Chapter 10
Population Structure and Life History Connectivity of Antarctic Silverfish (*Pleuragramma antarctica*) in the Southern Ocean Ecosystem

Julian Ashford, Lorenzo Zane, Joseph J. Torres, Mario La Mesa, and Alexander R. Simms

Abstract Antarctic silverfish (*Pleuragramma antarctica*) are the most important pelagic forage fish on the Antarctic continental shelf. They have an exclusively pelagic life history, including cryopelagic eggs and early larvae. The discovery of extensive distributions of eggs and larvae under fast-ice inside Terra Nova Bay, and the revelation that the aggregates were stable between years, suggested dispersal over the continental shelf by older larvae and juveniles and a return as adults to spawning areas, consistent with observations from the Antarctic Peninsula of large-scale adult movement inshore. This life history hypothesis holds promise for understanding population structure in silverfish found around the Antarctic continental shelf. However, the hypothesis is challenged by inconsistencies concerning the

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distribution of spawning and feeding areas, a low-energy life strategy, and lack of phylogenetic diversification.

We review recent and past population and genetic studies in the context of published literature on the physical environment, including hydrography and a recent geological reconstruction of Antarctic Ice Sheet deglaciation. We suggest physical-biological interactions between glacial trough systems, circulation, and life history processes in shaping distributions of silverfish along and across the shelf. We discuss how these processes may result in a richly diverse population structure around the Antarctic and over time, and show how the synthesis can help account for (1) variability in spawning and feeding areas over succeeding glacial cycles, (2) connectivity without invoking active migration on large spatial scales, and (3) persistence over successive glacial cycles without further phylogenetic diversification. Based on this synthesis, we make predictions concerning population structuring and genetic signatures of paleo-climatic events, and suggest multi-disciplinary approaches to test these in future research.

Keywords Population dynamics • Southern Ocean • Antarctic shelf • Antarctic fish

10.1 Introduction

Antarctic silverfish (*Pleuragramma antarctica*) are an important forage species in the marine ecosystem of the Southern Ocean, with a circumpolar range along the Antarctic continental shelf that extends to the South Orkney Islands (e.g. La Mesa and Eastman 2012; Duhamel et al. 2014) (Fig. 10.1). Unusually for a notothenioid, they have an exclusively pelagic life history, including a cryopelagic egg stage. The discovery of extensive distributions of eggs and larvae during November under fast-ice inside Terra Nova Bay in the Ross Sea (Vacchi et al. 2004) has stimulated interest in the processes structuring their populations and ecology. Recent sampling indicated that the aggregations were stable between years, restricted to embayments either side of the Campbell Glacier tongue, and associated with concentrations of platelet ice under the ice canopy (Vacchi et al. 2012; Guidetti et al. 2015). Distributions of young stages in the upper water column during December–January indicated dispersal over the continental shelf facilitated by the general circulation of the Ross Sea (La Mesa et al. 2010). Return as adults to spawning areas presumably completes the life cycle, consistent with observations from the Antarctic Peninsula (e.g. Daniels and Lipps 1982) of large-scale adult movement inshore.

This emerging life history hypothesis holds general promise for helping understand the population structure, as well as the distribution and abundance of silverfish around the Antarctic. Newly hatched larvae have been found in the south-eastern Weddell Sea (Hubold 1984), around the northern tip of the Antarctic Peninsula (Kellermann 1986; La Mesa et al. 2015), in Marguerite Bay (Donnelly and Torres 2008), and recently in the Bay of Whales in the eastern Ross Sea (Brooks and Goetz 2014). Growing evidence of population heterogeneity is consistent with life histories

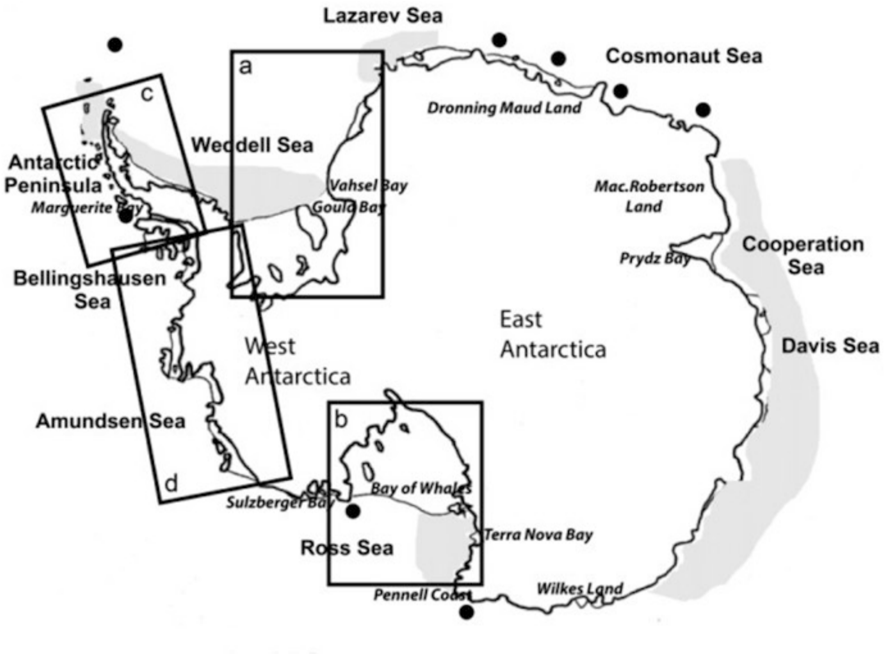

Fig. 10.1 Distribution of silverfish along the Antarctic continental shelf (Reproduced from La Mesa and Eastman 2012). *Black dots* indicate single record. *Frames* a, b, c, d enclose areas of interest whose details are shown in Figs. 10.2, 10.3, 10.4, and 10.5, respectively

linked to disparate spawning areas. Small but significant genetic differences detected both spatially and temporally (Zane et al. 2006) have been corroborated in a recent study (Agostini et al. 2015) that discounted panmixia, or random mixing, and indicated genetic structuring along the Antarctic Peninsula. Further evidence from differences in otolith chemistry (Ferguson 2012), reproductive measures (La Mesa et al. 2014), and distributions of faunal assemblages (Parker et al. 2015) also indicated spatial structuring.

However, several inconsistencies challenge the hypothesis in its present form. Firstly, La Mesa and Eastman (2012) pointed out that successive cycles of expansion and contraction of the Antarctic ice sheet (e.g. Anderson 1999) mean that current spawning areas, and feeding areas over the continental shelf, were covered over large periods during the evolutionary ecology of silverfish. Thus, a recent molecular phylogenetic study estimated that the Antarctic clade of notothenioids arose at approximately 22.4 Ma (million years before present, where present is defined as AD 1950) and Pleuragrammatinae, the neutrally buoyant clade to which silverfish belong, formed approximately 17 Ma (Near et al. 2012). The Pleuragrammatinae are characterized by only six species, including two members of the genus *Gvozdarus* (Eschmeyer et al. 2016) that are poorly known and not characterized at the molecular level. The latest split between the toothfish *Dissostichus mawsoni* and *D. eleginoides* occurred approximately 7.3 Ma, but earlier differentiation between *P.antarctica* and *Aethotaxis mitopteryx* dated at approximately 15 Ma (Near et al. 2012). By comparison, the Last Glacial Maximum (LGM) occurred at approximately 20 ka (kiloyears before present).

Secondly, the few species that are pelagic contrast with the spectacular diversification that occurred during late Miocene cooling (11.6–5.3 Ma) among benthic and bentho-pelagic Antarctic notothenioids. More than 100 species are currently recognized (Eastman 2005). Increased ice scouring, local extinction of the near-shore benthic fauna, survival of refugee populations in suitable areas, allopatric divergence and subsequent colonization of open niches have been invoked as the factors that allowed recurrent diversification of benthic and bentho-pelagic notothenioids (Near et al. 2012), as well as other Antarctic benthic taxa surviving the last glaciations (Thatje et al. 2008; Convey et al. 2009). In the Pleuragrammatinae, diversification is thought to have filled the niche space over the Antarctic shelf (Eastman 2005) consistent with a process of ecological speciation driven by divergent natural selection between environments (e.g. Schluter 2009). However, subsequent stability in the neutrally buoyant clade is harder to reconcile with mounting evidence of heterogeneity in shelf waters, both around the Antarctic and over time. The survival of only a few, old, highly divergent pelagic species suggests that lineage diversity was restricted either by increasing extinction rates or by reduced opportunities for speciation (Bortolotto et al. 2011). This raises the question: on an evolutionary time scale, how did silverfish adjust to environmental heterogeneity in a way that allowed populations to persist but without further phylogenetic diversification?

Thirdly, La Mesa and Eastman (2012) also pointed out that, in pelagic notothenioids, older fish do not maintain themselves in the water column by continuous swimming. Diversification from a benthic ancestry was achieved in large part through accumulation of lipids and paedomorphic adaptations, in which adult stages retain juvenile or larval features. Paradoxically in silverfish, this resulted in a pelagic species with an inactive, energy-efficient strategy that relies on extensive lipid sequestration in large sacs composed of adipocytes (Eastman and DeVries 1989). The resulting neutral buoyancy facilitates a sedentary lifestyle in which fish hang in the water column to feed (La Mesa and Eastman 2012). Questions immediately arise concerning silverfish movement: given the habitat constraint imposed on connectivity by their cryopelagic egg stage, how are the observed circumpolar distributions maintained? Secondly, how do adults return to spawning areas in order to close their life history? In this review, we start to resolve these issues by considering data from recent and past population studies in the context of glacial features and ice-sheet extent around the Antarctic continental shelf, as well as the shelf circulation and hydrography. We integrate the biological data with published studies on the physical environment, including a recent geological reconstruction of Antarctic Ice Sheet deglaciation. This synthesis showed that the ice sheet grounding line was near the shelf edge around much of the continent during the LGM, but the spatial pattern of deglaciation was highly variable (The RAISED Consortium et al. 2014). We suggest further development of the life history hypothesis that can account for variability in spawning and feeding areas, connectivity that does not rely on active swimming on large spatial scales, and persistence over successive glacial cycles without further phylogenetic diversification. In doing so, we take some initial steps towards an ecosystem perspective, with predictions concerning population structuring and genetic signatures of paleo-climatic events that can be tested in future research. Finally, we briefly consider some implications for other components of the ecosystem, including issues concerning fishing and climate variability.

10.2 Precedents

10.2.1 Prior Studies Suggest Early Life History Associated with Glacial Features on the Shelf

Kellermann (1986) noted that prior studies recorded silverfish early stages adjacent to ice shelves, which could be regarded as potential spawning areas. In particular, Hubold (1984) examined the spatial distribution of different age groups off ice shelves in the south-eastern Weddell Sea (Fig. 10.2). He found larvae <12.5 mm SL confined near the surface and associated with troughs off the Filchner Ice Shelf and Camp Norway. Higher post-larval concentrations (age 0+) coincided with troughs on the shelf as well, especially along the Filchner Ice Shelf in Gould Bay and Vahsel Bay, and also off the Brunt and Riiser-Larsen Ice Shelves. Distributions tended to be deeper with age. He noted the strong katabatic wind field and speculated that recruitment was influenced by yearly ice conditions associated with a polynya appearing along the coast during summer (Hubold 1984).

Extending out from under the Filchner Ice Shelf, Filchner Trough is the largest of a series in the south-eastern Weddell Sea that include the Ronne and Hughes Troughs (Fig. 10.2). Glacial reconstructions show that the grounding line, which delineates the limit where the ice sheet rested on the continental shelf, was near that of the present-day since 5 ka (Hillenbrand et al. 2012, 2014). However at 25 ka, it was located at the shelf break or on the outer shelf; off the Brunt and Quar Ice shelves, it had already retreated from the shelf edge (Hillenbrand et al. 2014). Ice streams extended along Filchner Trough to the outer continental shelf, sourced from both West and East Antarctica (Elverhoi 1981; Bentley and Anderson 1998; Larter et al. 2012; Hillenbrand et al. 2014). Available age constraints have not confirmed that the trough was filled with grounded ice during the LGM rather than a prior time period (Stolldorf et al. 2012; Hillenbrand et al. 2014), and the grounding line may have been confined to the inner shelf along the Ronne Trough, the Filchner Trough, and the continental margin farther east. Nevertheless, ice shelves are thought to have extended across these regions. Retreat was asynchronous: parts of the East Antarctic Ice Sheet (EAIS) retreated earlier than the West Antarctic Ice Sheet (WAIS) and the outer shelf off the Filchner Trough and farther east was free of grounded ice by between 15 ka and 10 ka (Stolldorf et al. 2012; Hillenbrand et al. 2014).

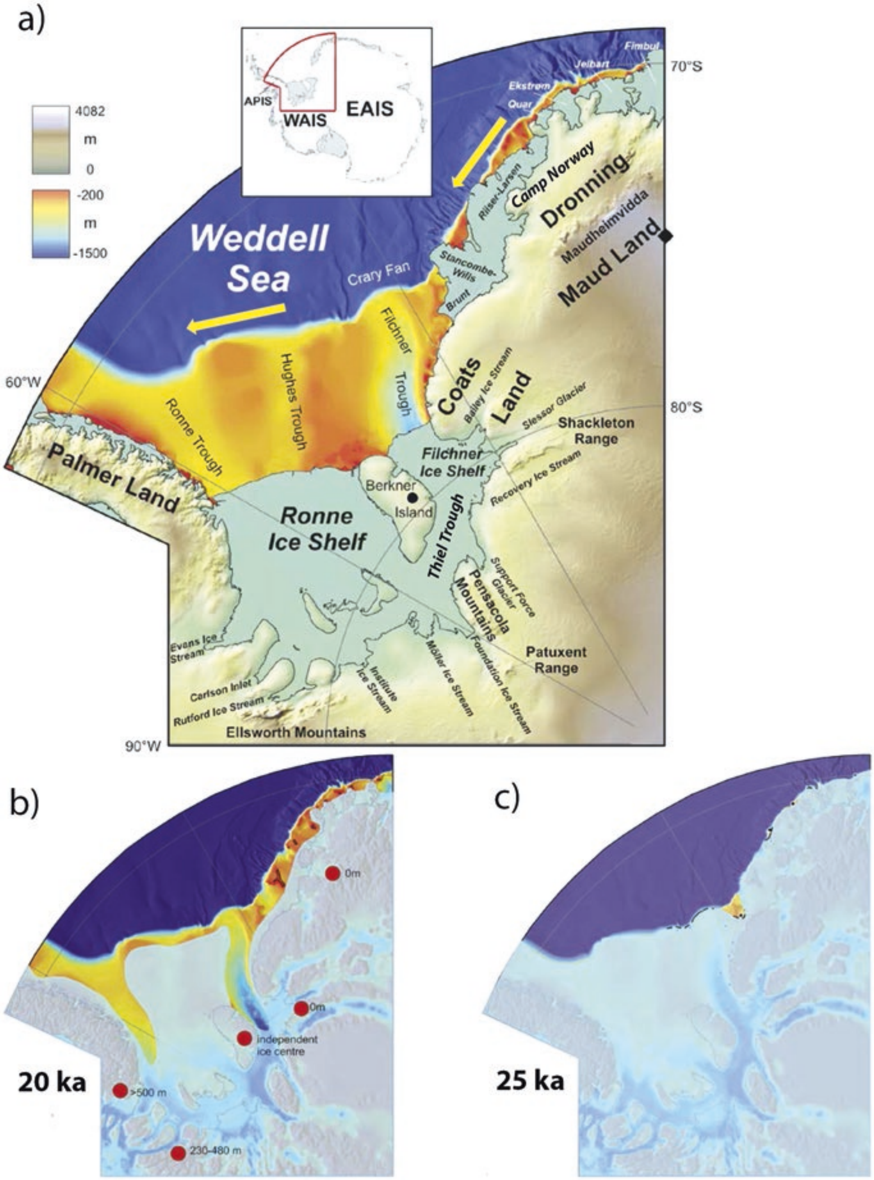

Fig. 10.2 South and southeastern Weddell Sea (Reproduced from Hillenbrand et al. 2014, Figs. 1, 8, and 12). (**a**) Shelf bathymetry and ice-sheet surface elevations (m above sea level). *APIS* Antarctic Peninsula Ice Sheet, *EAIS* East Antarctic Ice Sheet, *WAIS* West Antarctic Ice Sheet. *Yellow arrows* show direction of southern limb of Weddell Gyre. (**b** and **c**) Glacial reconstructions under alternative interpretations of available datasets (details in Hillenbrand et al. 2014): at 20 ka under Scenario A (**b**), at 25 ka under Scenario B (**c**)

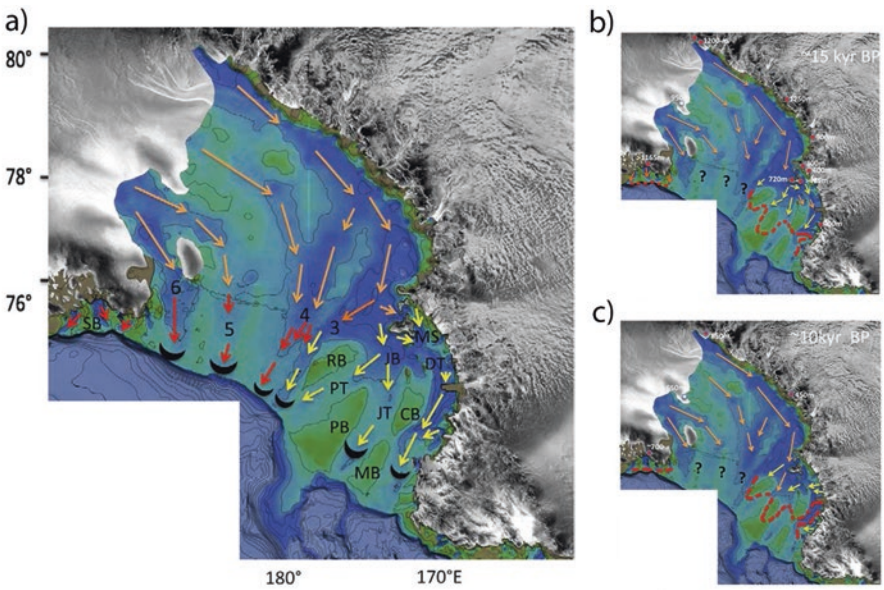

Fig. 10.3 Ross Sea (Reproduced from Anderson et al. 2014). (**a**) Bathymetry and paleo-drainage for maximum ice sheet advance showing ice draining East (*yellow arrows*) and West Antarctica (*red arrows*), with boundary at ca. 180° longitude. *Orange arrows* indicate inferred drainage in area beneath Ross Ice Shelf. – *Dark moon shapes* show grounding zone wedges; *MS* McMurdo Sound, *DT* Drygalski Trough, *CB* Crary Bank, *JB* JOIDES Basin, *JT* Joides Trough, *MB* Mawson Bank, *PB* Pennell Bank, *PT* Pennell Trough, *RB* Ross Bank, *SB* Sulzberger Bay. Trough numbering 3–6 using system by Mosola and Anderson (2006). *Insets*, also reproduced from Anderson et al. (2014), show inferred ice sheet elevations and grounding line (*dashed red lines*) in the western Ross Sea at (**b**) 15 ka and (**c**) 10 ka

In Terra Nova Bay, the David and Reeves Glaciers drain into the Drygalski Trough from the Transantarctic Mountains, directly offshore of the embayments where eggs and larvae were found in Silverfish Bay and the Gerlache Inlet. The Drygalski Trough is the largest of a series of cross-shelf troughs in the Ross Sea (Fig. 10.3). The region is also characterized by strong katabatic winds and a summer polynya, linked to considerable inter-annual variability in production that has been implicated in silverfish life history (La Mesa et al. 2010). However, an ice sheet occupied the Ross Sea embayment during the LGM, and it did not become largely ice-free until 7 ka (Licht et al. 1996; Hall et al. 2004; Anderson et al. 2014). Sourced from West and East Antarctica, the confluence was situated between Trough 3 and Trough 4 (numbering system used by Mosola and Anderson 2006) at approximately 180° longitude. The Drygalski Trough was occupied by ice streams draining from the EAIS, and the ice sheet was grounded north of Coulman Island (Anderson et al. 2014). Prior to 34 ka, an earlier ice sheet advanced to the edge of the continental shelf (Mosola and Anderson 2006). After the LGM, retreat followed a complex pattern with episodes of back-stepping and stability (Shipp et al. 1999; Domack et al. 1999; McKay et al. 2008). The grounding line reached the Drygalski Ice Tongue by 11 ka (Licht et al. 1996; Domack et al. 1999) but, outside of the trough, ice remained north of Terra Nova Bay until 8.2 ka (Baroni and Hall 2004) and did not retreat to the vicinity of Ross Island until ca 7.8 ka (Licht et al. 1996; Anderson 1999; McKay et al. 2008; Hall et al. 2013; Anderson et al. 2014) although more recent work suggests earlier deglaciation (McKay et al. 2016). By contrast, available age constraints suggest earlier retreat of the WAIS in the eastern Ross Sea where recently hatched larvae were found in the Bay of Whales (Brooks and Goetz 2014). The grounding line may have already been inshore of the shelf margin by the LGM, possibly forming a deep embayment (Licht et al. 1996; Bart and Cone 2012; Anderson et al. 2014).

Along the western Antarctic Peninsula (AP), the largest glacial feature on the shelf is Marguerite Trough, which extends from inside Marguerite Bay to the shelf break (Fig. 10.4, H). Donnelly and Torres (2008) caught 0+ age silverfish in Marguerite Bay during surveys in 2001 and 2002; large abundances of larvae and juveniles were found around the coastal fjords in the northern bay and inside George VI Sound. Nevertheless, the AP Ice Sheet (APIS) was grounded to the outer shelf edge during the LGM (Fig. 10.4) and contained ice streams that drained along cross-shelf bathymetric troughs (Pudsey et al. 1994; Evans et al. 2005; Heroy and Anderson 2005, 2007; O'Cofaigh et al. 2014). Off Marguerite Bay, the grounding line was located on the outer shelf and retreat was well underway by 14 ka (Kilfeather et al. 2011). Radiocarbon dating from glacial marine sediment indicated that retreat was initially slow between 13.5 and 12.6 ka across the outer to middle shelf but was rapid across the inner shelf around 9.6 ka (Bentley et al. 2011; Kilfeather et al. 2011). The larger inner fjords such as Neny Fjord were ice free by 9 ka (Allen et al. 2010) and the smaller fjords were ice free by around 6 ka (Simkins et al. 2013).

Farther to the north-east, Kellerman (1986) recorded silverfish post-larvae and juveniles in the Bransfield Strait and along the northern AP shelf during a series of surveys between 1976 and 1982. He hypothesized that larvae reach the Bransfield Strait by advection in water flowing from the north-western Weddell Sea around Joinville Island (e.g. Thompson et al. 2009). More recently, La Mesa et al. (2015) coupled otolith micro-increment data from larvae caught off Joinville Island with particle simulations from a circulation model, to predict where the larvae were spawned. They estimated two main areas of origin, one on the inner shelf off the Larsen A ice shelf connecting to the second at the shelf-break, both corresponding to the vicinity of the Larsen Inlet Trough (Fig. 10.4, L). The glacial reconstruction for the region (Evans et al. 2005; O'Cofaigh et al. 2014) shows ice streams that occupy the trough extending out to a maximum grounding position running along the shelf break (Fig. 10.4).

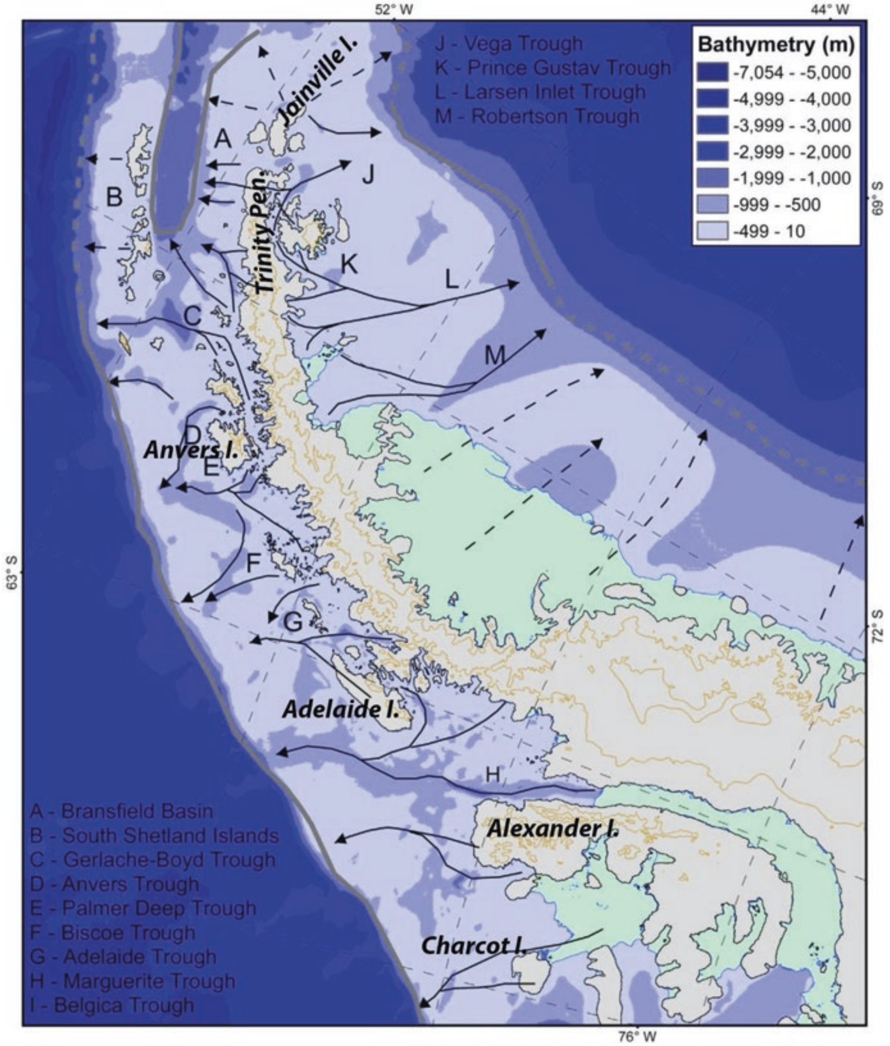

Fig. 10.4 Antarctic Peninsula (Reproduced from O'Cofaigh et al. 2014), showing reconstruction of ice streams and grounding line at LGM, with strong relationship to cross-shelf bathymetric troughs. *Arrowed lines* show ice-streams; *heavy grey line* shows LGM grounding line (*inferred where dashed*); modern ice shelves are shown in *light green*. *H* shows the Marguerite Trough system extending along Alexander Island from the ice shelf in George VI Sound (See also Fig. 10.9)

10.2.2 Geological Studies Document Widespread Distribution of Glacial Trough Systems Across the Shelf

Similar large trough systems occur across the shelf around the Antarctic and suggest present-day availability of silverfish habitat. In East Antarctica, the glacial trough in Lützow-Holm Bay reaches to the continental slope off Dronning Maud Land; Iceberg Alley and Nielsen Basin similarly dissect the shelf off Mac.Robertson Land (Mackintosh et al. 2014). Prydz Bay contains several large troughs, and glacial flow into the Amery Ice Shelf accounts for a substantial part of the drainage from the EAIS (Anderson 1999). Off Wilkes Land, the Mertz, Ninnis, Adelie and Clarie Troughs all originate at the mouths of ice streams draining the EAIS, and connect to the shelf edge (Mackintosh et al. 2014). Large trough systems are also found along the Pennell Coast (Anderson 1999), associated with ice flow from the northern edge of the Transantarctic Mountains and the EAIS.

Further east in Sulzberger Bay, drainage is from the WAIS. Similarly, the Dotson-Getz, Pine Island and Abbott Troughs in the Amundsen Sea, and the Belgica and Latady Troughs in the Bellingshausen Sea (Fig. 10.5), were all occupied by major ice streams that drained the WAIS and flowed across the continental shelf (Larter et al. 2014). North of Marguerite Bay, the AP is transected by systems that drain from the APIS. They include the Adelaide (Fig. 10.4, G), Biscoe and Anvers Troughs (Fig. 10.4, F and D respectively), and the Palmer Deep (Fig. 10.4, E), which may have been eroded by ice flowing in from the Gerlache Strait (Heroy and Anderson 2005). In the north-western Weddell Sea, the Prince Gustav Trough (Fig.10.4, K) is located to the north of the Larsen Inlet Trough, and the Robertson Trough (Fig. 10.4, M) is to the south (O'Cofaigh et al. 2014). By contrast, cross-shelf trough systems are relatively few in the southern Weddell Sea, because ice streams from the WAIS are directed eastward along the Thiel Trough into the Filchner Ice Shelf (Anderson 1999; Hillenbrand et al. 2014).

However, such habitat has varied considerably over time. Regional reconstructions show that, like the Weddell Sea and Ross Sea, ice extended to the edge of the shelf along the continental margin off much of East Antarctica including Wilkes Land (Mackintosh et al. 2014). Off West Antarctica, it extended to the shelf edge off Sulzberger Bay (Anderson et al. 2014) and along the Amundsen and Bellingshausen Seas (Larter et al. 2014), as well as the western and eastern AP (O'Cofaigh et al. 2014). Nevertheless, at 20 ka, the grounding line did not reach the shelf edge everywhere, and the local LGM and subsequent retreat were not synchronous (Anderson et al. 2002, The RAISED Consortium et al. 2014). The ice sheet retreat from Prydz Bay occurred by ca 13.5 ka (Domack et al. 1998) whereas, in Sulzberger Bay, most of the deglaciation is thought to have occurred in the last 11 ka (Anderson et al. 2014). In the Amundsen and Bellingshausen Seas, retreat varied considerably (Hillenbrand et al. 2010, 2013; Kirshner et al. 2012). It was well underway before 29 ka in the Belgica Trough (Hillenbrand et al. 2010), but not until 20 ka in the other major troughs (Larter et al. 2014). The grounding line retreated rapidly in the

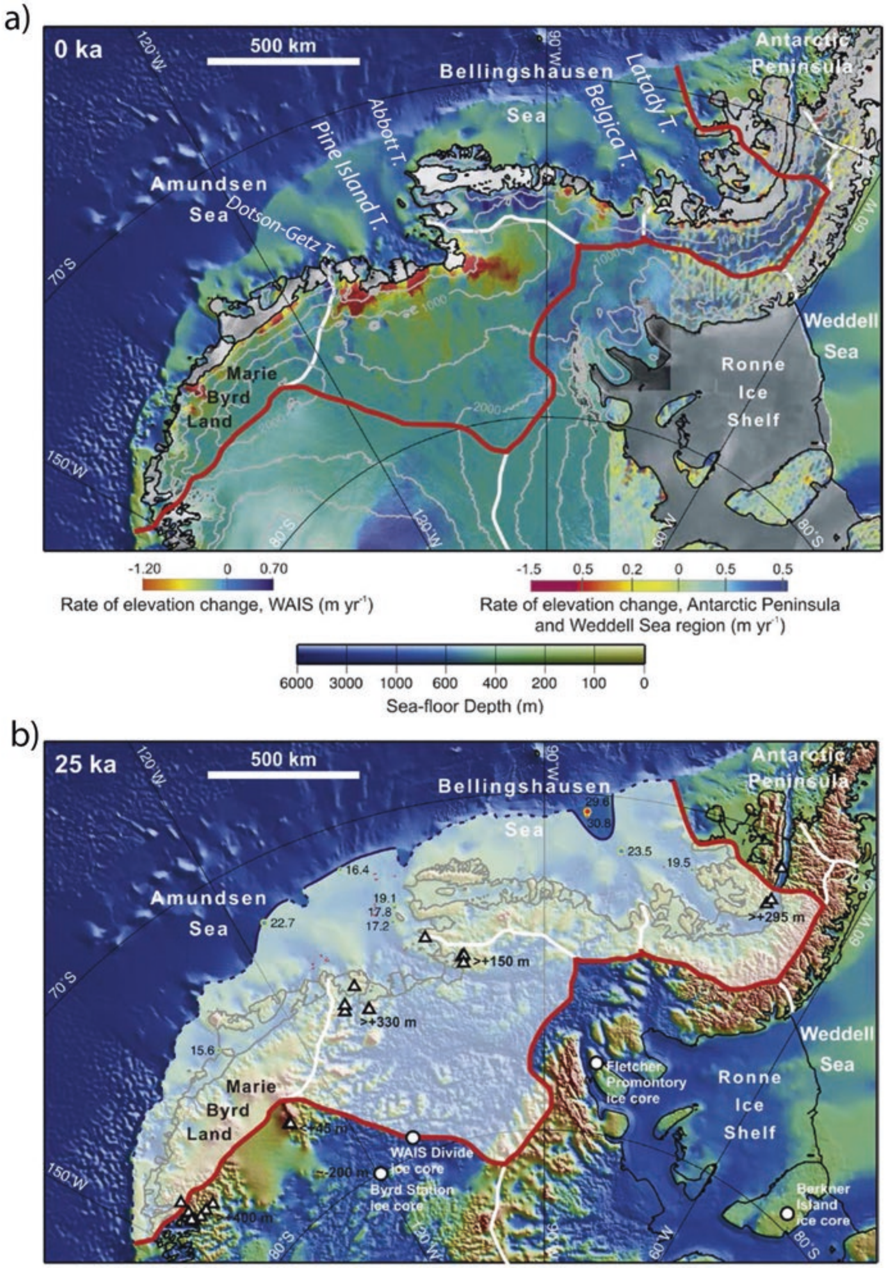

Fig. 10.5 Amundsen and Bellingshausen Seas (Reproduced from Larter et al. 2014). (**a**) Modern ice sheet configuration, showing surface elevation, ice sheets, and shelf bathymetry, (**b**) glacial reconstruction at 25 ka, showing extent of ice sheet as semi-transparent *white fill* and margin as *dark blue line* (*dashed* where less certain). *Thick white lines* mark major ice divides

Amundsen Sea to near modern limits by 10 ka (Lowe and Anderson 2002; Smith et al. 2011). By contrast in tributaries feeding into the Belgica Trough, it had reached the inner shelf in Eltanin Bay by 15 ka, but was very limited along the Ronne Entrance where it was still retreating at 5 ka (Larter et al. 2014). Initial retreat along the AP progressed southward over time; it also varied considerably between nearby troughs (O'Cofaigh et al. 2014). Retreat was earlier along the eastern AP than the western AP, and underway by 18 ka. From sampling in the Prince Gustav Channel, deglaciation and the transition to an ice shelf occurred prior to 11–12 ka (Evans et al. 2005). Grounded ice is likely to have been near its present configuration by 10 ka. However, fringing ice shelves remained more extended, with major retreat episodes suggested for the Larsen-A Ice Shelf between 3.8 ka and 1.4 ka (O'Cofaigh et al. 2014).

Recent consensus attributes thinning in modern ice shelves and retreat of grounded ice in ice streams to basal melting. Increasing inflow of warm Circumpolar Deep Water (CDW) along troughs, combined with topographic effects on ice flow and warm water inflow, may help explain the differences in retreat history between troughs (Larter et al. 2014). Topographic effects include bottlenecks and confluences in the configuration of ice streams, and submarine reverse slopes. These slopes are inclined towards the continent as a result of isostatic depression caused by the weight of the ice sheet that creates deep basins along the inner shelf (Larter et al. 2014).

10.2.3 Previous Studies Suggest Life History Associated with Ocean Circulation

Ocean circulation plays an important role in structuring populations across a range of Southern Ocean species (e.g. Loeb et al. 1993). The Antarctic Circumpolar Current (ACC) has been implicated in the transport of young Antarctic krill (*Euphausia superba*), entrained in fronts, from the western AP to South Georgia (e.g. Hofmann et al. 1998; Fach and Klinck 2006). According to simulations of the large-scale circulation, transport pathways connect widely separated regions of the Southern Ocean (Thorpe et al. 2007), and empirical studies suggest population structuring in *D. eleginoides*, a member of the neutrally buoyant clade of notothenioids, that is linked to the position of fronts and the direction of water flow (e.g. Shaw et al. 2004; Ashford et al. 2006, 2008). The Ross Gyre in the Southeast Pacific Basin (SPB) has also been implicated in the life history of *D. mawsoni* (Hanchet et al. 2008; Ashford et al. 2012). Matschiner et al. (2009) further pointed out that long larval and early juvenile pelagic stages, and connectivity generated by oceanographic currents, may promote gene flow around Antarctica in many notothenioid species. Damerau et al. (2012) found evidence of eastward gene flow in seven species from Elephant Island and the South Shetland Islands towards the South Orkney Islands. In the icefish *Chaenocephalus aceratus,* westward gene flow has been found as well (Papetti et al. 2009, 2012), and may be linked to an active post-larval stage (Ashford et al. 2010b). These results suggest that a complex interplay between oceanographic currents and life history features can act together to determine population structure, distribution and abundance across a range of notothenioid species.

Like La Mesa et al. (2010), earlier authors studying silverfish have linked dispersal from spawning habitat to regional circulation over the continental shelf. In the southeastern Weddell Sea, Hubold (1984) implicated surface Ekman transport induced by the katabatic wind field in transporting age 0+ post-larvae distributed over troughs to the offshore side of the coastal polynya and as far as the outer shelf edge. Moreover, he observed that post-larvae were largely absent over the Weddell Sea basin, and suggested that fish might be concentrated by the slope front, as well as locally by eddies. Kellermann (1996) proposed that, as well as connectivity from the north-western Weddell Sea (Kellermann 1986), extensive distributions of juvenile and adult silverfish found along the western AP shelf (e.g. Daniels and Lipps 1982) were the result of advection along the southern ACC from a source in the Bellingshausen Sea. He suggested advective pathways from the Bellingshausen to the shelf off the Biscoe and Palmer Archipelagos, and also inshore south of Anvers Island through the Gerlache Strait into the Bransfield Strait.

Genetic studies have also considered the potential effect of hydrography on silverfish connectivity. Zane et al. (2006) examined whether a pelagic life history and exposure to major circum-Antarctic currents resulted in weak population structure around the Antarctic. Genetic samples were taken in different years in the southeastern Weddell Sea off Halley Bay, in Terra Nova Bay and in the northern Bransfield Strait off Elephant Island and the South Shetland Islands. The results suggested considerable gene flow, but significant differences were found between years at Halley Bay and in a single comparison between Halley Bay and Terra Nova Bay. Similarly, Agostini et al. (2015) found evidence that supported geographic genetic structuring among silverfish sampled off the Larsen Ice Shelf, around Joinville Island, and along the southwestern AP, but also confirmed the weakness of genetic differentiation. They found genetic homogeneity between samples collected off the south-western AP at Marguerite Bay and Charcot Island and a weak net gene flow southward from the northern Peninsula. They suggested that these results, and considerable variability found between years, could be explained by dispersal from spawning areas into deeper water that exposes fish differentially to circulation features over the shelf. The resulting interplay between transport and retention determines spatial distributions along the AP.

Parallel studies found evidence corroborating connectivity along the south-western AP. Using the same fish as Agostini et al. (2015), Ferguson (2012) found differences in the trace element chemistry laid down in the otolith nuclei of fish sampled from the south-western AP and off Joinville Island in Antarctic Sound; however, there were no differences between fish from Marguerite Bay and off Charcot Island, consistent with a single population. Examining this further, La Mesa et al. (2015) found no structuring between Marguerite Bay and Charcot Island using reproductive metrics. Finally, Parker et al. (2015) found oceanic assemblages of invertebrates and fish mixing inshore over the western AP shelf, and silverfish strongly associated with neritic assemblages constrained along the northern and south-western coasts. They noted the contrast with prior distributions of silverfish, and suggested that a strengthening oceanic regime was consistent with increasing intrusion of CDW, notably along the Marguerite Trough (e.g. Dinniman and Klinck 2004). Building on the conclusions of Agostini et al. (2015), they hypothesized that, restricted inshore, dispersing silverfish are no longer exposed to circulation features over the outer shelf of the western AP, and this fundamentally alters their subsequent connectivity and distribution.

Taken together, these studies implicated physical-biological interactions between glacial trough systems, circulation and life history processes in shaping population structure and connectivity in silverfish, and hence gene flow and genetic differentiation. Moreover, compared to studies in other species, they highlighted the present-day importance of westward connectivity via the shelf circulation, and suggested diminishing influence of eastward transport in the ACC along the western AP slope. Because circulation is frequently constrained by topography, these interactions also suggest important associations between habitat and connectivity, ultimately structured by geological processes over successive glacial cycles.

10.3 Topography, Circulation and Connectivity Around the Antarctic Continental Shelf

10.3.1 Circumpolar Flow in the ACC

Frequently invoked as the major current shaping biological dispersal in the Antarctic, eastward flow in the ACC is concentrated in high-speed jets associated with fronts (e.g. Orsi et al. 1995, Fig. 10.6). The southern of these is the Southern ACC Front (SACCF), associated with shoaling of CDW towards the surface. The southern boundary of the ACC is located over the continental slope along the eastern Amundsen and Bellingshausen Seas (Orsi et al. 1995); off the western AP, flow along the slope is associated with the SACCF (Savidge and Amft 2009). The resulting eastward transport provides a potential pathway that can facilitate along-shelf movement of silverfish, consistent with Kellermann (1996). Connectivity with the shelf is facilitated by Upper CDW transported in the ACC that floods the shelf along the Peninsula. The intruding water mixes with intermediate Winter Water (WW) to form a deep layer of Modified CDW (e.g. Smith et al. 1999).

Downstream of the AP, the ACC southern boundary passes to the north of the South Orkney Islands (Fig. 10.7), where silverfish are found over the continental shelf (e.g. Jones and Kock 2009). However, further east, it moves far offshore, passing out into the southern Atlantic Ocean through a trough north of the South Sandwich Islands. Similarly, the SACCF is steered offshore by the Northwest Georgia Rise after looping around the eastern shelf of South Georgia.

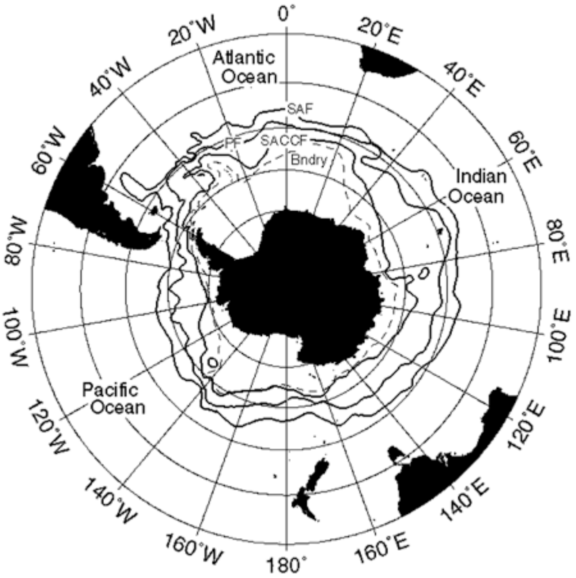

Fig. 10.6 The Southern Ocean (Reproduced from Ashford et al. 2008), showing the mean position of the main fronts in the Antarctic Circumpolar Current (ACC) (Orsi et al. 1995) in relation to West and East Antarctica. *SAF* Subantarctic Front, *PF* Polar Front, *SACCF* Southern ACC Front, *Bndry* southern boundary of the ACC

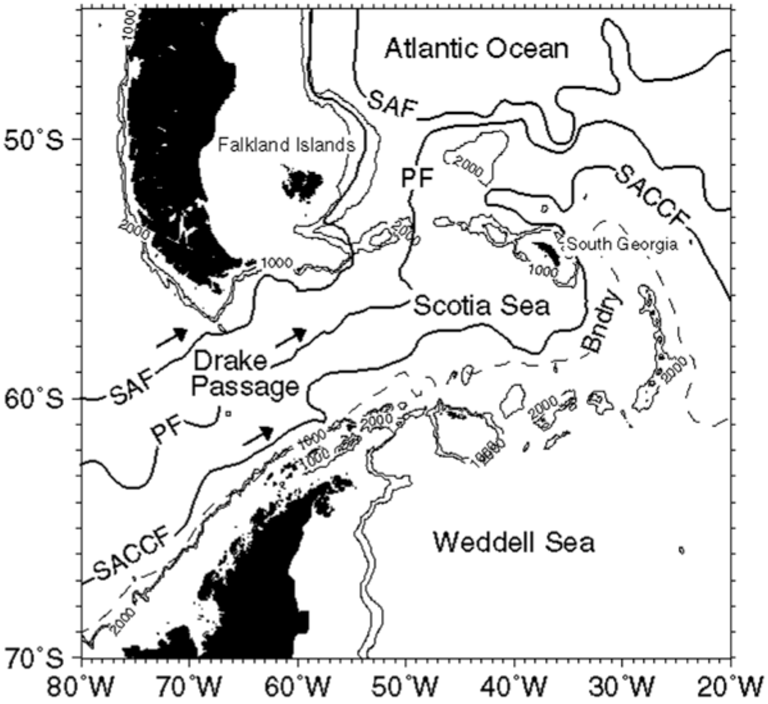

Fig. 10.7 The Drake Passage, Scotia Sea and southern Atlantic Ocean reproduced from Ashford et al. (2008), showing the frontal systems of the ACC (Orsi et al. 1995) in relation to the western Antarctic Peninsula and southern Scotia Ridge. Abbreviations as in Fig. 10.6

Silverfish have been found only rarely off South Georgia and the South Sandwich Islands (e.g. Trunov 2001). In contrast to the concentrations of krill, their sporadic occurrence argues that they are not entrained in the same ACC transport pathways in this region.

Continuing eastward, the ACC flows around the Weddell Gyre and southward, again bringing CDW close to the continental shelf along East Antarctica (Orsi et al. 1995). In the western SPB, the southern boundary follows the bathymetry along the Pacific-Antarctic Ridge: rapid shoaling of lower CDW marks the northward limit of the Ross Gyre, and it forms a warm, salty layer that reaches south to the continental slope. Further east, the ACC extends southward again, creating a bifurcation in the Amundsen Sea between eastward transport along the continental slope towards the AP, and westward transport along the eastern Ross Sea in the southern limb of the Ross Gyre. Thus, as a result of the large-scale circulation, these pathways can potentially transport fish larvae around the Southern Ocean. However, connectivity to habitats along the Antarctic continental shelf depends on the proximity of the southern boundary to the slope, its interaction with the shelf circulation, and the spatial availability of fish over their life history.

10.3.2 Along-Shelf Structuring

The southward extension of the ACC east of the Ross Gyre forces its eastward flow along the continental slope from the Amundsen Sea to the north-western AP. In sharp contrast, the flow of recirculating water along the southern limb of the Weddell Gyre is westward (e.g. Orsi et al. 1993; Loeb et al. 1993). In the western Weddell Basin, water flows northward (Fig. 10.8): in the Weddell Front off the continental slope; in the Antarctic Slope Front (ASF) along the slope; and in the Antarctic Coastal Current (CC) over the shelf (Thompson et al. 2009). Water transported in the Weddell Front flows around the Powell Basin to reach the South Orkney Islands, where Warm Deep Water (WDW) from the Weddell Sea is found over the southern shelf (Gordon et al. 2001; Heywood et al. 2004). The CC and ASF are steered by the topography to flow northwest around the tip of the Peninsula, forming transport pathways for along-shelf recruitment of silverfish from the Weddell Sea to larval aggregations in the Bransfield Gyre (Kellermann 1986; La Mesa et al. 2015). The two fronts merge at the mouth of the Bransfield Strait and a branch flows northeastward eventually into the southern ACC, while another forms a pathway that continues southwestward inshore along the Trinity Peninsula.

However, recent hydrographic evidence does not support extension of this advective pathway further southward through the Gerlache Strait, as suggested by Kellermann (1986). Similarly, the evidence does not support a strong advection pathway over the shelf south of Anvers Island and northward into the Bransfield Strait, as hypothesized by Kellermann (1996). Instead, westward flow off the northern AP forms the southwestward limb of the cyclonic circulation in the Bransfield

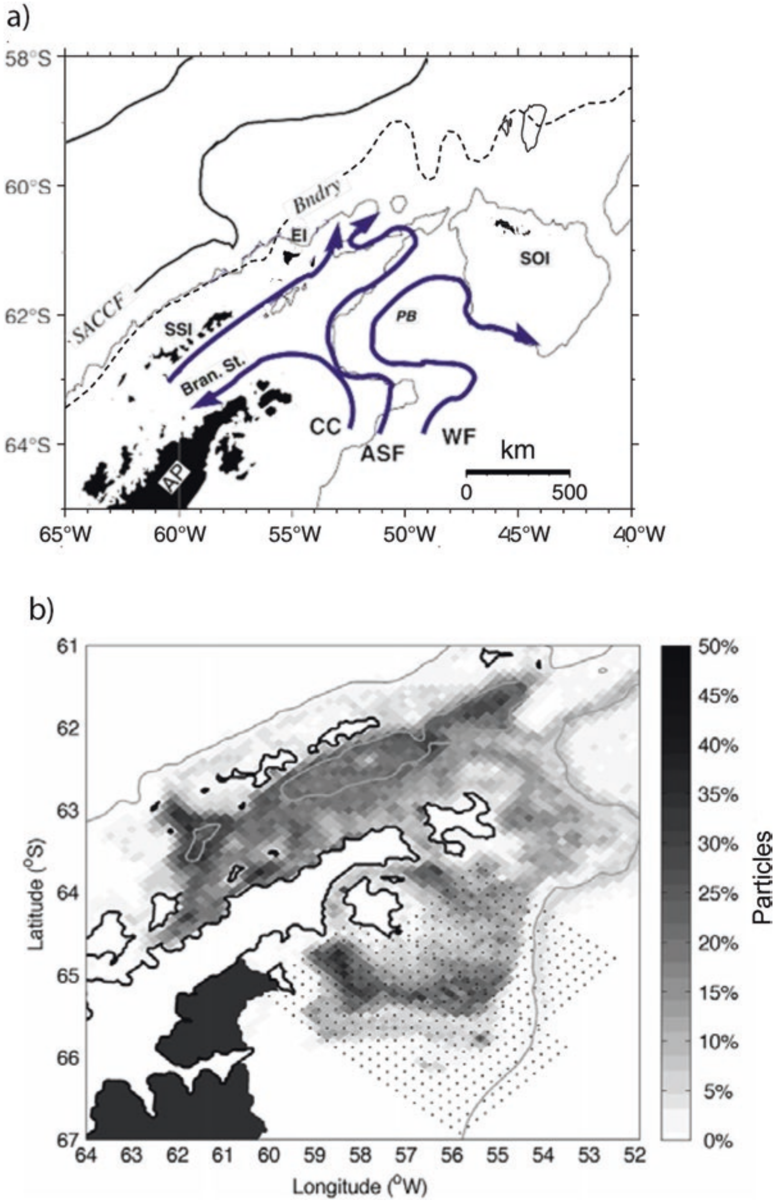

Fig. 10.8 The Western Weddell Sea and Bransfield Strait (**a**) Showing dominant currents, reproduced from Ashford et al. (2010b) and drawn originally from Thompson et al. (2009) (**b**) Distribution of simulated particles released along the eastern Antarctic Peninsula (Reproduced from La Mesa et al. 2015). Particles (%) indicate preferred transport pathways. *SACCF* Southern ACC Front, *Bndry* ACC southern boundary, *CC* Coastal Current, *ASF* Antarctic Slope Front, *WF* Weddell Front, *SSI* South Shetland Islands, *EI* Elephant Island, *SOI* South Orkney Islands, *Bran. St.* Bransfield Strait

Strait (Savidge and Amft 2009), and sharp changes in water properties (e.g. Smith et al. 1999) suggest a strong discontinuity that accounts for population structuring between silverfish found along the northern and southwestern AP (Ferguson 2012; Agostini et al. 2015; Parker et al. 2015). Minimal mixing between waters in the Gerlache Strait and south of Anvers Island, and a relatively shallow sill in the Neumayer Channel, create a barrier that prevents large-scale southward connectivity as fish age and move deeper during their migration. Nevertheless, mixing occurs between the water masses, and may account for the low levels of gene flow measured (Agostini et al. 2015). A strong western boundary current in the Bransfield Strait brings water from the Weddell Sea past the South Shetland Islands, potentially accounting for catches of silverfish in research trawls over the continental shelf (e.g. Jones et al. 2001).

Off the southwestern AP, Hofmann and Klinck (1998) described nearshore southward flow as part of a shelf-scale gyre, with circulation at the shelf-break dominated by the ACC. An independent southward circulation along the inner shelf has been described by Moffat et al. (2008). Strongly seasonal, the Antarctic Peninsula Coastal Current (APCC) is typical of coastal buoyant plumes with freshwater inputs largely from precipitation over the ocean and meltwater run-off from land (Moffat et al. 2008). A freshwater tongue in which the signature of WW is weak or absent extends laterally offshore to approximately 20 km, where a salinity front separates it from shelf waters. The velocity field shows a strong current co-located with the salinity front, extending to 150 m depth with surface velocities of 0.15–0.40 m s^{-1}. In winter, the formation of sea-ice and reduced horizontal gradients of seawater properties are associated with a shut-down of the APCC. Velocities rarely exceed 0.05 m s^{-1} and flow reverses episodically (Moffat et al. 2008).

The current creates a seasonal transport pathway along the inner shelf. The APCC reappears after the ice starts to retreat in late October, coinciding with spawning and hatching of silverfish. Based on drifter tracks (Beardsley et al. 2004), flow southward along Adelaide Island is thought to enter Marguerite Bay and exit around Alexander Island (Fig. 10.9). This generates a transport pathway that connects spawning in Marguerite Bay to areas where fish were caught over trough systems near Charcot Island. Based on evidence from otolith chemistry (Ferguson 2012), the fish are from the same population and movement occurs in the first year after hatching. The shallower distribution of young fish is consistent with the location of the APCC velocity front in the water column, ensuring exposure to westward transport. Moffat et al. (2008) pointed out that the front creates a favorable environment for biological production, suggesting that westward transport and foraging opportunities are correlated.

Indeed, coastal buoyancy forcing may be a general feature of silverfish population structure, connecting spawning areas to shelf distributions downstream. Dispersal along the APCC from spawning areas in Marguerite Bay is congruent with that predicted by La Mesa et al. (2015) for the northern Peninsula in which the CC connects spawning in the vicinity of the Larsen Inlet Trough to silverfish distributions around the Bransfield Strait. Moreover, APCC flow southward past Adelaide Island is thought to originate in the vicinity of Anvers Island (Moffat et al. 2008) and

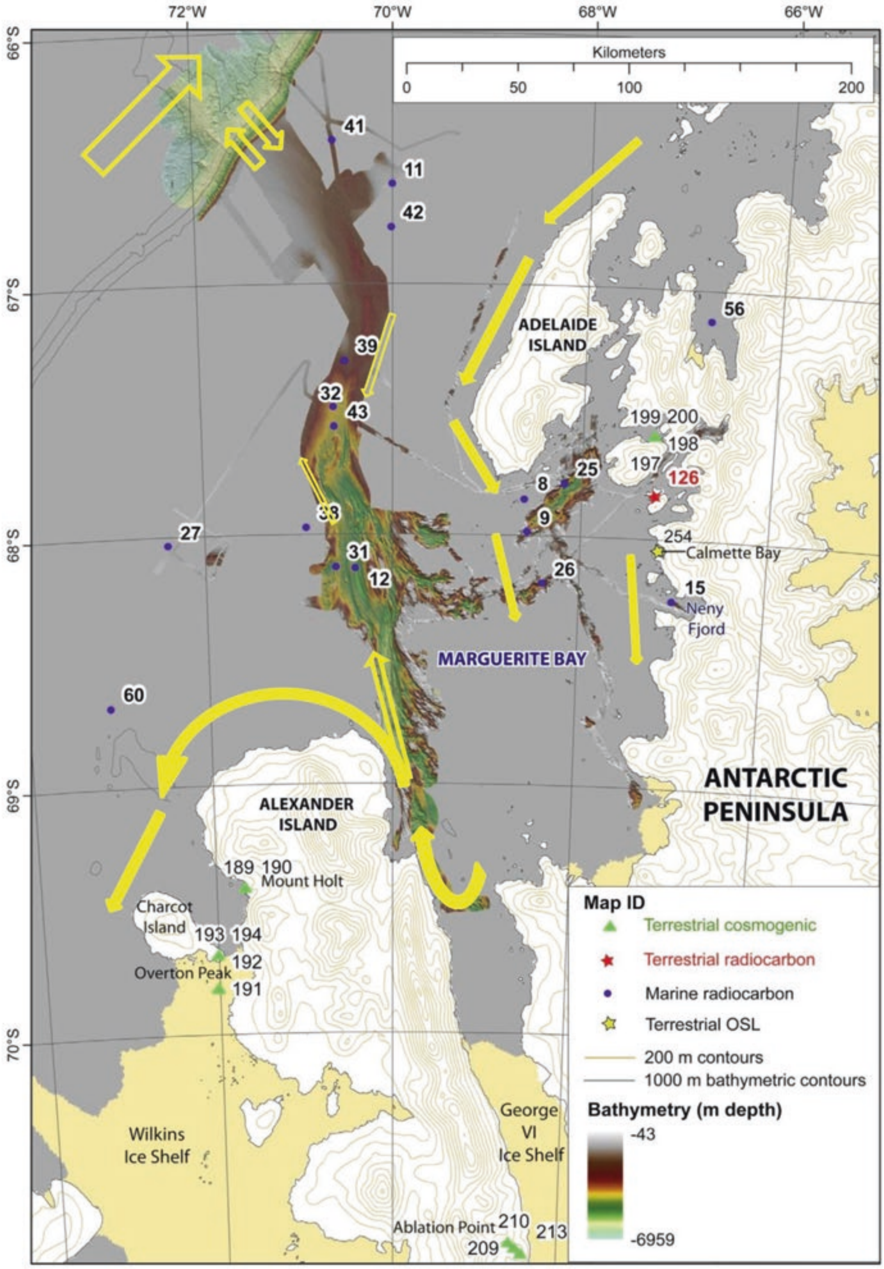

Fig. 10.9 Marguerite Trough showing bathymetry and location of marine radiocarbon samples (Reproduced from O'Cofaigh et al. 2014), with schematic of the shelf circulation. Net trough inflow and outflow (*transparent arrows at mouth*) based on Dinniman and Klinck (2004); location of the APCC (*filled arrows*) is drawn from Moffat et al. (2008). *Large arrow* indicates direction of flow over the shelf slope along the southern boundary of the ACC

a similar system may have operated historically along the mid-Peninsula. Thus, Parker et al. (2015) argued that a locally reproducing population would account for historic concentrations of silverfish south of Anvers Island, spawning under fast ice close to one of the trough systems that transect the AP at this latitude. Flow along the APCC that entrained young fish foraging in the surface layer would have connected spawning areas to distributions over the mid-Peninsula shelf. In conclusion, recent studies around the AP suggest that silverfish distribution and population structure may be closely related to the location and transport of coastal buoyancy plumes, and hence precipitation and meltwater run-off from ice-sheets along the shelf.

10.3.3 Cross-Shelf Structuring

If along-shelf flow from spawning habitat can help explain circumpolar distributions of silverfish over the shelf, how then do sufficient numbers of adults return to spawning areas to maintain individual populations? Consistent with Parker et al.'s (2015) argument for localized reproduction along the western AP, cross-shelf flow following the bathymetry along troughs may provide a recirculating mechanism. Inertia forces water onto or off the shelf where the shelf-break curves, notably off the Marguerite Trough and into the Biscoe and Anvers Troughs (Dinniman and Klinck 2004). The deeper, nutrient-rich Upper CDW driven upward by the shallowing bathymetry connects via the on-shelf flow to cross-shelf circulation. Off Marguerite Bay (Fig.10.9), cross-shelf flows at depth (Dinniman and Klinck 2004) contrast with broad jets in the upper layer that extend to a depth of 200 m (Savidge and Amft 2009). These follow the northeastern flank of the trough system inshore and the southwestern flank in a seaward direction at velocities of ca. 0.05 m s^{-1}. In the Marguerite Trough, adult fish distribute throughout the water column below 100 m, and notably around the interface where CDW and WW mix between 100 and 200 m (Fig. 10.10, Ferguson 2012). Water following bathymetric contours along the trough sides potentially facilitates connectivity between productive areas associated with mixing CDW, and spawning areas near the head of the trough. Other retention features may contribute. Piñones et al. (2011) found in simulations that cyclonic circulation in Laubeuf Fjord retained particles in deeper water, associated with a productivity hotspot. Moreover, the mean circulation field suggested retention of younger stages in a cyclonic eddy formed in the surface layer of Marguerite Bay, where offshore flow meandered to join inflowing water along the northeastern side of the trough (Piñones et al. 2011).

Interactions between flows across and along shelf may be important to connectivity between populations as well. Because intrusions of CDW are episodic and vary in intensity, the frequency and extent of their penetration are likely to influence the distance that silverfish disperse along the trough. Agostini et al. (2015) hypothesized that dispersal from spawning areas into deeper water exposes fish to circulation over the shelf, and the resulting interplay between transport and retention

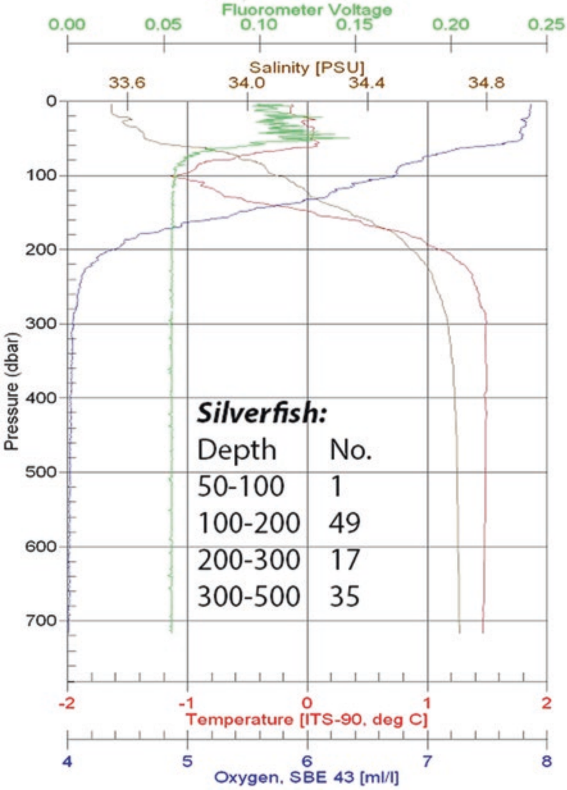

Fig. 10.10 Distribution of silverfish with depth and water properties in Marguerite Trough (latitude 068° 09.11, longitude 069° 59.63), April 2010. Volume of water sampled was approximately proportional to depth range

determines population structure and distribution. Variability in the frequency and penetration of CDW along the Marguerite Trough may regulate silverfish exposure to flow eastward along the shelf break, and hence connectivity with trough systems further to the northeast. Congruent with Kellermann's (1996) advective pathway along the southern ACC to south of Anvers Island, such a mechanism could help account for the historic observations of silverfish concentrations by Daniels (1982), with fish potentially sourced from troughs located upstream along the shelf as far as the bifurcation in the Amundsen Sea. Conversely, a strengthening oceanic regime that constrains silverfish distributions away from the slope (Parker et al. 2015), also shifts the population away from eastward connectivity along the ACC. Nevertheless, westward connectivity remains viable along the APCC. Water flowing along the shelf inshore becomes entrained in the trough circulation, providing a pathway for migration and gene flow between populations.

In the western Ross Sea (Fig. 10.11), similar considerations apply but with important differences. Inflow from the shelf-break follows the bathymetry along the west side of the series of banks oriented north-south on the shelf, with outflow on the eastern side (Dinniman et al. 2003). Lower CDW modified by mixing with AASW floods onto the shelf at the shelf-break in the vicinity of troughs separating the banks

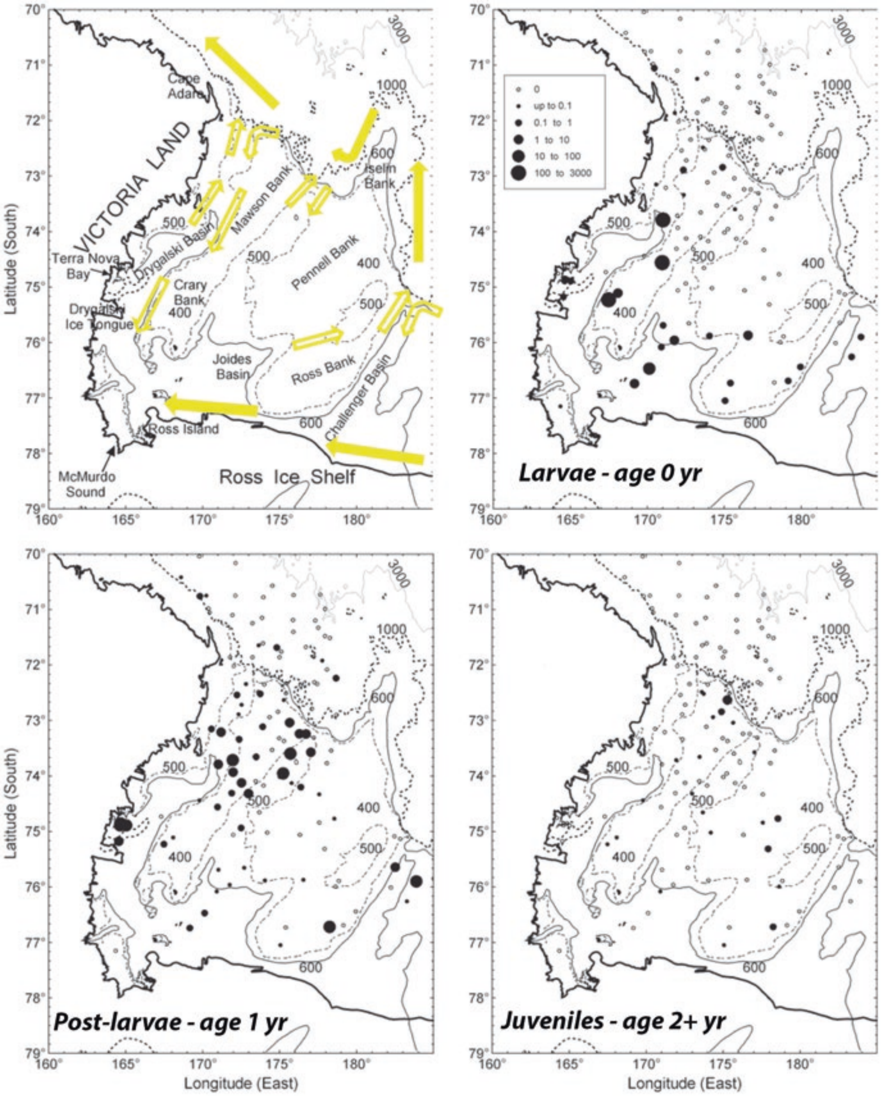

Fig. 10.11 Distributions of young silverfish in the upper water column of the western Ross Sea (Reproduced from La Mesa et al. 2010), in relation to the shelf circulation. *Upper left panel* shows schematic of westward flow along the Ross Ice Shelf and in the Antarctic Slope Current (*filled arrows*), and cross-shelf flow in inflows and outflows along troughs (*transparent arrows*). Other panels show standardized abundances of silverfish at pre-flexion, post-larval and juvenile stages in net tows that sampled to a maximum depth of between 130 and 300 m

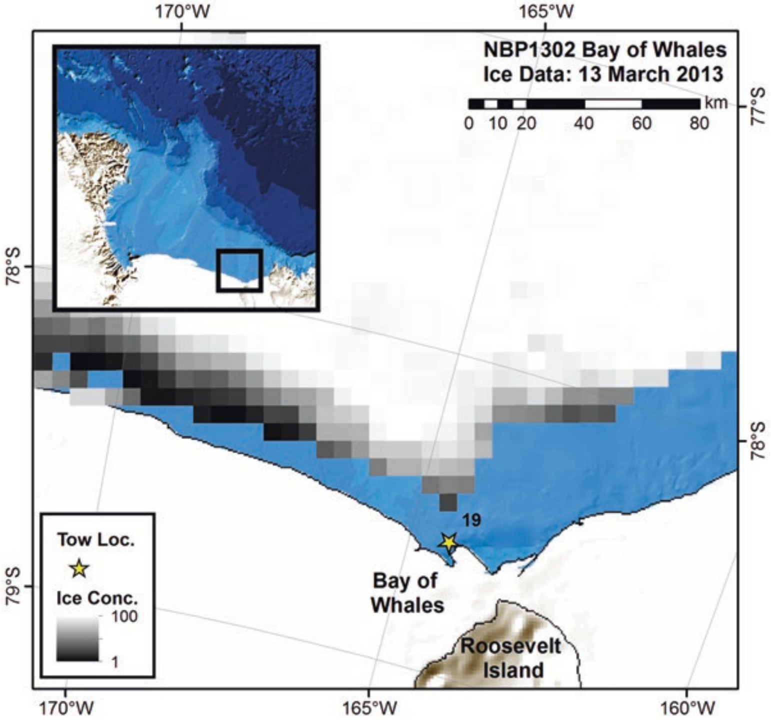

Fig. 10.12 Bay of Whales, showing ice concentration and site sampled by Brooks and Goetz (2014)

(e.g. Stover 2006; Orsi and Wiederwohl 2009). It meets equatorward flow of dense, cold High Salinity Shelf Water (HSSW), mixing to form Modified Shelf Water (Gordon et al. 2009). Consistent with La Mesa et al. (2010), young silverfish dispersing into the Ross Sea polynya from Terra Nova Bay encounter shelf outflow that follows the western side of the Drygalski Trough, facilitating movement to productive areas associated with inflowing nutrient-rich modified CDW. As fish age, they move deeper, away from surface waters. However, rather than returning fish to the spawning areas near the head of the trough, the inflow attenuates along the Crary Bank and into the Drygalski Basin, from where shelf outflow can facilitate movement back past Terra Nova Bay. Another difference from Marguerite Trough is that flow along the slope is westward in the Antarctic Slope Current (Dinniman et al. 2003; Locarnini 1994; Rickard et al. 2010). As a result, although silverfish can disperse in counter-clockwise flow around the Mawson and Crary Banks, eastward connectivity is severely constrained no matter how far fish disperse out over the shelf.

Similarly, in the eastern Ross Sea, cross-shelf circulation along bathymetric contours can facilitate movement between spawning in the Bay of Whales (Fig. 10.12) and feeding areas along the eastern troughs. Westward transport occurs along the Antarctic Slope Front, and a current that flows along the front of the Ross Ice Shelf. However, any eastward connectivity is severely constrained by the circulation.

10.4 Developing the Life History Hypothesis

10.4.1 Variability in the Structure of Marine Fish Populations

The previous section illustrates how physical-biological interactions can help resolve issues over connectivity that challenge the life history hypothesis. The present-day structure and hydrography of major trough systems provide a series of mechanisms that can help explain how an inactive, energy-efficient species moves between pelagic habitats occupied over its life history, and eventually returns to spatially constrained spawning areas necessary for a cryopelagic egg stage. Even before invoking behavior, predictable transport pathways along the shelf suggest how circumpolar distributions of silverfish can be maintained.

Nevertheless, a life cycle structured by hydrography implies considerable leakage. Biology can play a mitigating role through reinforcing behavior as well as physiological adaptation. For instance, as indicated by Moffat et al. (2008), fronts with rapid velocity shear are often zones of high productivity; fine-scale movement relative to feeding opportunities can facilitate entrainment in transport pathways supporting life history connectivity. Moreover, silverfish are unusually fecund for a notothenioid species, which renders them resilient under changing environmental conditions (La Mesa et al. 2014). It can also be seen as an adaptation to offset advective losses over their life history. Observations recorded by Daniels and Lipps (1982) among others suggest shoaling and aggregating behavior in adults as well, and active shoreward movement at spawning time. Active swimming that reinforces transport inshore would serve to optimize energy costs and reduce advective mortality.

The link between population structure and physical barriers has been widely recognized. Frontal systems, depth, or changes in gradients in water properties can obstruct directed movement and create spatial separation (e.g. Kingsford 1993; Loeb et al. 1993; Shaw et al. 2004). As a result, environmental variability can lead to changes in abundance through variation in mortality rate or self-recruitment, with their extent delineated by population boundaries. Yet ocean circulation can produce more complex population structure. Retention features can structure population diversity (Iles and Sinclair 1982), and currents that connect disparate areas can create opportunities for succeeding stages during the life history (e.g. Harden Jones 1968). But population membership can only be maintained if these trajectories eventually allow return to spawning areas (Sinclair 1988; Sinclair and Iles 1989), either by actively migrating adult stages (e.g. Cushing 1981) or facilitated by transport. Alternatively, fish can be entrained in trajectories that do not allow closure, becoming either non-breeding vagrants (Sinclair 1988) in habitats where abundance is determined by immigration and local mortality, or migrants if they eventually join another population to spawn. In the latter case, source populations with high recruitment relative to mortality can maintain sink populations in which self-recruitment is insufficient to offset mortality (Pulliam 1988; Polachek 1990). Interruptions to net migration can lead to extinctions of sink populations, even without local changes in births and deaths. As a result, variation in the spatial and temporal delivery of life stages between habitats can impact abundance and distribution over large areas.

Physical-biological interactions like these affect genetic differentiation and gene flow. High fecundity and early mortality can enhance the effect of genetic drift (David et al. 1997) in situations where many individuals fail to contribute to recruitment, and stochasticity associated with reproduction influences the proportion of individuals that contribute to the next generation (Hedgecock 1994). Several factors, including local oceanographic features such as troughs and upwelling nutrient-rich areas that exert temporary spatial constraints on individuals, can influence the success of parents and therefore the genetic composition in the pool of recruits (Aglieri et al. 2014). Among the consequences of variable reproductive success are a reduction in the effective genetic population size compared to census size, and a pattern of temporal genetic patchiness (unpatterned genetic heterogeneity) among local populations on a small spatial scale (Pujolar et al. 2009). Notably, both these effects have been observed in silverfish. Agostini et al. (2015) estimated the effective population size of silverfish collected off the western AP to be about 6500–11,000 individuals. They also found increasing differentiation over time between the southwestern and northern AP, and differences among length classes at Joinville Island. Zane et al. (2006) found a similar result for the Weddell Sea, with samples collected in 1989 differing significantly from samples collected in 1991.

Physical and population processes can interact with gene flow in complex ways. Populations exposed to divergent selection pressures can develop local adaptations even in the presence of high levels of gene flow (Canino et al. 2005; Hemmer-Hansen et al. 2007). Genetic differences at loci under selection often correlate with environmental variables (e.g. Milano et al. 2014), suggesting that there is a cost in terms of mortality associated with significant gene flow between locally adapted populations (Zane 2007). Similarly, the genetic-environment association (GEA) hypothesis (Bierne et al. 2011) predicts pre- or post-zygotic genetic incompatibilities that are independent from adaptation to habitats, and can determine a genetic load during immigration and successful reproduction. The GEA hypothesis has been recently invoked to explain growing evidence from genome-wide scans of genetic markers that show a much higher level of differentiation than expected under conditions of strong gene flow (Bierne et al. 2011). When incompatible genetic backgrounds come into contact, endogenous barriers negatively affect the fitness of immigrant offspring, increasing mortality and preventing the flow of certain combinations of alleles (Milano et al. 2014).

Moreover, range changes through expansion and contraction (e.g. MacCall 1990) can alter the spread and retention rate of mutations under selection pressure. They can also generate contact zones between populations that are adapted to different selective pressures or are genetically incompatible. In these cases, connections between divergent local populations can result in stable metapopulations in which genetic diversity is preserved at the cost of increased local mortality and extinction rates. Conversely, gene flow through immigration can homogenize differences between populations over the long term. The level of migrants needed to achieve homogenization is as low as one migrant per generation at equilibrium in an

Infinite Island Model (Waples and Gaggiotti 2006; see also Agostini et al. 2015 for silverfish in the AP). The evidence of weak but significant genetic differentiation in many Antarctic fish implies an ongoing exchange that is nevertheless insufficient to counteract genetic drift: in these situations, small increases in the level of connectivity can rapidly cause the differences to disappear, strongly impacting genetic structure.

However, rather than greater connectivity, recent observations in the AP suggest an increasing pattern of isolation for silverfish (Parker et al. 2015). Thus, in a stepping stone-type scenario, genetic differentiation between previously homogeneous adjacent populations seems reasonable, especially if temperature-related reductions in larval-stage duration (O'Connor et al. 2007) alter the complex spatial mechanisms of recruitment and connectivity between locations (Patarnello et al. 2011). Nevertheless, the accumulation of genetic differences through drift is extremely slow in populations of thousands of individuals. Ecological populations are generally nested within larger genetic units (Lowe and Allendorf 2010), since the amount of migration needed to maintain genetic homogeneity is far smaller than the lower bound required to render them ecologically independent (Bortolotto et al. 2011). As a result, inferences of genetic homogeneity should not be interpreted as implying the existence of a single ecological unit for management purposes. But conversely, heterogeneity can have complex causes: as well as discrete populations with independent recruitment and mortality, temporal genetic patchiness or mixing between two or more populations in different proportions can generate spatial variation in allele frequencies. Local populations that are connected, for instance in a metapopulation, also imply vital rates that are not independent, in which changes in connectivity can fundamentally influence their genetic structure and diversity.

10.4.2 Silverfish Population Structure: Variability Around the Antarctic

General theoretical considerations like these, taken with empirical evidence of interaction between physical forcing and life history processes, argue strongly for a richly diverse population structure in silverfish around the Antarctic. So far, there has been no comprehensive study at different spatial scales and over time. However, the series of studies from the AP indicate separation between Marguerite Bay and the northern Peninsula, with coherent feeding and spawning areas centered around the Marguerite Trough system. Similarities with fish found off Charcot Island can be explained by advection of young stages in the APCC along the coast of Alexander Island, but the lack of a return pathway suggests the Charcot fish are non-breeding vagrants. Lack of differentiation in the otolith trace element chemistry (Ferguson 2012) argues against mixing with a population reproducing locally off Alexander Island. Similarly, lack of any return pathway to the northern Weddell Sea suggests that fish reaching the Bransfield Strait and the shelf off the South Shetland Islands are vagrants. Low levels of gene flow are consistent with some southward emigration via hydrographic mixing in the Gerlache Strait. Emigration into the Bellingshausen and Amundsen Seas may also occur from the southwestern population by advection along the APCC. However, it remains unclear how far the coastal plume extends. It also remains unclear whether the trough systems downstream support suitable spawning areas that might account for distributions of silverfish caught off Marie Byrd Land and in the eastern Ross Sea (Donnelly et al. 2004).

In the northern Weddell Sea, the simulation study by La Mesa et al. (2015) predicted that larvae advected around Joinville Island largely originated in the Larsen Inlet Trough, suggesting a source population with a coherent life history. Nevertheless, Agostini et al. (2015) also found temporal instability in genetic frequencies. They hypothesized that physical-biological interactions during dispersal over the shelf may shape the genetic patterns observed, generating variability and hence genetic patchiness. However, the study also noted that the instability could reflect mixing with another unsampled population. Under this hypothesis, prevailing flow and the presence of several trough systems along the shelf imply advection from two or more source populations, themselves related through migration via flow along the coast and shelf slope. However, it has yet to be documented whether populations occupy the Prince Gustav, Robertson and Jason Troughs; or whether fish in Antarctic Sound represent a separate system with outflow into the southern Bransfield Strait. Although current evidence cannot discount genetic instability due to pulses of immigration from unsampled populations, the differences were weak and the hypothesis requires further testing.

Distributions of silverfish in the southeastern Weddell Sea gave a clearer indication of unidirectional movement between coherent populations linked to trough systems along the shelf. Hubold (1984) observed that warmer water reaches the shelf edge at depths of 500 m, and the troughs contained warm water at depth. He also noted a large cyclonic gyre over Filchner Trough. He hypothesized its involvement in the distribution of silverfish larvae. Thus, the gyre and an eddy system off Camp Norway represent retention areas for young fish following local hatching; dispersed over the shelf by cyclonic water movement and the katabatic wind field, they collect along the slope front accounting for concentrations found 30 km from shore. Moreover, consistent with westward connectivity, Hubold (1984) found post-larvae distributed over troughs along the shelf from Camp Norway to the Filchner Ice Shelf, as well as smaller numbers of 1 + yr. and adult fish. While the survey did not extend west of Filchner Trough, the relative paucity of trough systems along the southern Weddell Sea argue that any fish dispersing further westward may reach neighbouring populations only rarely, and mostly become vagrants instead.

By contrast, fish around the South Orkney Islands appear isolated. Although water transported in the Weddell Front flows around the Powell Basin to reach the South Orkney Islands, the obstacles to entrainment of silverfish in the current off the continental shelf and the distances involved make connectivity doubtful from either the northwestern or southeastern Weddell Sea. Evidence from otolith chemistry indicated structuring between fish caught in Antarctic Sound and over the South Orkney shelf (Ferguson 2012). By comparison, there was no differentiation along the shelf south of Coronation and Laurie Islands, suggesting that silverfish around the South Orkney Islands represent a separate and currently discrete population.

In the Ross Sea, the Antarctic Slope Current and the current along the ice shelf suggest pathways for westward advection from the eastern trough systems. However, Zane et al. (2006) found no genetic instabilities in the western Ross Sea. Moreover, homogeneity in the otolith nucleus chemistry of fish caught along the Drygalski Trough, Crary and Ross Banks (Ferguson 2012) corroborated a lack of mixing from the Bay of Whales and further east. The lack of connectivity suggested that either distances were too large relative to flow velocity; or alternatively, that fish in the Bay of Whales were spawned late in the season and seasonal flow along the ice shelf was limiting. Further west, outflow from the mouth of the Drygalski Trough and westward along the shelf may promote connectivity with extensive silverfish distributions found along East Antarctica (La Mesa and Eastman 2012). However, distances are large and, away from the surface, much of the outflow at the Drygalski mouth contributes to gravity flows that cascade down the slope (Gordon et al. 2009). Instead, recent evidence points to a single, discrete population in the western Ross Sea, centered on spawning in Terra Nova Bay. Several return pathways may be involved, facilitated by cross-shelf flow along bathymetric contours. Adult silverfish caught in trawls in the Drygalski Basin, acoustic backscatter indicating others in concentrations along the Drygalski and Joides Troughs, and comparatively large densities of juveniles along the Joides Trough (O'Driscoll et al. 2011), suggest trajectories along the Drygalski Trough, around the Mawson and Crary Banks, and around the Drygalski Basin.

10.4.3 Silverfish Population Structure: Variability over Time

The interaction between physical and life history processes also provides insight into how silverfish populations may have persisted over successive glacial cycles without giving rise to further phylogenetic diversification. Although current spawning areas and most of the continental shelf were covered during large periods, system shifts along troughs during ice sheet retreat and subsequent advance may have shaped complex and dynamically changing populations. Newly hatched fish in the Bay of Whales (Brooks and Goetz 2014) (Fig. 10.12) and in Gould Bay and Vahsel Bay (Hubold 1984) demonstrate that indentations along ice-sheets can provide the conditions necessary for spawning. As evident in Terra Nova Bay, active ice streams can help maintain ice distributions during ice-sheet retreat, creating embayments on either side with a source of meltwater and protection from near-shore advection. The relationships between CDW intruding into the deep basins inshore and the retreat of ice streams and break-up of ice-shelves along the AP (e.g. Dinniman et al. 2012; Larter et al. 2014) suggests that, as silverfish spawning areas retreated across the shelf, productive feeding areas increasingly advanced up troughs, mitigating variability in the distance between silverfish feeding and spawning grounds.

As ice sheets have retreated close to the coast, however, populations have become less exposed to circulation features associated with the outer shelf. Movement along the shelf-break and slope is reduced, and interaction with buoyancy-forced features inshore dominates connectivity instead. Increasingly, structure and processes at the head of the trough are important to the persistence of spawning areas: glacial dynamics, including the size and variability of ice flow and meltwater, and the configuration of the shoreline influence the predictable formation of fast ice. Along the western AP, such a mechanism is consistent with Parker et al.'s (2015) hypothesis that the recent disappearance of silverfish was due to extinction of a population south of Anvers Island as a result of regional warming. Recent failure of recruitment at Marguerite Bay suggests a similar extinction in process. Parker et al. (2015) also suggested a spatial connection between the two populations. Reductions in eastward connectivity could have contributed to the decline off Anvers Island if persistence depended on northeastward immigration from Marguerite Bay in a source-sink relationship.

The contrast with strong continuing recruitment in the Ross Sea implies variation at regional scales. Regions like the western AP that are strongly influenced by warming (e.g. Stammerjohn et al. 2008) show a higher rate of extinction related to the timing and intensity of succeeding cycles. Populations in regions like the Ross Sea where present-day warming trends lag, or that occupy deeply indented systems with continuing strong ice-streams, tend to survive as sources for westward connectivity. Moreover, the glacial reconstructions show regional variation in the timing of deglaciation that suggests differential changes in habitat availability, population structure, and connectivity during ice sheet retreat. Thus, the rapid retreat of the APIS across the inner shelf of Marguerite Bay around 9.6 ka (Bentley et al. 2011) meant that the deep inshore basins along the western AP were available before those in the Ross Sea. Retreat of the EAIS from Prydz Bay by ca 13.5 ka (Domack et al. 1998), and of the WAIS by 10 ka in the Amundsen Sea (Lowe and Anderson 2002), indicate much earlier availability than in Sulzberger Bay, where retreat occurred mostly in the last 11 ka (Anderson et al. 2014). In Belgica Trough, continuing retreat along the Ronne Entrance at 5 ka (Hillenbrand et al. 2010; Larter et al. 2014) suggests changes in habitat and circulation, with ongoing effects on silverfish abundance and life history connectivity.

Conversely, as ice sheets advance, it seems reasonable that many of these dynamics reverse. Changes in meltwater input would reduce buoyancy-driven westward connectivity during summer, just as currently during winter. With decreasing intrusion of warm water along troughs, feeding areas of surviving populations would trend outwards across the shelf, exposing fish to circulation features that provide new opportunities for connectivity and colonization. Consistent with the hypothesis of Parker et al. (2015), eastward connectivity could promote re-colonization of the Anvers and Biscoe Troughs as spawning areas became viable again after the warming phase ends. By subsidizing births, immigration from Marguerite Trough would stabilize any newly colonized population south of Anvers Island. Alternatively, consistent with Kellermann's (1996) hypothesis, connectivity eastward along the ACC could contribute vagrants from troughs in the Bellingshausen or Amundsen Seas to south of Anvers Island, accounting for historic distributions even without local self-recruitment. Similar considerations apply in the Weddell Sea. Katabatic activity further out over the slope and increasing exposure to circulation features offshore could promote westward connectivity to troughs downstream along the ASF, and colonization of the South Orkney Shelf along the Weddell Front.

At the LGM, however, the geological reconstructions demonstrate that the ice grounding line reached the shelf-break along large areas of the AP, Weddell and Ross Seas, as well as the Bellingshausen and Amundsen Seas and East Antarctica (Anderson 1999; O'Cofaigh et al. 2014; Hillenbrand et al. 2014; Larter et al. 2014; Anderson et al. 2014; Mackintosh et al. 2014; other references therein). An ice shelf is thought to have covered the Bransfield Strait, and the South Shetland Ice Cap extended onto the outer continental shelf (Simms et al. 2011). The resulting exposure to ice conditions and oceanic water at trough mouths implies a new set of extinction threats, with changes in the structuring of fast ice and the areas of productivity available, as well as the distances between them. Nevertheless, the sedimentary evidence indicates that the grounding line at the LGM may have been strongly indented inshore from the mouths of the Filchner and Drygalski Troughs (Hillenbrand et al. 2014; Anderson et al. 2014). In these systems, residual cross-shelf exchange may have allowed populations to persist, while others went to extinction. Re-colonization could then resume as the ice-sheet retreated back across the shelf once more.

Genetic data provide some corroborating evidence. Based on mitochondrial DNA sequencing and analysis of mismatch distribution, silverfish experienced a population expansion in the past (Zane et al. 2006). However, the timing needs clarification. The starting of the expansion was originally dated to about 120 ka, during the last (Eemian) inter-glacial period. This was revised to about 200 ka, corresponding to the beginning of the previous glacial period, after incorporation of new fossil and geological evidence in the molecular clock calibration (Janko et al. 2007). A concordant pattern of population expansion has been reported for Antarctic krill (Zane et al. 1998; Goodall-Copestake et al. 2010), suggesting a similar effect of paleo-climate on Antarctic pelagic species. However, for both silverfish and krill, the estimate of the date at which the expansion began suffers from lack of reliable calibration of the molecular clock and the width of the confidence interval associated with the point estimate. Thus, the original hypothesis that the expansion could be linked to a range expansion due to equator-ward migration of Antarctic planktonic ecosystems during cold periods (Charles et al. 1991) should be taken with extreme caution. In addition, both silverfish and krill studies were based on a single mitochondrial DNA marker, and the use of nuclear markers in krill provided discordant and much more recent estimates (Bortolotto et al. 2011). Finally, the approaches used for the estimation of the expansion are based on simplified approaches that assume one single population size change (mismatch distribution used in Zane et al. 1998, 2006) or limit the overall number of population size changes (skyride plots used in Goodall-Copestake et al. 2010). Nevertheless, the study of historical demography in Antarctic species, and in silverfish in particular, is still in its infancy and has great potential. It would benefit from the availability of a robust time frame for differentiation of notothenioids (Near et al. 2012); use of multiple mitochondrial and molecular markers; and application of new powerful approaches, such as those based on Approximate Bayesian Computation (Beaumont 2010) that allow comparison of complex scenarios of population changes (Marino et al. 2013).

Moreover, populations may have persisted during the LGM in areas other than the Filchner and Drygalski Troughs. Although deglaciation is not well constrained for much of the East Antarctic, available data suggest that the shelf remained ice free in Lützow-Holm Bay and along Prydz Channel (Mackintosh et al. 2014). In the Weddell Sea, the ice off Ronne Trough may have been strongly indented as well, providing conditions for a population to persist (Hillenbrand et al. 2014). Conversely, conditions in the Filchner and Drygalski Troughs may not have allowed persistence over time scales prior to the LGM. The grounding line appears to have reached the outer shelf in both systems during earlier glacial cycles (Hillenbrand et al. 2014; Anderson et al. 2014), whereas sampling along the continental slope indicated that glacial ice has not been grounded off Prydz Channel since the mid-Pleistocene (Mackintosh et al. 2014). This evidence suggests that population structure varied between glacial periods, with episodes of increased extinction rates, and re-colonization between troughs that enabled silverfish to persist over succeeding glacial cycles. Moreover, gene flow facilitated by the rapid bursts of connectivity involved may have made harder the evolution of reproductive isolation by divergent selection (Schluter 2009), hence limiting the opportunities for ecologically-based speciation.

10.5 Hypothesis Predictions and Testing

The preceding sections describe how the life history hypothesis can be developed conceptually by integrating past and recent population results with evidence from a range of studies examining physical components of the Southern Ocean ecosystem. Nevertheless, the resulting synthesis needs testing analytically using population and circulation models, and directly in the field. Advances in scientific theory become increasingly convincing as the possible outcomes of empirical testing become more specific and narrowly defined (Popper 1959), facilitating the use of powerful and highly targeted sampling and experimental designs. Particularly useful when examining physical-biological interactions, in this section we discuss several predictions concerning population structure that can be tested in further research.

Building on the results from La Mesa et al. (2015), the synthesis predicts a coherent population currently occupying the Larsen Inlet Trough, with spawning areas under fast ice near its head. Based on the distributions of young fish found by Hubold (1984), the same applies for the Filchner Trough and that off Camp Norway in the southeast Weddell Sea. Trough features associated with coherent silverfish populations appear to include the following: size; extension to the shelf edge; large active ice streams at their head, frequently associated with strong katabatic winds and a coastal polynya; and upwelling of warmer, nutrient-rich water over the shelf at their mouth. The occurrence of these features in trough systems in the Bellingshausen and Amundsen Seas, in particular the Belgica Trough, suggests suitable habitat to support silverfish populations.

The ACC also brings CDW close to the continent along East Antarctica (Orsi et al. 1995) where extensive distributions of silverfish are found over the shelf (La Mesa and Eastman 2012). Off Wilkes Land, large numbers of silverfish have been found south of the ASF, principally inshore along the western side of the Ninnis Trough and over the eastern Adélie Bank (Moteki et al. 2011). Post et al. (2011) described characteristic features: a deep inner basin adjacent to the Mertz Glacier Tongue, and oceanography dominated by the Mertz Polynya sustained by the katabatic wind field over Buchanan Bay. HSSW is formed there and modified CDW upwelling onto the shelf raises salinity and provides heat that contributes to sea-ice melting in the polynya. Large numbers of silverfish were also found associated with the Adélie Trough further west and out over the shelf (Moteki et al. 2011). This suggests spawning grounds under fast ice in the coastal bays along the George V Basin. Fish over the Adélie Trough may be the result of local reproduction or advection from the Ninnis system. In addition, concentrations in the Mawson, Davis, Cooperation, Cosmonaut and Lazarev Seas highlighted by La Mesa and Eastman (2012) suggest that at least some of the large cross-shelf troughs found west of Wilkes Land contain suitable habitat and maintain coherent populations that supply the shelf offshore and downstream. Although the topography is not as well described elsewhere off East Antarctica, systems in Lützow-Holm Bay, Iceberg Alley, Nielsen Basin and Prydz Bay appear promising candidates.

Spatial predictions like these facilitate the use of sampling frames in surveys that are highly targeted to cover the expected areas and timing of life history events (La Mesa et al. 2015). The hypothesis also predicts strong physical-biological relationships at each stage of the life history that are amenable to empirical measurement. Considered in the form of a life table, biological variables like adult fecundity rate (e.g. La Mesa et al. 2014) and the number of spawners are likely to be an important influence on egg abundance. So is the amount of habitat availability, indicating an expected relationship with ice extent and variables involved in platelet formation. Similarly, the katabatic wind field appears important in transport reaching productive larval habitat like polynyas so, as well as egg predation, local wind direction, velocity, and frequency can be expected to have strong relationships with larval abundance. Katabatic wind variables are also likely to influence the availability of larval habitat through their effect on polynya structure and extent, including upwelling of warmer water and hence temperature and salinity. Moreover, the hypothesis highlights how the retention of young fish in the population is likely to be influenced by interactions between offshore flow along the trough and buoyancy-forcing associated with advection losses along the inner shelf. As a result, strong relationships can be expected between juvenile abundance and variables describing trough flow such as the velocity, volume, and distance to intruding CDW, as well as inverse associations with rates of precipitation and meltwater run-off. For adults, the relative contributions of active swimming and transport needs further examination, but the velocity and volume of shelf outflow and flow along the slope are likely to influence losses by advection. A relationship between inflow along the trough and adult return to spawning areas can also be expected under the hypothesis.

Such physical-biological interactions suggest the geological features that are likely to be important predictors of population variability between troughs. Momentum-driven upwelling at points of curvature along the slope argues for the importance of formations like the Crary Fan off the mouth of the Filchner Trough, and the Belgica Trough Mouth Fan. The configuration of individual troughs, including the location of reverse slopes and glacial features like moraines, mega-scale glacial lineations and grounding zone wedges, are likely to be important in shaping eddies, meanders and areas of upwelling in the trough circulation. Areas where wind-driven mixing brings oxygen and iron rich meltwater to interface with upwelled deeper water are likely to be particularly productive. In turn, the influence of geological features on retention and transport, and the distribution of productive feeding areas, imply relationships with population vital rates and abundance, as well as connectivity.

These physical-biological relationships also lead to predictions under the life history hypothesis concerning the potential effect of glacial cycles on both genetic diversity and structuring. Thus, repeated cooling cycles can be expected to result in cyclic fluctuations of local population size, consistent with evidence of historic dietary shifts in predators (Emslie et al. 1998; Emslie and McDaniel 2002). If populations during the warmer period are more constrained along the coast and less exposed to the outer shelf circulation, increased fragmentation and reduced habitat availability may have resulted in decreases in population size. These reductions would have been followed by expansion during the cooling periods, when distributions shifted outward over the shelf, resulting not only in increased habitat availability (Zane et al. 2006), but also in increased mixing between previously isolated populations. Overall, these population size fluctuations might be expected to reduce genetic diversity. However, because estimates of effective population size are still in the order of thousands of individuals (Agostini et al. 2015), the reductions in population size may not have resulted in substantial genetic losses, making these episodes more difficult to detect. Even so, genetic analyses have already rejected the hypothesis of population size equilibrium and detected a signal of population expansion (Zane et al. 2006), and new analytical approaches show promise for detecting multiple fluctuations in population size and testing their correlation with glacial cycles (Beaumont 2010).

Predictions can be made for genetic structuring on recent time scales as well. Connectivity in both westward and eastward directions along the AP implies that, contrary to other Antarctic fish (Matschiner et al. 2009), unidirectional gene flow is not expected for silverfish in this region. The recent study by Agostini et al. (2015) supports this prediction, but the result was based on an indirect estimate of genetic connectivity, and further tests with direct approaches based on paternity or kinship analysis (Schunter et al. 2014) would be appropriate. Additionally, the relationship between connectivity and circulation implies potential for population differentiation from a stepping stone-type scenario. However, this may have been further complicated by episodic long distance dispersal events, especially along the shelf slope, and circum-antarctic gene flow that fluctuated over succeeding glacial cycles. As a result, differentiation may not be strongly related to distance. Future studies should focus on neighbouring populations, and the hydrodynamic and ecological features governing their separation and connectivity. Thus, they should be designed with sufficient power to resolve differentiation by using a large range of genetic markers and large sample sizes, incorporating a multidisciplinary approach that includes other fisheries population techniques. Because of the temporal heterogeneity demonstrated in silverfish (Zane et al. 2006; Agostini et al. 2015), experimental designs should also include temporal replicates to discriminate geographic differences from those over time, with sampling frames that exclude as far as possible mixtures of fish between populations.

Multi-disciplinary approaches to testing are particularly useful, incorporating markers that can cross-reference and complement the genetic information (e.g. Begg et al. 1999). As demonstrated by La Mesa et al. (2015), the extent of distributions downstream can be predicted through simulations using circulation models. For the related *D. mawsoni*, Ashford et al. (2012) complemented simulations with empirical data from age distributions and otolith chemistry, using genetic analyses by Kuhn and Gaffney (2008) to establish an external comparison. Where silverfish distributions are associated with troughs lacking features necessary to support a population, similarities in trace element chemistry in the nucleus can be used to test for vagrancy from the parent population. The reproductive study by La Mesa et al. (2014) usefully complemented approaches using otolith chemistry (Ferguson 2012), genetics (Agostini et al. 2015) and faunal assemblages (Parker et al. 2015) along the AP. Reproductive studies can also help identify spatial differences in fecundity (e.g. Riginella et al. 2015), and variation in gonad development indicative of vagrancy. By contrast, when advection is predicted to reach a trough occupied by a neighbouring population, mixing can be detected as a bimodal distribution in the nucleus chemistry, and reproductive studies used to help confirm that immigrants contribute to spawning. On the other hand, in situations where simulations predict that advection falls short, population separation can be tested by differentiation in the nucleus chemistry characterized by underlying unimodal distributions. Finally, spatial age distributions can effectively examine dispersal effects and demographic structuring related to life history movement.

10.6 Conclusion: Silverfish Population Structure in the Southern Ocean Ecosystem

In this chapter, we suggest further development of an emerging life history hypothesis that can enhance our understanding of population structure in silverfish. The synthesis helps resolve inconsistencies highlighted by previous authors concerning cyclical variability in spawning and feeding areas, connectivity without active large-scale migration, and persistence over successive glacial cycles without phylogenetic diversification. The hypothesis needs rigorous testing and further development, but it suggests broad potential implications for silverfish population structure and life history connectivity in the context of the Southern Ocean ecosystem.

Population considerations are important at an ecosystem level because of the role of silverfish as a forage species. For example, their disappearance from the diets of Adélie penguins nesting near Anvers Island may have been driven by reduced connectivity from Marguerite Bay along the shelf slope, as the distribution of neritic assemblages became increasingly constrained inshore (Parker et al. 2015). In the Ross Sea, silverfish form a large component in the diet of the toothfish *D. mawsoni* (Eastman 1985; La Mesa et al. 2004), which is fished commercially and follows life history movement to spawning grounds in the western Southeast Pacific Basin (Hanchet et al. 2008). Ontogenetic changes to neutral buoyancy may facilitate dispersal via trough outflows into the Ross Gyre (Ashford et al. 2012) and, as in silverfish, result from the accumulation of lipids during feeding. How the life history trajectories of the two species intersect in the southwestern Ross Sea, and along troughs connecting to the shelf edge, appears fundamental to the life cycle of *D. mawsoni*, and their entrainment in flows to spawning grounds off the continental shelf.

Population structure and life history connectivity are a critical step to predicting the abundance and distribution of silverfish, and their availability to higher components of the ecosystem. A life cycle can be considered as a continuity solution, linking areas within a physical system that imposes spatial constraints (Sinclair and Iles 1989). Such a solution demands at least one trajectory that returns adults to the areas where they were spawned. For silverfish that remain members in this way, births and deaths directly govern abundance and population persistence. By contrast, vagrants have no effect on whether a population persists or not, because they no longer contribute to spawning. Their abundance depends on supply and local mortality. In populations where immigration subsidizes recruitment (Pulliam 1988), both local births and supply are important. Estimates of effective population size (Agostini et al. 2015) suggest that a relatively small proportion of adult silverfish contribute to the next generation. Vagrancy is likely to be high. As a result, distinguishing the life history trajectories used by members from those of vagrants, and fish moving between populations, is an important step toward understanding the spatial dynamics that sustain higher predator assemblages.

Temporal variability in silverfish abundance may also have widespread implications for the marine ecosystem. Losses of silverfish in the rapidly changing system along the western AP have caused increasing concern among scientists. We argue that silverfish have persisted through successive glacial cycles and variation in population structure and size may form part of their, so far successful, response. Historical shifts in the diets of Adélie penguins near Anvers and Adelaide Islands (Emslie et al. 1998; Emslie and McDaniel 2002) indicate associations between episodes of cooling and silverfish availability to higher trophic levels. As a result, silverfish distribution and abundance can usefully be examined in relation to present-day glacial and hydrographic conditions. Changes in abundance compared to historical baselines can be helpful in gauging spatial responses to climate variability and warming trends. However, this synthesis suggests that anthropogenic effects should be considered in the context of their potential for disrupting normal population responses to succeeding phases of glacial cycles, for example by accelerating the rate of warming or intensifying the peaks and troughs. In this way, understanding the complex physical-biological interactions that determine life history connectivity can help resolve population structure in silverfish, and its relationship with variability in the Southern Ocean ecosystem.

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