antarctic benthos based on published data available (Table 1). Dispersal model results are also sensitive to larval mortality, which is typically assumed occur at a fixed level for the duration of the development and settlement periods. We chose not to prescribe any larval mortality during our simulations because pelagic larval mortality estimates are highly variable,

ranging from 3% to 20% of larvae per day (Rumrill 1990; Cowen et al. 2000; Doherty et al. 2004; Connolly and Baird 2010), and post-settlement processes (e.g., competition and predation) can cause mortality rates as high as 96% (Doherty et al. 2004). Therefore, settlement rates from our model represent the most optimistic estimate of larval supply to a location, while actual recruitment of individuals could be substantially lower.

We can assess the effects of mortality and population size on larval migration between locations with the equation  $P' = L * P * \exp(-m * PLD)$ ,  $P'$  is the number of larvae that survive and settle at a particular location,  $L$  is the larval supply from the origin location,  $P$  is the proportion of larvae settling at the desired end location,  $m$  is the daily rate of mortality, and  $PLD$  is the transport time. Our model estimated that 1.58% of high-dispersing larvae released from Andvord Bay with a pre-competency period of 120 days settled successfully within Flandres Bay. On average, these larvae spent 123.7 days in the water column. With an estimated larval mortality rate of 0.5% per day, only 0.85% of larvae are expected to successfully settle in Flandres Bay. If the mortality rate is increased to 5% per day, the percentage of successfully settling larvae is reduced to only 0.003% which is  $< 1$  individual per generation, and at a mortality rate of 20% per day, no larvae ( $2.85 \times 10^{-11}$ ) successfully settle in Flandres Bay. To maintain a migration rate of 100 individuals per generation, larval mortality could not exceed 0.4% per day. Conversely, the total larval supply required to

maintain 100 migrations per generation at 20% per day larval mortality is on the order of  $3.5 \times 10^{12}$  larvae. Assuming an individual fecundity of 10,000 as in our model, this requires a population of  $3.5 \times 10^8$  individuals which is one order of magnitude greater than the estimated population of the most abundant ophiuroid (*Ophionotus victoriae*) in the middle basin of Andvord Bay and three orders of magnitude greater than the least abundant asteroids (Grange and Smith 2013). Therefore, to maintain substantial ecological connectivity between Andvord and Flandres Bays without additional stepping-stone populations, organisms must have a very high fecundity and/or experience very low mortality during the dispersal process.

## Conclusions

We simulated the dispersal of larvae released from two glaciomarine fjords of the West Antarctic Peninsula using coupled high-resolution hydrodynamic and particle-tracking models. Our simulations revealed that ecologically relevant connectivity is lacking between neighboring fjords separated by less than 50 km for organisms assumed to have low-dispersal potential (e.g., tunicates and sponges) and was limited even for organisms that spend 120 days developing in the plankton (e.g., asteroids and other echinoderms). Katabatic winds increased the horizontal and vertical transport of larvae and indirectly increased the export of high-dispersing larvae from coastal fjords to the northern West Antarctic Peninsula and may be an important driver of connectivity between these regions. Future conditions within these glaciomarine fjords (e.g., increased sedimentation and estuarine circulation) may become increasingly important in controlling the vertical movement and overall dispersal of larvae especially to the broader WAP shelf region.

## Acknowledgments

We thank the United States Antarctic Program staff who assisted in data collection as well as the captains and crews of the AVIB 'Nathaniel B. Palmer' and ASRV 'Laurence M. Gould'. The technical support and advanced computing resources from the University of Hawaii Information Technology Services - Cyberinfrastructure are gratefully acknowledged.

## Funding

Funding for this research was provided by the National Science Foundation under grant OPP 1443680 to C.R.S.

## Conflict of interest

The authors declare no conflicts of interest.

## References

- Almany GR, Planes S, Thorrold SR, Berumen ML, Bode M, Saenz-Agudelo P, Bonin MC, Frisch AJ, Harrison HB, Messmer V, et al. 2017. Larval fish dispersal in a coral-reef seascape. *Nat Ecol Evol* 1:1–7.
- Arntz WE, Brey T, Gallardo VA. 1994. Antarctic zoobenthos. *Oceanogr Mar Biol Annu Rev* 32:241–304.
- Barbour JA, Parker RL, Kennel J. 2019. Package 'psd'.
- Ben-Shlomo R, Reem E, Douek J, Rinkevich B. 2010. Population genetics of the invasive ascidian *Botryllus schlosseri* from South American coasts. *Mar Ecol Prog Ser* 412:85–92.
- Bidegain G, Bárcena JF, García A, Juanes JA. 2013. LARVAHS: predicting clam larval dispersal and recruitment using habitat suitability-based particle tracking model. *Ecol Modell* 268:78–92.
- Bilton DT, Paula J, Bishop J. 2002. Dispersal, genetic differentiation and speciation in estuarine organisms. *Estuar Coast Shelf Sci* 55:937–52.
- Bingham BL, Young CM. 1991. Larval behavior of the ascidian *Ecteinascidia turbinata* Herdman; an in situ experimental study of the effects of swimming on dispersal. *J Exp Mar Bio Ecol* 145:189–204.
- Bosch I. 1989. Contrasting modes of reproduction in two antarctic asteroids of the genus *Porania*, with a description of unusual feeding and non-feeding larval types. *Biol Bull* 177:77–82.
- Bosch I, Beauchamp KA, Steele ME, Pearse JS. 1987. Development, metamorphosis, and seasonal abundance of embryos and larvae of the Antarctic sea urchin *Sterechinus neumayeri*. *Biol Bull* 173:126–35.
- Bosch I, Pearse JS. 1990. Developmental types of shallow-water asteroids of McMurdo Sound, Antarctica. *Mar Biol* 104:41–6.
- Bouchet P, Taviani M. 1992. The Mediterranean deep-sea fauna: pseudopopulations of Atlantic species? *Deep Sea Res Part A. Oceanogr Res Pap* 39:169–84.
- Brasier MJ, Harle J, Wiklund H, Jeffreys RM, Linse K, Ruhl HA, Glover AG. 2017. Distributional Patterns of Polychaetes Across the West Antarctic Based on DNA Barcoding and Particle Tracking Analyses. *Front Mar Sci* 4.
- Bryan-Brown DN, Brown CJ, Hughes JM, Connolly RM. 2017. Patterns and trends in marine population connectivity research. *Mar Ecol Prog Ser* 585:243–56.
- Buhl-Mortensen L, Heiseter T. 1993. Mollusc fauna along an offshore-fjord gradient. *Mar Ecol Prog Ser* 97:209–24.
- Cape MR, Vernet M, Pettit EC, Wellner J, Truffer M, Akie G, Domack E, Leventer A, Smith CR, Huber BA. 2019. Circumpolar Deep Water Impacts Glacial Meltwater Export and Coastal Biogeochemical Cycling Along the West Antarctic Peninsula. *Front Mar Sci* 6:1–23.
- Carroll D, Sutherland DA, Shroyer EL, Nash JD, Catania GA, Stearns LA. 2015. Modeling Turbulent Subglacial Meltwater Plumes: implications for Fjord-Scale Buoyancy-Driven Circulation. *J Phys Oceanogr* 45:2169–85.

- Chia FS, Buckland-Nicks J, Young CM. 1984. Locomotion of marine invertebrate larvae: a review. *J Can Zoo* 62:1205–22.
- Clarke A. 1992. Reproduction in the cold: thorsen revisited. *Invertebr Reprod Dev* 22:175–83.
- Clarke A. 2008. Antarctic marine benthic diversity: patterns and processes. *J Exp Mar Bio Ecol* 366:48–55.
- Clarke A, Griffiths HJ, Barnes DKA, Meredith MP, Grant SM. 2009. Spatial variation in seabed temperatures in the Southern Ocean: implications for benthic ecology and biogeography. *J Geophys Res Biogeosciences* 114:1–11.
- Connolly SR, Baird AH. 2010. Estimating dispersal potential for marine larvae: dynamic models applied to scleractinian corals. *Ecology* 91:3572–83.
- Cook AJ, Holland PR, Meredith MP, Murray T, Luckman A, Vaughan DG. 2016. Ocean forcing of glacier retreat in the western Antarctic Peninsula. *Science* 353:283–6.
- Cowen R, Gawarkiewicz G, Pineda J, Thorrold S, Werner F. 2007. Population Connectivity in Marine Systems: an Overview. *Oceanography* 20:14–21.
- Cowen RK, Lwiza KMM, Sponaugle S, Paris CB, Olson DB. 2000. Connectivity of marine populations: open or closed?. *Science* 287:857–9.
- Cowen RK, Sponaugle S. 2009. Larval Dispersal and Marine Population Connectivity. *Ann Rev Mar Sci* 1:443–66.
- Crandall ED, Toonen RJ, Selkoe KA, ToBo Laboratory. 2019. A coalescent sampler successfully detects biologically meaningful population structure overlooked by F-statistics. *Evol Appl* 12:255–65.
- Cunningham KM, Canino MF, Spies IB, Hauser L. 2009. Genetic isolation by distance and localized fjord population structure in Pacific cod (*Gadus macrocephalus*): limited effective dispersal in the northeastern Pacific Ocean. *Can J Fish Aquat Sci* 66:153–66.
- Damerau M, Matschiner M, Salzburger W, Hanel R. 2012. Comparative population genetics of seven notothenioid fish species reveals high levels of gene flow along ocean currents in the southern Scotia Arc. *Antarctica. Polar Biol* 35:1073–86.
- Damerau M, Matschiner M, Salzburger W, Hanel R. 2014. Population divergences despite long pelagic larval stages: lessons from crocodile icefishes (Channichthyidae). *Mol Ecol* 23:284–99.
- Demarchi M, Chiappero MB, Tatián M, Sahade R. 2010. Population genetic structure of the Antarctic ascidian *Aplidium falklandicum* from Scotia Arc and South Shetland Islands. *Polar Biol* 33:1567–76.
- Dierssen HM, Smith RC, Vernet M. 2002. Glacial meltwater dynamics in coastal waters west of the Antarctic peninsula. *Proc Natl Acad Sci* 99:1790–5.
- Doherty PJ, Dufour V, Galzin R, Hixon MA, Meekan MG, Planes S. 2004. High mortality during settlement is a population bottleneck for a tropical surgeonfish. *Ecology* 85:2422–8.
- Döös K, Kjellsson J, Jonsson B. 2013. TRACMASS - a Lagrangian trajectory model. In: Soomere T, Quak E, editors. Preventive methods for coastal protection: towards the use of ocean dynamics for pollution control. Cham: Springer International Publishing. p. 225–49.
- Egbert GD, Bennett AF, Foreman MGG. 1994. TOPEX/Poseidon tides estimated using a global inverse model. *J Geophys Res* 99:24821–52.
- Egbert GD, Erofeeva SY. 2002. Efficient inverse modeling of barotropic ocean tides. *J Atmos Ocean Technol* 19:183–204.
- Eidam EF, Nittrouer CA, Lundesgaard Ø, Homolka KK, Smith CR. 2019. Variability of sediment accumulation rates in an Antarctic fjord. *Geophys Res Lett* 46:271–80.
- Galley EA. 2004. Responses of benthic organisms on the deep Antarctic continental shelf to a highly seasonal food supply. PhD thesis. University of Southampton, UK.
- Galley EA, Tyler PA, Clarke A, Smith CR. 2005. Reproductive biology and biochemical composition of the brooding echinoid *Amphipneustes lorioli* on the Antarctic continental shelf. *Mar Biol* 148:59–71.
- Galley EA, Tyler PA, Smith CR, Clarke A. 2008. Reproductive biology of two species of holothurian from the deep-sea order Elaspoda, on the Antarctic continental shelf. *Deep Res Part II Top Stud Oceanogr* 55:2515–26.
- Gerritsen H. 2018. Package 'mapplots'.
- Giles EC, Petersen-Zúñiga C, Morales-González S, Quesada-Calderón S, Saenz-Agudelo P. 2018. Novel microsatellite markers for *Pyura chilensis* reveal fine-scale genetic structure along the southern coast of Chile. *Mar Biodivers* 48:1777–86.
- Grange LJ. 2005. Reproductive success in Antarctic marine invertebrates. PhD thesis. University of Southampton, UK.
- Grange LJ, Smith CR. 2013. Megafaunal communities in rapidly warming fjords along the West Antarctic Peninsula: hotspots of abundance and beta diversity. *PLoS One* 8:e77917.
- Hahn-Woernle L, Powell B, Lundesgaard Ø, van Wessem M. 2020. Sensitivity of the summer upper ocean heat content in a Western Antarctic Peninsula fjord. *Prog Oceanogr* 183:1–14.
- Haidvogel DB, Arango H, Budgell WP, Cornuelle BD, Curchitser E, Di Lorenzo E, Fennel K, Geyer WR, Hermann AJ, Lanerolle L, et al. 2008. Ocean forecasting in terrain-following coordinates: formulation and skill assessment of the Regional Ocean Modeling System. *J Comput Phys* 227:3595–624.
- Hastings A, Botsford LW. 2006. Persistence of spatial populations depends on returning home. *Proc Natl Acad Sci USA* 103:6067–72.
- Hedrick P. W., Miller PS. 1992. Conservation genetics: techniques and fundamentals. *Ecol Appl* 2:30–46.
- Hilario A, Metaxas A, Gaudron SM, Howell KL, Mercier A, Mestre NC, Ross RE, Thurnherr AM, Young C. 2015. Estimating dispersal distance in the deep sea: challenges and applications to marine reserves. *Front Mar Sci* 2:1–14.
- Hill AE. 1991. Advection-diffusion-mortality solutions for investigating pelagic larval dispersal. *Mar Ecol Prog Ser* 70:117–28.
- Hoffman JI, Peck LS, Linse K, Clarke A. 2011. Strong population genetic structure in a broadcast-spawning Antarctic marine invertebrate. *J Hered* 102:55–66.
- Hofmann EE, Klinck JM, Lascara CM, Smith DA. 1996. Water mass distribution and circulation west of the Antarctic Peninsula. *Antarct Res Ser* 70:61–80.
- Holsinger KE, Weir BS. 2009. Genetics in geographically structured populations: defining, estimating and interpreting  $F_{ST}$ . *Nat Rev Genet* 10:639–50.

- Hunter RL, Halanych KM. 2008. Evaluating connectivity in the brooding brittle star *Astrotoma agassizii* across the Drake Passage in the Southern Ocean. *J Hered* 99:137–48.
- Jablonski D, Lutz RA. 1983. Larval ecology of marine benthic invertebrates: paleobiological implications. *Biol Rev* 58:21–89.
- Jenkins A. 2011. Convection-driven melting near the grounding lines of ice shelves and tidewater glaciers. *J Phys Oceanogr* 41:2279–94.
- Kettle AJ, Haines K. 2006. How does the European eel (*Anguilla anguilla*) retain its population structure during its larval migration across the North Atlantic Ocean?. *Can J Fish Aquat Sci* 63:90–106.
- Klinck JM, Hofmann EE, Beardsley RC, Salihoglu B, Howard S. 2004. Water-mass properties and circulation on the west Antarctic Peninsula continental shelf in Austral fall and winter 2001. *Deep Res Part II Top Stud Oceanogr* 51:1925–46.
- Koppes M, Hallet B, Rignot E, Mouginot J, Wellner JS, Boldt K. 2015. Observed latitudinal variations in erosion as a function of glacier dynamics. *Nature* 526:100–3.
- Krug PJ. 2001. Bet-hedging dispersal strategy of a specialist marine herbivore: a settlement dimorphism among sibling larvae of *Alderia modesta*. *Mar Ecol Prog Ser* 213:177–92.
- Lambert G. 2005. Ecology and natural history of the protochordates. *Can J Zool* 83:34–50.
- Ledoux JB, Tarnowska K, Gérard K, Lhuillier E, Jacquemin B, Weydmann A, Féral JP, Chenuil A. 2012. Fine-scale spatial genetic structure in the brooding sea urchin *Abatus cordatus* suggests vulnerability of the Southern Ocean marine invertebrates facing global change. *Polar Biol* 35:611–23.
- Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, Holt RD, Shurin JB, Law R, Tilman D, et al. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett* 7:601–13.
- Levin SA. 1974. Dispersion and population interactions. *Am Nat* 108:207–28.
- Levin SA. 1976. Population dynamic models in heterogeneous environments. *Annu Rev Ecol Syst* 7:287–310.
- Leys SP, Ereskovsky AV. 2006. Embryogenesis and larval differentiation in sponges. *Can J Zool* 84:262–87.
- Ligges U, Short T, Kienzle P, Schnackenberg S, Billingham D, Borchers H-W, Carezia A, Dupuis P, Eaton JW, Farhi E, et al. 2015. Package ‘signal’.
- Lundesgaard Ø, Powell B, Merrifield M, Hahn-Woernle L, Winsor P. 2019. Response of an Antarctic Peninsula fjord to summer katabatic wind events. *J Phys Oceanogr* 49:1485–502.
- Lundesgaard Ø, Winsor P, Truffer M, Merrifield M, Powell B, Statscewich H, Eidam E, Smith CR. 2020. Hydrography and energetics of a cold subpolar fjord: Andvord Bay, western Antarctic Peninsula. *Prog Oceanogr* 181:1–16.
- Maldonado M. 2006. The ecology of the sponge larva. *Can J Zool* 84:175–94.
- Marquet P, Fortin M, Pineda J, Wallin D, Clark J, Wu Y, Bollens S, Jacobi C, Holt R. 1993. Ecological and evolutionary consequences of patchiness: a marine-terrestrial perspective. In: Levin SA, Powell TM, Steele JH, editors. *Patch Dynamics*, Vol. 96. Berlin Heidelberg: Springer-Verlag. p. 277–304.
- Matschiner M, Hanel R, Salzburger W. 2009. Gene flow by larval dispersal in the Antarctic notothenioid fish *Gobionotothen gibberifrons*. *Mol Ecol* 18:2574–87.
- McClintock JB, Pearse JS. 1987. Reproductive biology of the common Antarctic crinoid *Promachocrinus kerguelensis* (Echinodermata: Crinoidea). *Mar Biol* 96:375–83.
- McClintock JB, Amsler CD, Baker BJ, van Soest R. 2005. Ecology of Antarctic marine sponges: an overview. *Integr Comp Biol* 45:359–68.
- Mileikovsky SA. 1971. Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Mar Biol* 10:192–213.
- Mouquet N, E. Miller T, Daufresne T, M. Kneitel J. 2006. Consequences of varying regional heterogeneity in source-sink metacommunities. *Oikos* 113:481–8.
- Mouquet N, Loreau M. 2003. Community patterns in source-sink metacommunities. *Am Nat* 162:544–57.
- Mullineau LS, Mills SW. 1997. A test of the larval retention hypothesis in seamount-generated flows. *Deep Res I* 44:745–70.
- North EW, Adams EE, Schlag Z, Sherwood CR, He R, Hyun KH, Socolofsky SA. 2011. Simulating oil droplet dispersal from the deepwater horizon spill with a Lagrangian approach. *Geophys Monogr Ser* 195:217–26.
- North EW, Hood RR, Chao SY, Sanford LP. 2006. Using a random displacement model to simulate turbulent particle motion in a baroclinic frontal zone: a new implementation scheme and model performance tests. *J Mar Syst* 60:365–80.
- North EW, Schlag Z, Hood RR, Li M, Zhong L, Gross T, Kennedy VS. 2008. Vertical swimming behavior influences the dispersal of simulated oyster larvae in a coupled particle-tracking and hydrodynamic model of Chesapeake Bay. *Mar Ecol Prog Ser* 359:99–115.
- Nowacek DP, Friedlaender AS, Halpin PN, Hazen EL, Johnston DW, Read AJ, Espinasse B, Zhou M, Zhu Y. 2011. Super-aggregations of krill and humpback whales in Wilhelmina Bay, Antarctic Peninsula. *PLoS One* 6:e19173.
- Palmer AR, Strathmann RR. 1981. Scale of dispersal in varying environments and its implications for life histories of marine invertebrates. *Oecologia* 48:308–18.
- Palumbi SR. 1994. Genetic divergence, reproductive isolation, and marine speciation. *Annu Rev Ecol Syst* 25:547–72.
- Palumbi SR. 2003a. Population genetics, demographic connectivity, and the design of marine reserves. *Ecol Appl* 13:146–58.
- Palumbi SR. 2003b. Ecological subsidies alter the structure of marine communities. *Proc Natl Acad Sci* 100:11927–8.
- Paris CB, Chérubin LM, Cowen RK. 2007. Surfing, spinning, or diving from reef to reef: effects on population connectivity. *Mar Ecol Prog Ser* 347:285–300.
- Paris CB, Helgers J, van Sebille E, Srinivasan A. 2013. Connectivity modeling system: a probabilistic modeling tool for the multi-scale tracking of biotic and abiotic variability in the ocean. *Environ Model Softw* 42:47–54.
- Pearse JS, Bosch I. 1986. Are the feeding larvae of the commonest Antarctic asteroid really demersal?. *Bull Mar Sci* 39:477–84.
- Pearse JS. 1994. Cold-water echinoderms break “Thorson’s Rule”. In: Young CM, Eckelbarger KJ, editors. *Reproduction, larval biology, and recruitment of the*

- deep-sea benthos. New York: Columbia University Press. p. 27–43.
- Pearse JS, McClintock JB. 1990. A comparison of reproduction by the brooding Spatangoid echinoids *Abatus shackletoni* and *A. nimrodi* in McMurdo Sound, Antarctica. *Invertebr Reprod Dev* 17:181–91.
- Pearse JS, McClintock JB, Bosch I. 1991. Reproduction of Antarctic benthic marine invertebrates: tempos, modes, and timing. *Am Zool* 31:65–80.
- Pechenik JA. 1999. On the advantages and disadvantages of larval stages in benthic marine invertebrate life cycles. *Mar Ecol Prog Ser* 177:269–97.
- Peck LS, Convey P, Barnes D. 2005. Environmental constraints on life histories in Antarctic ecosystems: tempos, timings and predictability. *Biol Rev Camb Philos Soc* 81:75–109.
- Piñones A, Hofmann EE, Daly KL, Dinniman MS, Klinck JM. 2013. Modeling the remote and local connectivity of Antarctic krill populations along the western Antarctic Peninsula. *Mar Ecol Prog Ser* 481:69–92.
- Poulin É, Féral J-P. 1996. Why are there so many species of brooding Antarctic echinoids?. *Evolution* 50:820–30.
- Reijmer CH, van Meijgaard E, van den Broeke MR. 2005. Evaluation of temperature and wind over Antarctica in a Regional Atmospheric Climate Model using 1 year of automatic weather station data and upper air observations. *J Geophys Res D Atmos* 110:1–12.
- Riesgo A, Taboada S, Avila C. 2015. Evolutionary patterns in Antarctic marine invertebrates: an update on molecular studies. *Mar Genomics* 23:1–13.
- Rumrill SS. 1990. Natural mortality of marine invertebrate larvae. *Ophelia* 32:163–98.
- Ryan WBF, Carbotte SM, Coplan JO, O'Hara S, Melkonian A, Arko R, Weissel RA, Ferrini V, Goodwillie A, Nitsche F, Bonczkowski J, et al. 2009. Global multi-resolution topography synthesis. *Geochem Geophys Geosyst* 10:1–10.
- Sahade R, Tatián M, Esnal GB. 2004. Reproductive ecology of the ascidian *Cnemidocarpa verrucosa* at Potter Cover South Shetland Islands, Antarctica. *Mar Ecol Prog Ser* 272:131–40.
- Savidge DK, Amft JA. 2009. Circulation on the West Antarctic Peninsula derived from 6 years of shipboard ADCP transects. *Deep Res Part I Oceanogr Res Pap* 56:1633–55.
- Sciascia R, Straneo F, Cenedese C, Heimbach P. 2013. Seasonal variability of submarine melt rate and circulation in an East Greenland fjord. *J Geophys Res Ocean* 118:2492–506.
- Selkoe KA, Toonen RJ. 2006. Microsatellites for ecologists: a practical guide to using and evaluating microsatellite markers. *Ecol Lett* 9:615–29.
- Selkoe KA, Toonen RJ. 2011. Marine connectivity: a new look at pelagic larval duration and genetic metrics of dispersal. *Mar Ecol Prog Ser* 436:291–305.
- Schlag ZR, North EW. 2012. Lagrangian TRANSPORT (LTRANS) v.2 model User's Guide. Technical Report of the University of Maryland Center for Environmental Science, Cambridge (MD): Horn Point Laboratory. p. 1–183.
- Shanks AL. 2009. Pelagic larval duration and dispersal distance revisited. *Biol Bull* 216:373–85.
- Shanks AL, Grantham BA, Carr MH. 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecol Appl* 13:159–69.
- Shchepetkin AF, McWilliams JC. 2009. Correction and commentary for “Ocean forecasting in terrain-following coordinates: formulation and skill assessment of the regional ocean modeling system” by Haidvogel et al., *J. Comp. Phys.* 227:3595–624. *J Comput Phys* 228:8985–9000.
- Siegel DA, Kinlan BP, Gaylord B, Gaines SD. 2003. Lagrangian descriptions of marine larval dispersion. *Mar Ecol Prog Ser* 260:83–96.
- Siegel DA, Mitarai S, Costello CJ, Gaines SD, Kendall BE, Warner RR, Winters KB. 2008. The stochastic nature of larval connectivity among nearshore marine populations. *Proc Natl Acad Sci* 105:8974–9.
- Sköld M, Wing SR, Mladenov PV. 2003. Genetic subdivision of a sea star with high dispersal capability in relation to physical barriers in a fjordic seascape. *Mar Ecol Prog Ser* 250:163–74.
- Slatkin M. 1993. Isolation by distance in equilibrium and non-equilibrium populations. *Evolution* 47:264–79.
- Slatkin M. 1995. A measure of population subdivision based on microsatellite allele frequencies. *Genetics* 139:457–62.
- Smith DA, Hofmann EE, Klinck JM, Lascara CM. 1999. Hydrography and circulation of the West Antarctic Peninsula Continental Shelf. *Deep Res Part I Oceanogr Res Pap* 46:925–49.
- Spall MA, Jackson RH, Straneo F. 2017. Katabatic wind-driven exchange in fjords. *J Geophys Res Ocean* 122:8246–62.
- Stanwell-Smith D, Clarke A. 1998. Seasonality of reproduction in the cushion star *Odontaster validus* at Signy Island, Antarctica. *Mar Biol* 131:479–87.
- Stanwell-Smith D, Peck LS. 1998. Temperature and embryonic development in relation to spawning and field occurrence of larvae of three Antarctic echinoderms. *Biol Bull* 194:44–52.
- Stanwell-Smith D, Peck LS, Clarke A, Murray AWA, Todd CD. 1999. The distribution, abundance and seasonality of pelagic marine invertebrate larvae in the maritime Antarctic. *Philos Trans R Soc B Biol Sci* 354:471–84.
- Starr M, Himmelman JH, Theriault J-C. 1990. Direct coupling of marine invertebrate spawning with phytoplankton blooms. *Science* 247:1071–4.
- Straneo F, Cenedese C. 2015. The dynamics of Greenland's glacial fjords and their role in climate. *Ann Rev Mar Sci* 7:89–112.
- Strathmann RR. 1974. The spread of sibling larvae of sedentary marine invertebrates. *Am Nat* 108:29–44.
- Strathmann RR. 1985. Feeding and nonfeeding larval development and life-history evolution in marine invertebrates. *Annu Rev Ecol Systl* 16:339–61.
- Strathmann RR, Kendall LR, Marsh AG. 2006. Embryonic and larval development of a cold adapted Antarctic ascidian. *Polar Biol* 29:495–501.
- Sunnucks P. 2000. Efficient genetic markers for population biology. *Trends Ecol Evol* 15:199–203.
- Sutherland DA, Roth GE, Hamilton GS, Mernild SH, Stearns LA, Straneo F. 2014. Quantifying flow regimes in a Greenland glacial fjord using iceberg drifters. *Geophys Res Lett* 41:8411–20.
- Svendsen H, Thompson RORY. 1978. Wind-driven circulation in a fjord. *J Phys Oceanogr* 8:703–12.



- Swearer SE, Shima JS, Hellberg ME, Thorrold SR, Jones GP, Robertson DR, Morgan SG, Selkoe KA, Ruiz GM, Warner RR. 2002. Evidence of self-recruitment in demersal marine populations. *Bull Mar Sci* 70:251–71.
- Thatje S. 2012. Effects of capability for dispersal on the evolution of diversity in Antarctic benthos. *Integr Comp Biol* 52:470–82.
- Thornhill DJ, Mahon AR, Norenburg JL, Halanych KM. 2008. Open-ocean barriers to dispersal: a test case with the Antarctic Polar Front and the ribbon worm *Parborlasia corrugatus* (Nemertea: Lineidae). *Mol Ecol* 17:5104–17.
- Thorson G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol Rev* 25:1–45.
- van Sebille E, Griffies SM, Abernathey R, Adams TP, Berloff P, Biastoch A, Blanke B, Chassignet EP, Cheng Y, Cotter CJ, et al. 2018. Lagrangian ocean analysis: fundamentals and practices. *Ocean Model* 121:49–75.
- Van Wessem JM, Reijmer CH, Morlighem M, Mouginot J, Rignot E, Medley B, Joughin I, Wouters B, Depoorter MA, Bamber JL, et al. 2014. Improved representation of East Antarctic surface mass balance in a regional atmospheric climate model. *J Glaciol* 60:761–70.
- Vignal A, Milan D, SanCristobal M, Eggen A. 2002. A review on SNPs and other types of molecular markers and their use in animal genetics. *Genet Sel Evol* 34:275–305.
- Watson JR, Hays CG, Raimondi PT, Mitarai S, Dong C, McWilliams JC, Blanchette CA, Caselle JE, Siegel DA. 2011. Currents connecting communities: nearshore community similarity and ocean circulation. *Ecology* 92:1193–200.
- Weersing K, Toonen RJ. 2009. Population genetics, larval dispersal, and connectivity in marine systems. *Mar Ecol Prog Ser* 393:1–12.
- Wilson DS. 1992. Complex interactions in metacommunities, with implications for biodiversity and higher levels of selection. *Ecology* 73:1984–2000.
- Wilson NG, Hunter RL, Lockhart SJ, Halanych KM. 2007. Multiple lineages and absence of panmixia in the “circumpolar” crinoid *Promachocrinus kerguelensis* from the Atlantic sector of Antarctica. *Mar Biol* 152:895–904.
- Wilson NG, Schrod M, Halanych KM. 2009. Ocean barriers and glaciation: evidence for explosive radiation of mitochondrial lineages in the Antarctic sea slug *Doris kerguelensis* (Mollusca, Nudibranchia). *Mol Ecol Prog Ser* 18:965–84.
- Woodson CB, McManus MA. 2007. Foraging behavior can influence dispersal of marine organisms. *Limnol Oceanogr* 52:2701–9.
- Wright S. 1943. Isolation by distance. *Genetics* 28:114–38.
- Wright S. 1950. The genetical structure of populations. *Nature* 166:247–9.
- Xu G, McGillicuddy DJ Jr, Mills SW, Mullineaux LS. 2018. Dispersal of hydrothermal vent larvae at East Pacific rise 9–10° N segment. *J Geophys Res Ocean* 123:7877–95.
- Young CM, He R, Emler RB, Li Y, Qian H, Arellano SM, Van Gaest A, Bennett KC, Wolf M, Smart TI, et al. 2012. Dispersal of deep-sea larvae from the intra-American seas: simulations of trajectories using ocean models. *Integr Comp Biol* 52:483–96.
- Ziegler AF, Smith CR, Edwards KF, Vernet M. 2017. Glacial dropstones: islands enhancing seafloor species richness of benthic megafauna in West Antarctic Peninsula fjords. *Mar Ecol Prog Ser* 583:1–14.