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Tying policy to system: Does the Ross Sea region marine reserve protect transport pathways connecting the life history of Antarctic toothfish?

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ABSTRACT

A central objective of the Ross Sea region Marine Protected Area (MPA) is to protect areas important to the life cycle of Antarctic toothfish (*Dissostichus mawsoni*), a top fish predator and by far the region's most important commercial species. Juvenile toothfish predominate in deep basins along the inner continental shelf, whereas adults are found mostly along the continental slope and spawning areas on the Pacific-Antarctic Ridge. The inner basins connect to the continental slope via glacial troughs and predictable transport along each trough results in exchange with the Antarctic Slope Current as it flows westward. From the slope, two transport pathways, an eastern one from Iselin Bank and a western one that turns cyclonically along the flank of the Southeast Indian Ridge, connect northward to the Pacific-Antarctic Ridge, where the northern arm of the Ross Gyre and the Antarctic Circumpolar Current flow eastward. Using a circulation model to compare transport pathways connecting toothfish life history areas, we consider which inshore basins are likely most important in contributing to adult spawning aggregations; how transport pathways from each may be expected to influence distributions along the continental slope and Pacific-Antarctic Ridge; and how zonal transport pathways may promote export to areas downstream of the marine reserve. Although the MPA protects some critical life history pathways for toothfish, others remain vulnerable to commercial fishing, and we argue that those in adjacent areas along the Iselin Bank, Pacific-Antarctic Ridge and the Amundsen Sea might usefully be protected, discussing the range of policy instruments available. We also recommend consideration of transport pathways in deliberations for a proposed network of Southern Ocean MPAs, introducing a system-based tool using chemical tracers in otoliths that can test for toothfish movement between areas connected along the Antarctic Slope Current and Antarctic Circumpolar Current.

1. Introduction

Marine reserves that restrict resource utilization are an important ecosystem-based management tool for enhancing fisheries management, as well as conserving biodiversity [28,40]. Their objectives usually include promoting the conservation and recovery of commercially-targeted populations contained within their boundaries (e.g., [59]), yet equally important are the benefits for adjacent areas [36, 49]. However, the complex physical-biological interactions that influence population recovery and determine the rate and direction of export to neighboring areas are not well understood, in particular the effects of life history and population structure [34]. Data predicting how spatial relationships with habitat and transport pathways are likely to influence productivity and export can form a useful basis for designing more effective reserves [29,35].

The Ross Sea region Marine Protected Area (MPA) (Fig. 1A) was adopted by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) – the decision-making body that manages marine living resources in the Southern Ocean – in 2016 and came into force in 2017. Among the healthiest large marine ecosystems in the world, the Ross Sea region supports a lucrative international commercial fishery for Antarctic toothfish (*Dissostichus mawsoni),* the top fish predator in the Southern Ocean [31]. The MPA spans more than 2 million km^2 including large areas of the continental shelf and slope and

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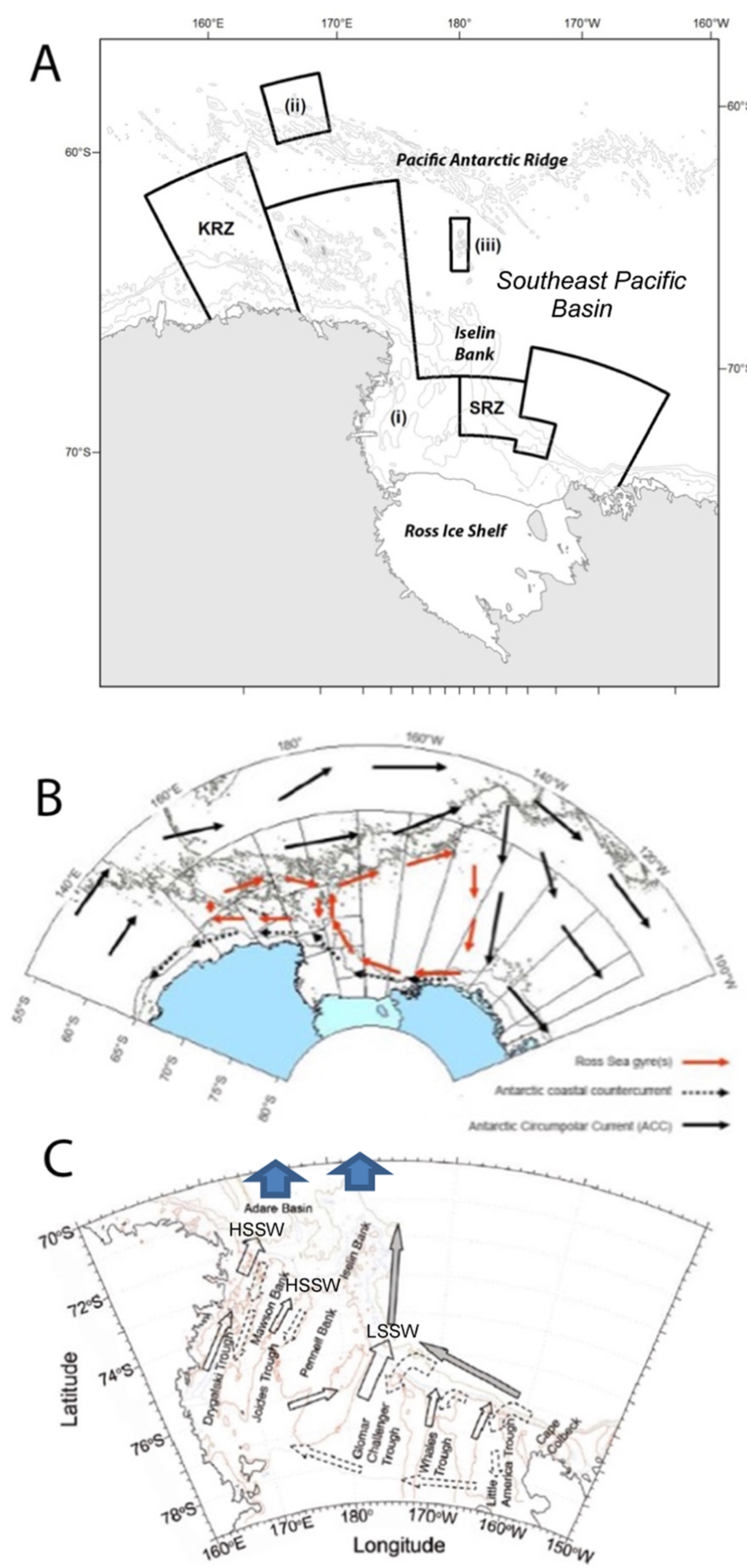

Fig. 1. Maps of Ross Sea region. Schematic in (c) shows main transport pathways on the shelf (transparent) and slope (grey), including those connecting northward to the Pacific Antarctic Ridge (blue). Also marked are Low Salinity Shelf Water (LSSW) in the outflow from Glomar Challenger Trough; High Salinity Shelf Water (HSSW) in the outflow from Joides Trough; and the higher salinity version (also marked HSSW) from the Drygalski Trough.

(a) Marine Protected Area reproduced from CCAMLR [16] (A), showing component areas of the General Protection Zone (i) over the continental shelf and slope, (ii) over the Pacific Antarctic Ridge; and (iii) in the western Southeast Pacific Basin; also Special Research Zone (SRZ) and Krill Research Zone (KRZ). (b) Life history working hypothesis (B) reproduced from Hanchet et al. [30]. (c) Circulation and topography over the shelf and slope (C) modified from Ashford et al. [4], including inner basins and glacial troughs.

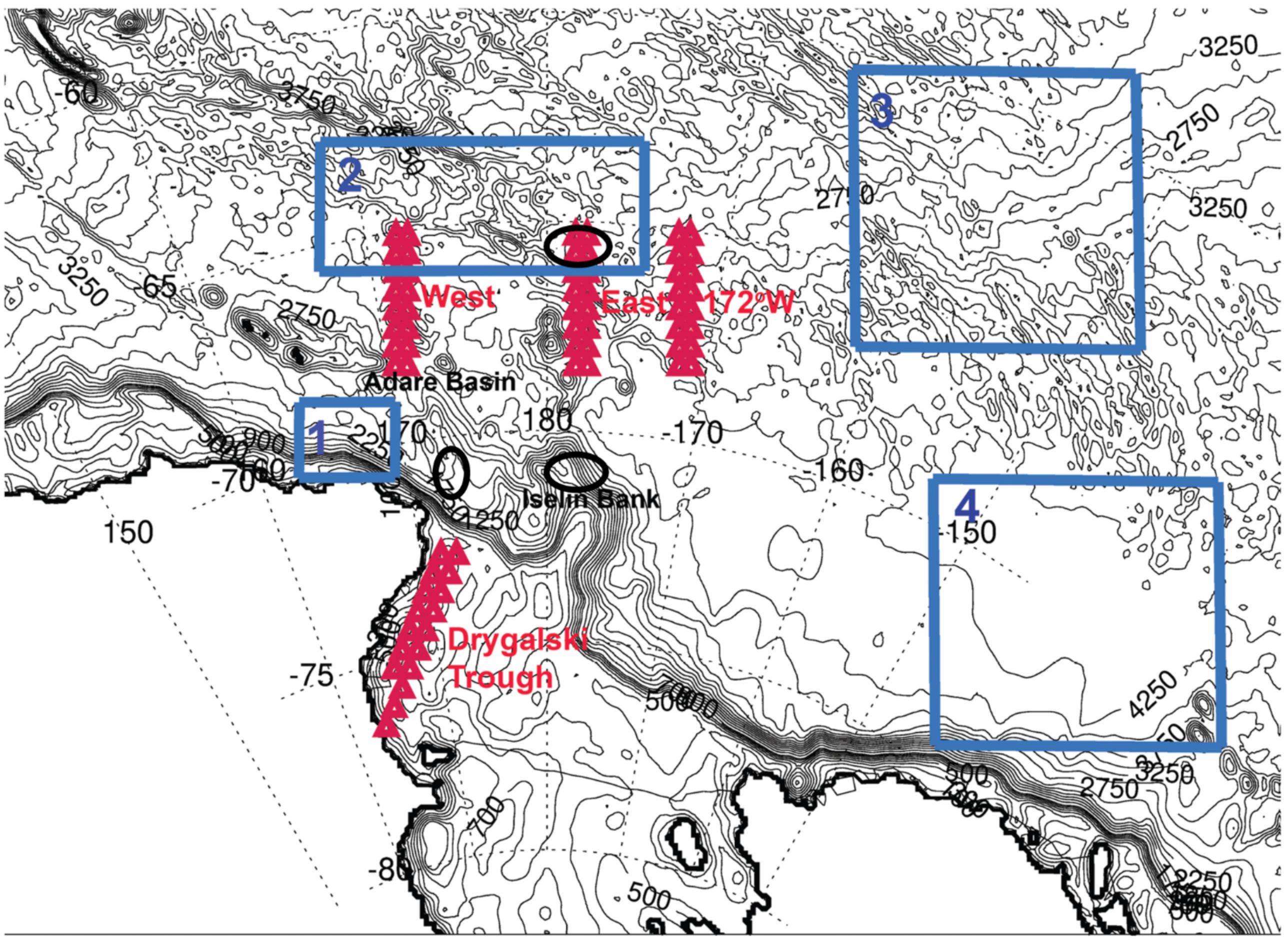

Fig. 2. Drifter release sites (red) located along 1) the eastern pathway from Iselin Bank to the Pacific Antarctic Ridge, 2) the western pathway from Adare Basin to the Pacific Antarctic Ridge, 3) the meridian at ~ 172°W, and 4) the Drygalski Trough; and the four destination boxes (blue) in the Ross Sea region 1) west along the continental slope past Cape Adare; 2) along the Pacific Antarctic Ridge north of Iselin Bank and Adare Basin; 3) along the Pacific Antarctic Ridge further east; 4) in the eastern arm of the Ross Gyre. Relevant sampling areas from Ashford et al. [4] for the Pacific Antarctic Ridge, Iselin Bank and Adare Basin are outlined in black.

seamounts in the north. It has three zones: the General Protection Zone comprises more than 70% of the MPA and prohibits fishing; the Special Research Zone permits limited fishing for toothfish; and the Krill Research Zone permits limited fishing for krill [16]. CCAMLR was the first international fisheries management body to adopt an ecosystem approach in its mandate [24], and the MPA was designed to protect ecosystem function and structure, including potential trophic interactions, seeking specifically to protect areas important to the life cycle of toothfish ([16], para 3). However, the efficacy of the MPA, including whether its boundaries will meet its conservation objectives, remains to be tested.

Fundamental gaps in knowledge regarding toothfish life history potentially undermine a full understanding of the role that the Ross Sea region MPA can play in conserving the toothfish population and generating benefits for adjacent areas. Among the most prominent gaps concerns the migration and dispersal pathways followed by each life stage [31]. In the working hypothesis currently guiding research in the region, spawning occurs over seamounts in the western Southeast Pacific Basin and along the Pacific Antarctic Ridge during winter [30,31], early stages are entrained eastward in the Ross Gyre to reach the continental slope in the Amundsen Sea, and an ontogenetic migration via the Ross Sea returns maturing fish and adults to spawning areas [46] (Fig. 1B). Yet older toothfish stages lack adaptations for active large-scale movement; instead, ocean circulation may structure connectivity [4]. Ontogenetic changes in toothfish from negative to neutral buoyancy during maturation [43] may be adaptive, potentially facilitating juvenile retention in productive areas on the shelf and transport of older stages to and from spawning areas [4,6]. As a result, a clear understanding of the physical system structuring the population and its life cycle can help in assessing the marine reserve and the efficacy of its boundary configuration for conserving toothfish.

Dispersal facilitated by the Southern Ocean circulation can shape Antarctic fish populations on large scales in spatially complex ways (e.g., [1–3,5,11,14,15,25], 2019; [23,60]). Models of the large-scale circulation have been utilized to help explore transport along the Antarctic Circumpolar Current (ACC) and over the continental shelf and slope (e.g., [2,21]). Experiments involving simulated particles can examine how fish might disperse along transport pathways, generating predictions that can be tested empirically using samples collected in the commercial fishery and during research surveys (e.g., [3]). In this way, a multi-disciplinary approach addresses the uncertainties involved in simulating physical processes, but the measure used for testing is critical. Most techniques employed by fish biologists to examine population structure cannot directly link fish to areas occupied earlier in their life history. Yet previous work on Antarctic toothfish [4] showed that minor and trace elements laid down in their otoliths distinguished fish potentially exposed to Circumpolar Deep Water (CDW) over the Pacific-Antarctic Ridge and outflows off the Ross Sea shelf involved in the production of Antarctic Bottom Water (AABW). Since fish subsequently carry this chemistry during dispersal, it can act as a tracer that enables powerful tests of modeling predictions. Moreover, because the chemistry is laid down within growth increments that are

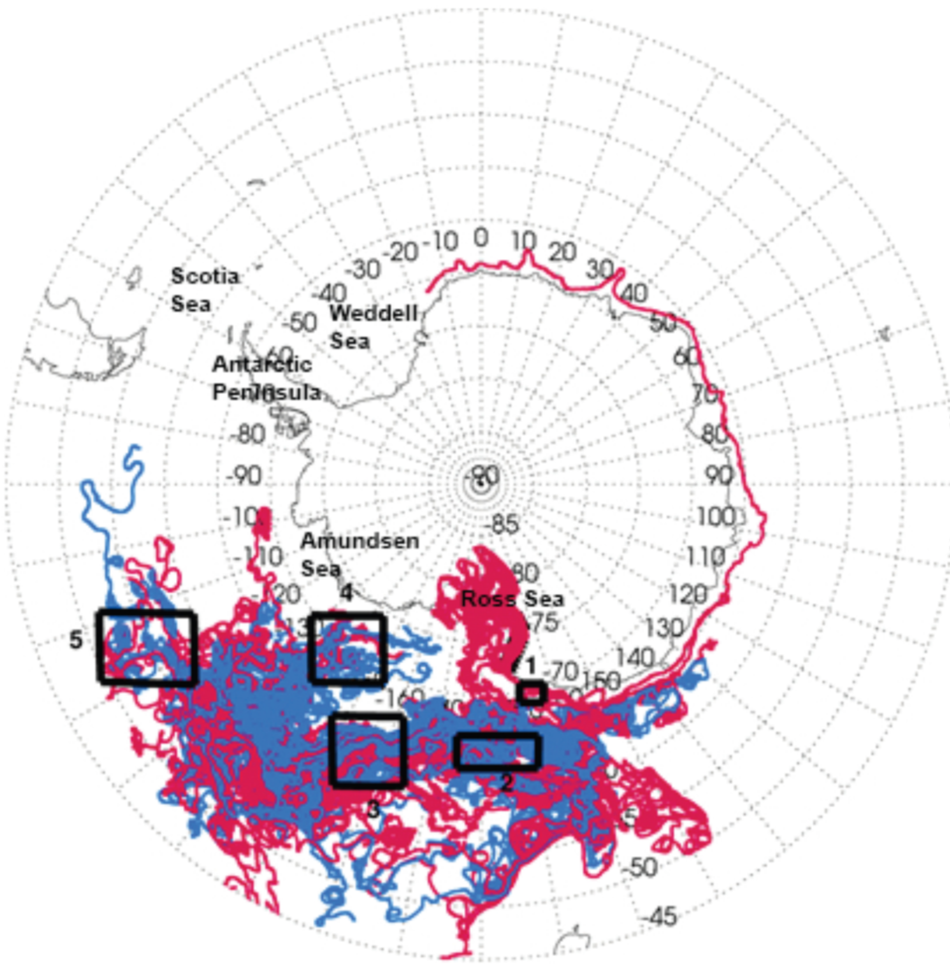

Fig. 3. Model output oriented with Prime (Greenwich) Meridian at top, showing drifter trajectories in relation to destination boxes 1–4 in Fig. 2, and destination box in the ACC (box 5). Releases in surface layer (blue) and bottom layer (red).

used for age estimation [8,32], the tracers can be related back to age and life stage.

A testing approach based on a combination of otolith chemistry, age distributions and particle simulations found strong evidence of a single population in the Ross Sea [4]. The simulations suggested two deep transport pathways from adult feeding areas along the slope to spawning areas over the Pacific Antarctic Ridge (see Fig. 1). The eastern one, northward from Iselin Bank, is associated with outflow of Low Salinity Shelf Water (LSSW) from the Glomar Challenger Trough that is involved in the production of low density AABW [52]. The western one, linked to High Salinity Shelf Water (HSSW) from the Joides Trough, is involved in the production of AABW [52] that flows down the slope into the Adare Basin (Fig. 1C). Another form of HSSW characterized by higher salinities cascades in gravity currents from the Drygalski Trough [52]. It supplies a deep current flowing westward along the continental slope, forming a potential transport pathway for maturing toothfish to areas off East Antarctica [4].

Here, our goal is to help develop a policy framework that explicitly reflects the physical system structuring toothfish life history. Using the model of the large-scale circulation in the Southern Ocean from Dinniman et al. [21], we test the efficacy of the Ross Sea region MPA by examining the current boundary configuration in relation to transport pathways that connect areas important to closing the life cycle of toothfish, as well as export from the Ross Sea. We generate predictions for toothfish stages dispersing along pathways within and adjacent to the Ross Sea region MPA, and assess otolith tracers for testing the predictions by examining successful classification between the Pacific-Antarctic Ridge, Iselin Bank and Adare Basin. The tracers are related to growth and physiology, which change dramatically between life stages undertaking movement, so we also test for ontogenetic differences that potentially confound environmental exposures to water masses entrained in these pathways.

2. Methods

2.1. Lagrangian particle tracking

We explored transport in the Ross Gyre, eastward along the ACC, and westward along the continental slope, in a simple experiment releasing particles in the large-scale circulation simulated using a numerical circulation model. The model was based on a high resolution version of the Regional Ocean Modeling System, configured for the Southern Ocean (for details, see [21]). The model domain extends from the Antarctic continental shelf northward past the Subantarctic Front in the northern ACC, and includes the cavity beneath the Ross Ice Shelf and the entire Ross Gyre. As such, the model includes regions within the boundaries of the Ross Sea region MPA, and also adjacent to the MPA and extending around the CCAMLR Convention area. The horizontal grid spacing is 10 km and the vertical resolution is determined by 32 terrain following vertical levels concentrated towards the surface and bottom. The simulation was for 10 years and used atmospheric re-analysis forcing for the year 2010. The model did not include ocean tides.

Neutrally-buoyant Lagrangian particles were initialized in areas along the eastern transport pathway northward from the Iselin Bank;

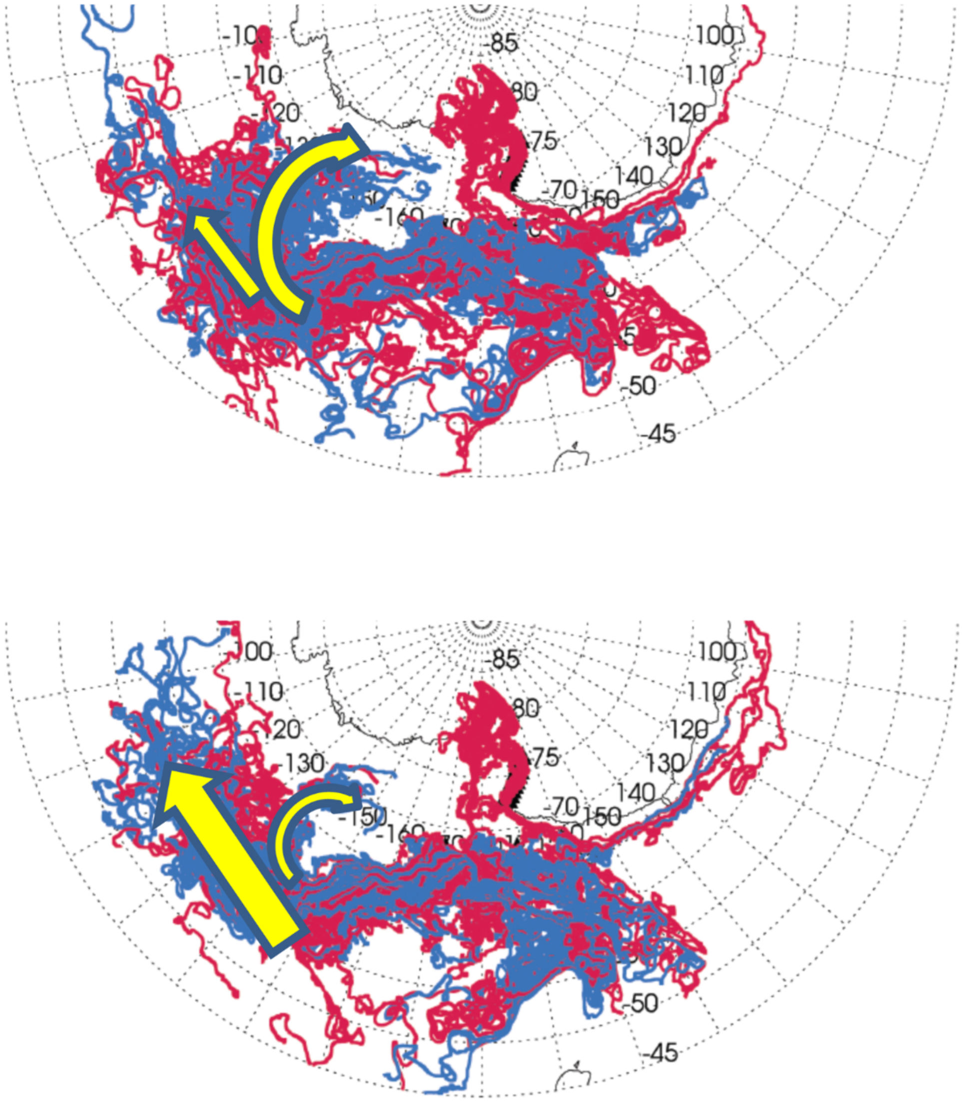

Fig. 4. Simulated drifter trajectories from the Ross Sea during winter (upper panel) and summer (lower panel). Releases in surface layer (blue) and bottom layer (red).

along the western pathway northward from the Adare Basin; and from the Drygalski Trough supplying westward flow along the continental slope (Fig. 2). The particles were advected within the model at every model time step using the full three dimension velocity fields of the model plus a random walk in the vertical direction (related to the parameterized model vertical diffusion, [33,57]). No behavior was simulated with the particles. The areas along the Iselin Bank and Adare Basin pathways were further divided into equal northern and southern sections. To compare transport closer to the center of the Ross Gyre, particles were also released along the meridian at ~ 172°W, divided into north-south sections. Particles were initialized in the bottom layer for all seven of the resulting locations, and in the surface layer for the six northern locations, during winter (July/August) and summer (January/February). Particles were tracked for three years and the trajectories examined to determine the dominant pathways. Of the 1356 released, the number were recorded arriving in destination boxes placed to cover the dominant pathways (1) west along the continental slope past Cape Adare; (2) along the Pacific Antarctic Ridge north of Iselin Bank and Adare Basin; (3) along the Pacific Antarctic Ridge further east; (4) in the eastern arm of the Ross Gyre; and (5) in the ACC (Fig. 3). For each location, the number arriving in each destination box was normalized by the number of releases, and the results presented as percentages.

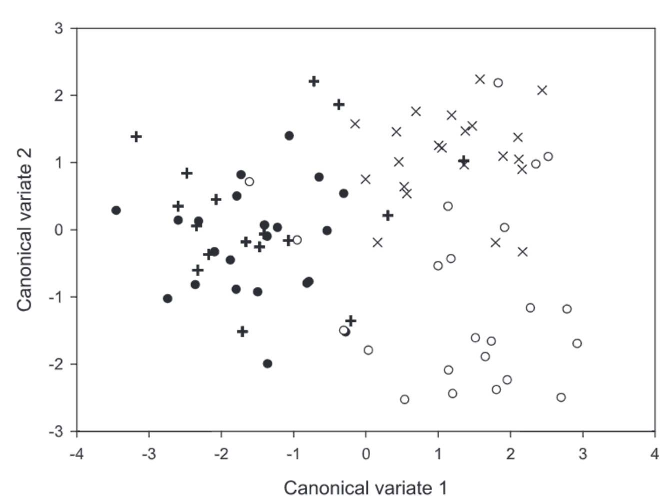

Fig. 5. Chemistry from otolith edges of Antarctic toothfish, showing relationships using canonical discriminant variates between maturing fish over the Pacific Antarctic Ridge (+), and adult fish from the same area (•), Iselin Bank (○) and Adare Basin (×) presented in Ashford et al. [4].

Table 1
Percentage of drifters from release sites reaching destination boxes 1) west along the continental slope past Cape Adare; 2) along the Pacific Antarctic Ridge (PAR in table) north of Iselin Bank and Adare Basin; 3) along the Pacific Antarctic Ridge further east; 4) in the eastern arm of the Ross Gyre; and 5) in the ACC (see Fig. 3). Release areas are highlighted in bold from which a high proportion of drifters reach the Pacific Antarctic Ridge north of Iselin Bank and Adare Basin, and further east.

	Destination Boxes						
Release sites	Section	No of releases	Western slope (1)	PAR west (2)	PAR east (3)	Ross Gyre (4)	ACC (5)
Drygalski Trough		204	17.2	3.9	2.4	0	0
Adare Basin	North	192	0.5	**97.9**	26.6	1.0	3.6
	South	192	7.3	**69.8**	14.1	1.0	1.0
Iselin Bank	North	192	0	**82.8**	**87.5**	10.4	21.4
	South	192	1.6	**71.9**	**56.8**	3.1	12.0
172°W meridian	North	192	0	13.0	**97.4**	14.1	22.9
	South	192	0	1.0	**100.0**	11.5	32.8

2.2. *Otolith chemistry analyses*

Since maturing toothfish potentially travel widely in the interval between becoming neutrally buoyant and achieving sexual maturity, we tested whether those reaching spawning areas were from the same population as the adults in Ashford et al. [4] and whether ontogenetic effects influenced the tracers between the two life stages. For this, we analyzed unpublished data measured from all the maturing fish ($n = 18$) taken over the Pacific Antarctic Ridge in the catch sampled in [4], see their Figs. 2b and 5, Table 1 for more details on catch and age composition), with validated ages [8] of 10–15 years incorporated as a single treatment within the fully randomized blocks experimental design used in that study. As for the published treatments, the single otoliths remaining for each fish after age analysis were sectioned and a Finnigan MAT Element 2 double-focusing sector-field inductively coupled plasma-mass spectrometer located at the Plasma Mass Spectrometry Facility at Woods Hole Oceanography Institutions (Woods Hole, Mass.) used to examine the chemistry. All randomization and other procedures were according to Ashford et al. [4]. Otoliths were analyzed for ^{48}Ca, ^{25}Mg, ^{88}Sr, and ^{138}Ba, (i) in the otolith nuclei, which reflects environmental exposure during the fishes' first summer, and (ii) along the otolith edges, which reflects environmental exposure before capture. They were then compared with adult fish (>15 years) from the same area of the Pacific Antarctic Ridge ($n = 23$), Iselin Bank ($n = 24$) and Adare Basin ($n = 24$) using multivariate analysis of variance (MANOVA).

For the edge chemistry, individual contrasts were used to test for differences between the maturing fish and each of the adult treatments. For both nucleus and edge analyses, after transforming data following Ashford et al. [4] we identified any outliers by plotting robust squared Mahalanobis distances of the residuals against the corresponding quantiles (QQ plot) of the χ^2 distribution [61]. We used Mardia's multivariate skewness and kurtosis measures ($\alpha = 0.05$) to test for multivariate normality; variance-covariance matrices were equal according to Bartlett's modification ($\alpha = 0.1$). To assess otolith chemistry as a tracer, we used multivariate discriminant analysis (MDA, [37]), estimating the rates at which material from the edges successfully classified exposures along the Iselin Bank and Adare Basin transport pathways and the Pacific Antarctic Ridge. Since there were no differences between maturing and adult fish over the Pacific Antarctic Ridge, these were pooled and compared to the adults caught over Iselin Bank and in Adare Basin. After pooling, $\chi2 = 0.07$ according to Bartlett's modification, so quadratic MDA was used. Classification error-rates were estimated by cross-validation based on equal prior probabilities.

3. Results

In the simulations, high proportions of particles (70–98%) released off the continental shelf along both the Iselin Bank and Adare Basin pathways reached the Pacific Antarctic Ridge (Table 1). However, far fewer from the Adare Basin pathway subsequently followed trajectories eastward and few reached the main pathways observed along the eastern arm of the Ross Gyre and ACC. Three to four times as many particles from the Iselin Bank pathway followed eastward trajectories along the Pacific Antarctic Ridge. Overall, the highest proportions of particles reaching the main pathways along the Ross Gyre (10.4%) and the ACC (21.4%) were from the northern section of the Iselin Bank pathway. This tendency was reinforced further east; from the 172°W meridian nearly all particles were transported eastward, and 11.5–14% reached the eastern arm of the Ross Gyre compared to 23–33% that passed into the ACC. From Drygalski Trough, only 3.9% of the particles reached the Pacific Antarctic Ridge, whereas 17.2% followed trajectories westward along the continental slope.

Table 2
Results from otolith chemistry for Antarctic toothfish. a) Multivariate analysis of variance comparing trace and minor element chemistry laid down i) in otolith nuclei and ii) along otolith edges, from maturing (mat) Antarctic toothfish over the Pacific Antarctic Ridge (PAR) with adults (ad) over the PAR, Iselin Bank (ISB) and Adare Basin (AB) sampled in [4]. b) quadratic multivariate discriminant analysis showing classification rates (%, bold values indicate rates of correct classification to sampling area).

a)	MANOVA Pillai's Trace				
Chemistry	Contrast	F	d.f.	p	Experimentwise $\alpha = 0.05$
Nucleus		1.3	9, 186	0.24	ns
Edge	PAR_{mat} vs PAR_{ad}	1.61	3, 55	0.20	ns
	PAR_{mat} vs ISB_{ad}	26.3	3, 55	< 0.0001	sig
	PAR_{mat} vs AB_{ad}	24.4	3, 55	< 0.0001	sig

b)		MDA % classification rates		
Area sampled	n	Classified to Area		
		PAR	ISB	AB
PAR	39	**92**	5	3
ISB	23	9	**74**	17
AB	22	0	14	**86**

Variability at smaller scales may affect connectivity as well. Whereas release from the northern section along the Iselin Bank pathway increased the proportion transported eastward, there was a small decrease at 172°W. Unlike the other offshore locations, a small proportion of particles (7.3%) released in the southern section of the Adare Basin pathway, just east of the Balleny Islands, traveled westward along the continental slope. Strong seasonal differences were observed: for drifters released both near the surface and bottom, the proportion returned towards the shelf in the eastern arm of the Ross Gyre was less among releases during summer (Fig. 4).

The otolith chemistry of maturing fish was consistent with the adult chemistry presented in Ashford et al. [4] (Table 2a). No outliers were detected in the nucleus data, and the maturing fish showed no significant differences from the adults (MANOVA Pillai's Trace; $F = 1.3$; d.f. = 9, 186; $p = 0.24$), indicating they were from the same population. Along

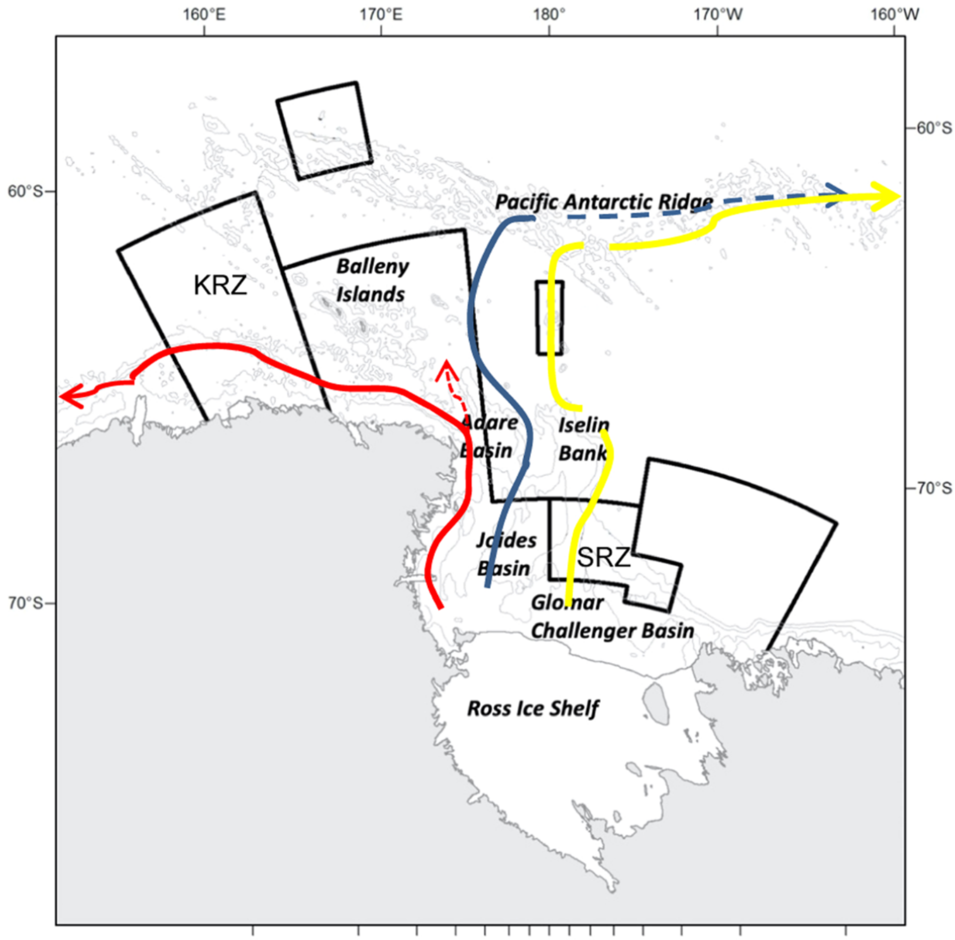

Fig. 6. Schematic comparing the boundaries of the Ross Sea region Marine Protected Area (MPA) with potential pathways supporting life history connectivity to the Pacific Antarctic Ridge and westward along the continental slope. i) from Glomar Challenger Basin via Iselin Bank (yellow); ii) from Joides Basin via Adare Basin (blue); and iii) from the Southwest Ross Sea and Drygalski Basin westward (red). Boundaries (black) indicate General Protection Zone of the MPA; Special Research Zone (SRZ) and Krill Research Zone (KRZ) are also shown along with major geographic features.

the otolith edges, five outliers were detected; two from the Adare Basin and one each from the other three treatments. Maturing fish showed no significant differences in their edge chemistry from the adults caught in the same time and place over the Pacific Antarctic Ridge (MANOVA Pillai's Trace; $F = 1.61$; d.f. = 3, 55; $p = 0.20$), and hence no ontogenetic effect in life stages reaching neutral buoyancy (Fig. 5). Like these adults, the maturing fish showed significant differences from adults on Iselin Bank (MANOVA Pillai's Trace; $F = 26.3$; d.f. = 3, 55; $p < 0.0001$) and in Adare Basin (MANOVA Pillai's Trace; $F = 24.4$; d.f. = 3, 55; $p < 0.0001$).

In the MDA (Table 2b), the edge chemistry successfully distinguished the Pacific Antarctic Ridge: only 8% (three of 39 fish) caught there were incorrectly classified elsewhere, and no fish taken from Adare Basin and only two fish from Iselin Bank were incorrectly classified to the PAR. For Adare Basin, 86% (19 of 22 fish) classified correctly; only one from the Pacific Antarctic Ridge and four from Iselin Bank were allocated there incorrectly. For Iselin Bank, 74% (17 of 23 fish) classified correctly; one from the Pacific Antarctic Ridge and three from Adare Basin classified there incorrectly. The overall error rate for the discrimination analysis was 15.8%.

4. Discussion

4.1. Transport pathways in relation to MPA boundaries

A simple experiment releasing simulated particles demonstrated the dominant transport pathways along which population retention and export can occur, which could be assessed in relation to the Ross Sea region MPA. The trajectories facilitate spatially-specific predictions concerning life history closure and emigration in toothfish that can be compared with the MPA boundaries. Several points were notable. Firstly, a much larger proportion of the simulated releases along the pathway northward from Iselin Bank eventually stayed in the Ross Gyre. Few releases from the pathway northward from Adare Basin did so. Secondly, an even larger proportion of the releases along the Iselin Bank pathway ended in trajectories along the ACC, but very few from the Adare Basin. Most releases along both pathways reached the Pacific Antarctic Ridge, but the Iselin Bank pathway was much more important for supplying the eastern ridge. Finally, consistent with earlier simulations by Hanchet et al. [30], some of the particles transported west along the slope came from the Adare Basin pathway, near the Balleny Islands. Nevertheless, a much larger proportion of releases from the Drygalski Trough reached westward, suggesting that it may also make an important contribution to westward export from the MPA, consistent with earlier modeling by Ashford et al. [4]. Overall, these results indicate the importance of the Iselin Bank pathway for connectivity from feeding areas along the continental slope of the Ross Sea to spawning grounds and eastward along the Pacific Antarctic Ridge. They also highlight the potential for connectivity westward from the Ross Sea region MPA, potentially along East Antarctica and as far as the Weddell Sea.

The circulation model does not include behavior which, superimposed on the background movement of water, may reinforce transport effects or increase variability. Nevertheless, the simulations indicate that significant amounts of directed behavior are not necessary for large proportions of fish to return to the continental slope or move into the ACC. The model may underestimate the formation of HSSW as a result of coarse resolution of the atmospheric forcing (~80 km, ERA-Interim reanalysis), and it does not include tidal forcing, which is significant in transforming HSSW into AABW in the Ross Sea [45,58]. The consequent under-estimate of benthic transport down the continental slope off the Drygalski Trough (e.g., [45]) suggests that transport along the continental slope from the Drygalski Trough may in fact be more intense, and westward export from the MPA more important than our results imply.

Our simulation results build on earlier work showing how the Ross Sea shelf and slope system, most of which is protected within the boundaries of the MPA, provides predictable opportunities for connecting toothfish life history. Deep basins along the inner continental shelf, the result of isostatic depression by the continental ice sheet, are associated with distributions dominated by juveniles that are protected within the General Protection Zone of the MPA [42]. These basins connect to the continental slope via glacial troughs exposed during ice sheet recession, which are also largely conserved within the General Protection Zone. Earlier simulations demonstrated transport pathways along the troughs connect to Iselin Bank and Adare Basin [4]: from the Glomar Challenger Basin, equatorward flow of dense, cold LSSW mixes with inflowing modified CDW, eventually contributing to the formation of Low Salinity AABW. Deep outflow of AABW from the mouth of the Glomar Challenger Trough is located within the Special Research Zone of the MPA (Fig. 6), from where it sinks down the slope to join a western boundary current providing a pathway northward to the Iselin Bank. Similarly, HSSW from the Joides Basin flows equatorward along Joides Trough within the General Protection Zone, providing a path down the slope into Adare Basin.

Taken with this earlier work, our simulations indicate that the MPA protects some of the transport pathways connecting areas important to the life cycle of toothfish, but not others. Connectivity from the Glomar Challenger system to the Pacific Antarctic Ridge via Iselin Bank generates opportunity for retention in the Ross Gyre. In consequence, the Glomar Challenger may be the most important system contributing to adult spawning aggregations along the Pacific Antarctic Ridge, and hence the productivity and persistence of the toothfish population. The pathway is protected where it spans the General Protection Zone, both over the shelf and around seamounts in the western Southeast Pacific Basin, and in the Special Research Zone where fishing is limited (Fig. 6). However, the pathway is not protected by the MPA along a large part of the deep western boundary current, the Iselin Bank and eastern Pacific Antarctic Ridge. Similarly, the pathway via the Joides system is also protected but transport northward from Adare Basin is not. Yet this may not be so important if the opportunities for connectivity eastward along the Pacific-Antarctic Ridge are much lower. The Drygalski system, fully within the General Protection Zone, connects to westward transport that is also protected, but along the slope away from the spawning areas (Fig. 6).

4.2. Developing system-based policy for toothfish conservation

CCAMLR comprises 26 Members (25 Nation States and the European Union) who collectively share the responsibility for managing Southern Ocean resources. All decisions, including adopting MPAs, must be made by consensus of all Members. Although the application of consensus decision-making has caused concern, the process airs disagreements and encourages dialogue that, over the years, has resulted in the Commission adopting a comprehensive set of conservation measures that address key management issues in the convention area [24], comparing well with Regional Fisheries Management Organizations [20]. The proposal for a Ross Sea Region MPA included an ambitious range of objectives covering science and protection, including biodiversity and fisheries management, that were adopted as a single conservation measure 91–05. Achieving consensus took many years as member states negotiated trade-offs, including between conserving ecological values and accommodating commercial fishing grounds for toothfish [9,13]. For example, the Iselin Bank (Fig. 1a) was a core priority area for conservation for meso-predators [7], but was also the primary commercial fishing grounds for toothfish [10] and was thus omitted from the MPA boundaries [13]. Earlier proposals for the MPA also envisaged greater protection extended to areas along the Pacific Antarctic Ridge.

Compromises like these are crucial for advancing policy. Arguably, adopting MPA objectives in a single conservation measure can help streamline management, strengthen protection, and mobilize public support. Set against this, the extended process risks elevating adversarial tensions between stakeholders, and a single measure lacks the flexibility of a coordinated series that target the same objectives individually [24]. Our results suggest as well that eventual agreement, while addressing some objectives, can result in only partial responses to others, reflecting resolution of stakeholder interests over the particulars of the system itself. Yet, unless tightly bound to the explicit biophysical structure on the ground, the outcome can end up undermining interests on all sides. With a life cycle linked to the Ross Gyre, toothfish life history movement through areas that remain open to concentrated fishing effort risks rendering careful protection over the rest of the life cycle ineffective [4]. Temporary benefits that might accrue for harvesters are offset as longer-term decreases in productivity set in. In this light, the simulations highlight earlier concern over vulnerability in the life cycle to fishing on the Iselin Bank (e.g., [4]), and demonstrate the Pacific Antarctic Ridge as another potential area of vulnerability; ontogenetic migration under the current working hypothesis suggests that the Amundsen Sea may be as well. As importantly, the specific transport pathways connecting these areas also need consideration.

What could effective protection look like? Surveys indicate that Antarctic silverfish, a closely related prey species of toothfish, dominates ichthyoplankton in the Ross Sea, comprising up to 99% of the catch (e.g., [39]). Aggregations of eggs and larvae occur under fast ice in Terra Nova Bay [56]. Interactions between life history and circulation are thought to drive distributions over the Ross Sea shelf: larvae disperse in outflow along the western side of Drygalski Trough, and mixing with trough inflow as the fish age enables return toward the inner shelf (Ashford et al., 2017, [11]). Secondary pathways underpinning life history closure may involve Joides and Glomar Challenger Troughs, connecting along the continental slope back to flows in the Drygalski Trough. Notably, all these pathways lie within the boundaries of the MPA, almost all within the General Protection Zone. Because of the importance of silverfish, the close correspondence between life history pathways and MPA boundaries helps address MPA objectives concerning ecosystem function and trophic interactions. Similar protection may be needed for areas important to the life cycle of toothfish, all the more because toothfish females grow much larger than males (e.g., [8]) and fishing large adults runs the risk of recruitment overfishing.

How to achieve this protection? The MPA comes up for review in 2027 [16], and this work suggests ways in which its boundaries might be tailored to target critical life history areas and transport pathways currently outside the General Protection Zone. Predictions based on transport indicate early emphasis on a potential primary pathway via Challenger Trough, Iselin Bank and the eastern Pacific-Antarctic Ridge; secondary pathways via Joides Trough and Adare Basin, and also Drygalski Trough, are likely less important. Nevertheless, consensus over changes that affect multiple objectives and stakeholders suggests that revisions might be difficult to achieve. A range of policy instruments are available: options might include introducing conservation measures for new reserves with limited objectives specific to toothfish life history, or narrower conservation measures aimed at limiting fishing in areas along targeted migration pathways. A critical consideration is that, whereas protection along the chain of life history areas will only be as good as its weakest link, consensus must include stakeholders with a commercial interest.

4.3. Downstream benefits, policy implications, and tools for testing

In this context, MPAs can increase returns to fishermen in neighboring areas (e.g., [49]), building support among commercial

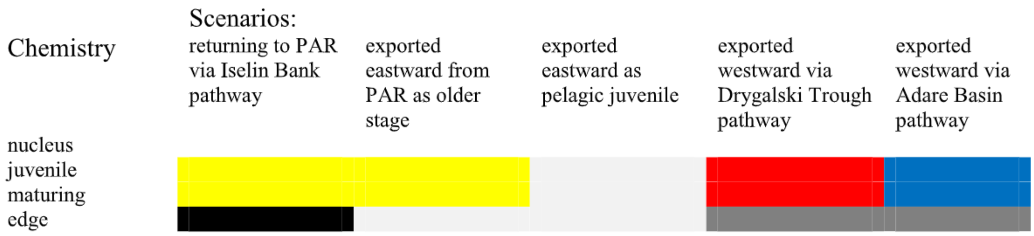

Fig. 7. Schematic illustrating expected sequences of otolith chemistry corresponding to scenarios concerning Antarctic toothfish from the Ross Sea population 1) retained within the population, 2) exported eastward at different life stages, and 3) exported westward from the Drygalski Trough and via the Adare Basin. Otolith chemistry laid down over the Pacific Antarctic Ridge during first year (white) and older stages (black); areas downstream east (light grey) and west (dark grey) of the Ross Sea region; pathways via Iselin Bank (yellow), Adare Basin (blue), Drygalski Trough (red).

stakeholders. Full productivity of the toothfish population resulting from protecting its life cycle, might deliver benefits for fishing elsewhere. Generally, spatial losses from a population are expected through geographic displacement from areas necessary for continued membership [51]. The fish exported from the Ross Sea region MPA may become non-breeding vagrants, or expatriates, in areas where abundance is determined by immigration and local mortality. Suitably tailored, protection conferred by a combination of the MPA and other policy instruments can help mitigate interruptions in the delivery of life stages and promote abundances and distributions well beyond its boundaries, potentially enhancing harvesting without detriment to the parent population.

The particle experiment highlighted how this might occur, through zonal transport in the ACC and along the continental slope. Contributions to export along the ACC implied a greater role for the Glomar Challenger than the Joides system in supplying toothfish to areas downstream. Critically, among releases further north, entrainment in the ACC and bathymetric steering along the Pacific Antarctic Ridge increased the proportion of particles exported eastward. Timing matters too: transport of the Ross Gyre varies considerably [22] whereas exchange with the ACC occurs on varying time scales [48]; in our simulations, the proportion of drifters exported was higher among releases during summer. Moreover, the Southern Boundary of the ACC marks the poleward extension of upper CDW and rapid shoaling of nutrient-rich deeper water. Its location above the Pacific Antarctic Ridge, closely associated with strong eastward flow in the Southern ACC Front, suggests a correlation between transport and productivity supportive of emigration towards the Antarctic Peninsula. However, the simulated trajectories indicated transport further north was dominant, especially during summer, indicating exchange with the Polar Front within the ACC. Elevated productivity associated with the front may help support adult emigration towards the Scotia Sea.

Similarly, gravity cascades down the slope from the Drygalski Trough connect to westward flow along the continental slope. Associated with a horizontal density gradient across the Antarctic Slope Front (ASF), the Antarctic Slope Current (ASC) continues around East Antarctica through the Weddell Sea as far as the South Scotia Ridge [26,55], potentially connecting the Ross Sea region MPA to shelf areas along its flow. Ross Sea silverfish reaching the ASF are thought to be exported along the slope (Ashford et al., 2017, [11]), with connectivity between multiple populations associated with trough systems along the ASC [14,15,62]. Additionally, movement along the ASC has been implicated in both species of the myctophid genus *Electrona* ([23,60], Zhu et al. in review), suggesting multi-species assemblages associated with westward export, and ready availability of food for toothfish emigration.

Further implications arise if emigrating toothfish eventually join another population to spawn. Source populations may maintain sink populations downstream, in which self-recruitment is insufficient to offset mortality [47]. Strategically placed networks of MPAs, currently under consideration for the Southern Ocean, can help protect populations linked by migration pathways. Thus far, CCAMLR's goal has been to work towards an ecologically representative system of MPAs based on benthic and pelagic regionalizations [12]. This could be complemented by considering connectivity, including migration and transport pathways for toothfish, in further design of Southern Ocean MPAs. Currently CCAMLR is considering proposals in the Weddell Sea, East Antarctic, and adjacent to the western Antarctic Peninsula [12]. Further particle modeling could help elucidate how effective these proposals would be in protecting toothfish population structure and connectivity.

Critically, otolith chemistry can help in testing the transport predictions. Under the working hypothesis, spawning along the Pacific Antarctic Ridge and subsequent exposure to the Ross Sea shelf should result in a sequence of tracers in the otolith nucleus and the material laid down by juveniles that is indicative of the Ross Sea population. Based on the discriminant analysis, most maturing fish and adults along the Pacific Antarctic Ridge should also show distinctive chemistry corresponding to the Iselin Bank pathway, and subsequent exposure to conditions along the Pacific Antarctic Ridge. This extended sequence, carried by spawning fish retained within the population, should also be present in fish in adjacent areas supplied as maturing fish or adults by eastward export from the MPA. By contrast, those supplied as pelagic juveniles will show only the nucleus chemistry before material corresponding to areas downstream. Areas supplied by westward export from the Ross Sea region MPA will carry the nucleus and juvenile sequence, and in some cases chemistry corresponding to the western pathway from Adare Basin, before material reflecting exposures off East Antarctica. Moreover, heterogeneity between the inner basins of the Ross Sea [44] augurs well, potentially generating sequences linking adult fish to nursery areas at basin scales (Fig. 7).

Further work is necessary to establish the sequence markers, and whether they separate sufficiently to allow classification from areas downstream of the Ross Sea. However, based on these data, combining circulation modeling with otolith chemistry appears a promising approach to examine how physical and biological processes interact in determining life history closure, and to separate breeding fish from those that are exported to neighboring areas. Designs that link circulation modeling with empirical testing based on biological response variables can help elucidate the effectiveness of reserve boundaries in promoting resource productivity and benefits downstream. We recommend further particle modeling at regional and circumpolar scales and across multi-year time periods, combined with otolith chemistry, to better understand toothfish movement across life history in space and over time. Through these experiments and additional modeling tools, connectivity involving source-sink dynamics and spillover effects from the MPA could be quantified [27,50,53]. This work would be strengthened if combined with field studies such as tag-recapture in and outside of the MPA [41,54]. Genetic studies too, can throw light on structuring and gene flow [18,19,38]. Collectively, a program incorporating combinations of these techniques would help inform whether the Ross Sea region MPA is meeting its objectives, and the role a network of MPAs might play in protecting toothfish populations around the Southern Ocean, and enhancing opportunities for harvesting. Here we show how a component combining circulation modeling with otolith chemistry to test life history hypotheses might be used to examine MPA efficacy, offering system-based tools for policy development that can be applied in the Antarctic and beyond.

CRediT authorship contribution statement

Julian Ashford: Conceptualization, Formal analysis, Funding acquisition, Methodology, Writing – original draft, Writing – review & editing. **Michael Dinniman**: Conceptualization, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Cassandra Brooks:** Conceptualization, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Lian Wei**: Conceptualization, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Guoping Zhu:** Conceptualization, Formal analysis, Methodology, Writing – original draft, Writing – review & editing.

Declaration of Competing Interest

The authors declare no competing interests.

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