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Critical Literature Review
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The ecological importance of Antarctic Silverfish

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Abstract

The Antarctic marine ecosystem is very unique. It supports a fast range of species ranging from phytoplankton to blue whales. Many of these species are endemic, including the Antarctic silverfish *Pleuragramma antarctic*um which is abundant throughout the Antarctic marine ecosystem.

P. antarcticum are the only truly pelagic fish in the Antarctic waters, and have an interesting life cycle that moves through the water column. Because of its high abundance and wide distribution, it is a key species in the in the Antarctic food web.

This review aims to understand what the ecological importance of Antarctic silverfish and the role that they play in the Antarctic food web. Leading on from this it is important to understand what the potential threats to their population are. Such as climate change which threatens vulnerable life stages habitats and fishing which does not impact *P. antarcticum* directly but indirectly through its predators and prey species.

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Introduction

The Southern Ocean is very important to the Earth Systems (Constable et al., 2014; Turner et al., 2009) and the Antarctic marine ecosystem within the Southern Ocean boundaries is very unique. It supports an array of species ranging from phytoplankton, fish, birds and marine mammals, many of these species are endemic to Antarctic. The fish fauna in the Antarctic waters is dominated by Notothenioidei (Eastman, 2005; Turner et al., 2009), the Antarctic silverfish *Pleuragramma antarcticum* (Boulenger, 1902) is part of this suborder.

P. antarcticum is abundant throughout the whole Antarctic marine system. It plays an important role in the Antarctic food web, as it is the main channel of primary production to the upper trophic levels (Pinkerton, Bradford-Grieve, & Hanchet, 2010). *P. antarcticum* are the only truly pelagic fish in the Antarctic waters, and have an interesting life cycle that moves through the water column (Wöhrmann, Hagen, & Kunzmann, 1997). They are the only species of Nototheniidae in Antarctic whose full cycle of life stages take place in the water column (Vacchi, La Mesa, Dalu, & Macdonald, 2004).

Because of its high abundance and wide distribution, *P. antarcticum* is a key species in the Antarctic food web, linking the plankton to the top predators. It is of interest to understand the ecological importance of *P. antarcticum* and the role they play in the Antarctic food web, and what the potential threats they face due to human induced pressures such as climate change and commercial fishing. As changes to Antarctica's environment, from climate change and fishing, could have significant impacts on *P. antarcticum* as their early life stages are closely linked to sea ice (La Mesa & Eastman, 2012). Due to the trophic importance of *P. antarcticum* this could have significant impacts on the connecting food chain.

Antarctic Silverfish

The majority of fish in Antarctic waters are part of the suborder Nototheniodei, which inhabit a range of niches (Wöhrmann et al., 1997) and provide one of the best examples of adaptive radiation by a marine vertebrate group (Turner et al., 2009). *P. antarcticum* are one of few truly pelagic fish in Antarctic waters (Wöhrmann et al., 1997), having evolved from a benthic origin. They inhabit the high Antarctic shelf and are the most abundant pelagic fish species, particularly in the Ross Sea (Pinkerton et al., 2013).

The high abundance and wide distribution make *P. antarcticum* a key species in the Antarctic marine ecosystem and food web (La Mesa & Eastman, 2012). The current stock status of the total population is unknown.

P. antarcticum have been commercially fished in the 1980's by Soviet Union vessels (Kock, 2007). Since this period there has been no commercial exploitation. Currently there is no interest in restarting a commercial fishery for *P. antarcticum*.

Habitat

P. antarcticum inhabit a circumpolar distribution around the whole of Antarctic waters, both in open waters and pack ice ranging from the surface down to 700 m (La Mesa & Eastman, 2012; Moline et al., 2008). Their habitat is characterised by constant low temperatures and high seasonal variation in terms of ice cover, light availability and primary production.

They form loose shoals (Fuiman, Davis, & Williams, 2002) and in the light months adult *P. antarcticum* display diel vertical migration, moving into deeper water during the day. This behavioural adaption is interesting as originating from a benthic origins this behaviour is not needed. It is thought this behaviour is exhibited as a predator avoidance tactic (La Mesa & Eastman, 2012; Robison, 2003).

The different life stages utilise separate vertical section of the water. Eggs and early larvae are found at the surface, while species between the lengths of 3.5 cm to 11 cm are caught from the surface to 400 m, and the largest individuals (10 cm +) are found in waters deeper than 400 m (La Mesa & Eastman, 2012).

Adaptations to the Antarctic environment

The suborder Nototheniodei are primarily benthic species. *P. antarcticum* evolved from a benthic dwelling ancestor and has evolved to specialise in the Antarctic pelagic waters. Adapting to the pelagic zone meant that *P. antarcticum* had to utilise the adaptations associated with Notothenioids with more specialised adaptations (Wöhrmann et al., 1997). The pelagic waters were largely uninhabited so the evolution to this would have provided *P. antarcticum* with an abundant food sources with little competition (La Mesa & Eastman, 2012).

To effectively inhabit the pelagic waters *P. antarcticum* had to develop a range of ecological, biochemical and physiological adaptations (La Mesa & Eastman, 2012), such as buoyancy. *P. antarcticum* are close to neutral buoyancy, despite not having a swim bladder. This is achieved through a number of ways including reduced skeletal ossification and retention of cartilage and accumulation of lipids (La Mesa & Eastman, 2012). *P. antarcticum* are very lipid rich, the amount of lipids increases with length of individuals. It has been hypothesised that the lipids sacs are a buoyancy mechanism rather than for metabolic use due to the low cell membrane surface area compared to the volume of the sacs (Eastman & DeVries, 1989).

To look at, it would be expected that *P. antarcticum* would have a similar activity levels to other species of similar body morphology, such as herrings. These two species demonstrate convergent evolution due to the similar body morphology (La Mesa & Eastman, 2012), but have very different lifestyles. *P. antarcticum* have many physiological features to suggest limited activity, such as a small amount of red muscle compared to other aerobic species.

The neutral buoyancy allows the *P. antarcticum* to use a ‘sit and wait’ feeding style, which is a similar feeding style to benthic species and allows them to conserve energy (La Mesa & Eastman, 2012; Wöhrmann et al., 1997). La Mesa & Eastman (2012) described *P. antarcticum* as an “ecological and physiological paradox, being a pelagic water column species with an inactive energy-conserving lifestyle” (La Mesa & Eastman, 2012, p. 255).

Due to the extreme environmental conditions *P. antarcticum* live in, they have developed a number of biochemical and physiological adaptations to withstand the cold waters (Wöhrmann et al., 1997). To survive in the freezing waters of Antarctica P. antarcticum, like many other fish species, have antifreeze glycopeptides, which protects *P. antarcticum* from the freezing water by lowering the freezing point of the body to below the freezing point for sea water (-1.9oC) (La Mesa & Eastman, 2012). Interestingly *P. antarcticum* also have a unique ‘*Pleuragramma* antifreeze glycopeptide’, which has a different carbohydrate and amino acid composition (Andreas Wöhrmann, 1995). The presence of the two antifreeze vary between life stages, with adults and post larvae having the highest concentrations as they inhabit the coldest waters (La Mesa & Eastman, 2012). And the early larval stages having very low levels of antifreeze as they utilise a barrier mechanism to prevent freezing (La Mesa & Eastman, 2012; Wöhrmann et al., 1997).

Life stages

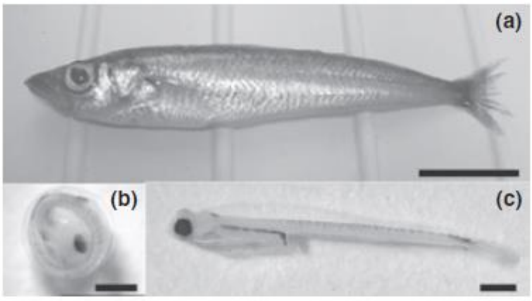

Figure 1: Antarctic silverfish in different life stages **a**) adult (scale= 50 mm), **b**) egg (scale= 1 mm), **c**) larvae (scale= 1 mm). Image from La Mesa & Eastman (2012).

All life stages take place in the pelagic zone which is very unique for a notothenioid fish, which are predominantly benthic (Vacchi et al., 2004). In winter adults migrate to inshore water to spawn (La Mesa & Eastman, 2012). It has been suggested that adults spawn upstream of the coastal currents, which allows larvae to be transported by these currents (Wöhrmann et al., 1997). The eggs produced are small (2 mm) and have a very high fecundity with females releasing 13,000 eggs (Wöhrmann et al., 1997). Compared to other Antarctic Notothenioids (apart from the Antarctic toothfish) *P. antarcticum* have the highest fecundity (La Mesa, Riginella, Mazzoldi, & Ashford, 2015).

Hatching areas are thought to occur in the coastal waters next to major continental ice shelves such as the Ross Sea and occurs between October and December (La Mesa & Eastman, 2012; Vacchi et al., 2004). The eggs are pelagic, and newly hatched larvae and eggs have been found under the sea-ice cover in the platelet ice in the Ross Sea (Vacchi et al., 2004). The eggs float under the sea ice, in the platelet ice which is thought to minimise predation (La Mesa et al., 2010; Vacchi et al., 2004). The reproductive cycle is closely linked with the seasonal zooplankton production.

Larvae hatch from November until December (Figure 1, c), with the yolk sac still attached to provide sufficient energy. As larvae grow into juveniles they are slowly transported to offshore waters which is where *P. antarcticum* start to differentiate through the water column and horizontally. This is thought to reduce cannibalism and competition for resources (La Mesa et al., 2010). The competition for food is also reduced by different life stages having different diets.

In the second year lipid deposits grow and juveniles recruit to the adult population between the ages of 3-5 years. They have slow growth rate which allows them to feed on mesozooplankton, and directs most the energy use into reproduction, antifreeze and lipid production (Hubold & Tomo, 1989). *P. antarcticum* reach sexual maturity around 7-9 years and can live until they are 21-35 years (Hubold & Tomo, 1989; Moline et al., 2008). The growth of *P. antarcticum* is one of the slowest known in marine fish (Hubold & Tomo, 1989).

Importance in the Antarctic food web

P. antarcticum play an important role in the Antarctic food chain, due to their abundance and circumpolar distribution. *P. antarcticum* demonstrate a wide predation plasticity and can switch between preferred prey species, with the main prey type being mesozooplankton. The preferred prey species changes between different locations and displays seasonal differences. La Mesa et al. (2010) found that Antarctic krill were the primary food source for *P. antarcticum* in the northern area of the Ross Sea, while ice krill were the primary food source for species living inside the Ross Sea.

The preferred prey species also varies during life stages, presumably due to the vertical separation of life stages, which reduces intra-specific competition. For example Pinkerton et al. (2013) found that post larval *P. antarcticum* in the Ross Sea fed predominantly on copepods, as did juveniles. For adults, copepods were a minor prey species in terms of mass, while fish were an important prey type which increased in importance with the length of P. antarcticum.

P. antarcticum are prey for a number of species including fish, marine mammals and birds in the Antarctic food chain (Pinkerton et al., 2013). In the Ross Sea where *P. antarcticum* make up 90% of the mid-water fish biomass (Smith, Ainley, & Cattaneo-Vietti, 2007), most top predators in this area feed on P. antarcticum. They are a prey species for skua, petrels, Adelie and Emperor penguins, Weddell seals, Antarctic toothfish and other fish, Minke whales and Orca (Smith et al., 2007). For example a study on Weddell seals found that *P. antarcticum* contributed between 70-100% of their diet (Burns, Trumble, Castellini, & Testa, 1998) and a study on a population of Emperor penguins found that *P. antarcticum* made up 95-100% of the fish component of their diet (Cherel & Kooyman, 1998).

Ainley et al. (2015) hypothesise that the predators such as whales and penguins regulate the prey (such as *P. antarcticum* and krill) vertical distribution and the abundance, which then reduces their impact on their prey species. This hypothesis is for the Ross Sea, where they describe the food chain as ‘wasp-waisted’ in that there is an abundance of top predators and primary production, but a relatively smaller abundance of mid-trophic level species such as P. antarcticum.

P. antarcticum are a critical trophic link in the Antarctic food chain and are considered a keystone species (Ghigliotti et al., 2016), creating a significant ecological importance to the Antarctic marine ecosystem. They channel the majority of primary production to the upper trophic levels. The high abundance of *P. antarcticum* significantly impact the species they are predating on. Many species that utilise *P. antarcticum* as a prey source heavily rely on it either year round or at certain times of the year. In the Ross Sea based on Pinkerton and Bradford-Grieve (2014) quantitative foodweb model, *P. antarcticum* had a high trophic importance in the Ross Sea ecosystem along with two other species types (mesozooplankton and small demersal fish). Due to the importance of *P. antarcticum* in the trophic system, research such as the impacts of climate change and other effects should be a priority (Pinkerton & Bradford-Grieve, 2014).

Potential future impacts to Antarctic Silverfish

Climate change

The environmental changes due to climate change in the Southern Ocean have been recorded in sea ice decline, temperature rise and ocean acidification (Flores et al., 2012). Casini et al. (2008) expressed that the impacts of climate change could have cascading effects from upper and lower trophic levels.

The effects of climate change on *P. antarcticum* will not be felt evenly throughout the Southern Ocean, and there has been significant regional variation in sea ice extent. The formation and duration of sea is dependent on the oceanic and climatic condition, these processes display annual variation and long term variation due to climate change. For example in the Ross Sea sea ice is increasing by 5% per decade, while in the west Antarctic Peninsular ice extent is decreasing by around 7% per decade (Kwok & Comiso, 2002; Turner et al., 2009). *P. antarcticum* early life stages are closely linked to the sea ice cover (Vacchi et al., 2004), which makes this vulnerable life stage very sensitive to the changes in sea ice extent and timing. The timing and extent of coastal polynyas of the Ross Sea and Weddell Sea could affect the abundance and size of *P. antarcticum* larvae (La Mesa et al., 2010; La Mesa & Eastman, 2012), as the reproductive cycle is linked to seasonal zooplankton production which is strongly influence by the timing and extent of coastal polynyas (La Mesa & Eastman, 2012).

The mid-waters of the Southern Ocean (to depths of 1000 m) have warmed more rapidly than other waters of similar depths around the world since the 1950's (Gille, 2002). Antarctic krill decline, as well as the decline of seabirds and seals has been linked to the warming of the Southern Ocean (Gille, 2002).The increased ocean temperatures will likely effects *P. antarcticum* as a polar species either directly it has adapted to low, stable temperatures or indirectly though the food chain, such as the changes to the abundance of Antarctic krill. Polar ecosystems are thought to be much slower to respond to environmental changes generally (Smith et al., 2007).

La Mesa et al. (2015) found during their study in the West Antarctic Peninsular that when sampling they were unable to find *P. antarcticum* in areas where they were historically abundant. They suggested that this population fragmentation was a result of rapid change in the shelf system, as the west Antarctic Peninsular has already experienced declines in sea ice and rapidly warming water. Due to the recent declines in *P. antarcticum* population, predators have replaced them with other fish species such as myctophids (Moline et al., 2008).

Climate change could impact *P. antarcticum* indirectly as well, through the food chain interactions. Phytoplankton are thought to change in abundance and composition of species which will impact on the whole Antarctic food web, as it relies on the abundance of primary production (Pinkerton & Bradford-Grieve, 2014). Phytoplankton have been reported in one study as a food source for early larvae but more research is needed to understand the importance of phytoplankton to *P. antarcticum* (Koubbi et al., 2007).

Climate change is likely to impact on *P. antarcticum* in a number of ways, however the resilience of *P. antarcticum* could be enhanced by having such a high fecundity.

Fisheries

Antarctic silverfish are not currently caught commercially (although have been in the past), but they are most likely indirectly effected by commercial fishing due to their food source (krill) and predators (toothfish) both being important fisheries.

The krill fishery catches have increased over recent years, this combined with krill being effected by climate change, are thought to have resulted in a population decrease (Flores et al., 2012). The decrease in the abundance of krill as a food source could negatively impact P. antarcticum, but due to the plasticity of feeding (mentioned earlier) the decrease in this prey species may not be as detrimental.

Antarctic toothfish are a top marine predator in the Antarctic marine food web. A significant decrease in Antarctic toothfish population could release *P. antarcticum* of a significant predator pressure. However, (Pinkerton & Bradford-Grieve, 2014) found that toothfish did not have a high trophic importance using their modelling system. So the top down effect on *P. antarcticum* may not be large.

The life histories of *P. antarcticum* (delayed sexual maturity, long life span, high mortality rates and low productivity) mean that any commercial harvesting needs very well managed, as this species would be very vulnerable to overfishing (La Mesa & Eastman, 2012). The importance in the food chain means that this species needs to be very well managed if there was ever a fisheries established.

Conclusion

P. antarcticum have adapted through stable environmental conditions to utilise the pelagic zone, which is unique for a species in the suborder Nototheniodei. The life stages of *P. antarcticum* are interesting due to vertical and horizontal separation of life stages. *P. antarcticum* play a very important role in the Antarctic marine ecosystem as they are vital part of the food web.

Due to the reliance on sea ice in the early vulnerable life stages (egg and larval stages) *P. antarcticum* are sensitive to changes in the sea ice cover and timing. The changes to sea ice due to climate change will affect these life stages. So far the changes to sea ice has not been consistent around Antarctica and it is likely that the affect to *P. antarcticum* will be variable.

Understanding the ecological change that will occur due to anthropogenic impacts on the Antarctic marine ecosystem is critical, as the Southern Ocean responds to climate change and the increased pressure from fisheries (krill and Antarctic toothfish). The future research needs to be focus on how *P. antarcticum* will be impacted from both these pressures, and what this will mean for the food web that they play such a vital role in. The actual stock status needs to be established, as without a population status it will make it very difficult to detect and prove population changes. Any changes in the abundance or distribution will likely have flow on effects to the species that depend on *P. antarcticum* as a food source, and the species that *P. antarcticum* predate on.

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