

Chapter 12

Impact of Climate Change on the Antarctic Silverfish and Its Consequences for the Antarctic Ecosystem

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Abstract *Pleuragramma antarctica* is the dominant forage fish of the coastal Antarctic, exhibiting a circumantarctic distribution and a well documented abundance in all shelf environments, from the high Antarctic Weddell and Ross Sea systems, to the milder waters of the western Antarctic Peninsula (WAP) shelf. Rapid regional warming on the WAP has produced a dichotomy in annual weather patterns between the high Antarctic systems and the WAP, resulting in swiftly rising midwinter air temperatures and fewer sea ice days during the annual winter cycle on the WAP, and little change in the Ross and Weddell Seas. The WAP shelf thus provides a model system for examining the potential effects of climate warming on an important Antarctic species.

Pleuragramma's life history is characterized by slow growth, late maturity, a high reproductive investment and an association with coastal sea ice for spawning and larval development. All those features will allow the species to weather episodic annual failures in recruitment, but not long term change.

Most effects of the increasing temperature associated with climate change will be indirect ones, as temperatures will not increase to the point where they are physiologically life-threatening in the short term. A recent survey of *Pleuragramma* distribution on the WAP shelf revealed a large break in its historical distribution in shelf waters, suggesting a collapse in the local population of silverfish there. The break occurred in the area that has been most heavily impacted by rapid regional warming: the northern mid-shelf including Anvers and Renaud Island. It may be that the multi-faceted effects of climate change are already at work in its local disappearance.

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12.1 Introduction

Clarke (1996) suggests three possible responses by a population of organisms experiencing an environmental challenge.

1. Migration: the species shifts to a more favorable area
2. Adaptation: the species evolves to shift the phenotypic reaction norm to better respond to the new environment (or can accommodate it within its existing phenotype)
3. Extinction: the species fails to adapt or migrate and becomes extinct (can be local extinctions if they reproduce in place and don't migrate appreciably)

The fact that polar species dwell in an end-member climatic regime limits the potential for migration. More favorable areas may be found within the polar biosphere itself due to regional variability, but excursions outside of the polar latitudes will not result in a more hospitable climate. In contrast, tropical species may shift poleward for temperatures more compatible with their "climate envelope" (Pearson and Dawson 2003).

The boundaries dictated by species' life history tactics, their behavior patterns such as foraging strategies, and their physiological breadth, or flexibility in dealing with warming temperatures, are important in assessing the vulnerability of individual species to changing climate. Once a species' boundaries are understood, they can be interpreted within the framework of observed and projected changes in climate to pinpoint vulnerabilities and evaluate the likelihood of survival.

The purpose of the present chapter is to identify the environmental challenges the Antarctic silverfish *Pleuragramma antarctica*, is facing now and likely to face in the immediate future. The western Antarctic Peninsula (WAP) shelf, currently the most rapidly warming region on the planet (Vaughan et al. 2003), is used as a reference and model system. The chapter is divided into a series of sections that initially summarize the distribution of *Pleuragramma* in the Antarctic system, the regional climatic differences it presently faces, and the challenges they present. Life history tactics are summarized and evaluated for vulnerabilities to the evolving physical and biotic environment of a changing climate. Physiological responses to changing seasonal temperatures and salinity fields are considered within the context of what is known about *Pleuragramma* and notothenioids in general. Potentially altered prey availability and composition are considered, as is the possibility of increased competition from oceanic pelagics in warming shelf waters. The chapter concludes with observed changes in the WAP shelf populations of silverfish, the importance of silverfish to the coastal Antarctic and recommendations for future research.

12.2 Geographic Distribution and Role as Prey

P. antarctica, given the common name Antarctic silverfish by DeWitt and Hopkins (1977), is the dominant pelagic fish in all regions of the coastal Antarctic (Kellerman 1996; Eastman 1993; DeWitt 1970; Ekau 1990). Unlike most notothenioids, which are associated with the benthos as adults, silverfish are found in the midwaters over the continental shelf from the surface to 500 m, and deeper in coastal canyons.

Pleuragramma's pelagic lifestyle makes it a key diet component of coastal Antarctic apex predators. The bottom fauna is inaccessible to many diving predators on the Antarctic continental shelf because its typical 500 m depth (Eastman 1993) is beyond their reach. Thus, because of their pelagic distribution, silverfish are an important prey source for flighted seabirds (Ainley et al. 1991) and the shallow-diving pygoscelid penguins (Bengtson et al. 1993; Williams 1995; Ainley 2002). They are also a significant part of the diet of deeper divers such as emperor penguins (Cherel and Kooyman 1998) and crabeater, Ross, Weddell, and leopard seals (Øritsland 1977; Lowry et al. 1988; Fuiman et al. 2002). Several species of fishes feed on *Pleuragramma* as well, including the notothenioids *Pagothenia borchgrevinki*, *Dissostichus mawsoni*, and *Gymnodraco acuticeps* (Eastman 1985), indicating that it represents a critical trophic link in the coastal system.

Pleuragramma is found in all coastal regions of the continental Antarctic, as well as several Antarctic and sub-Antarctic islands including those of the Scotia Arc (South Shetlands, South Orkneys, South Georgia, and South Sandwich islands) and the Balleny Islands of the Ross Sea region (MacDiamid and Stewart 2015, La Mesa and Eastman 2012). Its wide-ranging distribution and the vast size of the Antarctic continent means that the species experiences climate diversity within its natural range. Overall, the temperatures at which it is found range from -2 to 4 °C (Gordon et al. 1982), with the warmest in islands of the Scotia Arc and the coldest in all coastal regions of the Antarctic continent outside of the WAP shelf, where it encounters temperatures of -2 to 2 °C over the course of the year (Gordon et al. 1982). It is worth noting that the vast majority of its range has a year-round temperature of -2 °C throughout the water column and significant ice cover all year round (Zwally et al. 2002; Gordon et al. 1982). Since about 1950, climate records suggest a dichotomy in coastal climate between the Western Antarctic/Bellingshausen Sea region and the remainder of the Antarctic coastal system (Vaughan et al. 2003; Turner et al. 2005). Regional warming and loss of annual sea ice is far more pronounced in the WAP than the coastal Ross and Weddell Seas or the eastern Antarctic, which have remained cooler, retaining their high Antarctic character (Vaughan et al. 2003; Turner et al. 2005; Ducklow et al. 2007; Stammerjohn et al. 2008a) (Fig. 12.1).

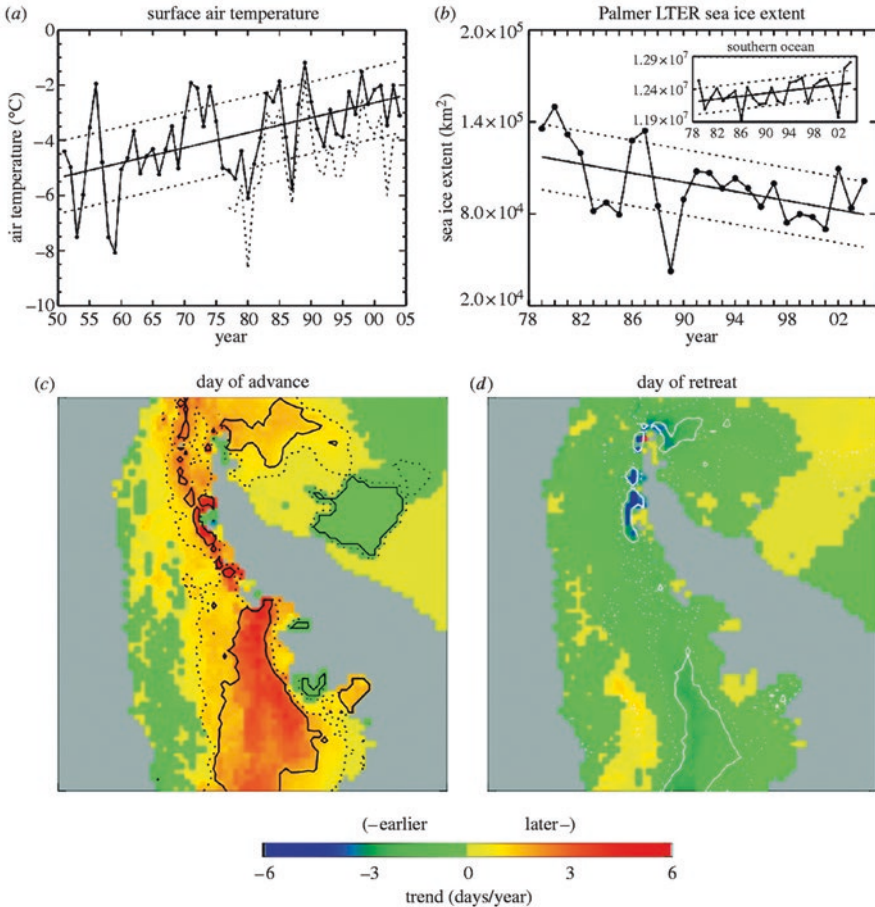


Fig. 12.1 (a) Annual average air temperature recorded at Faraday/Vernadsky Station ($65^{\circ}15' \text{ S}$, $64^{\circ}16' \text{ W}$) from 1951 to 2004. The linear regression fit (*solid*) and ± 1 standard deviation (*dotted*) about the fit are included. Annual average air temperature recorded at Rothera Station ($67^{\circ}34' \text{ S}$, $68^{\circ}08' \text{ W}$) from 1977 to 2004 is shown by the dotted curve. The standard error and significance were determined using the effective degrees of freedom ($N_{\text{eff}} = 24.8$) present in the regression residuals. Also included are the ± 1 standard deviation lines (*dotted*). (b) Annual average sea ice extent for the Palmer LTER region and for the Southern Ocean (*inset*) from 1979 to 2004. The linear regression fit (*solid*) and ± 1 SD (*dotted*) about the fit are included. Spatial maps of linear trends (1979–2004) in (c) day of advance and (d) day of retreat in the greater AP region (From Ducklow et al., *Marine pelagic ecosystems: the West Antarctic Peninsula*, *Philosophical Transactions B*, 2007, vol 362, issue n. 1477, Fig. 2, page 69, by permission of the Royal Society)

12.3 Physical Environment and Regional Change

12.3.1 *The High Antarctic*

The most complete data sets describing *Pleuragramma* distribution, abundance, and general biology come from three areas of the coastal Antarctic: the Weddell and Ross Seas, and the WAP shelf. The coastal Weddell and Ross Seas may be characterized as high Antarctic, with an isothermal water column on the shelf predominantly composed of $-2\text{ }^{\circ}\text{C}$ ice-shelf waters (Gordon et al. 1982). Though each system has experienced either the calving of massive icebergs (B-15, C-16 in the Ross Sea) or the break-up of ice shelves (Larsen and Filchner Ice Shelves in the Weddell Sea) within their respective embayments, each has retained a high Antarctic water column and a minimal reduction in annual sea ice days (Smith et al. 2007; Zwally et al. 2002; Jacobs and Giulivi 1998). A non-significant warming trend in annual surface temperature ($0.29 \pm 0.36\text{ }^{\circ}\text{C decade}^{-1}$) has been observed at Scott Base in the Ross Sea and a non-significant cooling trend ($-0.11 \pm 0.47\text{ }^{\circ}\text{C decade}^{-1}$) at Halley Station in the Weddell Sea during the period from 1958–2000 (Vaughan et al. 2003). From a climatic standpoint, observed changes in the Ross Sea and Weddell Sea embayments would have minimal impact on the life history (La Mesa and Eastman 2012) of *P. antarctica* living within them.

12.3.2 *The Western Antarctic Peninsula (WAP) Shelf: A Natural Experiment*

The hydrography of the WAP shelf is quite different from that of the Ross and Weddell Sea embayments. In contrast to the isothermal $-2\text{ }^{\circ}\text{C}$ water column found in the midwaters of the Ross and Weddell Sea continental shelves (Gordon et al. 1982), periodic intrusions of warm ($0\text{--}2\text{ }^{\circ}\text{C}$) circumpolar deep water onto the WAP shelf give it a consistently warmer pelagic environment (Hofmann et al. 1996, 1998). The WAP shelf has experienced dramatic changes in climate over nearly the same time frame (1951–2000) as the more limited change observed in the Ross and Weddell Seas. Designated as one of the three most rapidly warming regions of the world, the WAP shelf has increased in mean annual surface temperature at a rate of $0.56 \pm 0.43\text{ }^{\circ}\text{C decade}^{-1}$ since 1951 (Faraday/Vernadsky Station record, Turner et al. 2005); winter temperatures have increased even more profoundly ($1.09 \pm 0.88\text{ }^{\circ}\text{C decade}^{-1}$), resulting in present midwinter temperatures about $6\text{ }^{\circ}\text{C}$ higher than those observed in the 1950s. On the WAP shelf, sea ice advance and retreat shows coupling to the recent rapid regional warming of the system (Vaughan et al. 2003; Stammerjohn et al. 2008a), with a total of about 10 fewer sea ice days over the same time frame (Ducklow et al. 2007).

The WAP shelf provides a natural experiment, or model system, for examining the effects of climate change on silverfish. The major changes observed in the WAP system due to rapid regional warming include:

- Mean annual air temperature on the WAP shows an increase of 3.7 ± 1.6 °C century⁻¹ ($X \pm SD$; Vaughan et al. 2003). Its effects are important to marine life in that the increase in air temperature shows a coupling with the pattern of sea-ice advance, retreat and concentration (Weatherly et al. 1991; Vaughan et al. 2003; Turner et al. 2005; Stammerjohn et al. 2008a).
- Seasonal sea ice is advancing later in autumn and retreating earlier in spring, resulting in approximately 10 fewer sea ice days per year in the vicinity of Palmer Station (Ducklow et al. 2007). Between the years of 1979 and 2004 sea ice retreated a total of 31 ± 10 days earlier overall in the WAP/Bellingshausen Sea region (Stammerjohn et al. 2008b). In addition, reductions in sea ice concentrations have been noted within the pack ice (Vaughan et al. 2003). As might be expected, a North-South gradient in sea-ice advance and retreat dates exists along the shore on the WAP with the southernmost regions showing the least change and the northern mid-shelf region the greatest change (Stammerjohn et al. 2008a).
- Summer sea surface temperatures have risen by about 1 °C since 1950 (Meredith and King 2005).
- Seven ice shelves are in retreat or have already broken up and 87% of the glaciers on the WAP are in retreat (Vaughan et al. 2003; Schofield et al. 2010).
- Increasing temperatures result in reduced surface water salinity due to increasing glacial melt-water runoff and melting ice shelves (Moline et al. 2004, 2008). Vast areas west of the Antarctic Peninsula are covered by low salinity water (33.4–33.6‰; Moline et al. 2004), and the melt water plume extends to depths as great as 50 m (Dierssen et al. 2002).
- Increased landward influence of warm upper circumpolar deep water (UCDW) along the WAP over the last two decades described by Suprenand et al. (2015); Piñones et al. (2013b); Smith et al. (1999); Martinson et al. (2008); Martinson (2012) and Dinniman et al. (2012), effectively making the outer shelf a more oceanic system, particularly at depths below 200 m.
- Significant spatiotemporal changes in phytoplankton and zooplankton community structure were observed, with recurrent shifts from large diatoms to small cryptophytes (Moline et al. 2004) and episodic annual changes from a krill-dominated zooplankton community to a salp-dominated community (Loeb et al. 1997; Nicol et al. 2000; Atkinson et al. 2004).

12.4 Life History and Vulnerability to a Changing Climate

Species' life history traits provide an excellent framework for interpreting vulnerability to climate change (Pearson et al. 2014). Stearns (1992) lists the principal life history traits as: size at birth, growth pattern, size at maturity, age at maturity, number, size, and sex-ratio of offspring, age and size-specific reproductive investments, age and size-specific mortality schedules, and length of life. Data collected in the Ross and Weddell Seas as well as in the waters of the Antarctic Peninsula provide valuable information on a number of *Pleuragramma*'s life history traits. We summarize them here as a useful reference for interpreting climate change effects. For a more comprehensive treatment, see La Mesa and Eastman (2012).

12.4.1 Size at Birth

Pleuragramma hatch at an average length of 9.3 mm in the Ross Sea, with a range of 8–10 mm (Vacchi et al. 2004). Like most notothenioid fishes (Loeb et al. 1993; Kock 1992), it has a functional mouth at hatching and is theoretically capable of feeding right away. Hubold (1990) reported an average length of 9 mm for newly hatched *Pleuragramma* in the Weddell Sea, suggesting that variability in size at hatch is minimal from place to place.

12.4.2 Spawning

Spawning behavior of *Pleuragramma* is unknown. However, two lines of evidence provide suggestions. First, the data of Vacchi et al. (2004, 2012) confirm that *Pleuragramma* has pelagic eggs, and that they are found in high concentrations underneath the land-fast sea ice in Terra Nova Bay in the Ross Sea. Second, the observations of Daniels (1982) that thousands of *Pleuragramma* were observed under land-fast sea ice on three occasions in the June–October period suggests that *Pleuragramma* may form spawning aggregations under coastal sea ice in winter. At the very least, since Daniels (1982) observed the fishes feeding under the ice in Arthur Harbor vic. Palmer Station, it may be that the behavior of *Pleuragramma* in the winter months includes shoaling and movement inshore. It is believed that spawning takes place in the late winter, in the August/September time frame, and that embryos develop over a period of 60–75 days prior to hatching (Kock and Kellermann 1991; Ghigliotti et al. 2017a, b). Clearly, the presence of coastal sea ice at the time of spawning is important. At present, sea-ice is present at the time of spawning throughout the species' range.

In the one place where eggs were definitively located and collected, Terra Nova Bay in the Ross Sea (Vacchi et al. 2004, 2012), *Pleuragramma* eggs were found

floating in the platelet ice underneath 1.3 m thick sea ice. They were found to be hatching within the ice starting in mid-November. This was a very important finding, since it suggests that sea ice cover is important to *Pleuragramma*'s early life history. In addition, it confirmed that *Pleuragramma* has pelagic eggs, a conclusion first reported by Faleyeva and Gerasimchuk (1990) in a histological study on the gonads of *Pleuragramma*. As late as 1996 (Kellermann 1996) it was assumed that *Pleuragramma* had demersal eggs like many of the other notothenioids (Kock 1992). *Pleuragramma* eggs had been found earlier in the stomach of a primarily benthic species, *Trematomus scotti* (Hubold 1990), giving credence to the idea that the species had demersal eggs.

12.4.3 Growth and Ontogeny of Diet

In the Weddell Sea region, first year or age class 0 (AC 0) *Pleuragramma* appear in the plankton in late November to early December (Hubold and Tomo 1989); it is assumed that their hatch date is about 1 November. AC 0 *Pleuragramma* appear in the plankton a little later in the Terra Nova Bay region: December-early January (Granata et al. 2002; Guglielmo et al. 1998). Kellermann (1986) assumed a hatch date of early December for the *Pleuragramma* larvae captured in Antarctic Peninsula waters based on length distributions of post-larvae captured in the plankton there. Like the size at hatch, time of hatching is consistently in the November–December period in the three areas of the Antarctic where data are available: the Antarctic Peninsula, and the Ross and Weddell Seas (Vacchi et al. 2004; Kellermann and Kock 1991; Hubold and Tomo 1989; Kellermann 1986).

Post-larval *Pleuragramma* (10–30 mm – AC 0) are distributed largely in the upper 50 m where they feed on small *Limacina*, *Oncaea*, and *Oithona* (Hubold and Hagen 1997; Hopkins 1987; Hubold 1985) as well as nauplii and copepodites of calanoids. Koubbi et al. (2007) also found diatoms and tintinnids in the guts of young silverfish larvae, suggesting that omnivory in early life is another dietary option.

AC 1 larvae (30–55 mm) are found primarily below 50 m in the upper 200 m (Guglielmo et al. 1998) and still feed primarily on cyclopoids. However, once *Pleuragramma* reach a size of 60 mm a diet shift occurs, with the primary prey being *Calanoides acutus* and *Calanus propinquus* (Hubold and Hagen 1997; Hopkins 1987; Kellermann 1987). Fishes greater than 60 mm (Age 2+ – adult) are found primarily below 200 m, but some fraction (15–20%) of the age 2+ population can always be captured in the upper 200 m (Hubold 1984). Larger size classes of *Pleuragramma* (>100 mm) feed on furcilia, *C. acutus* and *C. propinquus*, *Metridia gerlachei*, *Rhincalanus gigas*, *Euphausia crystallorophias*, and *E. superba* (Hopkins 1987; Hubold 1985; Lancraft et al. 2004; Mintenbeck 2008).

Pleuragramma don't reach their juvenile "silverfish" appearance until in their third year (AC 2+) of life at lengths of 60–90 mm. As they grow larger, their diet shifts, their vertical distribution deepens and their eye diameter as a percentage of

body size grows larger (Hubold 1985) suggesting a developmental adjustment to promote visual acuity at greater depth. Data on length-at-age obtained using annular rings of otoliths (sagittae) suggest that *Pleuragramma* reach a size of about 200 mm in their 14th year of life (Reisenbichler 1993; Hubold and Tomo 1989). The annular rings of *Pleuragramma* sagittae suggested that the fish's largest sizes (245–250 mm) were about 21 years old (Hubold and Tomo 1989). At the moment, what is most certain is that *Pleuragramma* is a slow-growing, long-lived fish, even when considered among Antarctic fishes (La Mesa and Eastman 2012).

12.4.4 Buoyancy and Vertical Distribution

Despite its lack of a swim bladder, *Pleuragramma* is neutrally buoyant, allowing it to minimize energy expended in maintaining its vertical position within the water column. The lack of a swim bladder is compensated for by a reduction in bone mass and density, and by the static lift provided by large lipid deposits stored in subcutaneous and intramuscular lipid sacs (Eastman and DeVries 1982; Eastman 1985). Whether the functional role of lipids in the lipid sacs is limited to buoyancy (see Maes et al. 2006) or if they also serve as an energy reserve (see Eastman and DeVries 1989, Hagen and Kattner 2017) is still not clear.

Vertical distribution within the water column differs with age. Two elements of *Pleuragramma*'s vertical distribution are clear. First, fishes AC 2+ and younger are found primarily in the upper 200 m, with the youngest fishes found highest in the water column. Second, vertical distribution of fish 3+ and older is uncertain, other than the fact that they are found deeper in the water column. Data from Southern Ocean GLOBEC (Donnelly and Torres 2008) were in good agreement with older literature in that AC1+ fish were found mainly in the upper 100 m and AC2+ fish in the 100–200 m depth stratum in Marguerite Bay.

Limited data are available on diel periodicity during seasons where there is a diel period. During the austral fall in the Croker Passage, north of Anvers Island in the Gerlache Strait on the WAP shelf, juvenile and adult *Pleuragramma* (length greater than 60 mm) performed a diel vertical migration, changing their center of distribution from approximately 600 m during the day to approximately 300 m at night. A sizable fraction of the population (ca 20%) reached the 100–200 m depth stratum at night (Lancraft et al. 2004). The same was observed in the eastern Weddell Sea: here, adult *Pleuragramma* were found to spend most of the day close to the sea floor at water depths greater than 350 m. At night the shoals moved up into the upper water column to feed on zooplankton at the pycnocline (Plötz et al. 2001; Mintenbeck 2008).

12.4.5 *Growth and Diet in a Changing Environment*

The change in the timing of sea-ice retreat observed over the last 25 years (Stammerjohn et al. 2008a) on the northern mid-Peninsula coincides roughly with the time of *Pleuragramma* hatching – episodically leaving the hatching eggs and young larval fish without a sea-ice refugium and more vulnerable to predation. Key parameters for the condition and survival of pelagic fish larvae are prey abundance, prey type and seasonal timing (Beaugrand et al. 2003). It is very likely that changes in sea-ice dynamics will involve alterations in all of these three parameters.

The prey taxa of early *Pleuragramma* larvae, like *Pleuragramma*, exhibit a circumantarctic distribution (Everson 1984; Smith and Schnack-Schiel 1990). However, prey taxa also have species-specific phenologies, with reproduction tied to photoperiod, sea-ice retreat, and phytoplankton production (Atkinson 1991). Cyclopoids, like *Oncaea* and *Oithona*, and the calanoid *M. gerlachei*, remain active in the winter months (Hopkins et al. 1993b) and are able to reproduce when food in the form of phytoplankton comes available. Most of the important calanoids (*C. propinquus*, *C. acutus*, *R. gigas*) exhibit a fairly strict phenology of winter dormancy or diapause (Hopkins et al. 1993b; Atkinson 1991). The breaking of diapause, reproduction, and appearance of eggs and copepodites must match up with the hatch time of *Pleuragramma* or they will be unavailable as fuel. Thus, it would appear that timing of prey reproduction is a key element for survival of young *Pleuragramma* larvae. If it occurs too early, prey sizes may exceed those that are optimum for survival.

12.4.6 *Size at Maturity*

Agreement on size at sexual maturity is a little better than that for age at maturity. Visual and histological studies (Faleeva and Gerasimchuk 1990) suggest that fish collected in the Mawson Sea spawn at 13–16 cm standard length for the first time, with more variability in size at first reproduction in males than females. Hubold (1985) reported that fish in the Weddell Sea first show gonadal development at a size of 12.5 cm and Reisenbichler (1993) reported that McMurdo Sound fish did not show appreciable gonad development until approximately 16 cm. Agreement between those three studies and others (La Mesa and Eastman 2012) is quite good, with a consensus figure of 13–16 cm.

12.4.7 *Age at Maturity*

If the size at sexual maturity, 13–16 cm SL, is applied to the Hubold and Tomo (1989), Reisenbichler (1993), or Sutton and Horn (2011) growth curve, *P. antarctica* begins reproduction at an age of 6–9 years or about 55% of its maximum size

(Kock and Kellermann 1991). Gerasimchuk (1992) as reported in La Mesa and Eastman (2012) observed an age at maturity of 4–5 years for silverfish of 13–16 cm in the Mawson Sea. However, all studies reporting a size at sexual maturity consistently place it at 13–16 cm, which in at least three studies of length at age (Hubold and Tomo 1989; Reisenbichler 1993; Sutton and Horn 2011) corresponds to an age at maturity of 6–9 years. The species thus shows little difference in size at maturity between regions. Differences in reproductive age between studies are likely due to differences in aging techniques, but three of four give a consensus age of 6–9 years. Deferring reproduction until midway through life allows for greater initial fecundity when reproduction occurs and higher later fecundity through growth (Stearns 1992). For a fish with high natural mortality such as *Pleuragramma* (La Mesa and Eastman 2012), delayed maturity does increase the risk of individual reproductive failure, but the trade-off apparently confers increased individual fitness.

12.4.8 Age-Specific Reproductive Investments

GSI (Gonadosomatic index: the percentage of total fish weight made up by the gonad) for *Pleuragramma* varies between 13 and 46 (Kock and Kellermann 1991), suggesting that, though variable, reproductive investments are quite high. For comparison, GSI's of other nototheniids, *Pleuragramma*'s benthic dwelling relatives, vary between 9 and 29 with a mean of about 16. Other data support a case for high reproductive investment. Relative fecundity of *Pleuragramma* has been reported as 124.9 ± 4.4 eggs g^{-1} ($X \pm SD$; Gerasimchuk 1987) and 70–190 oocytes g^{-1} wet mass (La Mesa et al. 2014), which is 3–5 times that of any of the other nototheniids (Kock and Kellermann 1991) but 4–8 times less than the relative fecundity of other small pelagic fish species such as clupeids (e.g. Alheit and Alegre 1986). Table 12.1 is an estimate of the energy invested in reproduction relative to that invested in metabolism and in somatic growth for three calculated levels of GSI: 15, 25, and 45. Investments in somatic growth were obtained from equations in Reisenbichler (1993) who determined caloric values for *Pleuragramma* tissues through proximate analysis (protein, lipid, carbohydrate, water, ash). Reisenbichler's growth curve, virtually identical to that of Hubold and Tomo (1989), was used to estimate growth in mass. Data for *Pleuragramma* metabolism are from Martinez and Torres (2017).

Table 12.1 An estimate of energy (Kcal/year) invested in reproduction relative to that invested in metabolism and in somatic growth for three calculated levels of GSI: 15, 25, and 45

| Age (year) | Somatic growth | Metabolism | Reproductive energy | | |
|------------|----------------|------------|---------------------|--------|--------|
| | | | GSI 15 | GSI 25 | GSI 45 |
| 7 | 8.81 | 47.98 | 3.51 | 5.86 | 10.54 |
| 8 | 11.92 | 62.25 | 5.30 | 8.84 | 15.91 |
| 9 | 15.56 | 78.49 | 7.64 | 12.73 | 22.91 |
| 10 | 19.75 | 96.70 | 10.60 | 17.67 | 31.80 |

Reproductive energy was calculated using the conservative approach, that energy invested in gonadal development was equivalent in caloric value to somatic tissues. Clearly, reproductive investment by *Pleuragramma* is quite high; at a GSI of 45, it eclipses the energy invested in somatic growth per year.

Metabolism and growth command the lion's share of the assimilated energy of carnivorous fishes (Brett and Groves 1979), generally about 75%. In the case of *Pleuragramma*, within the total energy devoted to growth and metabolism, reproduction commands between 6 and 27% depending on the year and GSI. Maintaining such a high reproductive output requires a high level of feeding success and excellent physiological condition. Reproductive output will most likely decrease or cease altogether (skip spawning – see Ghigliotti et al. 2017a) if the spawning population is directly or indirectly stressed due to environmental alterations or disturbances.

12.4.9 Mortality Schedules

Estimates of the instantaneous rates of natural mortality (M) vary from 0.25 to 2.21 (La Mesa and Eastman 2012), which is on the high end for notothenioids in general (Kock, 1992; La Mesa and Eastman 2012), reflecting its role as a linchpin prey item for apex predators (Eastman 1985) in the coastal Antarctic. As for most species, it is assumed that mortality decreases with increasing size. Multiple years of recruitment failure, or absence of spawning activity due to poor feeding conditions, coupled with a high natural mortality make silverfish particularly susceptible to local population extinctions (Parker et al. 2015).

12.4.10 Length of Life

It is believed that *Pleuragramma* are capable of living to at least 14 years of age (La Mesa and Eastman 2012; Sutton and Horn 2011; Reisenbichler 1993; Hubold and Tomo 1989). The maximum size is not at issue; it is about 25 cm (La Mesa and Eastman 2012). A long life coupled with reproductive maturity at about the halfway point allows the fish multiple opportunities (7–8 years at minimum) for successful reproduction, a valuable attribute in an environment that is highly variable even without the added uncertainties of climate change. A long life thus may be considered a strength rather than a vulnerability in a high Antarctic climate pattern. If a warming environment results in direct competition for a limiting resource (Lancraft et al. 2004) with a species that exhibits earlier maturity and a shorter generation time, e.g. *Electrona* on the WAP shelf, the species could eventually be displaced.

12.4.11 *Capsule Summary of Life History*

Pleuragramma is a long-lived, slow growing fish with a tie to coastal sea ice for spawning and early larval development. Sexual maturity occurs at a length of 13–16 cm, which, by conventional reading of otoliths yields an age of 6–9 years (La Mesa and Eastman 2012), and in favorable conditions are capable of reproducing yearly after maturity, though skip spawning is also possible. Young larvae are primarily distributed in the upper 100 m. Dispersal of silverfish is considered to be maximal in the first 2 years of life. Center of distribution deepens as the fish age. Fish exhibit vertical migrations as juveniles and adults (Lancraft et al. 2004; Plötz et al. 2001) and shoaling behavior has been observed both by divers and with “critter cams” mounted on seals (Fuiman et al. 2002). Slow growth, late maturity, and an apparent tie to coastal sea ice all contribute to the species’ vulnerability to a warming regional climate on the WAP shelf.

12.5 Effects of Climate Change

Life history traits including reproductive output, individual growth, fitness, development and survival are vulnerable to environmental alterations and may be affected directly or indirectly by changes in temperature, salinity, prey availability and composition, competition and predation.

12.5.1 *Temperature and Salinity*

Ambient temperature is one of the major drivers controlling the rate of metabolic processes in ectothermic organisms such as fish. The temperature range where physiological functions perform at optimal level, is species-specific (and sometimes also region-specific). Though not necessarily lethal, temperatures outside the optimum range may affect physiological efficiency, thereby impairing fish growth rate and lifetime fecundity (Pörtner et al. 2001; Pörtner and Peck 2010). Moreover, in some fish species ambient water temperature determines the sex-ratio of the offspring (e.g. Brown et al. 2015; Ospina-Alvarez and Piferrer 2008) which may impact reproductive output in the longer term. Temperature has been shown to affect development and growth rate of the early developmental stages of fishes (embryos and larvae) (Fukuhara 1990; Hufnagl and Peck 2011).

There are no experimental data describing temperature and/or salinity effects on *Pleuragramma*, except for one study on freezing resistance of larvae (Cziko et al. 2006). Nothing is known about upper temperature limits. A number of studies have addressed temperature effects on closely related notothenioids and several species were found to be highly stenothermal with an upper lethal temperature of 4–6 °C

(Somero and DeVries 1967; Robinson 2008), while the cryopelagic *P. borchgrevincki* exhibits high thermal tolerance and acclimation capacities to elevated temperatures of >4 °C (Seebacher et al. 2005; Robinson 2008; Robinson and Davison 2008).

In the Ross and Weddell Seas, *Pleuragramma* is found exclusively in the very cold ice-shelf waters (-2 °C) typical of its high Antarctic coastal distribution (Hubold and Ekau 1987; DeWitt 1970; Donnelly et al. 2004). On the WAP shelf, silverfish experience temperatures ranging from -2 to 2 °C (Lancraft et al. 2004; Donnelly and Torres 2008). Two single adult individuals were caught far north, off South Georgia Island and the South Shetland Islands (Trunov 2001), suggesting a certain degree of thermal flexibility; however, water temperatures close to the sea floor where these fish were caught were about 1.5 °C, which is within the range fish are also exposed to off the WAP. At present, the best data available suggest that temperatures over the known range of *Pleuragramma* are not physiologically life-threatening. However, species often exhibit thermal preferences (Brett 1952), that may be due to physiological trade-offs between metabolism and growth or simply prey distributions. In Marguerite Bay on the WAP, *Pleuragramma* was found in highest abundance in the most neritic environments and not on the outer shelf (Donnelly and Torres 2008).

Experimental studies on the impact of salinity changes on notothenioid fish are extremely scarce and limited to few species, which were found to be tolerant towards large fluctuations in salinity (O'Grady and DeVries 1982).

Data from non-Antarctic fish species show ontogenetic differences in vulnerability towards changes in temperature (Pörtner and Farrell 2008; Pörtner and Peck 2010) and sea water salinity (Varsamos et al. 2005), with early developmental stages such as eggs and larvae being more sensitive than adult fish. In the case of *Pleuragramma*, there is some indirect evidence that larvae and juveniles might be vulnerable to changes in temperature and salinity. Larvae and juveniles are mostly found associated with water masses of particular temperature and salinity (e.g. Hubold 1984; Kellermann 1986; Slósarczyk 1986; Guglielmo et al. 1998; Granata et al. 2002). West of the Antarctic Peninsula, larvae and juveniles were clearly confined to cold and high salinity water masses of Weddell Sea origin (Slósarczyk 1986). Based on combined datasets of fish abundances in water of Weddell Sea and Bellinghousen Sea origin, Slósarczyk (1986) calculated the range of approximate optimum water temperature (-0.50 to $+0.45$ °C) and salinity (~ 34.10 – 34.62 ‰) for *Pleuragramma* larvae and juveniles in the Bransfield Strait. Though changes in salinity induced by climate change might be a locally restricted phenomenon, dense aggregations of larvae and juveniles that are both concentrated close to the coast/shelf ice in the upper water layers might be affected. Moline et al. (2004) found vast areas west of the Antarctic Peninsula covered by low salinity water (33.4 – 33.6 ‰), and the melt water plume extended to depths as great as 50 m (Dierssen et al. 2002).

However, whether the occurrence of larvae and juveniles in particular water masses really reflects thermal and salinity optima or preferences, or maybe just major transport pathways, remains to be verified. Nevertheless, there is some evidence that larvae are actually highly sensitive to increasing temperatures from

observations on board a research vessel: *Pleuragramma* larvae from the southern Weddell Sea, held in aquaria on board, were observed to shrink and to die immediately at water temperatures >0 °C (Hubold 1990).

12.5.2 Prey Availability and Composition

The environmental alterations off the Antarctic Peninsula are causing significant spatiotemporal changes in phytoplankton and zooplankton community structure. Recurrent shifts are observed from large diatoms to small cryptophytes (Moline et al. 2004) and from a krill-dominated zooplankton community to a salp-dominated community (Loeb et al. 1997; Nicol et al. 2000; Atkinson et al. 2004). Unlike krill, salps are able to feed efficiently on very small particles ± 1 μm (Madin 1974; Kremer and Madin 1992; Fortier et al. 1994). Alterations in zooplankton community composition due to climate forcing have been observed world-wide, and often include a shift from larger to smaller zooplankton species, especially in copepods (e.g. in the southern North Sea, Helouët and Beaugrand 2007; and in the Humboldt Current ecosystem, reviewed in Alheit and Niquen 2004). Shifts in size distribution from large to small phytoplankton organisms in the Southern Ocean may thus favor the prevalence of smaller zooplankton species such as the cyclopoid copepods. Fishes, particularly small pelagic zooplankton consumers, are known to be highly sensitive to indirect effects of climate forcing such as alterations in prey abundance, prey composition, and prey size (see McFarlane et al. 2001; Benson and Trites 2002; Beaugrand et al. 2003; Alheit and Niquen 2004).

Pleuragramma mainly preys upon copepods and different life stages of krill (see 12.4.3). There are indications for size selective feeding in larvae as well as in adults from studies on stomach contents (Hubold and Ekau 1990; Lancraft et al. 2004; Mintenbeck unpublished data), with adults neglecting prey below a certain size limit, but it is unknown whether the selective feeding behaviour is obligate or facultative. Moreover, compared to most other notothenioids, *Pleuragramma* is a specialist feeder with a narrow food spectrum (Mintenbeck et al. 2012). *Pleuragramma* might therefore be extremely vulnerable to changes in zooplankton composition in general, and to changes in zooplankton size-structure in particular.

Pleuragramma larvae strongly depend on time of appearance, abundance and type of prey. A mismatch between hatching and prey availability due to climate change-induced phenological shifts might significantly compromise larval condition and survival (see, e.g. Wöhrmann et al. 1997; La Mesa et al. 2010; La Mesa and Eastman 2012). Early postlarvae exhibit only low levels of reserve lipids, early stages therefore depend on the availability of prey and thus on synchronous hatching of copepod offspring (Wöhrmann et al. 1997). However, despite low lipid levels, larval *Pleuragramma* can starve for about 3 weeks (Hubold 1992) and adults are also assumed to be able to cope with periods of food deprivation due to their low metabolic requirements (Wöhrmann 1998), so there is a certain degree of plasticity. Larvae and juveniles, however, were observed to feed all year long (Kellermann and

Schadwinkel 1991) and overall lipid content of adult individuals shows no pronounced seasonal variation (summer-winter), both indicating that the large lipid deposits are primarily used as buoyancy aid and not as energy reserve during winter months (Hubold and Hagen 1997), as e.g. in Antarctic myctophid fish (Donnelly et al. 1990). However, the functional role of lipids in *Pleuragramma* is still not fully understood. If the functional role of lipids in Antarctic silverfish is exclusively restricted to buoyancy (see, e.g. Maes et al. 2006), starvation capability is extremely low. If lipid stores, or at least parts of them are used as energy reserves in case of food deprivation (see, e.g., Eastman and DeVries 1989), the reduced lipid content will negatively affect buoyancy and thereby energetics underlying dispersal and migration (vertical and horizontal).

Prey quality may be as important as prey availability to young *Pleuragramma*; condition of *Pleuragramma* larvae varied strongly with food composition (copepods vs. diatoms; Koubbi et al. 2007). Likewise, condition of adult fish may be affected by a shift in zooplankton towards a salp-dominated community, as has been observed off the WAP. Gelatinous zooplankton, such as salps, are occasionally consumed by fishes (including notothenioids) and flighted seabirds (Ainley et al. 1986), acting as “survival food” when preferred zooplankton prey are not abundant (Kashkina 1986; Mianzan et al. 2001). Energy density and nutritive value of gelatinous species are extremely low when compared to crustaceans such as krill and copepods (e.g. Clarke et al. 1992; Donnelly et al. 1994; Torres et al. 1994). Low energy food may affect survival, growth, body condition and reproductive output of consumers such as *Pleuragramma*, in turn making the species a low quality prey item for its warmblooded predators (see Österbloom et al. 2006, 2008; Ruck et al. 2014).

12.5.3 Competition and Predation

In vast areas around the Antarctic continent an oceanic, offshore pelagic fish community and a neritic pelagic fish community are readily distinguished (e.g. in the Weddell and Ross Seas; DeWitt 1970; Hubold and Ekau 1987; Lancraft et al. 1991; Donnelly et al. 2004). The oceanic community is typically dominated by myctophid fish and the neritic fish community is almost exclusively composed of *Pleuragramma* and early developmental stages of other notothenioid fish species. As the oceanic and neritic communities are usually clearly separated at the shelf break, there is no pelagic fish species seriously competing with *Pleuragramma* for prey in the high Antarctic. However, on the West Antarctic Peninsula (WAP) shelf, the neritic and oceanic communities overlap, resulting in a mixed pelagic community (Donnelly and Torres 2008).

The oceanic fraction of the mixed community is dominated by the myctophids *Electrona antarctica* and *Gymnoscopelus* spp., and the neritic fraction is mainly represented by *Pleuragramma*. *E. antarctica* and *Gymnoscopelus* spp. both mainly feed on copepods, in particular *C. acutus*, *C. propinquus* and *M. gerlachei*, and on

ostracods and euphausiids (Hopkins et al. 1993a; Saunders et al. 2015), so there is very high overlap in prey composition between the myctophids and *Pleuragramma*, making competition for food in this region likely.

The degree of overlap between oceanic and neritic communities was found to be directly correlated to local hydrodynamic conditions, i.e. to the mixture of cold shelf water masses and warmer and more saline circumpolar deep water (Donnelly and Torres 2008; Cullins et al. 2011). The absence of myctophid fish in other coastal Antarctic regions where cold ($-2\text{ }^{\circ}\text{C}$) and less saline ice shelf water prevails (e.g. Ross and Weddell Seas), is explained by the absence of antifreeze glycoproteins (AFGPs) in the oceanic species (Cullins et al. 2011). The occurrence of oceanic species on the WAP with its warmer mid-depths ($2\text{ }^{\circ}\text{C}$), suggests that, with more widespread warming of shelf water masses due to climate change, oceanic myctophid fish may increasingly invade other high Antarctic regions, perhaps becoming a serious competitor of *Pleuragramma* for zooplankton on a larger spatial scale. Growth and time to first reproduction happen much faster in myctophid fish than notothenioid species (Greely et al. 1999; Linkowski 1987), so population density may increase rapidly. Ongoing climate change might thus result in competitive suppression of *Pleuragramma* populations.

However, populations may not exclusively be suppressed by competition, but also by top-down pressure, namely predation. Predation on *Pleuragramma* is pervasive. All developmental stages are important food sources and are heavily preyed upon by a multitude of predators, including piscivorous fish, seals, seabirds and penguins (Castellini et al. 1984; Eastman 1985; Green 1986; Plötz 1986; Klages 1989; Hureau 1994; Burns et al. 1998; Cherel and Kooyman 1998; Daneri and Carlini 2002; La Mesa et al. 2004). Under stable conditions the populations of *Pleuragramma* can sustain this exploitation, but in a changing Southern Ocean, where krill are in decline and salps are more pervasive (as observed at the WAP; Loeb et al. 1997; Nicol et al. 2000; Atkinson et al. 2004), krill consumers may rely more heavily on pelagic fish resulting in increased predation pressure on *Pleuragramma*.

Competition and predation alone are unlikely to cause a collapse of *Pleuragramma* populations. However, the cumulative effects of several stressors working in tandem, e.g. competition, predation, changing prey spectrum, reduced sea ice, episodic recruitment, and the physiological effects of warm temperature work together to put a high level of pressure on the species.

12.6 *Pleuragramma* on the WAP Shelf: Mechanisms Underlying Its Response to Rapid Regional Warming

Pleuragramma has been extensively sampled on the WAP shelf as part of large multi-investigator programs and smaller individual efforts, providing a historical record of its larval and adult distribution since 1976 that is unique in the Antarctic

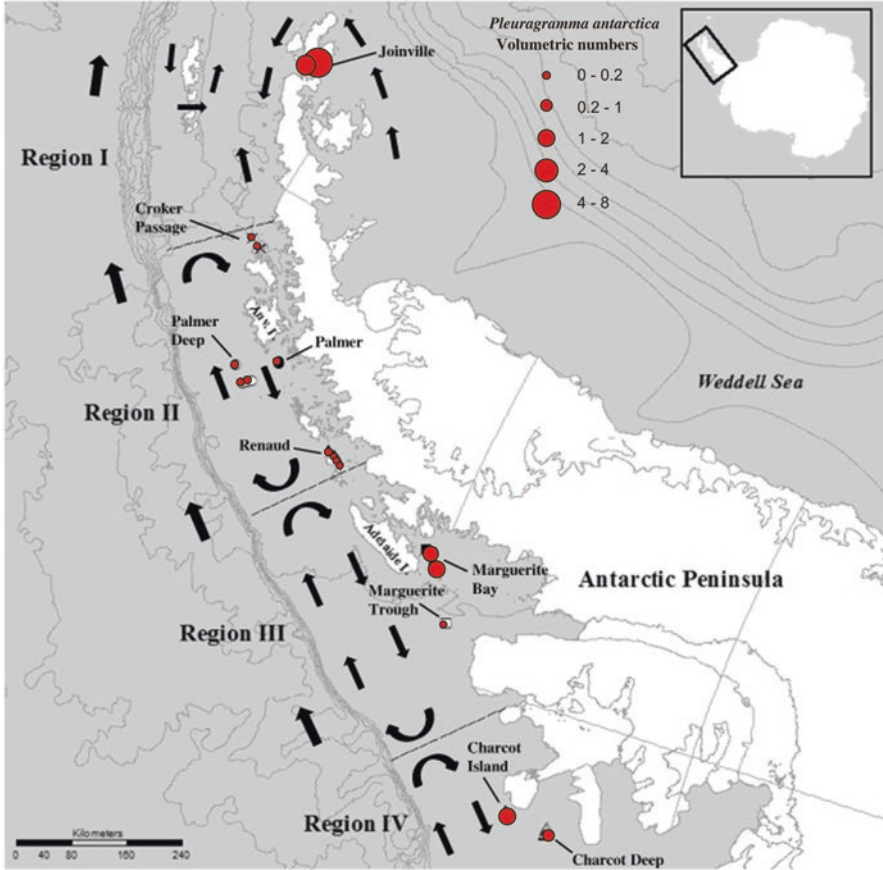


Fig. 12.2 Distribution of *P. antarctica* (number $\times 10^4 \text{ m}^{-3}$ in the upper 500 m) on the western Antarctic Peninsula shelf in the austral fall of 2010. Results from 32 trawls (Data from Parker et al. 2015)

system. Taken together, the historical information confirmed a continuous distribution of *P. antarctica* from the Antarctic Sound in the Northern Peninsula to Marguerite Bay in the south up to at least 1990, when targeted sampling for *Pleuragramma* became less frequent (Parker et al. 2015; Ross et al. 2014; Kellermann 1996).

In an effort to assess the current status of *Pleuragramma* on the WAP shelf, a study was undertaken in austral fall of 2010 (Parker et al. 2015). Samples were collected at nine sites within the historic distribution of *Pleuragramma* along the WAP (Fig. 12.2) with a 10-m² Multiple Opening and Closing Net and Environmental Sampling System (MOCNESS) outfitted with six 3-mm mesh nets (Wiebe et al. 1976, 1985). A total of 32 trawls were successfully completed, with 7 conducted during the day and 25 at night.

Sites were located within four hypothesized hydrographic regimes (Fig. 12.2), based on observed shelf circulation patterns (Parker et al. 2015; Hofmann et al. 1996; Stein 1983). The regimes, designated as peninsular regions, were delineated as follows. Region I comprised the northern peninsula including Joinville Island, Antarctic Sound, and the Bransfield Strait. It is strongly influenced by cold-water flow from the Weddell Sea. Region II was the northern mid-peninsula, including Anvers Island and the Biscoe Islands community where regional warming has produced a marked decline in spring (November) sea ice (Ducklow et al. 2007; Stammerjohn et al. 2008a, b). Region III was the southern mid-peninsula (Marguerite Bay) community including the Marguerite Bay system. Region IV was the southern peninsula (Charcot Island) community roughly defined by Lazarev Bay on the north and an as yet undefined boundary well south of Charcot Island. Model results suggest that the gyral circulation in Region III reaches closure near Lazarev Bay, and a third gyral circulation is set up just north of Charcot Island, reaching closure further south (Piñones et al. 2011, 2013a, b). For purposes of discussion, the different regions described above (shown in Fig. 12.2) will be used for convenience in discussing peninsular locations.

Silverfish were captured at Joinville Island in Region I, Marguerite Bay in Region III, and in the vicinity of Charcot Island in Region IV. One fish was captured in Croker Passage, an area in Region II where they were formerly abundant (88 individuals 10^3 m^{-2} in the upper 200 m; Lancraft et al. 2004). A continuous distribution of juvenile and adult silverfish along the WAP shelf in the 1970s and 1980s (Daniels and Lipps 1982; Reisenbichler 1993) was highly discontinuous in early fall of 2010. The question is: what does a gap in a formerly continuous distribution mean for silverfish on the WAP?

12.6.1 *Paleohistory of Silverfish on the WAP*

Part of the answer to *Pleuragramma*'s disappearance from Region II is provided by observed shifts in paleo-climate. Two studies of abandoned penguin rookeries along the WAP show evidence of shifts in paleo-diet in the Adélie penguin (*Pygoscelis adeliae*) in response to past warming and cooling periods. The first study, located in the vicinity of Palmer Station in Region II (Emslie et al. 1998), and covering a time span from approximately 644 to 250 years BP (Before Present), shows a shift in the non-euphausiid component of Adélie diets from primarily silverfish during cool periods to primarily squid (*Psychroteuthis glacialis*) during warm periods of the WAP's environmental history. Abandoned rookeries of Marguerite Bay (Region III) showed an identical trend in a study encompassing 6000 years of paleohistory (6000 years BP to modern), with diets shifting from primarily silverfish in cooler periods to squid in warmer (Emslie and McDaniel 2002). Clearly, silverfish have exhibited up and down trends in population numbers on the WAP throughout the Holocene.

12.6.2 *Mechanisms Underpinning the Disappearance of *Pleuragramma* in Region II: Alternate Hypotheses*

Ultimately, *Pleuragramma*'s absence from Region II reflects an absence in recruitment of young fish accompanied by attrition in the older size classes due to predation or migration. In the late 1980s, larval silverfish showed an abrupt and persistent drop in numbers in the northern mid-peninsula region (Region II) (Kellermann 1996), which persists to the present day (Ross et al. 2014). Ross et al. (2014) attribute the loss of larval *Pleuragramma* to three possible causes: (1) loss of connectivity to a distant source population, (2) loss of a local source population, or (3) decrease of larval survival in the northern mid-peninsula. Any of the three alternatives would potentially result in an absence of recruitment, leading eventually to local extinction. It will be useful to consider each possibility in light of what is presently known about *Pleuragramma* on the peninsula.

12.6.2.1 The “Larval Pump” Hypothesis

Much thought has been given as to how a high-Antarctic species such as *Pleuragramma* has succeeded in the warmer waters of the WAP shelf. Youngest post-larvae (10–12 mm) were rarely captured on the peninsula in the many larval surveys conducted from the 1970s through the early 1990s (Kellermann 1996), and then not in high abundance (Kellermann 1986), which argued against local source populations, particularly when compared to the numbers found in the Weddell and Ross Seas. Instead, recruitment of *Pleuragramma* to the waters of the WAP shelf was attributed to larval dispersal, a “larval pump”, from spawning centers associated with the ice shelves in the western Weddell Sea (e.g. Larsen Bay) and the continental Bellingshausen Sea southwest of the Peninsula (Kellermann and Schadwinkel 1991). In the larval-pump hypothesis, larvae originating in the Weddell Sea, notably in Larsen Bay, are transported from the Weddell Sea via the Weddell Gyre/Antarctic Peninsula Coastal Current (APCC) as it flows through the Antarctic Sound and as it bends around Joinville Island (Fig. 12.2; Stein 1983; Hubold 1992; Hofmann et al. 1996; La Mesa et al. 2015) and into the eastern Bransfield Strait, eventually proceeding south with the APCC. Larvae originating in the other hypothetical spawning site, the continental Bellingshausen south of the peninsula, would be transported northeast in the upper 100 m of the Antarctic Circumpolar Current (ACC), merging with the general northeasterly flow at the shelf break along the peninsula, and making their way further inshore via the cross-shelf gyral flows in the vicinity of Alexander Island, Renaud Island, and the southern Bransfield Strait (Fig. 12.2; Hofmann et al. 1996; Piñones et al. 2011, 2013a, b).

Pleuragramma larvae have been present in most samples taken from the Bransfield Strait in the 1970s through the 1990s (Kellermann 1986, 1996; Loeb 1991; Morales-Nin et al. 1998) and more recently (Lipsky 2006; Loeb et al. 2006; Jones et al. 2006; La Mesa et al. 2015) though numbers have been highly variable.

Recent modeling of larval transport for *Pleuragramma* originating in the Weddell Sea corroborates the dispersal path described above, both in terms of trajectory and timing relative to hatch-date (La Mesa et al. 2015). Once in the Bransfield Strait, larvae could theoretically be transported south via the APCC, potentially to the Palmer Archipelago, the Biscoe Islands, and Marguerite Bay (Niiler et al. 1991; Moffat et al. 2008). Flow in the upper 200 m of the Gerlache Strait east of Anvers Island is generally north (Savidge and Amft 2009), so dispersal of larvae further south via the Gerlache Strait would be severely constrained by the circulation. Successful transport south would require that larvae be in the west central Bransfield Strait (Niiler et al. 1991; Moffat et al. 2008).

Whether the “larval pump” was ever a major supplier of *Pleuragramma* larvae from either the Weddell Sea or from the Bellingshausen for recruitment to the WAP shelf is a matter of conjecture, but it is highly unlikely that it has been contributing any in recent years. Ross et al. (2014) report that no *Pleuragramma* larvae were captured on the slope or outer shelf from 1993–2008, ruling out any input from the Bellingshausen via the Antarctic Circumpolar Current (ACC). Similarly, in samples from the Anvers Island region (Region II of Parker et al. 2015) no larvae were present from 1996–2008. The implication is that few larvae originating in the Weddell Sea survived the transit from the cold waters of the Bransfield Strait to the warmer region near Anvers Island. There is no evidence for present connectivity between the Weddell Sea and Region II.

Further evidence ruling out strong connectivity from the Northern to Southern peninsula is provided by genetics and otolith microchemistry of fish collected in Region I and Regions III and IV. Genetic analyses performed on fish captured in the 2010 survey described in Parker et al. (2015) showed that Marguerite Bay and Charcot Island fish comprised a single, panmictic population that was differentiated from the Joinville Island fish (Agostini et al. 2015). Microchemical analyses of otolith nuclei showed similar results. No significant differences were detected in isotopic ratios between fish captured in Marguerite Bay and near Charcot Island (Ferguson 2012) suggesting that *Pleuragramma* from Marguerite Bay and Charcot Island are part of one contiguous population. A separate population of silverfish was found at Joinville Island using the same techniques. Results of those studies coupled with the fish distributions observed in Parker et al. (2015) provide three lines of evidence that there is little connectivity between silverfish populations in the northernmost region at Joinville Island and the two southernmost regions at Marguerite Bay and Charcot Island.

12.6.2.2 Reproducing Populations on the WAP Shelf

An alternate hypothesis to the continuous replenishment of WAP silverfish populations by larvae from distant sources is that reproduction has been occurring in local populations on the WAP shelf, supplementing the larvae supplied by advection (Parker et al. 2015). Candidates for spawning locations would include Palmer Station’s Arthur Harbor (cf. Daniels 1982), Crystal Sound, and Marguerite Bay.

Each may have hosted reproducing populations of *Pleuragramma*, but changing seasonal sea ice dynamics presently leave only Crystal Sound and Marguerite Bay as possibilities for local reproduction. Recruitment in local populations would be highly vulnerable to unfavorable sea-ice conditions brought about by a changing climate.

Larval captures in the Marguerite Bay region reported by Ross et al. (2014) and the presence of fish sufficiently large to be of reproductive age captured in Parker et al. (2015) support reproduction on the shelf. Larvae captured by Ross et al. (2014) were of the correct size to have been spawned there.

If the three hypotheses for absence of silverfish larvae in Region II stated in Ross et al. (2014) are revisited in combination with results from Parker et al. (2015), what is happening to silverfish on the peninsula becomes a bit clearer. Essentially, all three reasons for silverfish disappearance have converged in Region II, driven by the poleward movement of the ACC. The increased landward influence of warm upper circumpolar deep water (UCDW) along the WAP over the last two decades described by Suprenand et al. (2015), Piñones et al. (2013b), Smith et al. (1999a), Martinson et al. (2008), Martinson (2012) and Dinniman et al. (2012), has made the outer shelf a more oceanic system, particularly at depths below 200 m (Ashford et al. 2017). Nowhere has this eastward encroachment been more pronounced than in Region II.

12.6.2.3 Loss of Connectivity to a Distant Source Population

A potential larval source in the Weddell Sea is well established based on recent (La Mesa et al. 2015) and multiple older references (Kellermann 1996) that considered the Bransfield Strait as a nursery ground for *Pleuragramma*. Circulation in the Bransfield Strait, though complex, would allow some southward transport of larvae though the strait itself and into Region II. However, in recent years, once transported into the increasingly oceanic waters of Region II, they apparently do not survive (Ross et al. 2014). Any Weddell Sea larvae drifting south past Anvers Island and the Biscoe Islands will encounter a warmer water column and an altered prey spectrum. Clearly, hypothesis 3, decrease of larval survival, applies here as well.

Northward larval transport from the Bellingshausen via the ACC is also not supported by the Ross et al. (2014) larval survey, which found no silverfish larvae in outer shelf or slope samples. Though alluded to repeatedly (e.g. Kellermann 1996), a location for the source populations in the Bellingshausen Sea was never provided in the literature.

Northward transport of larvae produced in the Marguerite Bay region would also be possible, but the demonstrated absence of larvae in shelf/slope stations coupled with the highly episodic appearance of any northeasterly coastal flow (Moffat et al. 2008) precludes any likelihood of serious northward larval transport. Region II is effectively cut off from larvae originating to the north and south of it.

12.6.2.4 Loss of a Local Source Population

P. antarctica is a cold-water, neritic species, not found in oceanic waters during its juvenile or adult stages (De Witt 1970; Lancraft et al. 1989, 1991; Donnelly et al. 2004; Donnelly and Torres 2008) despite an entirely pelagic life history (La Mesa and Eastman 2012) and a rich prey spectrum in oceanic waters. Increasing influence of warm oceanic waters (upper circumpolar deep water) on the shelf will likely push its distribution further toward the inner shelf, a trend observed in Marguerite Bay during the 2001, 2002 GLOBEC program (Donnelly and Torres 2008).

Historical observations in the vicinity of Palmer Station and the Biscoe Islands, e.g. Daniels (1982) and Daniels and Lipps (1982), strongly suggest that Antarctic silverfish were quite abundant in Region II during the 1970s (Kellermann 1996). Region II shows the most pronounced effects of rapid regional warming on the peninsula, including mean annual temperatures that have increased by 5.7 ± 2.0 °C century⁻¹ since 1951 (Vaughan et al. 2003) and a consistently earlier sea ice retreat at about the time-of-hatch for *Pleuragramma* eggs (Fig. 12.1; Stammerjohn et al. 2008a). Region II also showed a virtual absence of silverfish during Parker et al. (2015). The fact that *Pleuragramma* spawns under coastal sea ice and that eggs apparently develop and hatch in a nursery of platelet ice when it is available (Vacchi et al. 2004, 2012) points to regional warming and its effects on seasonal sea ice dynamics as an important element in the species' absence in Region II. Phenology of reproduction in the local silverfish population may have been disrupted by early ice retreat, resulting in the absence of a sea ice refugium prior to hatching, with an accompanying change in predation pressure and altered prey spectrum for larvae, resulting in multiple years of poor local recruitment. It is highly likely that a local breeding population formerly existed in Region II, but that it is no longer present, either due to attrition or migration.

12.7 Consequences for the Ecosystem

Pleuragramma is a shoaling fish (Fuiman et al. 2002) that can attain very high densities. For example, in the southern Weddell Sea the biomass of silverfish was estimated to be 1 ton km⁻² (Hubold 1992). Adults undertake nocturnal migrations from deeper waters into upper water layers, where dense shoals provide an easily accessible food source for warmblooded animals living on the ice (Fuiman et al. 2002; Plötz et al. 2001; Lancraft et al. 2004; Mintenbeck and Knust unpublished data). This key species in the high Antarctic food web is threatened by climate change on several levels, making a reduction in its population density probable in the long run.

The ecosystem response to climate forcing detected so far off the WAP may be observed in other marine ecosystems worldwide. A common pattern emerging from the climate-driven alterations in the world's oceans is that the pelagic realm is always the first and/or the strongest to respond (reviewed in Mintenbeck et al. 2012). Among fishes, pelagic species in short plankton-based food chains often undergo

strong fluctuations in stock density (e.g. clupeids; Alheit and Niquen 2004), with severe consequences for warm-blooded apex predators (e.g. Alheit 2009; Arntz 1986; Cury et al. 2000).

Something similar may be expected in the long run for the Southern Ocean. If climate change proceeds and extends towards other regions of the coastal Antarctic, it is very likely that *Pleuragramma* will be affected by direct and/or indirect climate forcing. The potential consequences involve a decrease in nutritive value of the fish for predators and a decline in population density due to reduced reproductive output or increased mortality. As a polar species, *Pleuragramma* has no option for escape to a more favorable climate, nor is an evolutionary adaptation that keeps pace with the rate of change very likely (see Somero 2010). Notothenioid fish are evolutionarily adapted to stable (cold) environmental conditions without major disturbances, which is also reflected in *Pleuragramma*'s life history traits such as slow growth and low relative fecundity (compared to non-notothenioid pelagic fish, reviewed in Mintenbeck et al. 2012). A recovery of the population after the stock has declined is accordingly questionable. If *Pleuragramma*, in the worst case, disappears from the ecosystem, many species will lose their main food source.

Whether such a loss can be replaced within the food web by, e.g., invading myctophid fish or demersal notothenioid fish remains to be seen. Demersal notothenioids also contribute to the diet of Antarctic warm-blooded animals (Casaux et al. 2006; Coria et al. 2000; Plötz et al. 1991), but they neither occur in shoals, nor do they undertake regular vertical migrations into upper water layers, making their exploitation in vast areas on the deep shelf more costly in terms of capture efficiency and time and energy investment. Myctophids, which also undertake daily vertical migrations (e.g. Lancraft et al. 2004), might be able to substitute for Antarctic silversfish in the high Antarctic marine food web. One possible candidate is *Electrona antarctica*. Its circumantarctic distribution in waters seaward of the shelf break and south of 60° S (e.g. Lancraft et al. 1989, 1991) make it attractive as a potential replacement for *Pleuragramma* in the coastal system. Currently, its lack of anti-freeze proteins physiologically exclude it from the ice-shelf waters of the Antarctic coast (Cullins et al. 2011), but it is found in abundance at typical shelf depths and in deeper coastal canyons in the warmer waters of the WAP (Parker et al. 2015; Donnelly and Torres 2008; Lancraft et al. 2004). It has a maximum age of 4 years, and is believed to broadcast spawn in multiple batches in its last year of life (Greely et al. 1999). The diet of *E. antarctica* is similar to that of *Pleuragramma*, with copepods being its main prey in its early years and juvenile krill as it reaches its maximum size (Lancraft et al. 2004).

E. antarctica undertakes strong diel vertical migrations; in oceanic waters it is found in the upper 300 m at night and between 600 and 1000 m during the day (Lancraft et al. 1989, 1991). Morphologically, it is well suited to the nearly constant reduced light levels typifying the habitat of a vertically migrating mesopelagic fish. It has a dark dorsum and a full suite of ventral and lateral photophores in addition to large, well developed eyes. Further, it exhibits little plasticity in its diel behavior with no evidence of swarming, or shoaling. Unlike *Pleuragramma*, it is not found over shallow bottom depths.

Piñones et al. (2016) note an increasing presence of circumpolar deep waters in cross-shelf canyons in the Ross Sea shelf area, so eventually *E. antarctica* may be able to make its way onto the Ross Sea shelf via coastal canyons as on the WAP shelf. In past climatic regimes, the Ross Sea has been an open water marine environment (45,000 to 27,000 years BP; Emslie et al. 2007), which would suit the species' life strategy well. However, this scenario is far in the future, even at the current rate of warming.

A fully functional substitution requires not only an alternative species similar in terms of diet, abundance, size, and energetic value, but also in terms of availability and accessibility. The dense shoals of *Pleuragramma* provide an easily accessible food source for warm-blooded predators, in particular when shoals migrate up into upper water layers. *E. antarctica* does not occur in such dense shoals, and its success as a potential substitute for *Pleuragramma* in the diet of apex predators also depend on their vertical migration pattern at high latitudes; e.g. during 24 h daylight in austral summer, longer periods of time are spent at great depth (Donnelly et al. 2004), out of the reach of most predators.

Clearly, systemic shifts affecting *Pleuragramma* will cause strong responses in food web structure. The long-term consequences for the ecosystem's top predators and for overall ecosystem functioning remains unclear, so far. However, if no species will be able to provide functional compensation within the food web, the consequences for the entire system are most likely severe.

12.8 Future Research

There are still many gaps and uncertainties in our knowledge on *Pleuragramma*'s fundamental ecology and life history traits that needs to be filled or verified. Future research, e.g., should verify the role of sea ice in *Pleuragramma*'s ecology and reproductive ecology and spawning sites.

The standard method for analyzing the effects of environmental alterations on fish species is the experimental approach, where single variables or even variable combinations can be manipulated to test for a response. Experimental approaches would definitely help to verify the assessment of *Pleuragramma*'s vulnerability to climate change inferred so far only from indirect evidence and knowledge on closely related species.

Experimental studies on Antarctic silverfish are extremely scarce due to its soft and fragile body structure, making the capture and cultivation of live specimens extremely difficult. Some of the few successful experimental approaches include studies on the freezing resistance of eggs and larvae (Cziko et al. 2006), on yolk resorption in starving yolk-sac larvae (Hubold 1992), haemoglobin system of adult fish (Tamburrini et al. 1997), and feeding behavior and prey preferences of juvenile *P. antarctica* (Fanta 1999).

Sampling of adults in good condition from research vessels using traditional fishing methods, such as trawls, is very difficult. However, careful sampling of early

stages through holes drilled in the ice, as successfully done in Terra Nova Bay (Vacchi et al. 2004), may provide the best solution to collect *Pleuragramma* individuals alive for experimental studies. Such experimental approaches should test for the direct effect of changes in water temperature and salinity on fitness and survival and the acclimation capacities of this species. This will allow for further insights into actual sensitivity of these vulnerable life stages to alterations in environmental parameters. Feeding experiments with different life stages may help to elucidate selectivity in prey choice (size and type of prey) and the impact of prey quality on fish condition.

Also studies focusing on spatial and/or temporal variability in life history traits or fish condition could further elucidate the role of particular environmental parameters (abiotic and biotic) in controlling the state of individuals and populations (e.g., Ruck et al. 2014). For such an approach specimens from regions with different environmental regimes might be compared based in traditional measures (e.g. stomach contents, fatty acid composition, condition indices, etc.), but also using advanced methods. A recent study investigated the internal structure of preserved *Pleuragramma* using Magnetic Resonance Imaging (MRI; Bock et al. 2017). This modern tool may provide novel insights into, e.g. the structure of *Pleuragramma*'s lipid sacs, and may open new opportunities for studies on the impact of climate change on Antarctic silverfish.

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