


Early life history connectivity of Antarctic silverfish (*Pleuragramma antarctica*) in the Ross Sea

Cassandra M. Brooks^{1,2}  | Jilda Alicia Caccavo³ | Julian Ashford⁴ | Robert Dunbar¹ | Kimberly Goetz⁵ | Mario La Mesa⁶ | Lorenzo Zane³

¹School of Earth, Energy and Environmental Sciences, Stanford University, Stanford, CA, USA

²Environmental Studies, Sustainability, Energy and Environment Complex, University of Colorado Boulder, Boulder, CO, USA

³Dipartimento di Biologia, Università di Padova, Padova, Italy

⁴Department of Ocean, Earth and Atmospheric Sciences, Center for Quantitative Fisheries Ecology, Old Dominion University, Norfolk, VA, USA

⁵National Institute of Water and Atmospheric Research, Wellington, New Zealand

⁶Istituto di Scienze Marine, UOS di Ancona, Ancona, Italy

Correspondence

C. M. Brooks
Email: cassandra.brooks@colorado.edu

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Abstract

A recent population hypothesis for Antarctic silverfish (*Pleuragramma antarctica*), a critical forage species, argued that interactions between life history and circulation associated with glacial trough systems drive circumpolar distributions over the continental shelf. In the Ross Sea, aggregations of eggs and larvae occur under fast ice in Terra Nova Bay, and the hypothesis predicted that dispersing larvae encounter outflow along the western side of Drygalski Trough. The outflow advects larvae towards the shelf-break, and mixing with trough inflow facilitates return toward the inner shelf. To examine the hypothesis, we compared samples of *P. antarctica* collected near Coulman Island in the outflow, along Cray Bank in the inflow, and a third set taken over the rest of the Ross Sea. We ruled out misidentification using an innovative genetic validation. Silverfish larvae comprised 99.5% of the catch, and the highest population densities were found in Drygalski Trough. The results provided no evidence to reject the population hypothesis. Abundance indices, back-calculated hatching dates, length distributions and growth were congruent with a unified early life history in the western Ross Sea, constrained by cryopelagic early stages in Terra Nova Bay. By contrast, a sample in the Bay of Whales revealed much smaller larvae, suggesting either a geographically separate population in the eastern Ross Sea, or westward connectivity with larvae spawned nearby by fish sourced from troughs upstream in the Amundsen Sea. These results illustrate how hypotheses that integrate population structure with life history can provide precise spatial predictions for subsequent testing.

KEYWORDS

Ross Sea, Antarctic silverfish, physical-biological interactions, large-scale circulation, glacial trough systems, Circumpolar Deep Water, life history connectivity, population structure

1 | INTRODUCTION

In the Southern Ocean ecosystem, Antarctic silverfish (*Pleuragramma antarctica*) are a critical forage species that, with Antarctic krill (*Euphausia superba*), typically connect producer trophic levels to those of higher predators (Granata, Zagami, Vacchi, & Guglielmo, 2008; La Mesa & Eastman, 2012; La Mesa, Eastman, & Vacchi,

2004; Smith, Ainley, & Cattaneo-Vietti, 2007; Smith, Ainley, Cattaneo-Vietti, & Hofmann, 2012). The connections occur throughout its life history, which is exclusively pelagic, and the species has a circumpolar distribution over the continental shelves around the Antarctic, including the sub-antarctic South Shetland and South Orkney Islands. In the western Ross Sea (Figure 1a), *P. antarctica* dominates the ichthyoplankton comprising up to 99% of the total

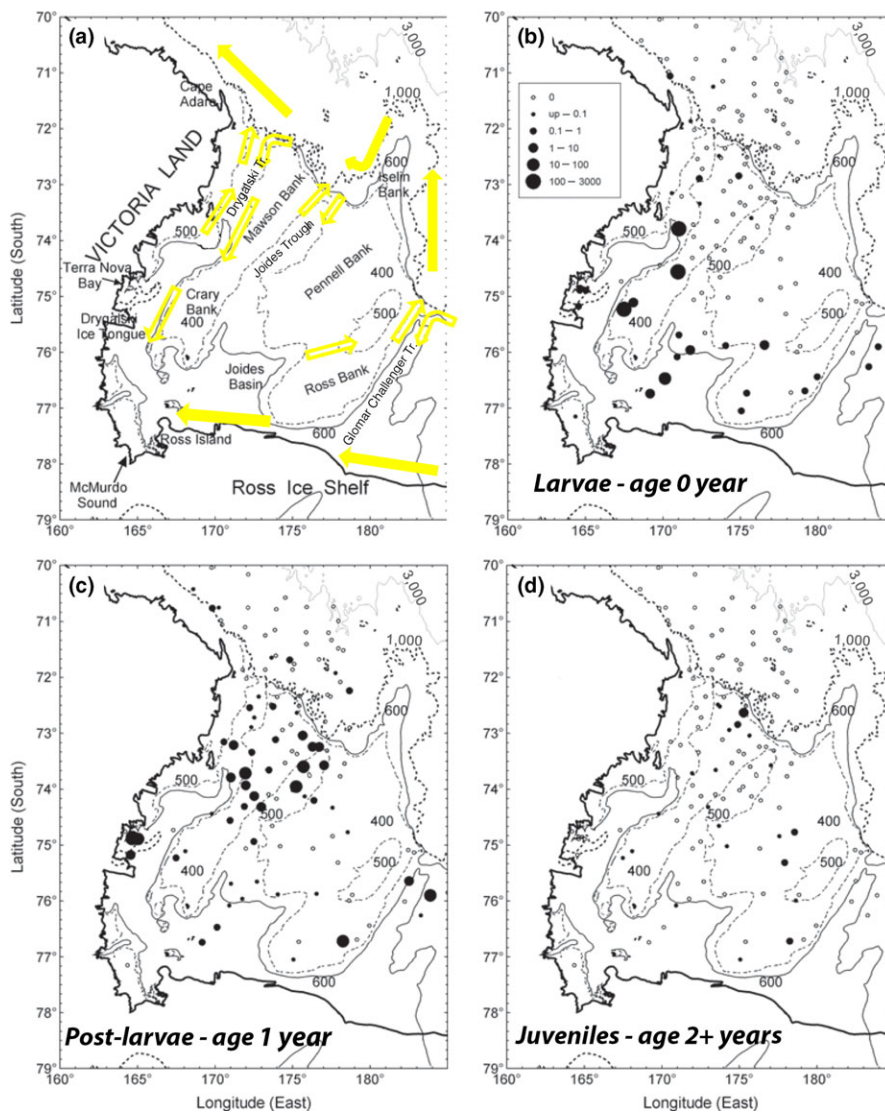


FIGURE 1 Distribution of young silverfish in the upper water column of the western Ross Sea in relation to the shelf circulation, reproduced from La Mesa et al. (2010) and Ashford et al. (2017). Geographically labelled schematic of westward flow along the Ross Ice Shelf and in the Antarctic Slope Current and Front system (filled arrows), and cross-shelf inflows and outflows along troughs (transparent arrows; [a]). Standardized abundances of silverfish at larvae (b), post-larval (c), and juvenile stages (d) in net tows that sampled to a maximum depth of between 130 and 300 m

catch in research surveys over the continental shelf (Granata et al., 2002; Guglielmo, Granata, & Greco, 1998; La Mesa et al., 2010; Vacchi, La Mesa, & Greco, 1999), and occurring in concentrations that extend over the shelf-break and slope (La Mesa et al., 2010; O'Driscoll, Macaulay Gavin, Gauthier, Pinkerton, & Hanchet, 2011).

Aggregations of *P. antarctica* eggs and larvae are consistently found inshore, under winter fast ice in Terra Nova Bay (Guidetti, Ghigliotti, & Vacchi, 2015; Vacchi, La Mesa, Dalu, & Macdonald, 2004; Vacchi et al., 2012) and the species relies on an inactive, energy-efficient strategy (La Mesa & Eastman, 2012), especially in older stages. Lipid sequestration in large sacs composed of adipocytes (Eastman & DeVries, 1989) results in neutral buoyancy and low-energy behavior in which fish are suspended in the water column to feed (La Mesa & Eastman, 2012). *P. antarctica* distribution can be explained by dispersal in regional circulation over the continental shelf (Agostini et al., 2015; Ferguson, 2012; Hubold, 1984; La Mesa, Piñones, Catalano, & Ashford, 2015; La Mesa et al., 2010; Parker et al., 2015). In Terra Nova Bay, the eggs occupy a layer of platelet ice under the fast ice and hatch from mid-November

through December (Vacchi et al., 2004, 2012). A potential second hatching extends into early January (Granata et al., 2002). The larvae have a mean hatching length of 9–9.3 mm standard length (SL; Vacchi et al., 2004, 2012). La Mesa et al. (2010) found distributions of young stages in the upper water column during summer surveys of the western Ross Sea between December and early February (Figure 1). Larvae (SL 7–18 mm, age 0; Figure 1b) were found in large numbers along the western side of the Mawson and Crary Banks, and in smaller numbers in Terra Nova Bay and the Joides Basin. In contrast, post-larvae (SL 30–57 mm, age 1; Figure 1c) occurred in concentrations over the outer shelf corresponding to the Drygalski and Joides Troughs and the Mawson Bank, and along the Glomar Challenger Trough further east (La Mesa et al., 2010). La Mesa et al. (2010) also noted that most *P. antarctica* captured were in areas characterized by a layer of warmer Circumpolar Deep Water (CDW); and the young stages were generally confined to the surface 100 m in the water column, where a productive environment provides favorable conditions for growth (La Mesa & Eastman, 2012). Early growth rates were estimated at 0.15–0.25 mm/day (Guglielmo et al.,

1998; Hubold, 1985; La Mesa et al., 2010), and juveniles aged 2+ were also found near the shelf-break before moving to depth with age.

In a subsequent review of the population structure of *P. antarctica*, Ashford, Zane, Torres, La Mesa, and Simms (2017) developed this life history hypothesis further, arguing that distributions across and along the shelf are maintained by interactions between life history and the circulation associated with glacial trough systems. The circulation in the Ross Sea is generally bathymetrically controlled and the trough systems are oriented north/south, connecting the shelf-break to the inner shelf (Figure 1a). Intrusions of warm CDW from the continental slope are carried along the eastern side of the troughs (Dinniman, Klinck, & Smith, 2003; Orsi & Wiederwohl, 2009) and modified by mixing with Antarctic Surface Water. The modified CDW (MCDW) meets equatorward flow of dense, cold Shelf Water, mixing to form Modified Shelf Water and eventually Antarctic Bottom Water that flows in gravity currents down the slope (Gordon et al., 2009). In the Drygalski and Joides Troughs, southward jets carry the MCDW towards the inner shelf at velocities of 0.3 m/s and disperse it across the neighbouring Mawson and Pennell Banks (Kohut, Hunter, & Huber, 2013). Although reports indicate larvae of *P. antarctica* in McMurdo Sound and off Ross Island (summarized in Ghigliotti, Herasymchuk, Kock, & Vacchi, 2017), the existence of nursery grounds remains undetermined with no evidence so far of consistent aggregations such as those observed in Terra Nova Bay (Ghigliotti et al., 2017). Moreover, otolith chemistry from adults showed no evidence of

mixing, implying a single population in the western Ross Sea (Ferguson, 2012). Developing the life history hypothesis, Ashford et al. (2017) suggested that larvae dispersing from Terra Nova Bay encounter the shelf outflow along the western side of the Drygalski Trough, which advects them toward the shelf-break and productive areas associated with nutrient-rich MCDW. As they grow older, they either mix with the trough inflow, which facilitates return toward the inner shelf (Figure 1a), or reach the slope front (Hubold, 1984) and become entrained in westward flow along the Antarctic Slope Current and Front system (AFS; Ashford et al., 2017).

During February and March of 2013, a United States National Science Foundation (NSF) research cruise in the Ross Sea provided an opportunity to examine cross-shelf dispersal via the trough circulation predicted by the life history hypothesis. By February, larvae of *P. antarctica* are considered to have largely dispersed from Terra Nova Bay to be entrained in flows along the Drygalski Trough. In this paper, we compare three sets of samples; the first taken along Crary Bank corresponding to the inflow including MCDW with a second set taken in the outflow near Coulman Island, and a third set of samples taken from the rest of the Ross Sea: over the Joides and Glomar Challenger Troughs, south of Crary Bank and in the Joides Basin, and at the southern end of the Little America Trough in the Bay of Whales (Figure 2). We examine relative abundances between the three sets of samples in relation to water structure, and length frequency distributions in the context of reported early growth rates and hatching times from the nursery ground at Terra Nova Bay. We also report on a recently hatched group of larvae found late in the

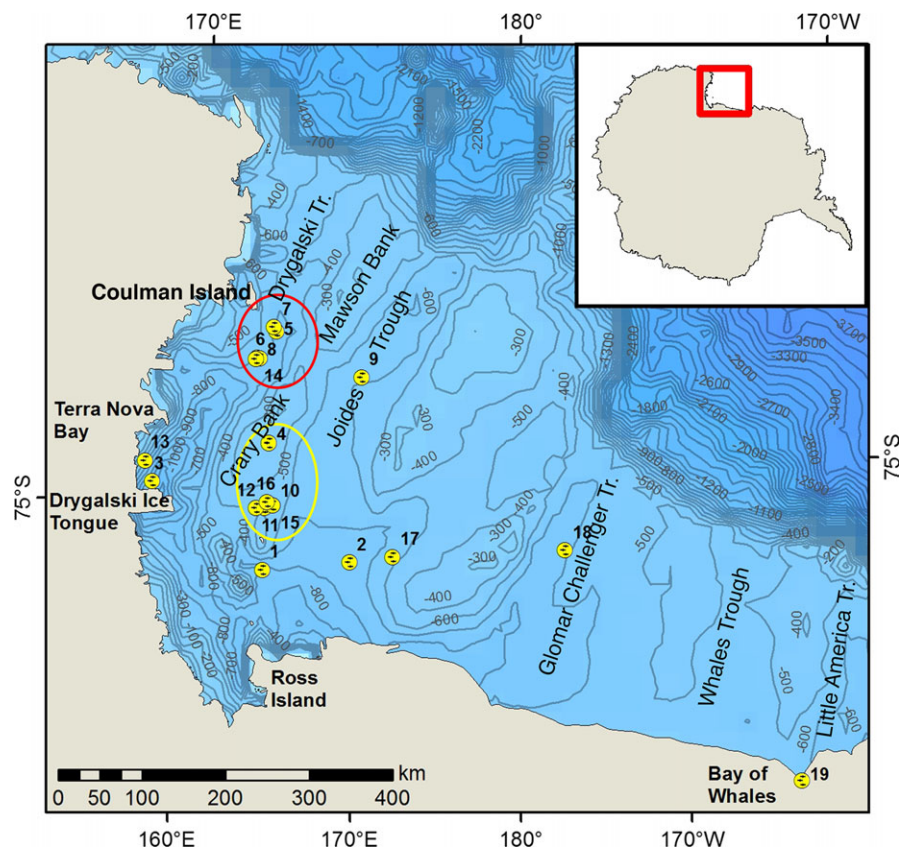


FIGURE 2 Map of the Ross Sea showing locations sampled by Tucker trawl during February and March 2013. Inflow locations along Crary Bank (yellow circle; Locations 4, 10, 11, 12, 15, 16); outflow locations near Coulman Island (red circle; Locations 5, 6, 7, 8, 14)

cruise in the Bay of Whales; a validation method that used genetic markers to test species identifications based on morphological characteristics; and sea-ice distribution in relation to connectivity during early life.

2 | MATERIALS AND METHODS

NSF research cruise NBP13-02 deployed during February–March 2013 to measure the carbon flux in the Ross Sea towards the end of the Antarctic summer, in particular along the edge of the Ross Sea polynya. During these operations, larval fish were sampled at 19 different locations (Table 1, Figure 2) using a Tucker Trawl equipped with either of two nets, one 2 × 2 m mouth and mesh size 700 µm, the other 1 × 1 m mouth and mesh size 300 µm. Thirteen locations were successfully sampled using both nets, towed in succession off the stern of the vessel diagonally through the water column. Tows using the 700 µm net targeted the top 100 m of the water column, while operations using the 300 µm net targeted depths between the surface and ca 300 m; however, this varied with conditions and depth of the water column. The volume of water sampled was measured using a General Oceanics Digital Flowmeter (Model 2030 series), and abundance indices were calculated by normalizing the number of fish caught by volume sampled.

Tows deployed at Locations 4, 10, 11, 12, 15 and 16 corresponded to inflow along the Drygalski Trough and western side of Cray Bank; Locations 5, 6, 7, 8 and 14 corresponded to the outflow along the trough; and Locations 1, 3, 9, 13, 17, 18, and 19 elsewhere in the Ross Sea provided a spatial comparison (Figure 2). Hydrographic data including temperature, salinity and oxygen were collected at each location using CTD casts. At all locations, the presence or absence of MCDW, detected via the CTD casts, was used to confirm that tows corresponded to trough inflow and outflow, respectively. Sea ice data, at 6.25 km resolution, was also examined at sampling locations. This was obtained from the daily Advanced Microwave Scanning Radiometer sea ice concentration data from the University of Bremen (<http://www.iup.uni-bremen.de/seaice/amr/>). All larval fish were sampled from each tow and identified according to morphological characteristics using the guide developed by Kellermann (1989). Standard length (SL) of specimens was measured to the nearest mm. In the case of large catches (>100) of *P. antarctica*, subsamples were selected by thoroughly mixing the catch in a container of seawater and pouring off a volume containing approximately 100 individuals. All fish selected in this way were measured except a small number that were damaged by the net. An adult (SL 171 mm) and a juvenile fish (SL 62 mm) were captured in the 700 µm net at Location 4; an adult (SL 120 mm) in the 700 µm net at Location 12; and two juveniles (SL 49 mm, 52 mm) at Location 18. These individuals were not included in the analysis.

Location no.	Latitude	Longitude	700		300	300 V	
			Date	Depth (m)	Date	Date	Depth (m)
1	-76.417500	167.940300	13 Feb	80	13 Feb		180
2	-76.502152	171.995050	16 Feb	100	16 Feb		195
3	-75.193183	164.177433	22 Feb	91	22 Feb		291
4	-75.082350	169.338017	25 Feb	138	25 Feb		283
5	-73.914742	170.429200	26 Feb	136	26 Feb		386
6	-74.152610	169.506485				27 Feb	379
7	-73.861473	170.368683				28 Feb	348
8	-74.163972	169.604202				1 Mar	334
9	-74.531800	173.530030	2 Mar	83	2 Mar		376
10	-75.750870	169.001587	2 Mar	172	2 Mar		343
11	-75.758728	168.604355	4 Mar	151	4 Mar		325
12	-75.746433	168.239333	5 Mar	264	5 Mar		414
13	-74.956133	164.137667			6 Mar		408
14	-74.165317	169.457317				7 Mar	278
15	-75.752200	168.998400	8 Mar	135	8 Mar		355
16	-75.706467	168.773333	9 Mar	312	9 Mar		151
17	-76.500833	174.010133	10 Mar	143	10 Mar		326
18	-76.492900	-177.968383				11 Mar	338
19	-78.587250	-164.365677	13 Mar	155	13 Mar		320

TABLE 1 Sampling locations in the Ross Sea

Tucker trawl net type 700 and 300 refers to mesh size (µm); V indicates vertical tow off the starboard side; Depths (m) refer to deepest part of the water column sampled.

To test that identification of *P. antarctica* larvae by morphological characteristics was correct, samples were frozen for later genetic analysis. A total of 70 larvae were selected for DNA extraction from tows using the 700 μm net for which frozen larvae were preserved. For locations in the western Ross Sea, 44 larvae ranging from 15 to 26 mm SL were selected by stratified random sampling from the nine tows with the largest catches. For Location 19 in the Bay of Whales, 26 whole larvae were adequately preserved for analysis, and all were used. Genomic DNA was extracted from whole larvae using a standard salting-out protocol. Total genomic DNA was diluted to approximately 100 ng/ μl for use in PCR amplification, and stored at -20°C . The 16S large ribosomal unit and the D-Loop control region of mitochondrial DNA were amplified by PCR (see Figure S1 for details). Approximately 528 base pairs (bp) of 16S rDNA and 349 bp of the D-Loop region were amplified and sequenced (See Figure S1 and Table S1 legends for details). The resultant mitochondrial DNA sequences were then aligned against seven 16S rDNA and sixteen D-Loop region corresponding to sequences of *P. antarctica* retrieved from the nucleotide database NCBI (see Table S1 for GenBank accession numbers). GenBank sequences from three of the most closely related notothenioids *Aethotaxis mitopteryx*, *Dissostichus mawsoni* and *D. eleginoides* (Near et al., 2012) were also included as outgroups (see Table S1 for GenBank accession numbers). The proportion of nucleotide positions at which two sequences differed represented by the p distance was used to calculate genetic distance in MEGA. In addition, a neighbour-joining tree was drawn using the Kimura 2-parameter substitution model, with tree robustness confirmed by 1,000 bootstrap replications.

To describe the growth rate of the larvae, an exponential model was applied to the length frequency distributions over the period of sampling, as reported in previous studies (Hubold, 1985; Keller, 1983; Kellermann, 1986). The model was fitted by linear regression on \log_e transformed data in the form:

$$\log_e \text{SL} = \log_e a + gt,$$

where SL is the standard length in mm, a is the initial SL, g is the instantaneous growth rate and t is time in days. Specific growth rate representing the daily percentage change in size (G , % SL/day) was calculated by multiplying the instantaneous growth rate g by 100, allowing comparison with growth rates from different geographical areas and size ranges. The distribution of hatching dates was back-calculated by applying the growth model to individual size of survivors and date of capture, and pooled by week. We assumed no selective mortality related to different hatching periods (Campana & Jones, 1992) and a minimum size at hatching of 8 mm, corresponding to the minimum size found during field operations.

3 | RESULTS

Tows using both the 700 and 300 μm nets were completed for Locations 4, 10, 11, 12, 15 and 16 along Cray Bank, Location 5 off

Coulman Island, and Locations 1, 2, 3, 9, 17 and 19 over the rest of the Ross Sea. Because of severe winds near Coulman Island, towing operations using the 700 μm net were suspended at Locations 6, 7, 8 and 14, and the 300 μm net was towed vertically off the starboard side of the vessel. At Location 13, the 700 μm net failed and was not retrieved; at Location 18, only the 300 μm net was deployed using a vertical tow (Table 1).

3.1 | Hydrography and sea-ice

Along Cray Bank in the trough inflow, stratification occurred at approximately 30–50 m, with a well defined mixed layer at Locations 11, 12, 15 and 16, although not at Location 4 (Figure 3a). As expected, a layer of warm water was found between 40 and 100 m at all the Cray Bank locations, which was associated with a pronounced oxygen minimum indicating MCDW (Figure 3a). Off Coulman Island in the outflow, surface mixing reached ca 30 m at Location 5 and there was strong stratification at 40–60 m at Locations 6, 8 and 14 with relatively low salinity in the surface layer (Figure 3b). As expected, the hydrographic data showed no evidence of MCDW. A layer of warm water was found at a depth of 30–60 m at Location 5, which was warmer and somewhat deeper at Locations 6, 8 and 14, but this was not associated with an oxygen minimum. However, at the northernmost Location 7, a temperature maximum and oxygen minimum was found between depths of 40–80 m, indicating MCDW (Figure 3b).

Elsewhere, mixing reached 80 m at Location 3 in Terra Nova Bay near the Drygalski Ice Tongue, and more than 140 m at Location 13 in front of the Reeves Glacier (Figure 3c). At Location 1 south of Cray Bank, a warm mixed layer reached ca 50 m; colder water beneath was associated with an oxygen minimum at 60 m. Further east in the Joides Basin, the warm surface layer reached 100 m at Location 2 with a layer of warm water below showing an oxygen minimum between 100 and 150 m, indicating MCDW. At Location 17, the mixed surface layer was colder and MCDW was present but slightly deeper. The temperature in the surface layer was warmer at Location 9 in the Joides Trough, and MCDW was present deeper than at the Drygalski Trough locations, with an oxygen minimum between 80 and 100 m (Figure 3c). MCDW was deeper still at Location 18 in the Glomar Challenger Trough, with surface mixing down to nearly 100 m. Finally, Location 19 in the Bay of Whales showed much less variation in oxygen and temperature over the water column, and lower oxygen at the surface compared to elsewhere (Figure 3c).

Locations along Cray Bank and near Coulman Island were close to the ice edge (Figure 4), with a sharper transition near Coulman Island. Sea-ice covered most of the Drygalski Trough between Coulman Island and Terra Nova Bay, and the western side of Cray Bank. Ice cover was much less dense at sampling locations in the rest of the Ross Sea; Locations 3 and 13 were in the Terra Nova Bay polynya, and open water at Location 19 was consistent with the Ross Ice Shelf polynya. Locations 1, 2, 3 and 9, sampled earlier in the season, showed a relatively warm, well mixed surface layer, whereas the

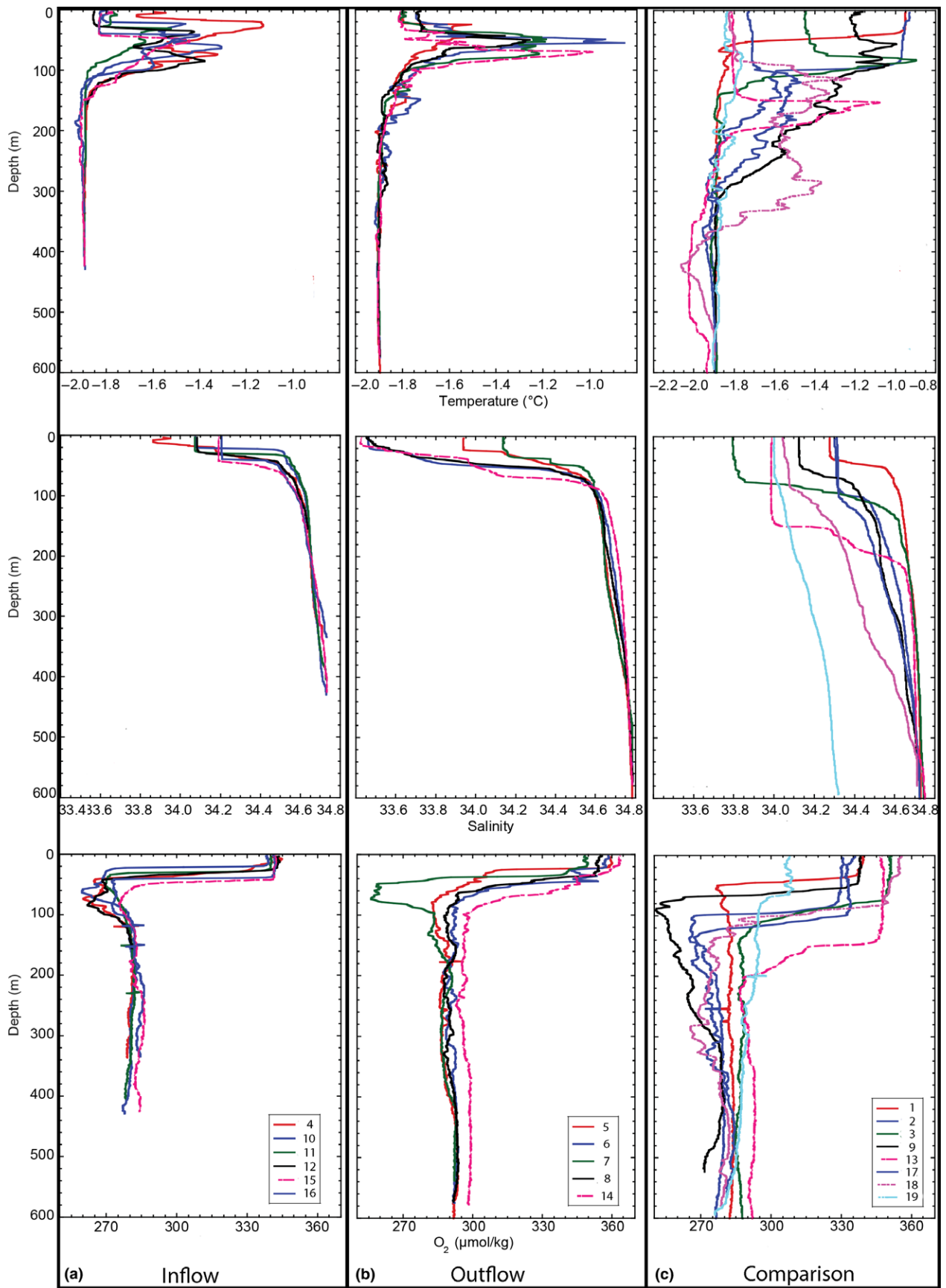


FIGURE 3 CTD profiles showing temperature, salinity and dissolved oxygen for inflow (a) and outflow (b) locations, and locations in the rest of the Ross Sea (c) for comparison

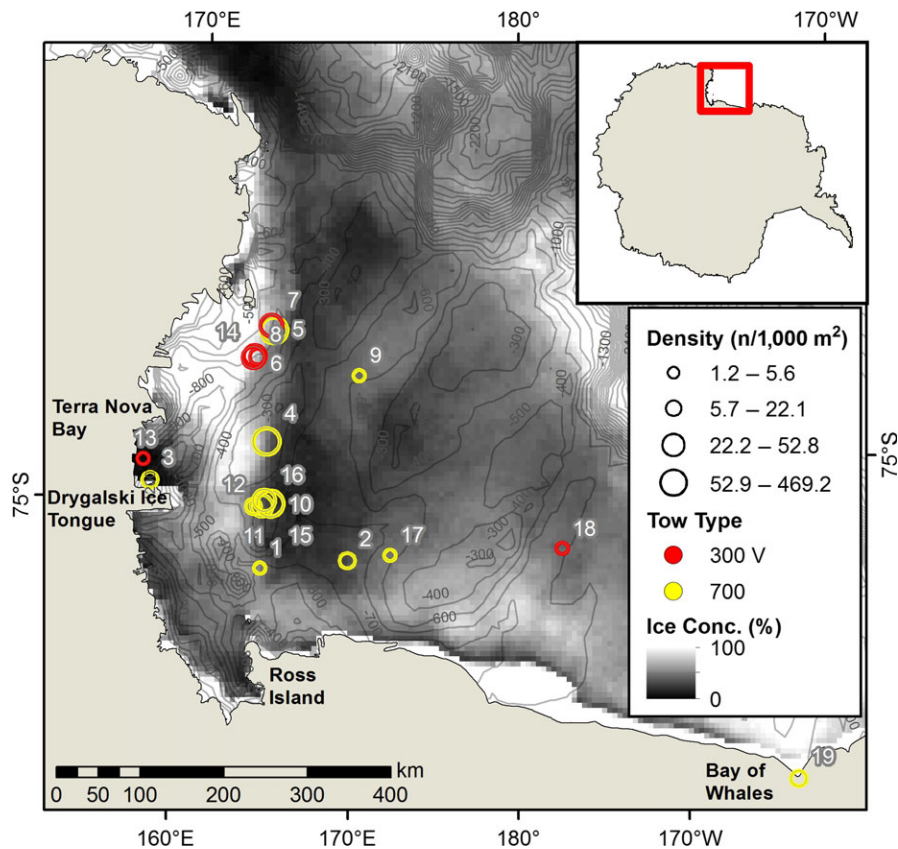


FIGURE 4 Bathymetric map of the Ross Sea, Antarctica showing average ice cover over the duration of the sampling period (13 February–16 March), in relation to abundance indices measured using the 700 μm net (yellow). Abundance indices for vertical tows with the 300 μm net (red) are shown at locations where the 700 μm net could not be deployed due to wind conditions. Since the 700 μm net failed at Location 13, the abundance index shown is for the corresponding diagonal tow of the 300 μm net. Shading represents 100% ice cover (white) to 0% (black)

surface was colder at Locations 13, 17 and 18 sampled later in the season, indicating seasonal cooling. However, freshening in the surface layer contributed strongly to stratification, notably at Locations 6, 8 and 14 near Coulman Island, consistent with melting sea-ice. By contrast at Location 19, weak stratification and freshening throughout the water column (Figure 3c) was consistent with upwelling from deeper melting processes along the front of the ice shelf.

3.2 | Genetic validation

The genetic analyses confirmed the identification of *P. antarctica* larvae by morphological characteristics. As detailed in Table S3, the newly obtained Ross Sea larval sequences were extremely similar to the existing GenBank sequences for *P. antarctica* (uncorrected divergence 0.001 with 16S and 0.004 with D-Loop) and different from those of the outgroups included in the analysis (minimum uncorrected divergence 0.048 with 16S and 0.139 with D-loop). In a neighbour-joining tree, the larval sequences from both the western Ross Sea and Bay of Whales clustered in a single clade with the *P. antarctica* sequences from the NCBI database with 100% bootstrap support, and were clearly differentiated from the D-loop sequences of the phylogenetically closest species (Figure S2, 16S rDNA and Figure S3, D-Loop).

3.3 | Spatial distribution

Based on the validated morphological identifications, more than 99% of the overall catch from all combined tows consisted of larvae of *P. antarctica*. Species from other families were represented, including Channichthyidae, *Trematomus* spp., Bathydraconidae, Paralepididae and Artedidraconidae (Table 2), but these contributed only 50 fish out of a total of 9,519 individuals caught.

For *P. antarctica*, abundance indices were higher using the 700 μm net than the 300 μm net, which sampled much deeper in the water column (Table 3). Using the 700 μm net, the indices varied from 22 to 469/1,000 m³ off Coulman Island and along Cary Bank; with the 300 μm net, they varied between 12 and 32/1,000 m³ off Coulman Island and were <7/1,000 m³ everywhere else (Table 3). Only at Location 1 was the abundance index lower using the 700 μm net. Although weather conditions prevented direct quantitative comparison between the three sample sets, the abundance index along Cary Bank reached 430 fish/1,000 m³ at Location 4 using the 700 μm net, and was still high further south (22–96/1,000 m³) relative to areas in the rest of the Ross Sea (2–21 fish/1,000 m³). Indices at Locations 10, 15 and 16 were higher (53–96 fish/1,000 m³) than further west at Locations 11 and 12 (28 fish/1,000 m³ and 22 fish/1,000 m³ respectively). However, the highest

Family	Taxa	Tows present	Total no.	Total %
Nototheniidae	<i>Pleuragramma antarctica</i>	1–19	9,469	99.47
	<i>Trematomus</i> spp.	3, 4, 6	5	0.05
Channichthyidae	Unid.	1, 3, 4,	5	0.05
	<i>Chaenodraco wilsoni</i>	4	2	0.02
	<i>Chionobathyscus dewitti</i>	8	1	0.01
	<i>Chionodraco</i> spp.	5, 6, 11, 12, 14, 16	10	0.11
	<i>Cryodraco antarcticus</i>	11	1	0.01
	<i>Pagetopsis macropterus</i>	4	2	0.02
	<i>Pagetopsis maculatus</i>	3, 15	9	0.09
Artedidraconidae	<i>Dacodraco hunteri</i>	3, 4, 15, 19	7	0.07
	<i>Dolloidraco longedorsalis</i>	8, 11	2	0.02
Bathydraconidae	Unid.	9, 10	3	0.03
	<i>Racovitzia glacialis</i>	17	1	0.01
Paralepididae	Unid.	10, 17	2	0.02
Total collected specimens			9,519	

TABLE 2 Total larval fish abundance and composition from the 19 tow locations

abundance index using the 700 μm net was at Location 5 (469 fish/1,000 m^3) and the highest using the 300 μm net were all similarly off Coulman Island (Table 3).

In the rest of the Ross Sea, abundance indices using the 700 μm net were low at Locations 1, 2 and 17 south of the Crary Bank and in the Joides Basin, and at Location 9 in Joides Trough (2–10 fish/1,000 m^3). At Location 18 in the Glomar Challenger Trough, no tow was taken using the 700 μm net and the abundance index for the 300 μm tow was very low (1 fish/1,000 m^3). Indices were only higher in Terra Nova Bay at Location 3 (21 fish/1,000 m^3 using the 700 μm net) and Location 13 (6 fish/1,000 m^3 using the 300 μm net; Table 3).

3.4 | Length, growth rate and hatch dates

The average length of larvae caught at Locations 1–17 between 13 February and 10 March was 17.4 mm (Figure 5). Almost all sampled specimens (99.94%, 1,654 specimens measured) were less than 30 mm, indicating they were hatched during the current season (Figure 5; La Mesa, Piñones, et al., 2015). The average size sampled by both nets increased over the sampling period. Pooling larvae sampled by both nets (Figure 5) and estimating the growth rate from larvae smaller than 30 mm SL based on the exponential model fitted to the length frequency distributions (Figure 5a), the daily percentage change in size (G) was 1.25%/day, and the growth rate at the mean size of 18.3 mm was 0.23 mm/day. Hatch dates were spread over two months (December and January), with a single peak occurring in the last week of December (Figure 5b).

By contrast, the tow in the Bay of Whales (Location 19) using the 700 μm net yielded *P. antarctica* with a mean SL of 10.59 mm, and the fish were significantly smaller than those caught at Locations 1–17 (*t* test; *p* value < .001). Larger fish (19 mm and 41 mm) were

also sampled in the tow at Location 19, which may have hatched earlier in the current season or in the previous one. When these were excluded, the mean SL was 9.80 mm (*SD* = 0.86 mm). Assuming the same growth curve as for the western Ross Sea, the larvae would have hatched from 15 February to 13 March.

4 | DISCUSSION

4.1 | Examining the life history hypothesis

As observed in earlier studies, *P. antarctica* larvae dominated the ichthyoplankton in the western Ross Sea, comprising more than 99% of the fish sampled. As reported by La Mesa et al. (2010), the highest population densities were in the Drygalski Trough, along Crary Bank and near Coulman Island. Despite sampling relatively late in the summer, larvae were also present in Terra Nova Bay. Relatively few were found elsewhere. The results provided no evidence to reject dispersal via the trough circulation as predicted by the life history hypothesis, demonstrating high concentrations in the outflow and inflow that were consistent with expected transport from spawning inshore at Terra Nova Bay.

Length distributions were larger than La Mesa et al. (2010), consistent with sampling later in the summer, and the average length of the larvae increased over the course of the sampling period at a rate similar to that reported in the literature (Guglielmo et al., 1998; Hubold, 1985; La Mesa et al., 2010). Back-calculated hatching dates covered the range previously found from mid-December to early January, and largely matched reported hatching events in Terra Nova Bay (Granata et al., 2002; Vacchi et al., 2004, 2012). Overall, the abundance and size data supported a unified early life history expected for a single population of *P. antarctica* in the western Ross Sea, constrained by cryopelagic early stages under fast ice in Terra Nova Bay.

TABLE 3 Standard length (SL, mean \pm SD, and range), number caught and abundance indices ($n/1,000\text{ m}^3$) for *Pleuragramma antarctica*, caught by (a) 300 micron nets, (b) 700 micron nets

Location	No. caught	Abundance index	No. measured	Average SL (mm)	Range SL (mm)
(a)					
1	31	3	31	15.54 (± 3.59)	12–34
2	48	5	48	17.9 (± 1.72)	14–22
3	1	0	1	19	19
4	23	7	23	13 (± 1.98)	10–18
5	93	28	93	16.25 (± 1.95)	13–22
6	76	33	72	16.14 (± 1.96)	13–22
7	55	29	53	15.64 (± 1.55)	13–20
8	22	12	20	17.5 (± 1.91)	13–21
9	2	1	2	22.5 (± 3.54)	20–25
10	24	7	23	19.57 (± 1.34)	17–22
11	1	0	1	12	12
12	6	2	6	19.67 (± 0.52)	19–20
13	16	6	16	23.31 (± 1.85)	21–28
14	50	32	48	17.81 (± 1.68)	14–22
15	13	5	13	19.62 (± 2.02)	15–22
16	1	0	1	23	23
17	1	1	0		
18	2	1	2		
19	0	0	0		
Tow	No. caught	Abundance index	No. measured	Average SL (mm)	Range SL (mm)
(b)					
1	7	2	6	10.17 (± 1.83)	8–12
2	60	10	58	16.5 (± 1.54)	13–36
3	144	21	131	18.77 (± 2.11)	14–31
4	3,402	430	77	16.23 (± 1.95)	11–21
5	3,538	469	97	17.54 (± 1.63)	14–22
9	35	5	35	20.34 (± 1.66)	16–23
10	668	96	296	17.5 (± 1.67)	14–22
11	213	28	206	19.56 (± 1.89)	15–23
12	141	22	108	20.01 (± 1.83)	16–25
15	435	67	105	21.09 (± 3.54)	15–49
16	291	53	109	21.39 (± 2.36)	15–35
17	10	2	9	21.11 (± 4.43)	16–26
19	59	11	51	10.59 (± 4.61)	8–41

However, in the eastern Ross Sea, sampling in the Bay of Whales showed a clear discontinuity. Only a single tow was undertaken, but the mean length of larvae (SL 9.8 mm) indicated strong spatial structuring. There is considerable uncertainty over the distribution of egg and larval aggregations around the Antarctic (Ashford et al., 2017; Ghigliotti et al., 2017). Nevertheless, recently hatched larvae of 10 mm in length have previously been reported in the Bay of Whales, earlier in the season between mid-December and mid-

January (Biggs, 1982). *Pleuragramma antarctica* show remarkable consistency in reproductive timing and behavior under a variety of environmental conditions (La Mesa, Riginella, Mazzoldi, & Ashford, 2015), yet hatch dates in December and January for fish in our sample would demand virtual cessation of growth until their capture in mid-March. Instead, recent hatching in the vicinity of the Bay of Whales appears a better explanation. Late hatching may reflect multiple hatching events (Granata et al., 2002; Keller, 1983), the longer season and higher productivity of the Ross Ice Shelf polynya (Arrigo, van Dijken, & Strong, 2015), or the southern location of the Bay of Whales (78.5°S) relative to Terra Nova Bay (74.83°S).

4.2 | Cross-shelf dispersal in the western Ross Sea

Refining the scenario for dispersal using our results during the 2013 summer, eggs incubated under the fast ice between Gerlache Inlet and Cape Washington (shown in Figure 6 in relation to sampling locations 3 and 13) would have been initially retained in association with platelet ice. Based on back-calculation, most larvae hatched during the last three weeks of December and first two weeks of January. Moving into the water column, the larvae would have encountered surface Ekman transport induced by the katabatic wind field (Hubold, 1984; La Mesa et al., 2010) notably off the Reeves Glacier that, flowing past Cape Washington to the offshore edge of the Terra Nova Bay polynya and the western Drygalski Trough, would have exposed them to northward transport in the trough outflow to Coulman Island. The distribution of ice cover made it unlikely that the katabatic winds over Terra Nova Bay advected larvae eastward as far as Cray Bank.

Considering the timing of these events, advection northward from Cape Washington at a velocity of 0.1 m/s, similar to that found in the surface layer in the Joides Trough (Kohut et al., 2013), would have taken in the order of 14 days, suggesting that fish sampled between 26 February–1 March off Coulman Island were originally entrained in the trough circulation in mid-February. The timing coincided with a series of strong wind events recorded at Mario Zucchelli Station after 5 February (Figure 7), consistent with enhanced connectivity between the fast ice stretching from Gerlache Inlet to Cape Washington and the outer edge of the polynya. Earlier series of wind events in the last week of December and commencing 15 January suggest similar periods of enhanced dispersal (Figure 7). From Coulman Island, subsequent advection in southward jets, documented at velocities of 0.2 m/s in the surface layer by Kohut et al. (2013), would have taken in the order of seven days to pass along the Cray Bank. As a result, fish sampled off the southern Cray Bank may have been part of the same advection event out of Terra Nova Bay as those caught off Coulman Island.

However, the high concentration of larvae at Location 4 were caught too early to have been advected in the same event. Instead, the period of high katabatic winds commencing on 15 January was associated with open water off southern Victoria Land (Figure 7) and, prior to our sampling period, a pulse of wind-

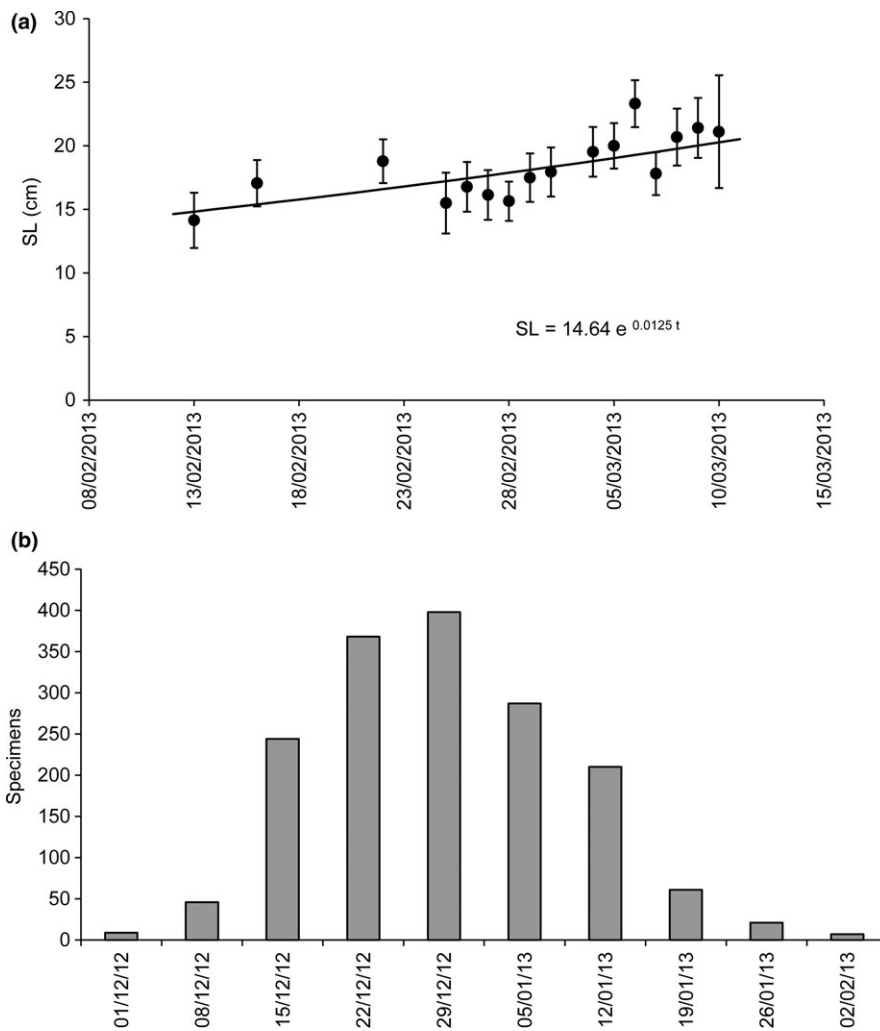


FIGURE 5 Length distributions for *Pleuragramma antarctica* sampled between 13 February to 13 March 2013 in the Ross Sea. Standard length (mean \pm SD) all larvae pooled, with estimated exponential equation growth relationship (a), and back-calculated hatch dates (b). First day of sampling 13 February 2013; all dates reported in day/month/year (DD/MM/YY). Locations reflect order of sampling; with the Bay of Whales sampled last on 13 March

induced Ekman transport in the surface layer may have carried larvae past Cape Washington, reaching across the trough to generate an alternative, episodic pathway to the Crary Bank. Notably, the congruence in length distributions between Location 4 and locations off Coulman Island indicated that the dispersal events were from the same pool of larvae, presumably accumulating during the hatching period under the fast ice between Gerlache Inlet and Cape Washington.

Sea ice distribution may also be important. The trajectory northward from the edge of the Terra Nova Bay polynya was covered with ice during sampling: transported northward to emerge from under the ice near Coulman Island, the water at Locations 6, 8 and 14 was characterized by freshening near the surface, whereas a pronounced mixed layer was found further from the ice margin at Locations 5 and 7. Similarly over southern Crary Bank, more open conditions were associated with a well developed mixed layer above MCDW. The ice distribution may have had other effects as well. Meltwater from sea-ice is one of the largest sources of dissolved iron to the euphotic zone (McGillicuddy et al., 2015). Melting, especially near the ice edge, combined with wind action at the surface, is likely to strongly influence conditions for growth and survival of *P. antarctica* larvae. Such sea-ice interactions with the circulation

and life history suggest an important development to the scenario, in which growth and survival decline when the ice edge does not lie over Drygalski Trough and larval trajectories are geographically separated from meltwater inputs. In years when the two coincide, successful recruitment may result in strong cohorts connecting production to higher trophic levels.

4.3 | Retention by trough systems and transport along shelf

The life history hypothesis predicted that trough circulation facilitates retention of fish in populations of *P. antarctica*, and that advection across and along the shelf helps to maintain distributions around the Antarctic (Ashford et al., 2017). In the western Ross Sea, La Mesa et al. (2010) found post-larvae (age 1+ yr) and juveniles (2+ yr) on the outer shelf (Figure 1c,d). Cross-shelf transport northward reaching the AFS, would result in advection westward to areas of the shelf along East Antarctica past Cape Adare, similar to the description by Hubold (1984) for the south-east Weddell Sea. The hypothesis suggested a mechanism by which fish mixing between trough outflows and inflows regulates along-shelf advection, versus retention and return toward the inner shelf.



FIGURE 6 Geography of Terra Nova Bay, including Mario Zucchelli Station (MZS) and showing sampling Locations 3 and 13

Our results suggest physical effects that are potentially involved. The trough near Coulman Island is notable for its curvature and narrowing, as well as a reverse slope and glacial discontinuities like grounding zone wedges (Anderson et al., 2014) that may help promote mixing both in vertical and horizontal directions. The unexpected presence of MCDW at Location 7 may have been due to a meander or eddy. Given the proximity of the coast, wind events like those encountered during sampling may also be involved. These potential effects, concentrated near Coulman Island, argue for the importance of the area for entrainment in southward flow. Dilution with increasing dispersal along the trough, rates of mixing between outflowing and inflowing water, and variation in the outflow to the outer shelf, would then help account for spatial variation in abundance indices, as well as retention within the population and advective losses along the continental shelf.

Predictions of population structure and connectivity are less straightforward for the Bay of Whales. In much the same way as for the western Ross Sea, dispersal by katabatic winds off the Ross Ice

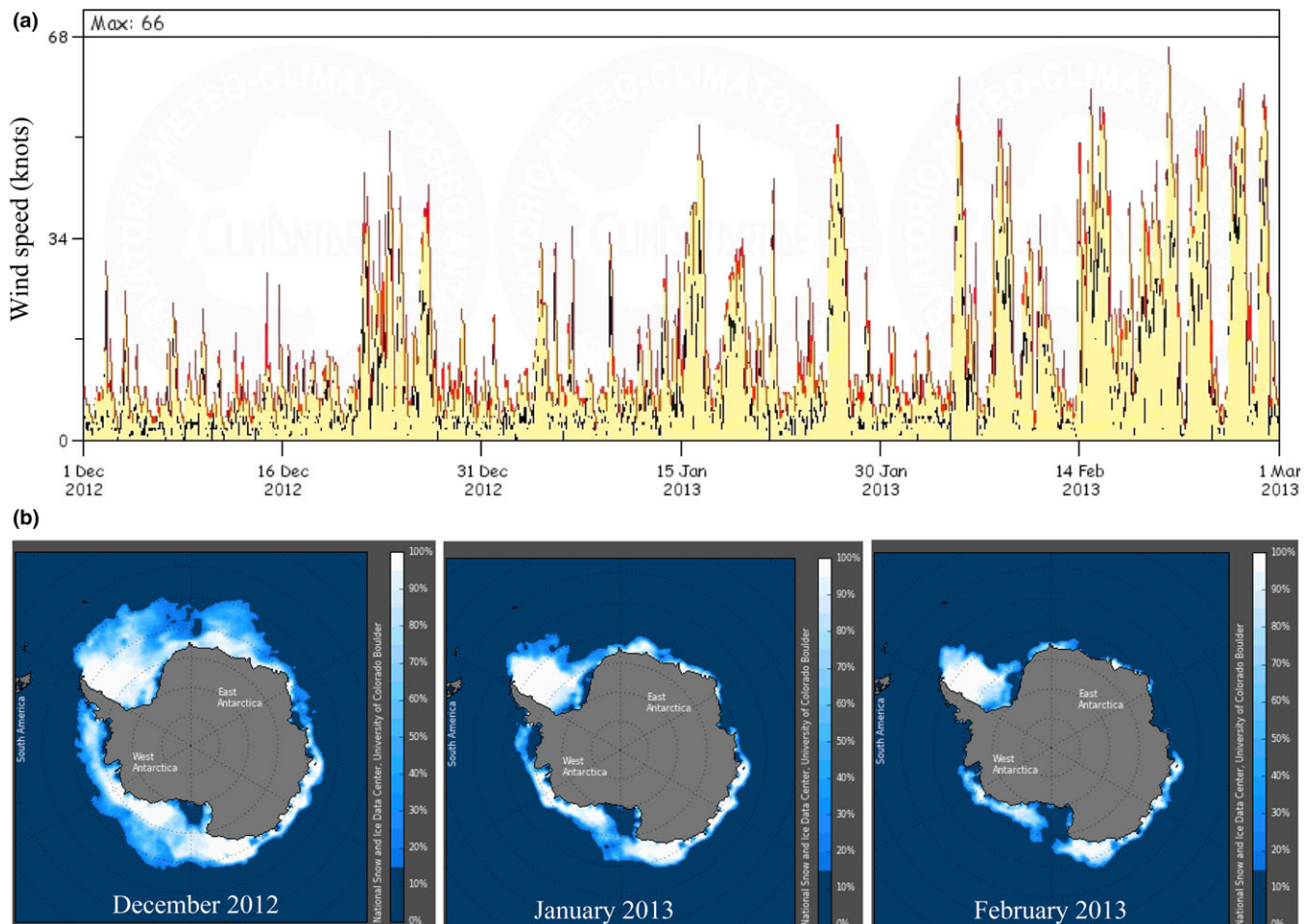


FIGURE 7 Wind velocities at Terra Nova Bay station (a), and sea ice concentration around the Antarctic during the months December 2012–February 2013 (b). Data and information for the wind velocities were obtained from the Meteo Climatological Observatory at Mario Zucchelli Station and Victoria Land of PNRA -<http://www.climantartide.it>. Sea ice concentrations were obtained from Fetterer, F., Knowles, K., Meier, W., & Savoie, M. (2016) updated daily. Sea Ice Index, Version 2. Boulder, Colorado USA. NSIDC: National Snow and Ice Data Center. <https://doi.org/10.7265/n5736nv7>

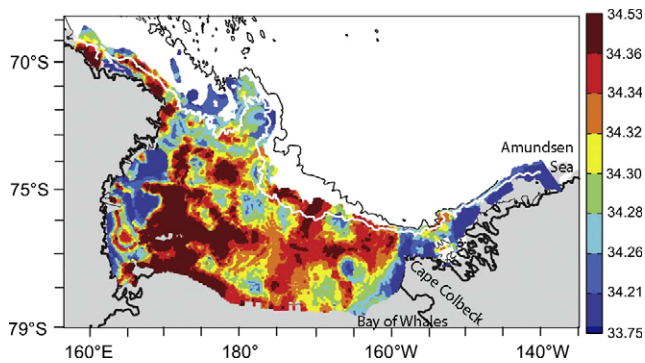


FIGURE 8 Average salinity for the surface density layer in the Ross Sea, reproduced from Orsi and Wiederwohl (2009) in their Figure 5. Fresher AASW that flows south of Cape Colbeck corresponds to the Antarctic Coastal Current. Isobaths: 1,000 m (white); 3,000 m (black)

Shelf may connect the nursery ground of a geographically discrete population (Brooks & Goetz, 2014) to outflowing water along the Whales Trough (Orsi & Wiederwohl, 2009) consistent with a coherent early life history spatially constrained by incubation under fast ice in the vicinity of the Bay of Whales. However, late hatching, or lack of growth, raises questions over subsequent larval survival and recruitment. In addition, how fish would close their life history is unclear: water is transported poleward along Little America Trough, located east of Whales Trough (Orsi & Wiederwohl, 2009), but connectivity is limited. Flow along the slope is westward, constraining return to potential nursery grounds under fast ice in the vicinity of the Bay of Whales. Considerable uncertainty remains over whether the larvae represent a true nursery ground (Ghigliotti et al., 2017), and more work is required to resolve the physical-biological interactions by which retention and self-recruitment could support a discrete population in the eastern Ross Sea.

Moreover, the life history hypothesis suggests a competing explanation based on along-shelf advection. In contrast to the AFS, the westward Antarctic Coastal Current (AACC, e.g., Moffat, Beardsley, Owens, & van Lipzig, 2008; Núñez-Riboni & Fahrbach, 2009) is a feature typical of coastal buoyant plumes, with freshwater inputs from precipitation over the ocean, meltwater run-off from land and sea-ice and glacial melting (Dutrieux et al., 2014; Moffat et al., 2008). The AACC is thought to be involved in the delivery of larvae spawned in the western Weddell Sea to adult assemblages in the Bransfield Strait (La Mesa, Piñones, et al., 2015), and from Marguerite Bay to Charcot Island (Agostini et al., 2015; Ferguson, 2012). It is also located inshore along the Amundsen Sea, flowing around Cape Colbeck and sharply south towards the eastern Ross Ice Shelf (Orsi & Wiederwohl, 2009; Figure 8). Larvae in the Bay of Whales were too small to have been advected themselves, but large aggregations of older *P. antarctica* occur inshore along the western Amundsen Sea and around Cape Colbeck (Donnelly, Torres, Sutton, & Simoniello, 2004). As in the western Weddell Sea, advective losses in the AACC past Cape Colbeck may survive to join adult assemblages downstream. Such vagrants (Sinclair, 1988) may still spawn as adults where they encounter suitable conditions along the Ross Ice Shelf, including in the Bay of Whales, but the

lack of a coherent spatial trajectory to underpin their life cycle inhibits their ability to self-recruit successfully.

Further research is needed to address these questions, especially since multi-decadal freshening of shelf water in the southwestern Ross Sea has been linked to melting of continental ice in the Amundsen Sea and transport westward along the shelf (Jacobs & Giulivi, 2010; Jacobs, Giulivi, & Mele, 2002). Strengthening connectivity over time, with larger and more stable spawning events, may lead to colonization if changing conditions allow life cycle closure and a stable population to form (Ashford et al., 2017). Due to heavy ice conditions and difficulties of access and sampling, the eastern Ross Sea is understudied compared to western areas. However, multi-disciplinary approaches combining techniques that include genetics (Agostini et al., 2015), otolith chemistry (Ferguson, 2012), age distributions and circulation modelling (La Mesa, Piñones, et al., 2015), reproduction (La Mesa, Riginella, et al., 2015), and community studies (Parker et al., 2015) successfully tested population hypotheses along the Antarctic Peninsula. Spatial heterogeneity between discrete populations contrasts strongly to homogeneity between exported fish and their parent population, providing a useful test around which field sampling can be designed. Resolving life history and population structure in a critical forage species can help unravel the complex physical-biological interactions that link producers and higher predators in the Southern Ocean ecosystem.

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ORCID

Cassandra M. Brooks  <http://orcid.org/0000-0002-1397-0394>

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