Chapter 9

Reproductive Strategies of the Antarctic Silverfish: Known Knowns, Known Unknowns and Unknown Unknowns

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Abstract Reproduction is a key step of a species life history and includes a suite of strategies and tactics enacted to allow the maximization of reproductively active offspring in relation to available energy and parental life expectancy. Gender system, oogenesis pattern, maturation schedule, shifts in habitat utilization, spawning seasonality, mating behavior, and fertilization pattern are among the traits involved in the process of species adaptive optimization of reproduction.

In this frame, here we review the reproductive traits of the Antarctic silverfish (*Pleuragramma antarctica*) based on the available macroscopic and histological data. Then, we will step forward by focusing on two aspects of this species' reproduction: (i) skipped spawning; (ii) potential location of reproduction sites along the Antarctic coasts.

Keywords Antarctic fish • Ovarian maturation • Atresia • Skip spawning • Nursery area

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9.1 Introduction

It is widely accepted that reproduction encompasses a whole suite of strategies which enable the species to maximize its reproductive output in relation to the available energy and parental care (Murua and Saborido-Rey 2003). The optimization of these two components is achieved through an adaptive process fine tuning reproductive traits such as the gender system, oogenesis pattern, maturation schedule, shifts in habitat utilization, spawning seasonality, mating behaviour, and fertilization pattern. A thorough understanding of the reproductive characteristics of a species is paramount not only for understanding its biology and ecology, but also for management purposes. Here we focus on the reproductive features of the Antarctic notothenioid *Pleuragramma antarctica* (Antarctic silverfish), a dominant fish in high-Antarctic shelf and slope waters (Duhamel et al. 2014) where the species plays a similar key role in the food web as does krill in the Seasonal Pack-ice Zone (SPZ).

The evolution and adaptation of Antarctic notothenioids is closely linked to the opening of the Drake Passage and the subsequent cooling and other changes that occurred (Eastman 1993). The next 20 million years provided ample time to shape many aspects of their biology and ecology, including reproduction.

Antarctic notothenioids share a number of reproductive traits such as low fecundity, large eggs (size spanning between 2 and 5 mm), prolonged gametogenesis, and group-synchronous oocyte maturation (e.g. Kock and Kellermann 1991; Shandikov and Faleeva 1992; Calvo et al. 1999; Kock 2005; La Mesa et al. 2003, 2007, 2008; Parker and Grimes 2010). Despite the fact that they share common features of their reproduction on the one hand, notothenioids exhibit a high diversity in reproductive strategies. For example, most Antarctic notothenioids lay demersal eggs (e.g. Kock and Kellermann 1991; Kock and Everson 1997; van der Molen and Matallanas 2004; Kock 2005) that, in a number of species, are deposited in nests and guarded (e.g. Kock et al. 2006; Jones and Near 2012; Ferrando et al. 2014). Others lay pelagic eggs, which drift in the upper part of the water column up to several months (e.g. Yukhov 1982; Kock and Kellermann 1991).

Here, we review the reproductive traits of the Antarctic silverfish. We focus on two aspects of their reproductive strategy: (i) skipping annual spawning when unfavourable conditions prevail; (ii) identifying locations where the species are known to spawn and/or potentially spawn along the Antarctic shelves and slope.

9.2 Reproductive Traits of Antarctic Silverfish

In his monography of Antarctic fish, Andriashev (1965) compiled what was known on the Antarctic silverfish until the mid-1960s. Reproduction was one of the biological characteristics of which little beyond that spawning occurred apparently in austral winter and larvae were first recorded from October–December was known (Regan 1916; DeWitt and Tyler 1960).

The Soviet Union started commercial fishing in the Southern Ocean in the late 1960s. Soviet scouting and commercial fishing vessels were fishing close to the Antarctic continent from the second half of the 1970s. Aggregations of the Antarctic silverfish were discovered in the northern Weddell Sea, in the Prydz Bay and Ross Sea in the late 1970s by FRV *Mys Yunony* (Shust 1998). Comparatively little was published in the accessible Soviet scientific literature at that time. These exploratory fishing cruises confirmed that the species was apparently one of the most abundant fish species in the high-Antarctic. In particular, the abundance and biomass of this fish in the north-western part of the Weddell Sea was considered as very high. In 1985, the relative biomass of *P. antarctica,* even in the less productive central area of the Weddell Sea, was 300 kg/km^2 (Shust 1998). Some data on catches of *P. antarctica* by Soviet trawlers during exploratory fishing reported in CCAMLR documents can be found in Koubbi et al. (2017).

The species is drawn to greater depths than other plankton-feeders, and adult *P. antarctica* are generally found at depths beyond 300 m (Sosinski and Skora 1979; Shust et al. 1984; Ekau 1990).

German Antarctic expeditions, conducted between 1979 and 1981 to the Weddell Sea down to the Filchner Shelf Ice, found that Antarctic silverfish larvae made up to 95% of the plankton biomass obtained from net catches. Of particular interest was the occurrence of larvae between 8 and 12.5 mm standard length in January–February, which reinforced Andriashev's assumption of a winter spawning of the species (Hubold 1984). The presence of silverfish eggs in the stomach of the benthic nototheniid *Trematomus pennellii* (Ekau et al. 1987) first suggested that eggs may be deposited on the bottom (Kellermann 1986). However, the very thin membrane of eggs, and significant yolk deposits, made pelagic eggs more likely. The finding of early embryonated eggs under the fast ice in September (Ghigliotti et al. 2015), and their location in the upper part of the platelet ice, close to the solid ice, as found later in the season (Guidetti et al. 2015), confirmed that eggs were positively buoyant, and floating in their latest stage of development before hatching.

Unfavorable weather and ice conditions during the winter period have thus far limited year-round sampling of adult individuals which could provide an unambiguous determination of when and where Antarctic silverfish spawn. For the time being histological methods are considered to be the only techniques which could provide further insight into the process and cycle of gonad maturation.

A time series of 10 year of data collected during austral summer (December–April) to East Antarctica (Cosmonauts, Commonwealth and Mawson Seas) allowed Faleeva and Gerasimchuk (1987, 1990) to refine information on length and age at sexual maturity, which had previously been overestimated due to the limitation of macroscopic observations. Furthermore, their investigations provided evidence that in early autumn the Antarctic silverfish gonads are still far from pre-spawning condition, supporting the notion of a winter or even winter/spring spawning (June to September).

The presence of sometimes large numbers of oocytes in regression state some 2–3 months prior to spawning suggests that a proportion of Antarctic silverfish females does not spawn annually and that the process of gonad maturation can be

Table 9.1 Length and age at sexual maturity as reported in the scientific literature

Region	Sex	SL (cm)	Age (years)	Refs.
East Antarctica Cosmonauts Sea	f	14–16	5–6	[1]
	m	13–15	4–5	
East Antarctica Commonwealth Sea	f	14–15	5–6	[1]
	m	13–15	4–5	
East Antarctica Mawson Sea	f	15–16	5–6	[1]
	m	13–15	4–5	
Weddell Sea	f/m	15.8		[2]

interrupted in case of unfavorable environmental conditions, thus saving energy for survival (Faleeva and Gerasimchuk 1990). Later studies extending the geographic range of such investigation by including the Antarctic Peninsula (La Mesa et al. 2015a) and Ross Sea (Ghigliotti et al. 2017) confirmed the presence of readsorbing follicles sporadically present or massively occurring in the ovaries.

9.2.1 *Macroscopical Observations*

The Antarctic silverfish is a gonochoristic dimorphic species. Males are characterized by on average smaller size, and pelvic fin which are longer than in females (Gerasimchuk 1987a) (please note that the spelling might change according to the Russian or Ukrainian transliteration as Gerasimchuk or Herasymchuk, respectively).

Differences between sexes have also been detected in the length at which specimens reach sexual maturity (Table 9.1) that is smaller in males and larger in females. [1] Gerasimchuk (1992); [2] Duhamel et al. 1993.

In the early austral summer, the gonadosomatic index (GSI) of sexually mature individuals, a widely used proxy of gonad development that expresses gonad weight as a percentage of total body weight, is low (ranging from 1 to 2% in both sexes). The GSI is slowly increasing towards the end of summer but in early autumn it is still well below 15–30%, usually found in females of many nototheniids and channichthyids immediately prior to spawning (Kock and Kellermann 1991; Duhamel et al. 1993) (Table 9.2 and references therein).

In low-Antarctic nototheniids and channichthyids, there appears to be a trend in the same species of increasing egg size and decreasing relative fecundity towards higher latitudes (Kock and Kellermann 1991), i.e. the same species generally produces more eggs at South Georgia than in the South Shetland Islands. Antarctic silverfish do not appear to follow that trend (Hubold 1992). Although not as high as in some Patagonian and low-Antarctic nototheniid species (e.g. Brickle et al. 2006), relative fecundity in Antarctic silverfish is fairly high (Table 9.3), and coupled with a relatively small egg diameter of about 2 mm.

Table 9.2 Range and variability in gonad maturity coefficient (GSI) of Antarctic silverfish specimens at maturity over the stage III, from various Antarctic areas, during the Southern Hemisphere summer and early autumn

Month	Region	Sex	n	GSI range	GSI mean ± σ	Refs.
January	East Antarctica	f	143	1.00–4.48	1.47 ± 0.46	[1]
		m	44	1.00–3.56	1.36 ± 0.45	[1]
February	East Antarctica	f	247	1.03–4.98	1.78 ± 0.51	[1]
		m	160	1.08–8.06	2.11 ± 0.94	[1]
	Weddell Sea	f	67	1.3–3.6	2.20 ± 0.49	[2]
		m	53	1.0–4.9	2.40 ± 0.81	[2]
	Ross Sea	f	25	0.97–3.43	2.20 ± 0.51	[4]
		m	16	1.29–4.50	2.23 ± 0.77	[4]
March	East Antarctica	f	400	1.07–5.00	2.64 ± 0.78	[1]
		m	291	1.00–9.27	4.77 ± 1.57	[1]
April	Antarctic Peninsula Charcot Island	f	41	1.48–3.46	2.25 ± 0.06	[3]
		m	15	1.09–4.00	2.87 ± 0.20	[3]
	Antarctic Peninsula Marguerite Bay	f	46	1.54–4.35	2.62 ± 0.08	[3]
	Antarctic Peninsula Joinville Island	f	3	1.29–5.25	3.27 ± 1.98	[3]

n sample size, *GSI* GonadoSomatic Index. References: [1] Faleeva and Gerasimchuk (1990); [2] Duhamel et al. (1993); [3] La Mesa et al. (2015b); [4] Ghigliotti et al. (2017)

9.2.2 Histological Data

Progress and timing of gonad maturation occurs in the three investigated areas, East Antarctica (Faleeva and Gerasimchuk 1990), Antarctic Peninsula (La Mesa et al. 2015b), and Ross Sea Region (Ghigliotti et al. 2017) at a similar time of the year. Within the 4 months of the austral summer, males pass through two stages: a resting stage is observed early in the season with inactive, sometimes dividing, spermatogonia at the periphery of the seminal gland, residual spermatozoids, and epithelium desquamation in proximal part of the testicular tubule. Active spermatogenesis then occurs the further summer progresses. It is characterized by intensive spermatogonial proliferation and emergence of primary spermatocytes. Limiting investigations to visual observation of testicles often resulted in over-estimation of maturity stage given the comparatively large size of the testis. Testis has often been found to occupy the rear 2/3 or the entire abdominal cavity and to be turbid white and yellowish. Nevertheless, spermatogenesis completion and emergence of spermatozoids had never been observed.

As notothenioids in general (see Shandikov and Faleeva 1992), females of Antarctic silverfish close to spawning are characterized by having group synchronous ovaries which consists of a batch of eggs maturing and ovulate in the current season, and a second batch of previtellogenic much smaller oocytes representing the next season's spawn. Oocytes in the primary growth stage are homogeneous in size. A large nucleus occupies most of the cell surrounded by a thin strongly basophilic layer of cytoplasm (Fig. 9.1a). They are regularly occurring along with a cohort of

Table 9.3 Absolute and relative fecundity (calculated in relation to weight) in developing females of the Antarctic silverfish collected in various Antarctic regions

Region	n	size range (cm)	OD (μm)	F_{abs} range	F_{abs} mean ± σ	F_{rel} range	F_{rel} mean ± σ	Refs.
EA (MS)	30	15.4–25.6	450	4315–17,774	7499 ± 2868	67.7–156.8	124.9 ± 4.4	[1]
AP (CI)	12	n.a.	400	2953–11,613	6818 ± 1968	78–193	136 ± 39	[2]
AP (MB)	12	n.a.	400	3637–11,492	6700 ± 1934	108–189	157 ± 45	[2]
AP (JI)	2	n.a.	400	10,043–10,174	10,109 ± 7148	119–171	145 ± 103	[2]
RS	25	13–19	460	2360–6700	4939 ± 1289	65.8–188.4	111.3 ± 27.8	[3]

n sample size, *OD* maturing oocyte minimum diameter, *EA* East Antarctica, *MS* Mawson Sea, *AP* Antarctic Peninsula, *CI* Charcot Island, *MB* Marguerite Bay, *JI* Joinville Island, *RS* Ross Sea, *n.a.* not available. References: [1] Gerasimchuk (1987b); [2] La Mesa et al. (2015b); [3] Ghigliotti et al. (2017)

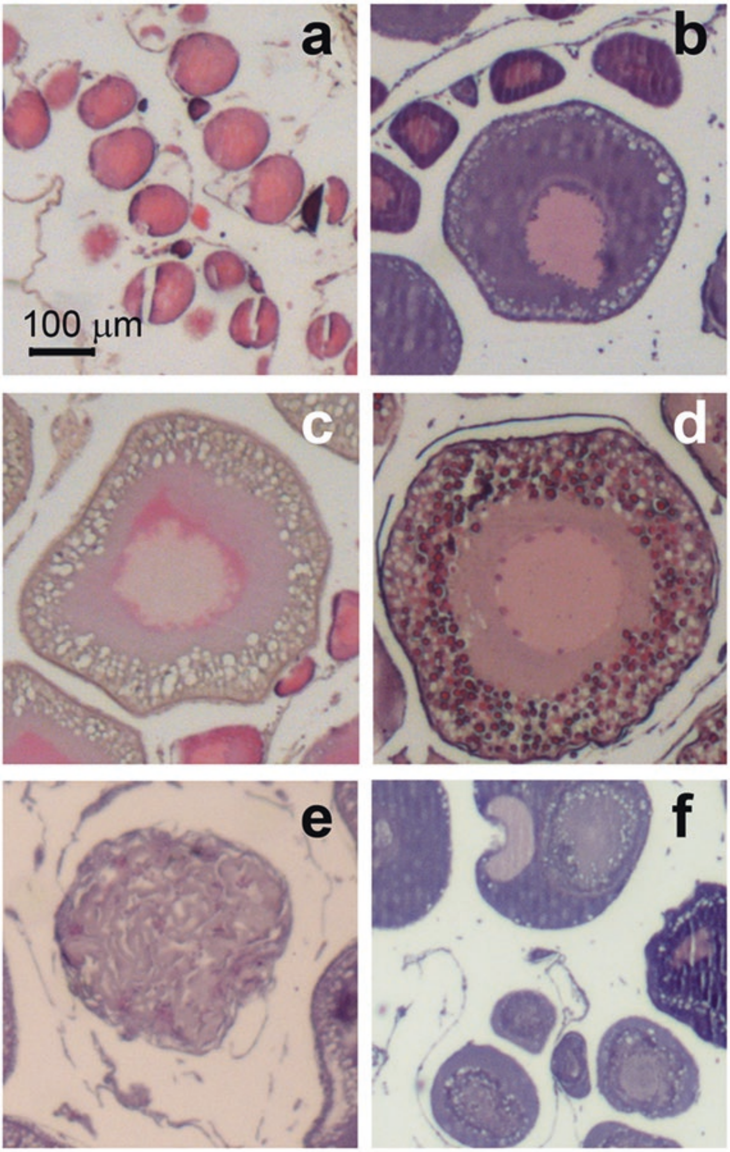

Fig. 9.1 Antarctic silverfish ovary. Cross sections of regular and reabsorbing follicles, hematoxylin-eosin stained: primary growth oocytes (**a**), initial alveolus oocyte (**b**), cortical alveolus stage oocyte (**c**), vitellogenic oocyte (**d**), post-ovulatory follicle (**e**), alpha atretic follicles (**f**). Scale bar = 100 µm

oocytes in various stages of trophoplasmatic growth. Three distinct stages of vitellogenic cells have been observed: initial alveolus (IA), cortical alveolus (CA), and vitellogenic (Vtg). The cells are round with a thin acidophilic layer at the periphery of the cytoplasm (the future zona radiata) beneath the follicle. The nucleus is spherical in the IA cells (Fig. 9.1b), and becomes irregularly shaped, with niches along its wall, in the CA (Fig. 9.1c) and Vtg (Fig. 9.1d) cells. A large number of basophilic nucleoli are accumulated at the periphery of the nucleus; small grainy basophilic, not marginated, nucleoli are sometimes interspersed in the nucleoplasm or circularly displaced around the central area of the nucleus. Vesicles start to be accumulated at the periphery of the cytoplasm, in a few rows (IA), many rows (CA) or multiple rows occupying almost the entire cytoplasm (Vtg). In the vitellogenic oocytes, yolk granules start to be deposited from the periphery of the oocyte toward the centrally located nucleus.

In January and February post ovulatory follicles (POFs), reaching 1600–1800 µm in size, were occasionally observed in the ovaries (Faleeva and Gerasimchuk 1990; Ghigliotti et al. 2017). They are clearly recognizable as having completely homogenized yolk, reduced lumen, convoluted shape and deep folded membrane (Fig. 9.1e).

The presence of developing follicles undergoing resorption (atretic follicles) is reported from the majority of females exhibiting maturing gonads from East Antarctica (Faleeva and Gerasimchuk 1990), a few females from the Antarctic Peninsula (La Mesa et al. 2015a), and a large number of maturing females from the Ross Sea Region (Ghigliotti et al. 2017). In most cases, the atretic process is reported to be in its initial phase (alpha atresia): oocytes shrinking in size, distorted follicles, disorganization of the cytoplasm in the oocyte, fragmentation of the chorion with cytoplasm flowing out, deformation and sometimes dissolution of the nucleus are among the most commonly described features (Fig. 9.1f).

9.3 Skipped Spawning: A Reproductive Strategy in the Antarctic Silverfish?

Field observations to be conducted year-round close to the Antarctic continent are still extremely difficult, dangerous, and cost-expensive. In particular, winter investigations suffer from these constraints. The limitations in mind, the available information nevertheless allows to develop a hypothesis with respect to the reproductive strategy which is probably followed by Antarctic silverfish.

Spawning is likely to occur in austral winter and early spring (July to end of August, beginning of September). This hypothesis is supported by the fact that both male and female gonads are developing but still far from spawning in late summer. The presence of newly hatched larvae in November (e.g. Hubold 1984; Vacchi et al. 2012) provides additional support for winter spawning of the Antarctic silverfish. The presence of large numbers of atretic follicles, also known as mass ovarian atresia, in the months leading up to spawning suggest that Antarctic silverfish are able to skip the process of gonad maturation when unfavorable living conditions are encountered. This may be interpreted as a tactic in order not to jeopardize survival of the fish.

A number of observations in recent years suggest that in other Antarctic fish species, such as mackerel icefish at South Georgia, 10–20% of the fish do not spawn each year. In years when feeding conditions were poor such as in those years when few krill was transported to South Georgia, up to 60% of mackerel icefish are able to interrupt the maturation process of the ovaries in order to save energy to sustain their living (Kock and Everson 2003). Skip spawning has been hypothesized for a number of Patagonian, Sub-Antarctic, and Antarctic species, Patagonian toothfish *Dissostichus eleginoides* (Arana 2009), the Antarctic toothfish *D. mawsoni* (Parker and Grimes 2010), the blackfin icefish *Chaenocephalus aceratus* (Vanella et al. 2005), the mackerel icefish *Champsocephalus gunnari* (Kock and Kellermann 1991; Kock and Everson 2003), and the pike icefish *C. esox* (Calvo et al. 1999).

Over evolutionary time, skipped spawning occasionally enacted when unfavorable environmental and physiological conditions prevail, can be interpreted as a manifestation of phenotypic plasticity in a species, in a wider adaptive sense. In other words, the capability to skip spawning, demonstrated at individual level, can be viewed as a facet of the overall specific reproductive strategy influencing the reproductive potential of fish populations and thus enhancing the species fitness (Jorgensen et al. 2006; Rideout and Tomkiewicz 2011; Shaw and Levin 2011).

The Antarctic silverfish is suggested to perform energy costly spawning migrations from open waters to ice-laden coastal waters where they were born or where environmental conditions are similar to those experienced at the larval stage following a homing-behaviour (Koubbi et al. 2011). In such a scenario, the capability to down-regulate the oocytes development through follicular atresia would reduce individual reproductive investment during breeding migration, at annual scale, but would result in a long-term adaptive advantage for the populations (Ghigliotti et al. 2017).

9.4 Reproduction Areas: Evidences and Hypotheses

There is sufficient evidence now to support the hypothesis that Antarctic silverfish reproduction occurs in coastal areas along major continental ice shelves (e.g. Faleeva and Gerasimchuk 1990; Eastman 1993; Hubold 1990; Kellermann 1987; La Mesa et al. 2010; Moline et al. 2008; Vacchi et al. 2012). However, running ripe females and males have never been sampled. Nevertheless, information is available on known and potential nursery areas of early larvae. They can serve as a proxy for the location of spawning grounds. In its wider sense, the term “nursery area” is used to define those regions or habitat where larvae, post-larvae and early juveniles of a given species occur and reside in significant amounts, with a substantial potential to contribute to the renewal of the adult fish population (Beck et al. 2001). Given the diversity in the life histories and developing times of the various species, a nursery area in its wide definition does not necessarily coincide with the place where reproduction occurs (Harden-Jones 1968). Being Antarctic fish characterized by a protracted larval development, in order to limit vagueness we will use the term “nursery area” in its strict sense, considering nursery grounds only areas where larvae up to 25 mm SL (0+ age class) have been recorded. Records of larger larvae, post-larvae, and juveniles, although important for reconstructing the life history of the Antarctic silverfish, have been excluded from our analysis because of the high spatial dispersal of these stages (La Mesa et al. 2010).

Early stages of silverfish, namely embryonated eggs or 0+ larvae (up to 25 mm SL), have been recorded in various locations around the Antarctic continent. In order to attempt a rough quantitative comparison among localities, the abundance of early life stages of Antarctic silverfish available in the scientific literature are ranked into four categories (see Table 9.4 and pertaining legend). By coupling the presence

Table 9.4 *Pleuragramma antarctica,* hatching and nursery areas along the Antarctic coasts

Region locality	Typology	Life stage (SL)	Period	Abundance	References
Ross Sea					
Terra Nova Bay	HA NG	Eggs & larvae (mean 9.3 mm)	Sep., Nov., early Dec.	++++	Vacchi et al. (2004), (2012), Guidetti et al. (2015), and Ghigliotti et al. (2015)
Terra Nova Bay (North side)	NG	Larvae 0+ (mean 13.9 mm)	Jan., Feb.	++++	Guglielmo et al. (1998) and Granata et al. (2000)
McMurdo Sound	LNG	Larvae 0+ (18–25 mm)	Oct., Nov.	+++	Outram (2000)
McMurdo Sound	ID	Larvae 0+ (mean 8.9 mm)	Nov. – Jan.	++	DeWitt and Tyler (1960)
McMurdo Sound	ID	Larvae 0+ (mean 14 mm)	18–21 Feb.	++	Hopkins (1987)
Ross Island	ID	Larvae 0+ (6–7 mm – 15–19 mm)	14 Dec. – 21 Feb.	++	Regan (1916)
Bay of Whales	LNG	Larvae 0+ (mean 10 mm)	mid Dec. – Mid Jan.	+	Biggs (1982)
Bay of Whales	LNG	Larvae 0+ (mean 9.8 mm)	Mar.	+	Caccavo et al. (2015), Brooks and Goetz (2014)
D'Urville Sea					
Pierre Lejay Bay	NG	Larvae 0+ (mean 17.3 mm)	Jan. – early Feb.	++++	Koubbi et al. (1997)
MGT & Commonwealth Bay	NG	Larvae 0+ (mean 13.8 mm)	Jan.	++++	Koubbi et al. (2011)
Davis Sea					
Gauss Station (Wilhelm II coast)	LNG	Larvae 0+ (20 mm)^a	22 Nov. – 01 Dec.	++++	Pappenheim (1912)

(continued)

Table 9.4 (continued)

Region locality	Typology	Life stage (SL)	Period	Abundance	References
Cosmonauts and Cooperation Seas					
Prydz Bay	NG	Larvae 0+ (mean 15 mm)	Jan. – Feb.	++++	Williams (1991)
Cosmonauts Sea and Prydz Bay	?	Larvae 0+ (18 mm)	Jan. – Mar.	+	Van de Putte et al. (2010)
Weddell Sea					
Vestkapp (Eastern Weddell Sea)	LHA	Hatched larvae	mid Nov.	unrep.	Hubold (1990)
FIS (Vahsel and Gould Bays)	NG	Larvae 0+ (8–25 mm)	end Jan. – early Mar.	++++	Keller (1983) and Hubold (1984)
R-LIS (Camp Norway – Halley Bay)	NG	Larvae 0+ (8–16 mm)	Jan.	++++	Hubold (1985) and White and Piatkowski (1993)
Antarctic Peninsula					
Tip AP-North West Weddell Sea	LHA		December	unrep.	Kellermann (1986) and La Mesa et al. (2015b)
S-W AP-North Bellinghausen Sea	LHA			unrep.	Kellermann (1986)
Bransfield Straits	LNG	Larvae 0+ (means 15.9–20.2 mm)	Jan. – Feb.	++	Kellermann (1986) and Sinque et al. (1986)
Bransfield Straits	LNG	Larvae 0+ (17.7 to 26.7 mm)	26 Feb. – 3 Mar.	++	Jones et al. (2014) and La Mesa et al. (2015b)
Bransfield Strait-Marguerite Bay	LNG	Larvae 0+ (15.0–19.8 mm)[a]	early Jan. – mid Feb.	+++	Ross et al. (2014)
Gerlache Strait	LNG	Larvae 0+ (16.8–23.4 mm)	19 Jan. – 15 Feb.	++	Morales-Nin et al. (1995)
Marguerite Bay	LNG	Larvae 0+ (9–13 mm)	Dec.	++	Outram (2000)

Localities are grouped by region. Acronyms have occasionally been used to make the table more easily readable: *MGT* Mertz Glacier Tongue, *FIS* Filchner Ice Shelf, *R-LIS* Reeser-Larsen Ice Shelves, *AP* Antarctic Peninsula, *HA* Hatching Area, *LHA* Likely Hatching Area, *NG* Nursery Ground, *LNG* Likely Nursery Ground, *ID* Insufficient Data to draw any hypothesis, *SL* Standard Length. Abundance of Antarctic silverfish specimens have been expressed as follows: + = sporadic occurrence (<10), ++ = moderate occurrence (10–100), +++ = high occurrence (101–1000), ++++ very high occurrence (>1000); unrep = abundance not reported in the paper

[a] Size range referred to the Total Length (TL) not Standard Length

of the various Antarctic silverfish early stages and their abundance, each of the locations has been assigned to one of the following typology: (i) Hatching Area (HA, area where hatching eggs have been recorded), (ii) Likely Hatching Area (LHA, area in which eggs have never been found but just hatched larvae have been found abundant), (iii) Nursery Grounds (NG, area where early larval stages are occurring in large or very large numbers) and (iv) Likely Nursery Grounds (LNG, where silverfish larvae up to 25 mm SL were recorded in limited amount).

Terra Nova Bay (TNB), in the Ross Sea, is the only area from where embryonated eggs and newly hatched larvae have been recorded. In TNB, Antarctic silverfish embryonated eggs have been found floating in large quantities among platelet ice under the sea-ice in September (Ghigliotti et al. 2015). Mass hatching has directly been observed in November (Vacchi et al. 2004, 2012; Guidetti et al. 2015). In the same areas, early larvae (7–9 mm SL) have been recorded in abundance in the following summer months (Guglielmo et al. 1998; Granata et al. 2000). This makes TNB both a hatching area (HA) and a nursery ground (NG) and strongly supports the notion that mass spawning occurs in the northern part of the Ross Sea. The finding, during several annual surveys, of adult silverfish remains trapped in the sea-ice in the TNB nursery area is a further strong indication for spawning in the northern Ross Sea (Vacchi et al. 2012). Alternative hypotheses are that eggs are spawned close to the sea-ice and remain in a challenging environment for all the embryonic development period, or dispatched in deeper ice-free water and then rise in the water column later on owing to their buoyancy and local hydrodynamic flows (Vacchi et al. 2012).

Although lower in numbers, larvae had been collected on several occasions in southern parts of the Ross Sea. *P. antarctica* early larvae were collected at Ross Island during the "Discovery" and "Terra Nova" Expeditions (Regan 1916). Early larvae were collected in McMurdo Sound during spring and summer months (DeWitt and Tyler 1960; Hopkins 1987; Outram 2000). Recently, several newly-hatched larvae, which were genetically assigned to *Pleuragramma,* were sampled in mid-March in the Bay of Whales, eastern Ross Sea (Brooks and Goetz 2014; Caccavo et al. 2015). This finding, together with the occurrence of a number of 10 mm long larvae, previously reported by Biggs (1982) in the same area, strongly suggests the potential role of the Bay of Whales in the eastern Ross Sea as a nursery ground for this species.

In the D'Urville Sea region, annual surveys carried out from 1996 to 2010 (Koubbi et al. 1997, 2009, 2011) provided data to identify a second nursery ground for *Pleuragramma*. The Terre Adélie coastal area (Pierre Lejay Bay) and seabed depression adjacent to the Mertz Glacier Tongue and Commonwealth Bay hosted *P. antarctica* larvae in large numbers with mean size of 17.3 and 13.8 mm SL, respectively. At Pierre Lejay Bay a dense aggregation of Antarctic silverfish larvae, extending about 1.8 by 1.5 nautical miles, was noticed. Such an aggregation was made of at least 17/m^3 individuals, while densities in the remainder of the study area were on average lower than one individual/m^3 (Koubbi et al. 1997).

In other regions of the Indian Sector, an interesting record on the mass occurrence of early-stage *Pleuragramma* in Wilhelm II coast (Davis Sea) came from the Heroic Age of the Antarctic Expeditions around the turn to the Twentieth century. From 22 November to 1 December 1902 more than one thousand *Pleuragramma* larvae of about 20 mm TL were taken by fine-meshed tow-nets at the German Gauss Station (Pappenheim 1912). These large density suggest the presence of another nursery ground in the Davis Sea.

A survey carried 1991 in the Prydz Bay region (Cooperation Sea) identified another nursery ground. In 93 near-surface tows (30–50 m depth) of 30 min duration with the International Young Gadoid Pelagic Trawl (IYGPT, *P. antarctica* constituted the most important part of the catch. Up to 9100 individuals/30 min haul occurred in the central part of the bay. Most of the fishes were age class I juveniles of 45 mm SL but a noticeable part of the catch was also represented by *Pleuragramma* larvae of 15 mm SL (Williams 1991). A recent extensive survey in the pelagic zone of the Cosmonauts Sea and Prydz Bay (Van de Putte et al. 2010) confirmed the occurrence of Antarctic silverfish fingerlings of age class 2+ (54–95 mm SL) and larvae of age class 0+ in coastal waters of Prydz Bay, although in low numbers.

The Weddell Sea region has been studied in some detail for the presence and abundance of ichthyonekton since 1979/1980 (Hempel et al. 1983; Kellermann 1986; Hubold and Ekau 1987; Ekau et al. 1987; Piatkowski 1987; Boysen-Ennen and Piatkowski 1988; Hubold 1990; Piatkowski et al. 1990; White and Piatkowski 1993). Larval *P. antarctica* typically predominated shelf waters of the southern and southeastern Weddell Sea (Keller 1983; Hubold 1985, 1990) representing some 90% of the fish larvae in summer (Hubold 1990; Piatkowski et al. 1990). *P.antarctica* larvae ranging 8–16 mm SL in size, were aggregating in the upper 25–50 m of the water column over the continental slope and innershelf depressions located in the southern Weddell Sea off the Filchner Ice Shelf and in the south eastern part of Weddell Sea in January–February (Hubold 1984, 1985). The density of larvae peaked at 3000–4000 individuals/1000 m^3 (Keller 1983) and supports the hypothesis that *P. antarctica* hatched near Vestkapp by mid-November (Hubold 1990), making this zone a likely hatching area (LHA) for the species.

A large number of ichthyoplankton surveys were performed in the western Antarctic Peninsula (wAP) since 1975/1976 (Kellermann 1986; Kellermann and Schadwinkel 1991, Kellermann and Kock 1988; Loeb 1991; Morales-Nin et al. 1995; Donnelly and Torres 2008; Jones et al. 2014; Ross et al. 2014; Parker et al. 2015; Mintenbeck and Torres 2017). Typically, the number of fish larvae up to 25 mm SL was low, ranging from zero to about one hundred individuals in the catches (higher numbers of more developed postlarvae and juveniles were routinely collected).

At least, three sites of wAP (Bransfield Strait, Gerlache Strait, and Marguerite Bay) can be considered as LNGs. In these wAP areas, the larval density is generally 10 times less than in the Weddell Sea. A substantial decline has occurred in the northernmost location of larvae after 1999–2000 (Ross et al. 2014). Despite the occurrence of substantial numbers of larvae, it remains unclear so far if Antarctic silverfish spawn successfully in the wAP region. Recruitment of *Pleuragramma* to the waters of wAP shelf has been attributed to larval dispersal from spawning occurring in the western Weddell Sea (Kellermann 1986; La Mesa et al. 2015b) and the Bellinghausen Sea, southwest of the wAP (Kellermann and Schadwinkel 1991). A LHA could be located in the northwestern Weddell Sea. Larvae originating from this area could be transported from the Weddell Sea via the Weddell gyre/Antarctic Coastal Current as it flows through the Antarctic Sound and around the tip of the

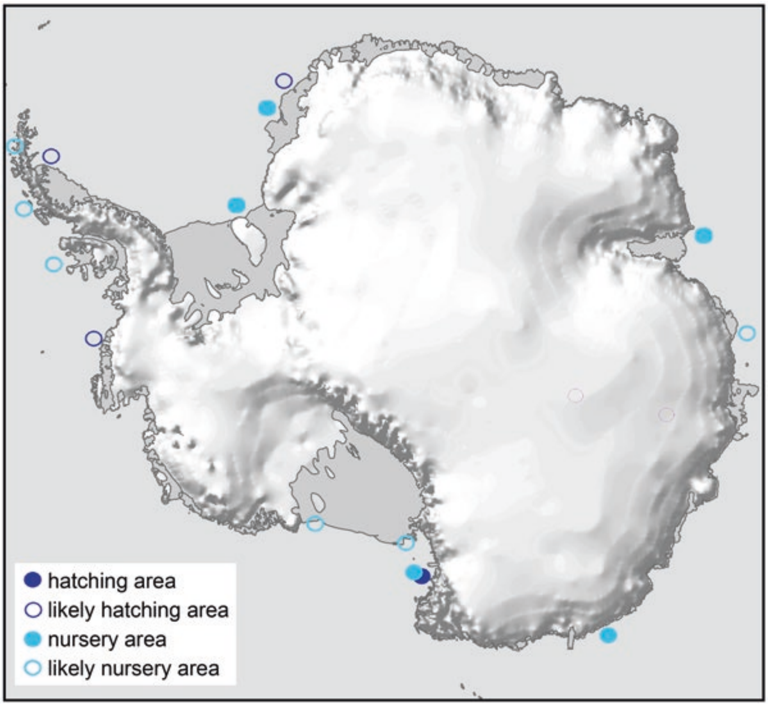

Fig. 9.2 *Pleuragramma antarctica* actual hatching areas, likely hatching areas, nursery areas and likely nursery areas are mapped

Antarctic Peninsula into the eastern Bransfield Strait (La Mesa et al. 2015b). Larvae originating from the other LHAs in the Bellinghausen Sea south of the Peninsula could be drifted northeast by the Antarctic Circumpolar Current merging with the general northeasterly flow at the shelf break along the Peninsula (Mintenbeck and Torres 2017).

The resulting distribution of hatching areas, likely hatching areas, nursery areas and likely nursery areas along the coasts of Antarctica is shown in Fig. 9.2.

Hubold (1984) related the retention of developing eggs and young stages in the Weddell Sea to the presence of polynyas that are known to act as hydrographic engines, and that are widespread along the Antarctic coast (e.g. Kern 2009). However, no evidences are available to date that might confirm or reject this interesting hypothesis.

9.5 Conclusive Considerations

Scientific knowledge on the reproduction cycle of the Antarctic silverfish has improved in the past 30 years, with most of the information originating from the Ross Sea. In Fig. 9.3 the year-round events characterizing the Antarctic silverfish reproduction in the Ross Sea are shown along a timeline.

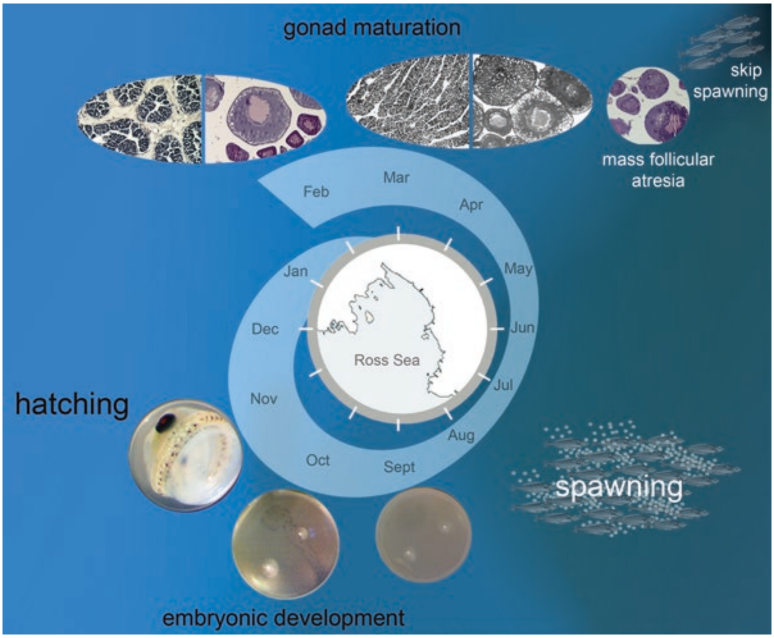

Fig. 9.3 Diagrammatic representation of the year-round events related to the Antarctic silverfish reproduction in the Ross Sea summarizing what reported in current literature. Pictures correspond to actual data, drawings stand for events whose timing or happening is indirectly deduced

Besides illustrating actual information, Fig. 9.3 also highlights areas where knowledge are still lacking. Indeed, the time of spawning is still approximate, but it is likely to occur from July to September. Moreover, the occurrence of small larvae as late as February–March may suggest that spawning is extending over a comparatively long period of several months. Eggs are pelagic but if they are released in surface waters or close to the sea-floor from where they may rise later is still unknown. Logistic constraints have historically limited year-round field activity, however future scenarios in this regard are encouraging.

For instance, newly established permanent Antarctic Stations are expected to provide new opportunities for Antarctic silverfish winter sampling, such as the new Korean Jang Bogo Station in the Ross Sea, in close vicinity of the Silverfish Bay – Cape Washington hatching area, that already offered the possibility to extend backwards to September the sampling of embryonated eggs (Ghigliotti et al. 2015).

In addition, advances in the logistic capabilities of research vessels, by allowing to operate year-round in ice-covered waters, could further improve both a geographical and temporal extension of researches focusing on the Antarctic silverfish life cycle and reproduction.

New tools for non-invasive, spatial and temporal extensive surveys have been developed in recent years improving researches by visual and acoustic methods

(Azzali et al. 2010; O'Driscoll et al. 2011; Fox 2015; Guidetti et al. 2015). The definition of Antarctic silverfish adults acoustic target strength (Azzali et al. 2010), and the improvement of acoustic technology in general (reviewed in O'Driscoll et al. 2017), provides new possibilities for recording silverfish presence, abundance and movements over a wide time frame.

On the whole, the availability of new infrastructure for all-year-round research in the Southern Ocean, progress in remote sensing and image processing technology offer the possibility to collect data in areas and periods previously unattainable, laying the bases to step forward in the knowledge of the Antarctic silverfish reproductive strategies.

Acknowledgments This work is also intended as a tribute to the memory of Tatiana I. Faleeva who greatly contributed to the knowledge on the reproductive biology of the Antarctic silverfish.

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