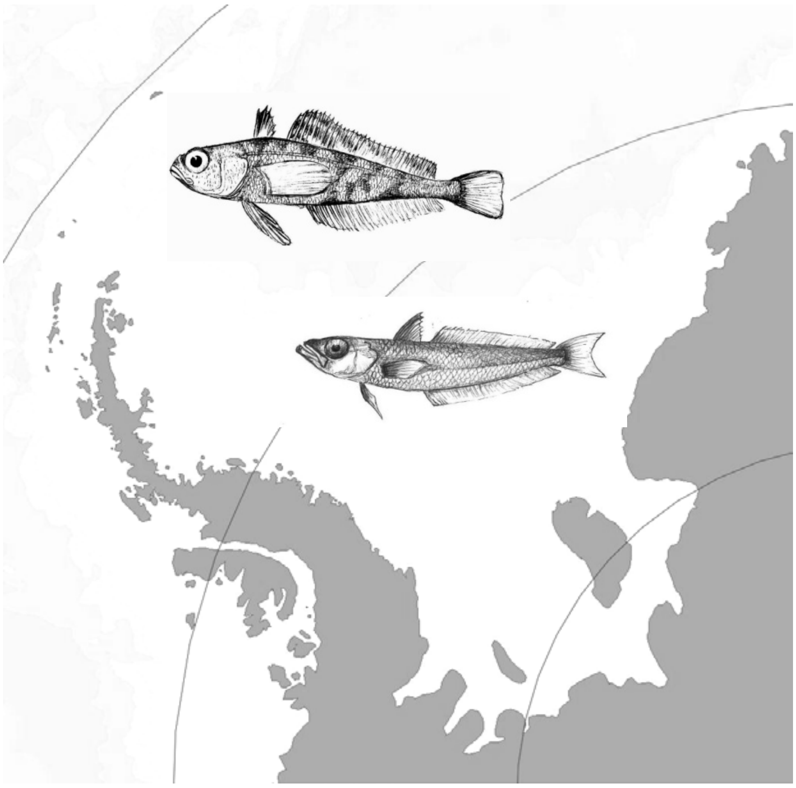
University of Applied Sciences Bremen
Alfred-Wegener Institute for Polar and Marine Research

MASTER THESIS

GROWTH PRODUCTION OF TWO NOTOTHENIOID FISH SPECIES FROM DIFFERENT GEOGRAPHICAL REGIONS OF THE ANTARCTICA



Submitted by Maj Wetjen

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supervised by:

Prof. Dr. Heiko Brunken (1st supervisor)

University of Applied Sciences Bremen

Dr. Rainer Knust (2nd supervisor)

Alfred-Wegener Institute for Polar and Marine Research

Growth production of two notothenioid fish species from different geographical regions of Antarctica

Wachstumsleistungen zweier antarktischer Fischarten aus unterschiedlichen Verbreitungsgebieten der Antarktis

Cover pictures

Map: Weddell Sea and Antarctic Peninsula: Ocean data view

Fish pictures: *Trematomus eulepidotus* (Nototheniodae): Maj Wetjen

Pleuragramma antarcticum (Nototheniodae): Maj Wetjen

ABBREVIATIONS

B	biomass
°C	degree Celsius
Cf	condition factor
cm	centimeter
DW	dry weight
e.g.	exempli gratia (for example)
et al.	et alii (and others)
g	gram
GSI	gonadosomatic index
HSI	hepatosomatic index
k	growth coefficient
kJ	kilojoule
kcal	kilocalories
KS-test	Kolmogorov–Smirnov test
$L\infty$	asymptotic length
L_{max}	maximum length
M	mortality
MCA	metabolic cold adaptation
n	number of individuals
P	production
PAGP	*Pleuragramma*-antifreeze-glycopeptide
R^2	coefficient of determination
SD	standard deviation
SL	standard length
t	time
t_0	time/age when length of fish is zero
TL	total length
t_0	time of hatching
VBGF	von Bertalanffy growth function
W_∞	asymptotic weight
WW	wet weight
WT	total weight
$ZW\infty$	mortality estimated by $W\infty$
$ZL\infty$	mortality estimated by $L\infty$
α	Greek alpha (significance level)
Φ	growth performance index

ABSTRACT

To date, the ecology and in particular mechanisms influencing the growth and the distribution of Antarctic fish are still poorly understood. This study provides data about the age and growth of two dominant notothenioid fish species: the pelagic keystone species *Pleuragramma antarcticum* and the benthopelagic species *Trematomus eulepidotus*. Fish were sampled from different geographical regions of the Antarctic waters during expeditions with the research vessel POLARSTERN in 2003/2004, 2011, and 2012. Age was determined by sagittal otolith increment analysis. By applying the von Bertalanffy growth formula, growth curves for both species from the different study sites of the Antarctica were generated in order to assess their growth performance. Analysis revealed a maximum age of 13 years for *P. antarcticum* and 19 years for *T. eulepidotous*. Both species had relatively slow growth with growth coefficients (*k*) of 0.16 – 0.25 for *P. antarcticum* and 0.11 – 0.23 for *T. eulepidotus* and neither grew especially large. Nevertheless, *T. eulepidotus* achieved larger maximum lengths than *P. antarcticum* overall. Both species had significantly higher growth rates and a better nutritional condition at lower latitudes of the South Shetland Islands compared to the more southern areas of the eastern Weddell Sea. In this study, growth performances of the two species from different geographical areas are presented and compared both intra- and interspecifically. After Ccomparing these data, it is evident that both species grow faster at higher annual mean temperatures. Furthermore, fast growth coefficients were associated with lower maximum ages and therefore, seem to reduce the longevity of fish.

ZUSAMMENFASSUNG

Kenntnisse über die Ökologie, vor allem im Bereich der Wachstumsleistungen und der Verbreitung von antarktischen Fischen sind derzeit noch sehr rar. Diese Arbeit liefert Informationen über das Wachstum zweier antarktischer Fischarten, zum einen von der pelagisch lebenden Art *Pleuragramma antarcticum* und zum anderen von der bentho-pelagischen Art *Trematomus eulepidotus*. Die Individuen wurden während der Expeditionen mit dem Forschungsschiff POLARSTERN in den Jahren 2003/2004, 2011 und 2012 in unterschiedlichen Regionen der antarktischen Gewässer gefangen. Das Alter der Fische wurde zunächst mittels der sagittalen Otolithen bestimmt. Anschließend wurden anhand der Alters- und Längendaten für die unterschiedlichen Untersuchungsgebiete von Bertalanffy Wachstumskurven erstellt. Unter allen untersuchten Individuen konnte für *P. antarcticum* ein maximales Alter von 13 Jahren nachgewiesen werden. *T. eulepidotus* erreichte ein höheres maximales Alter von 19 Jahren. Beide Arten wiesen ein relativ langsames Wachstum auf. Die ermittelten Wachstumskoeffizienten lagen innerhalb aller Untersuchungsgebiete bei k = 0.16 – 0.25 für *P. antarcticum* und k = 0.11 – 0.23 für *T. eulepidotus*. Auch das Längenwachstum ist eher gering mit einer Maximallänge von unter 30 cm für beide Arten. Dennoch erreicht *T. eulepidotus* insgesamt größere Maximallängen als *P. antarcticum*. Beide Arten zeigten ein schnelleres Wachstum und eine bessere Kondition in den nördlicheren Gebieten bei den Südlichen Shetlandinseln als in den höheren Breiten des östlichen Weddell Meeres. Diese Arbeit gibt Aufschluss über die Wachstumsleistungen beider untersuchten Arten in unterschiedlichen geographischen Gebieten der Antarktis. Die ermittelten Wachstumsleistungen wurden sowohl intraspezifisch innerhalb der unterschiedlichen Gebiete als auch interspezifisch zwischen den beiden Arten analysiert und verglichen. Die Datenanalyse hat gezeigt, dass der Wachstumskoeffizient (k) beider Arten von der Umgebungstemperatur beeinflusst wird. Je höher die Temperatur, desto schneller das Wachstum. Schnelleres Wachstum geht aber wiederum mit einem geringeren Maximalalter einher. Ein schnelleres Wachstum scheint demnach die Langlebigkeit der Fische herabzusetzen.

CONTENTS

1 INTRODUCTION

Fish play a major role in the Antarctic ecosystems. The fish fauna of the Antarctic waters is, with respect to other marine systems of lower latitudes, predominantly populated by demersal organisms while the pelagic zone is only sparsely inhibited. Despite constant environmental conditions, different regions of the Antarctic waters show differences in their fish fauna (SCHWARZBACH 1988). Fish play a significant role in the higher latitudes for endemic warm-blooded animals such as the Weddell seals and emperor penguins, whereas krill is of great importance in sub-Antarctic and in oceanic regions (HUBOLD 1992). Particularly in terms of biomass, the significance of fish is great as they are an essential food source not only for high-level predators but also for other predator fish (HUREAU 1994). They are the most important prey for squid in the oceanic waters as well as for warm-blooded predators in the high-Antarctic zone. The pelagic *Pleuragramma antarcticum* plays a major role in the trophodynamics of the high-Antarctic zone, whereas mesopelagic fish are of importance in the ice-free zone and in the oceanic regions of the seasonal pack-ice zone (KOCK 1992). Being both prey and predator, fish are a pivotal connecting link between lower and higher trophic levels.

With eight families and 43 genera, Notothenioidei is the dominant endemic perciform suborder of the Antarctic fish fauna (EASTMAN & EAKIN 2000; BARRERA-ORO 2002; JOHNSTON 2003). The extreme environmental conditions and cold temperatures strongly influence its metabolic-processes (VERDE *et al.* 2006) and therefore, notothenioids show several important features for cold adaptation (CLARKE & JOHNSTON 1996; PATARNELLO *et al.* 2011). In comparison to fish from other regions, Antarctic fish show slower physiological processes (VERDE *et al.* 2006). As a result, their growth is slower (MORALES-NIN *et al.* 2000) and they reach smaller maximum sizes. However, they reach higher ages than comparable temperate fish species (BRODTE *et al*. 2006; HILDEBRANDT *et al.* 2011).

Growth is a quantitative aspect of development and it is known to control mortality rates as well as the rate of reproduction in fish (NIKOLSKII 1969). Growth or production of fish is defined as the elaboration or synthesis of fish tissue over time. It can be calculated as the change in biomass, size, energy (calories), carbon, or nitrogen over a specified time interval and includes somatic growth as well as the development of the gonads (MARSHALL & BRECK 1990). To get information about the growth of fish, the age is often determined via otolith increment analysis as the growth of otoliths correlates with the growth of fish (BOEHLERT 1985). Otoliths retain structures of banding patterns or rings that reflect the punctuated nature of growth with the highest potential of temporal resolution, compared to other structures, such as bones or scales that can be used for age determination as well (CHAMBERS & MILLER 1995).

There are many factors influencing the growth of fish. The most important ones are temperature, food quality and quantity (NAUMANN 2010) and the energy allocation for growth. Temperature is one of the abiotic key factors in marine ecosystems because it influences metabolic processes and shapes the distribution limits of fish (LANGENBUCH *et al.* 2003; SANDERSFELD 2012). Under optimal environmental conditions, fish can grow throughout their life. An optimal temperature will therefore improve the growth and reproduction of fish. The growth rate of fish is decreasing with increasing age. The maximum growth rate and approximate size that can be reached by an individual is still genetically defined (HILDEBRANDT 2009). It is widely known that most Antarctic fish grow slowly (CLARKE & NORTH 1991) and are more sensitive to temperature variations than marine fish from boreal latitudes (PECK *et al.* 2004). In addition, pelagic fish from the Antarctic shelf regions seem to be more susceptible to environmental changes than the benthic fish communities which are more resistant to fluctuations (MINTENBECK 2008). As the Antarctic marine ecosystem developed into a stable environment over the last millions of years, the Antarctic waters are characterized by constant cold temperatures, high oxygen levels and a distinct seasonality in the ice regime and in the primary production. All of these factors control the life cycle of fish in these areas (CLARKE 1988, WÖHRMANN 1997).

Because of their specialization to cold conditions, a lot of Antarctic species have become highly cold-stenothermal. Most species have just very narrow temperature windows (PÖRTNER & KNUST 2007) of upper lethal temperatures of 6 °C (SOMERO & DEVRIES 1967). This specialization led to a less active and rather sluggish lifestyle (MARK *et al.* 2005).

Not only the temperature is an important factor influencing the growth of fish but also food limitation and the high seasonality of the polar regions (CLARKE & NORTH 1991). Because sufficient light for growth of phytoplankton is only available for a short period of time during polar spring and summer, the overall primary production and the food quantity is quite low (HILDEBRANDT *et al.* 2011). Further, changes in salinity and rising CO_2-concentrations may have direct physiological effects on marine organisms. Changing environments always have certain impacts on the organisms that occupy these habitats. Over a longer period of time, these changes will either lead to a successful adaptation of the organisms or to a collapse of their populations if they are unable to sustain these new living conditions. In marine ecosystems changing temperatures are frequently the main cause for failing survival (PECK *et al.* 2004).

The ongoing climate change will affect individual organisms or even whole populations and communities, and therefore, the entire ecosystem. It will have an impact either directly or indirectly. All life stages of these organisms, their growth and reproduction, may be affected by changes in the water temperature, in the sea level, in the wind and storm regimes or in the food web (PÖRTNER *et al.* 2001, PÖRTNER *et al.* 2008). Furthermore, the climate change may result in habitat loss due to a reduction of sea ice. It may even lead to acute-heat death of the stenothermal Antarctic fish if the temperature rises a few degrees above their normal habitat temperature (SOMERO 2009). The recovery and recolonization of Antarctic waters after disturbances e.g. iceberg strandings is known to take much longer than in tropical areas which are affected by shattering actions of a similar degree (GERDES *et al.* 2008). A reduction of fish in the Antarctic waters will have substantial consequences for the entire ecosystem as fish play a major role in the food web of the Antarctica. Especially, the migrating species *P. antarcticum* is the most important food source for upper consumers in the Weddell Sea (HUBOLD 1992) and it contributes to the bentho-pelagic coupling by vertical feeding migrations (KNUST *et al.* 2012).

This study provides data about the age and growth of *P. antarcticum* and *T. eulepidotus* from different areas of the Antarctic Ocean. Their age population structure was determined in order to investigate their population dynamics and their growth within their natural environment. Having obtained the age and length data, inferences were drawn about their growth rates. Studies on the relation between age and growth of fish are important because fish have an intermediate growth and over time, many aspects of their biology change with changing body size. Aging of fish is of importance for the understanding of the population dynamics of single species and is necessary for a good management (BALTZ 1990). In addition, the comparison of the growth performance of species from different geographical regions offers the potential to get an insight into the ecological key factors influencing their growth. A better knowledge of these processes will help to estimate possible future shifts of distribution boundaries in the context of climate change. The aim of this study was a comparative analysis of the growth of these two fish species from different Antarctic regions from an ecological point of view. Therefore, the study was performed with guidance of the following central questions:

- How can the growth performance of *P. antarcticum* and *T. eulepidotus* be described in their natural environment?

- Are there intraspecific differences in the growth regarding different regions of the Antarctic waters?

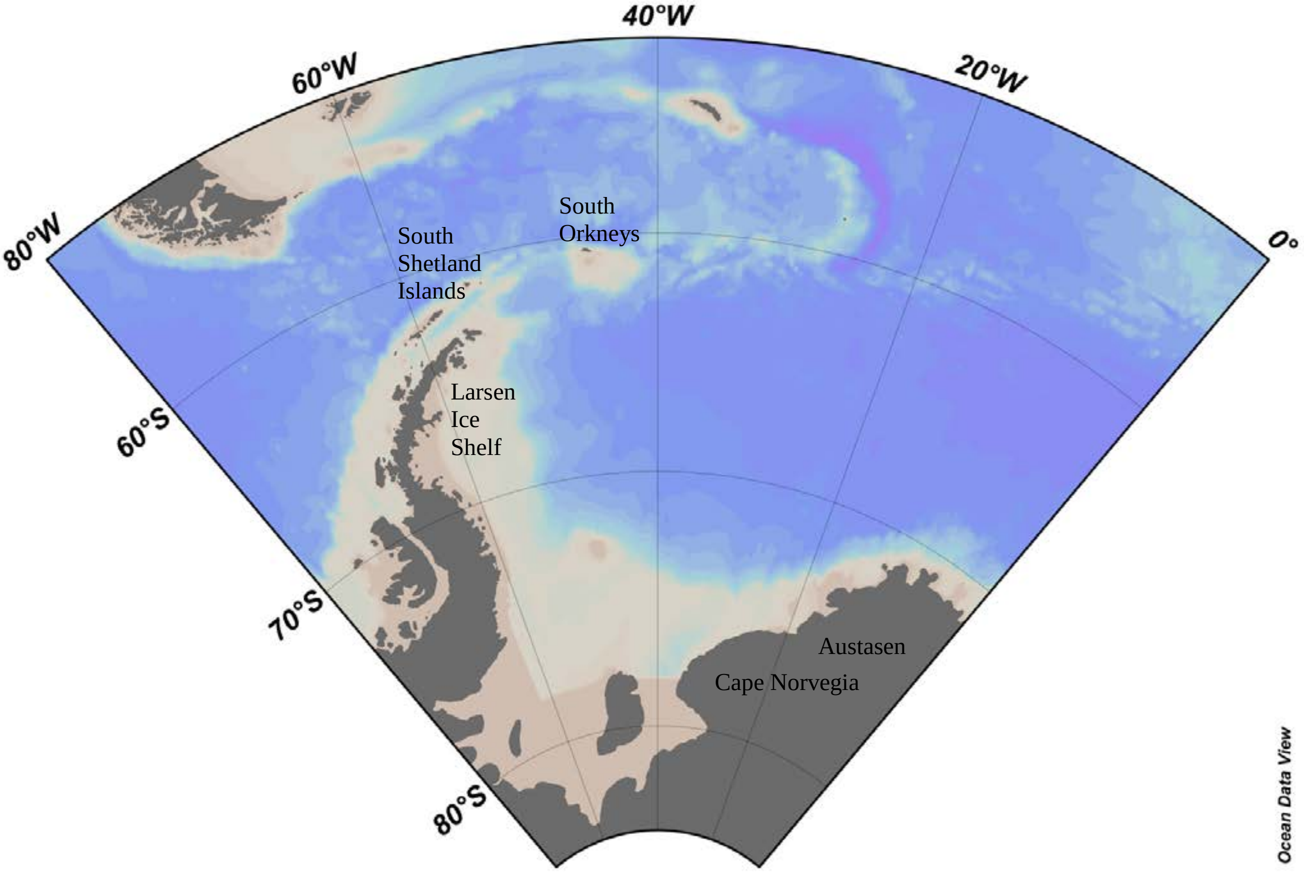
- Are there interspecific differences in the growth of *P. antarcticum* and *T. eulepidotus*?

- Which are the most important factors influencing the growth performance of these two species?

2 AREAS OF INVESTIGATION

Fish were caught at different sites of the Antarctic waters. Fig. 1 gives an overview of the different areas of investigation. Two sample stations were within the high-Antarctic waters, Austasen and Cape Norvegia. The other investigated areas of the Larsen Shelf, the South Shetland Islands and the South Orkneys belong to the area surrounding the Antarctic Peninsula in the sub-Antarctic waters. Stability of water temperatures is known to increase and temperatures to decrease from the north (sub-Antarctic) to the south (high-Antarctic).

Figure 1: Investigated areas of the Antarctic waters.



2.1 South Orkneys

The South Orkneys belong to the scattered islands of the Southern Ocean and are located in the southern part of the Scotia Sea, to the north-east of the Antarctic Peninsula. Coronation

Island and Laurie Island are the biggest Islands within the island group of the South Orkneys (Coria *et al.* 2011). In total, this group of islands comprises an area of 622 km² of which 85 % are covered by glaciers (Rubin 2008). Water depth is known to vary greatly in the proximity. In the north, depths of up to 5000 m were observed. In the south, on the contrary, the descent is more gradual with water depth of 150 m at the shelf (Everson 1970). The amount of caught fish around the South Orkney Islands was large in the years of 1977/78. However, yields seemed to have dropped in the following years and stock sizes declined distinctly after 1981/82 due to intense fishing (Kock 1992).

2.2 South Shetland Islands

The South Shetland Islands consist of a group of eleven bigger and several smaller islands which are located parallel to the northernmost part of the Antarctic Peninsula. The South Shetland Islands are separated from the Antarctic Peninsula by the Bransfield Strait (Smellie 1979). In the southern part the Bransfield Strait is influenced by the waters of the Bellingshausen Sea and in the eastern part, it is influenced by cold and salt-rich water from the Weddell Sea (Kellermann 1986).

King George Island

King George Island is the biggest of the South Shetland Islands and is located 62.1 °S/ 58.4 °W (Travassos & Simões 2004). As an offshore island (100 km distance) it belongs to the Antarctic Peninsula. Over 90 % of the actual island is covered by ice (Bu Jeol *et al.* 2008). King George Island just shows slight variations in air temperature and a relative high humidity (Ferron *et al.* 2004). From the area around King George Island, different types of soils and plant cover are recorded: extended areas of meadows with higher plants as well as large lichen heaths and barren soils (Bölter 2009).

Elephant Island

Like King George Island, Elephant Island belongs to the South Shetland Islands and is located at 61°10`S and 55°14`W. Elephant Island got its name because of the many elephant seals seen around that island in the nineteen-twenties (MILLS 2003). It lies beyond the northernmost extent of the continental Antarctica and it is separated from the Antarctic Peninsula by the deep basins of the Bransfield Strait. These contain dense waters formed from mixtures of the Antarctic shelf waters (MEREDITH *et al.* 2003). Elephant Island is about 19 km wide and 39 km long.

2.3 Antarctic Peninsula

The Antarctic Peninsula region is defined as the area between 62° - 75 °S and 55° - 80 °W. This region is one of the most dynamic climate systems on earth and responds rapidly to climate changes (INGÓLFSSON *et al*. 2003). The impact of regional warming in the last 50 years already resulted in changes in the ecological structure. The mean seasonal sea surface temperature variation at the Antarctic Peninsula shows temperatures that are usually above 0 °C between January and March. In autumn and winter, when the region is covered by ice, temperatures are generally below 1 °C (MURPHY *et al.* 2012).

Larsen Shelf

The Larsen Shelf is located 67 °S next to the Antarctic Peninsula in the western Weddell Sea. The Larsen Shelf consists of the Larsen A, Larsen B and Larsen C ice shelves. The Larsen A and Larsen B ice shelves are already prove of the consequences of the global warming, as they came off in the years 1995 and 2002. The Larsen C ice shelf seems to be rather stable for the moment (ROTT *et al.* 2011). The waters around Larsen shelf area show water depths of 350 m on average. It further is traversed by troughs that can be deeper than 500 m. The continental slope is formed quite plain and shallow. The area around the Larsen Shelf is characterized by oxygen-rich waters and cold temperatures (GORDON 1998). The Larsen Shelf is affected significantly by direct precipitation, basal congelation and terrestrial ice streams (HOLZ 2001).

2.4 Eastern Weddell Sea

The Weddell Sea is almost entirely covered by sea ice throughout the year (HUBOLD 1984). During summer, an ice free polynya forms parallel to the shelf barrier in varying extension and is shifted westwards each winter (GORDON *et al.* 2007). The shelf water of the eastern shelf reaches depths of circa 500 m where the warm deep water abuts the continental slope (HUBOLD 1992). The continental slope of the eastern Weddell Sea is quite steep with a declination of about 9 % (HOLZ 2001). Waters of the Weddell Sea are characterized such as the Larsen Shelf by cold and stable temperatures, with surface water temperatures between +2 and -1.8 °C and a salinity commonly between $34.0 – 34.5*10^{-3}$ (HUBOLD 1992).

Cape Norvegia

Cape Norvegia is located at the south-eastern part of the Weddell Sea (ULLOD 2003). On the one side it outlines most eastern part of the eastern Weddell Sea coast and on the other side the most northern part of the Riiser-Larsen Ice Shelf. The area around the shelf of Cape Norvegia is without or with just a few small stones. The surface is generally high populated by bryozoa and sponge associations (EKAU & GUTT 1991). It is an area with a high primary production rate and it undergoes relatively low iceberg transits (ISLA *et al.* 2006).

Austasen

The area of Austasen is characterized by grounded icebergs (“ice resting place”) due to a high density and transit of icebergs above the shelf (GUTT & STARMANS 2001; ISLA *et al.* 2006). The fauna in the shallow waters is dominated by bryozoans, sponges, gorgonians and asteroids (ARNTZ & GUTT 1999).

3 METHODS

3.1 Investigated Species

Both model organisms, *Pleuragramma antarcticum* and *Trematomus eulepidotus*, belong to the family Notothenidae. With 13 genera and 49 species it is the most diverse family, not only in habitat and distribution, but also in size and body form (EASTMAN, 1993). Of these 49 species, 15 are non-Antarctic and 34 are Antarctic species (DI PRISCO 2009).

Pleuragramma antarcticum, Boulenger 1902

The Antarctic silverfish, *P. antarcticum* is not only the most frequent species in the continental shelf areas (61° S – 78° S) of the Antarctica (HUBOLD & TOMO 1989); moreover it is the only pelagic living species of the notothenioidei (WÖHRMANN *et al.* 1997). It is distributed only in the waters around Antarctica in depths down to 700 meters (O´DRISCOLL *et al.* 2011). In the midwater fish fauna of continental shelf areas of the Ross Sea and the Weddell Sea *P. antarcticum* accounts for over 90 % of the fish communities in number as well as in biomass (LA MESA *et al.* 2004; VACCHI *et al.* 2004; SUTTON & HORN 2011). Consequently, it plays an important role in the diet of endemic Antarctic mammals like seals, birds, penguins and other predator fish (LA MESA *et al.* 2004; GRANATA *et al.* 2009) and may even rival krill in its ecological significance (RADTKE *et al.* 1993). *P. antarcticum* mostly feeds on copepods and amphipods, but sometimes also on larval fish (PINKERTON *et al.* 2010). During its life cycle *P. antarcticum* undertakes vertical migrations in the south-eastern Weddell Sea. Thus, larvae remain mainly in the surface waters of about 20 m (KNUST *et al.* 2012) at temperatures of < -1.8 °C, juveniles prefer warmer waters at temperatures of > -0.5 °C while adults are mostly found at the shelf at temperatures of < -2 °C (WÖHRMANN 1997) and water depths of 60 – 200 m (KNUST *et al.* 2012).

P. antarcticum (Fig. 2) is a relatively slow growing fish species with a moderate life span. In the Ross Sea individuals showed body lengths of 4.6 - 22.9 cm (SUTTON & HORN 2011)

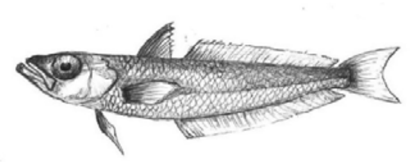


Figure 2: ***Pleuragramma antarcticum***

and in the western Weddell Sea near to the Antarctic Peninsula their body lengths ranged from 1.1 - 24.5 cm (HUBOLD & TOMO 1989). However, their maximum length is supposed to be 26 cm. The maximum age of the oldest individuals determined via otolith readings was slightly over 30 years (RADTKE *et al.* 1993). *P. antarcticum* reaches maturity at an age of 7 - 9 years. In November 12000 - 18000 eggs per female are deposited (KOCK & KELLERMANN 1991) by which their official "birthday" is defined to be the 1th of November (SUTTON & HORN 2011).

Trematomus eulepidotus, Regan 1914

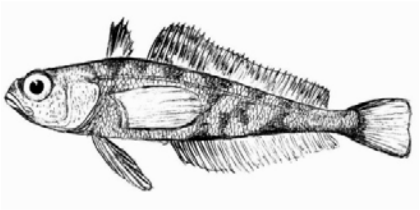


Figure 3: ***Trematomus eulepidotus***

This bentho-pelagic species is particularly found at the shelf of the eastern and southern Weddell Sea in depths of 200 - 410 m, occasionally also in deeper waters down to 630 m (SCHWARZBACH 1988). It is a circum-Antarctic species with its main distribution at the continental shelf and nearby costs and islands (DAMERAU *et al.* 2012). The blunt scalyhead, *T. eulepidotus* (Fig. 3), is mainly found swimming directly above the substratum (EKAU & GUTT 1991) but migrates to the upper waters for feeding (EL-SAYED 1994). Since the percentage of adult *T. eulepidotus* is distinctively higher during the summer months in the Weddell Sea, it is suggested that they undertake vertical migration as it is done by *P. antarcticum*. *T. eulepidotus* is the second most abundant species in the Weddell Sea and represents about 11 % of the fish biomass (EKAU 1990). It preys on organisms in the water column (DAMERAU *et al*. 2012). Adults mostly feed on euphausiacea whereas small individuals primarily feed on gastropods and copepods (KLINGENBERG & EKAU 1996; MINTENBECK 2001). Male *T. eulepidotus* are known to reach maturity later than females (DUHAMEL *et al.* 1993). In the Weddell Sea males showed maximum lengths of 21.7 cm and maximum ages of 14 years, whereas females showed maximum lengths of 29.3 cm and maximum ages of up to 21 years (EKAU 1988). *T. eulepidotus* seem to spawn relatively late for the first time in their life. Spawning takes place when individuals have reached about 70 - 75 % of their maximum length. Their reproductive effort in terms of the gonadosomatic index (GSI) is quite high reaching 20 - 30 % in females (LA MESA *et al*. 2008). It is suggested that *T. eulepidotus*- larvae hatch in May/June, so that the early larval development is expected to occur in winter (KELLERMANN 1990). An official “birthday” is not yet known for this species.

3.2 Sampling

Fish were caught during expeditions with the research vessel POLARSTERN in the years 2003/2004 (ANTXXI-2), 2011 (ANTXXVII-3), and 2012 (ANTXXVIII-4). Sampling took place at different sites in the Antarctic waters. Individuals were caught in the eastern Weddell Sea (Cape Norvegia and Austasen), the Scotia Arc (South Orkneys), the South Shetland Islands (King George Island and Elephant Island) westward to the Antarctic Peninsula, and at the eastern part of the Antarctic Peninsula (Larsen A, B, and C ice shelves) (Fig. 1). Table 1 shows an overview of all sampled stations. Different types of fishing gear were used during the three expeditions: bottom trawls (BT), benthopelagic nets (BPT), Agassiz trawls, 3 m (AGT), and small Agassiz trawls, 1.5 m (AGTs). Trawling took place at water depths between 122.8 and 890.0 m. Fish were sorted by species, and the total length (TL) and standard length (SL) measurements were rounded down to the nearest whole centimeter. In the case of *P. antarcticum,* the total length could not always be established, since the tail fin sometimes folds up and prevents a precise measurement. Here, the standard length was the primary measurement used for further analysis. Fish weights were recorded within an accuracy of 1 g. During weighing, differentiation was made between the total weight and the gutted weight of the fish. In addition, the gonad weight and the liver weight were taken. Finally, individuals were sexed as well. In juveniles it was not possible to sex every individual distinctively. Therefore, these individuals were only documented as juvenile (J).

Sagittal otoliths were extracted and preserved dry and clean for subsequent age determination. Altogether, there were 866 otoliths (433 otolith pairs) available for age determination. Of these, 274 pairs belonged to the species *P. antarcticum,* and 159 pairs belonged to the species *T. eulepidotus*.

Table 1: Sampled stations within the areas of investigation. BPT = benthopelagic net, AGT = Agassiz trawl (3 m), AGT`s = small Agassiz trawl (1.5 m), BT = bottom trawl.

Expedition	Station	Area	Latitude	Longitude	Depth (m)	Gear	Number of individuals	
							P. ant.	*T. eul.*
ANT-XXI/2	PS65-299	Austasen	70°48.54`S	10°42.57`W	468.0	BPT	10	-
ANT-XXI/2	PS65-314	Cape Norvegia	72°50,65`S	19°36.21`W	484.0	BPT	10	-
ANT-XXI/2	PS65-39	Cape Norvegia	71°06.63`S	11° 32.72`W	166.0	AGT	-	10
ANT-XXVII/3	PS77-218-2	South Orkneys	61°10.85`S	45°43.87`W	337.7	BT	20	-
ANT-XXVII/3	PS77-222-6	King George Is.	62°19.09`S	58°36.44`W	459.2	BT	20	-
ANT-XXVII/3	PS77-222-7	King George Is.	62°19.10`S	58°36.62`W	451.5	BT	17	-
ANT-XXVII/3	PS77-228-3	Larsen A south	64°54.96`S	60°31.97`W	308.5	BT	6	-
ANT-XXVII/3	PS-77-231-3	Larsen A south	64°54.79`S	60°30.80`W	354.5	BT	28	-
ANT-XXVII/3	PS77-235-8	Larsen B seep	65°31.71`S	61°33.00`W	450.5	BT	61	-
ANT-XXVII/3	PS77-237-2	Larsen C north	66°12.48`S	60° 9.68`W	381.0	BT	2	-
ANT-XXVII/3	PS77-243-2	Larsen C north	66°16.74`S	60°16.02`W	402.0	BPT	3	-
ANT-XXVII/3	PS77-250-8	Larsen B seep	65°22.54`S	61°42.45`W	828.0	BPT	40	-
ANT-XXVII/3	PS77-256-3	Larsen A north	64°45.84`S	60°23.41`W	890.0	BPT	20	-
ANT-XXVII/3	PS77-269-3	Cape Norvegia	71°21.38`S	12°38.71`W	488.0	BPT	7	-
ANT-XXVII/3	PS77-269-4	Cape Norvegia	71°21.38`S	12°42.02`W	448.0	BPT	30	-
ANT-XXVII/3	PS77-269-6	Cape Norvegia	71°26.52`S	12°35.49`W	509.0	BPT	10	-
ANT-XXVII/3	PS77-226-6	Larsen A	64°91.35`S	60°60.16`W	277.7	AGT	-	10
ANT-XXVII/3	PS77-257-2	Larsen A	64°54.85`S	60°38.67`W	168.5	AGTs	-	6
ANT-XXVII/3	PS77-281-1	Austasen	70°48.93`S	10°32.69`W	288.5	BT	-	7
ANT-XXVII/3	PS77-286-1	Austasen	70°50.64`S	10°36.11`W	249.0	BT	-	5
ANT-XXVII/3	PS77-291-1	Austasen	70°50.50`S	10°35.24`W	281.7	BT	-	8
ANT-XXVII/3	PS77-292-2	Austasen	70°50.07`S	10°34.73`W	276.7	BT	-	3
ANT-XXVII/3	PS77-300-1	Austasen	70°50.48`S	10°35.28`W	280.2	BT	-	2
ANT-XXVII/3	PS77-301-1	Austasen	70°50.99`S	10°35.23`W	265.7	BT	-	5
ANT-XXVII/3	PS77-308-1	Austasen	70°51.30`S	10°35.35`W	250.5	BT	-	4
ANT-XXVIII/4	PS79-199-1	Elephant Is.	61°4,78`S	56°01.76`W	244.8	BT	-	4
ANT-XXVIII/4	PS79-209-1	Elephant Is.	60°51,53`S	55°30.25`W	290.2	BT	-	2
ANT-XXVIII/4	PS79-214-1	Elephant Is.	61°02.58`S	55°45.51`W	111.8	BT	-	2
ANT-XXVIII/4	PS79-218-1	Elephant Is.	61°00.53`S	55°58.39`W	299.2	BT	-	3
ANT-XXVIII/4	PS79-219-1	Elephant Is.	61°00.68` S	55°58.03`W	304.6	BT	-	8
ANT-XXVIII/4	PS79-220-1	Elephant Is.	61°02.59` S	55°57.03`W	273.0	BT	-	4
ANT-XXVIII/4	PS79-240-1	Elephant Is.	61°38.75`S	57°05.83`W	463.6	BT	-	2
ANT-XXVIII/4	PS79-242-1	Elephant Is.	61°35.88`S	57°16.68`W	423.0	BT	-	3
ANT-XXVIII/4	PS79-244-1	Elephant Is.	61°38.86`S	57°47.52`W	322.2	BT	-	1
ANT-XXVIII/4	PS79-248-1	King George Is.	62°46.71`S	61°36.10`W	146.0	BT	-	1
ANT-XXVIII/4	PS79-259-1	King George Is.	61°59.99`S	59°14.73`W	129.1	BT	-	1
ANT-XXVIII/4	PS79-260-1	King George Is.	61°51.74`S	59°15.47`W	259.5	BT	-	1
ANT-XXVIII/4	PS79-263-1	King George Is.	61°40.43`S	58°51.46`W	366.1	BT	-	3
ANT-XXVIII/4	PS79-243-1	Elephant Is.	61°38.21`S	57°32.72`W	425.4	BT	-	1
ANT-XXVIII/4	PS79-268-1	King George Is.	62°15.61`S	55°18.44`W	366.1	BT	-	15
ANT-XXVIII/4	PS79-269-1	King George Is.	62°27.59`S	55°15.62`W	227.3	BT	-	1
ANT-XXVIII/4	PS79-234-1	Elephant Is.	61°17.42`S	56°01.25`W	279.7	BT	-	4
ANT-XXVIII/4	PS79-236-1	Elephant Is.	61°22.28`S	56°10.24`W	293.1	BT	-	2
ANT-XXVIII/4	PS79-273-1	Elephant Is.	62°22.04`S	55°57.65`W	336.6	BT	-	25
ANT-XXVIII/4	PS79-283-1	Elephant Is.	61°01.75`S	55°48.50`W	122.8	BT	-	18

3.3 Otolith Preparation

Initially, all otoliths were weighed to an accuracy of 0.01 mg (Sartorius LA 230S). Direct weighing has the advantage of precise weight specification, whereby it is necessary for all otoliths to be isolated from any debris which could falsify measurements.

The maximum diameter was measured under a stereomicroscope (Leica MZ12.5) with the help of the Cell^{B} computer program and a microscope camera (Color View, Olympus Soft Imaging Solutions). In both species investigated, the maximum diameter of the otoliths was taken because it is more precise than measuring from rostrum to postrostrum. Measurements from rostrum to postrostrum are not accurately definable, especially in nearly circular but still irregular otoliths (HUBOLD 1989). When weighing and measuring the diameter of the otoliths, a distinction was made between right and left sagittae of every individual based on the location of the sulci of the otoliths. A sulcus located at the left side of the otolith is the right otolith of the fish and vice versa (Fig. 4).

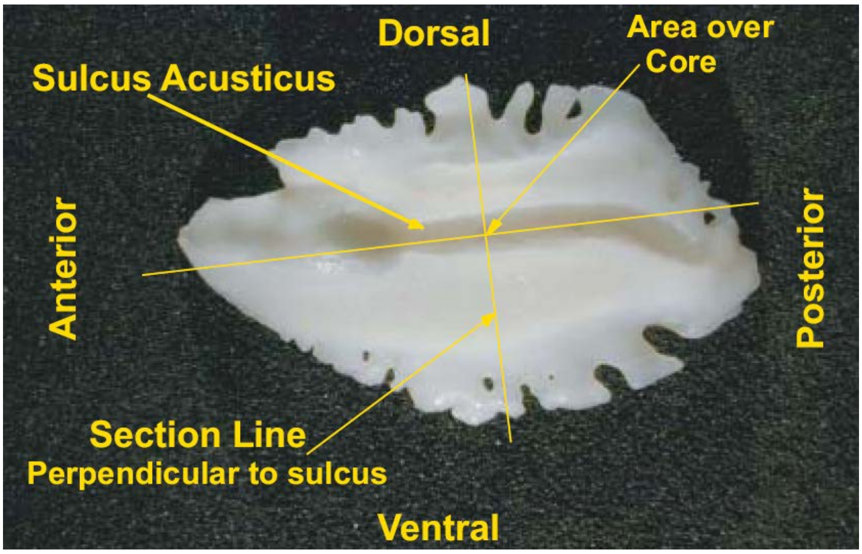


Figure 4: Schematic illustration of a right sagittal otolith (JENKE 2002).

Due to the high diversity of osteichthyes and their high variability in growth performance, otoliths, and morphology, a general method for otolith preparation and analysis is not practical.

Since the otoliths of *P. antarcticum* are quite small and readable merely by transferring them into a few drops of glycerin during the period of examination, it was not necessary to perform any further treatment. Otoliths that were difficult to read were stored in glycerin for longer periods of up to 96 hours, as glycerin is known to clarify the structures. When storing such otoliths in glycerin for a prolonged period, the appearance of the annual rings was checked regularly under a stereomicroscope to prevent the structures from clarifying to an unreadable extent. Photographs of all otoliths were taken.

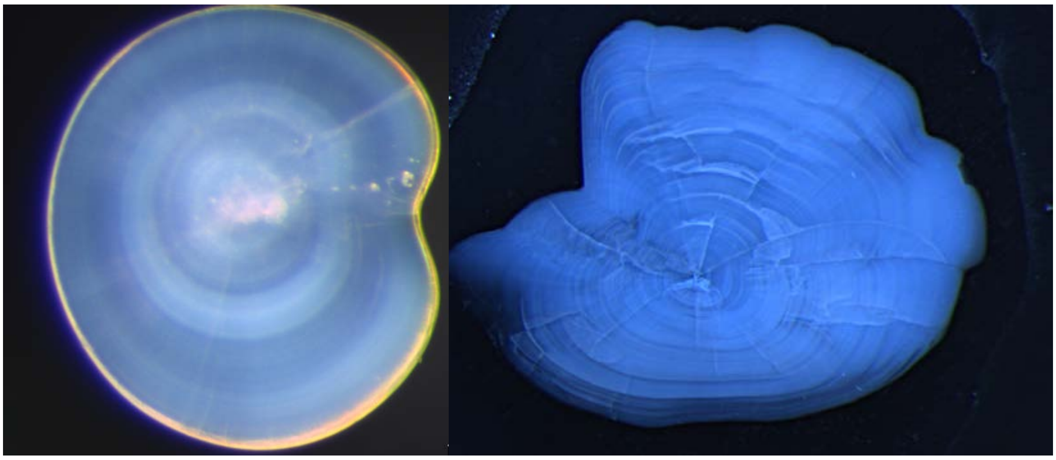


Figure 5: Otolith of a) a juvenile *P. antarcticum* in glycerin and b) of *T. eulepidotus* (polished).

Single otoliths of *T. eulepidotus* were fixed with cyanoacrylate onto black plastic lids so that the plain side with the sulcus was on the bottom. After drying, the otoliths were sanded down to the nucleus, whereby water was used for cooling. The progress of polishing was checked regularly under a stereomicroscope. Polishing was done by using two different grinders (Struers, DAP-6 and DAP-7). Grain size was either 1200 or 2400. A photograph of every single otolith was taken after being polished.

Depending on the thickness of each otolith, they were examined under the stereomicroscope using either transmitted or reflected light. The otoliths were examined at different perspectives, since the ring structures may appear differently from different viewing angles. Turning the otoliths to different positions under the stereomicroscope was meant to ensure that the ring structures were consistently present from every point of view and no misinterpretation was done. To increase the contrast of the otolith structures, the photographs were treated with an unsharp mask (Adobe Photoshop CS 3 Extended, Version 10.0, Adobe Systems Inc.) which improves the appearance of details by increasing acutance. The actual age was determined by counting the hyaline winter rings with the aid of the Cell^B computer program by drawing an axis from the nucleus to the margin of the otoliths. Hyaline and opaque zones were distinguished and considered to form an annulus together. Any outmost increment that was hyaline was not counted, as the growth of the corresponding year was not complete at that point.

To avoid mistakes in determining the age, otoliths that were difficult to read were evaluated by a second additional reader, and all otoliths were read twice to increase the accuracy of age determination. Otoliths with an unclear formation of annuli, where the age of the fish could not be determined exactly, were not included in the subsequent data evaluation and analysis.

3.4 Mathematical and Statistical Analyses

3.4.1 Otolith Size and Shape

For the purpose of investigating whether left and right otoliths of individuals had identical growth, tests were conducted to reveal any significant differences in their maximum diameters and weights. Therefore, the first thing that was tested was the distribution of the available data pairs of the respective left and right otolith diameters. The same procedure was done for the data pairs of left and right otolith weights. To test for normal distribution, the Kolmogorov–Smirnov test (KS-test) was used. Since the data did not have a normal distribution and the data pairs were matched, the Wilcoxon signed-rank test (significance level $\alpha = 0.05$) was then used to examine whether the data of the respective otolith pairs differed significantly ($p < 0.05$) in diameter or weight.

3.4.2 Age and Growth

The age of the fish ascertained by annual increment analysis was standardized by the month of capture. The official "birthday" of *P. antarcticum* is defined to be the 1st of November (SUTTON & HORN 2011). For *T. eulepidotus* there is not a clearly defined hatching date, but it is known to spawn in the spring-summer months (KOCK & JONES 2005). Therefore, its "birthday" was considered to be the 1st of June for the calculations in this study. These dates were used as the hatching dates for both fish species.

$$Age_{norm} = Age_{annuli} + \left(\frac{Month\ of\ capture}{12}\right) \tag{1}$$

The Bertalanffy growth function is used in fisheries to model the growth of fish as a function of age and is based on the antagonistic effects of anabolism and catabolism. Length growth was assessed by fitting the age-length data to a von Bertalanffy growth function (BEVERTON & HOLT 1957):

$$L_t = L_\infty * [1 - e^{-k} * (t - t_0)] \tag{2}$$

where L_∞ is the theoretical maximum length or asymptotic length; L_t is the length at a point in time; k is the growth coefficient which indicates the rate of change in length; and t_o

represents the age or time when length is theoretically zero. The parameter t_0 was set to zero in all analyses to avoid positive t_0 -values.

In this study, L_∞ was defined using the maximum observed length (L_{max}) for each population of the different areas of investigation. L_∞ was calculated by using the following formula (TAYLOR 1958):

$$L_\infty = \frac{L_{max}}{0.95} \tag{3}$$

Not only the asymptotic length but also the asymptotic weight (W_∞) was calculated, the latter of which was estimated by the following equation according to PAULY (1985):

$$W_\infty = \frac{W_{max}}{0.86} \tag{4}$$

The length-weight relation can be described by the statistical regression of length to weight:

$$W = a * L^b \tag{5}$$

where W is the weight of the fish, L is the length of the fish, and a and b are the constants to be calculated.

Growth curves of the particular regions were compared using the method according to KAPPENMAN (1981). With this method, two different hypotheses were tested. Hypothesis M_1 specifies that there will be no significant difference between the growth curves of two areas under investigation, whereas M_2 specifies that the growth curves of both areas under investigation differ from each other. The data used to make the selection (M_1 or M_2) are pairs of age-length measurements of fish from each of the two populations tested. For each data pair (age/length) of each individual, the van Bertalanffy growth parameters and the theoretical length of the fish were calculated from the distinct data sets (M_2) and the combined data sets (M_1) by excluding the regarded data pair from the estimation. Next, the theoretical length was subtracted from the actual observed length for every fish to get the difference between the observed and the predicted fish length. Subsequently, the result was squared. The total sum of these squares under M_1 and M_2 is D_1 and D_2, respectively. If the sum of the squares of the differences between observed and predicted lengths under M_l does not exceed the sum of the squares of the differences between observed and predicted lengths under M_2 ($D_1 < D_2$), the data are better predicted by one growth curve than by two, and hypothesis M_l should be selected. Is $D_1 > D_2$, the investigated growth curves show a significant difference (M_2) and are better described by two distinct growth curves.

3.4.3 Production

The estimation of the annual production in length and weight of both species from the different areas investigated was based on the von Bertalanffy growth function. The results refer to the time span of one year (from the first year of age to the second, from the second to the third, etc.). The average lengths per age were calculated by the von Bertalanffy growth function (2), the average weight then being converted by the length-weight relation formula (5). Extrapolation was done to the determined maximum age of the population.

$$p = \left(L_{(t+1)^b} * a\right) - \left(L_{(t)^b} * a\right) \tag{6}$$

where p indicates production per year, $L_{(t)}$ the length at time (t), $L_{(t+1)}$ the length in the following year $(t+1)$ and a and b are constants of the particular population concerned.

Moreover, production (P) of the entire population in biomass per year per 1,000 square meters was calculated. Assuming that the fish stocks are stable and in balance, annual production adjusts the mortality of fish. Hence, natural mortality is equal to the production rate P/B. Fish production is used to estimate the quantity of new tissue created by a cohort or population. It provides the understanding of trophic ecology and sets the limit on food/energy availability for higher trophic levels (MERTZ & MYERS 1998). Production (*P*) can be assessed by the following formula:

$$P = B * M \tag{7}$$

where *B* represents the biomass in grams per area and *M* the mortality rate.

Knowing production *P* and biomass *B* the production rate *P/B* can be estimated easily.

Mortality of both species was calculated for each investigated area based on two different means of estimation. Natural mortality includes all possible causes of death, such as predation or senescence and diseases (BRODZIAK *et al.* 2011), except fishing (PAULY 1980).

To estimate the mortality, initially the formula according to HEWITT & HOENIG (2005) was used. This formula assumes that approximately 1.5 % of the fish population is still alive at their maximum age:

$$M = \frac{4.22}{t_{max}} \tag{8}$$

t_{max} is the value for longevity and is known to be related to the parameter *k* of the von Bertalanffy growth equation. t_{max} can be calculated as follows (PAULY 1980):

$$t_{max} = \frac{3}{k} + t_0 \tag{9}$$

This formula is only applicable for small fish with asymptotic lengths of ≤ 50 cm, whereas in larger fish, the value of the denominator becomes < 3 (PAULY 1980).

Mortality can also be calculated by the parameters k, W_∞, and L_∞ of the von Bertalanffy function and mean water temperature T. The parameter k is known to increase due to factors that bring about stress and an increase of O_2 consumption. Therefore, k has a direct correlation with the longevity of individuals (PAULY 1980). Mortality shows the highest correlation with the value of k, but also with the size of fish and therefore directly with the environmental temperature. Thus, mortality was also estimated by the equation according to PAULY (1980), whereby mortality can be calculated using the asymptotic weight ($W\infty$) or asymptotic length ($L\infty$), respectively:

$$\log M = -0.2107 - 0.0824 \log W\infty + 0.6757 \log k + 0.4627 \log T \tag{10}$$

and

$$\log M = -0.006 - 0.279 \log L\infty + 0.6543 \log k + 0.4634 \log T \tag{11}$$

Here, W_∞, L_∞ and k are parameters of the von Bertalanffy growth formula (2), and T is the mean annual water temperature, or in the case of polar fish, the physiologically effective temperature of cold-adapted Antarctic fish. In this study, T = 12 °C was used for all calculations.

Both methods were used for estimating mortality and will be compared and discussed with regard to their applicability, accuracy, and precision.

3.4.5 Condition

The condition factor (Cf) was estimated for each individual of the sample and is used to obtain information about the corpulence and condition of the fish. Thus, it gives information about the nutritional condition (MÜLLER 2003). The condition factor was calculated as follows:

$$Cf = 100 * \frac{W\,(g)}{TL\,(cm)^3} \tag{12}$$

where W is the total weight and TL is the total length of the individual.

Furthermore, the gonadosomatic index (GSI) was calculated for both species from each area of investigation. The GSI indicates the maturity level of the gonads of individuals. It illustrates the proportion of the gonad weight compared to the total weight of the fish, thereby providing information about the reproductive condition. The index is only comparable within a species:

$$GSI = \frac{W_{gonads}\,(g)}{W\,(g)} * 100 \tag{13}$$

where W_{gonads} is the weight of the gonads and W is the total weight of the individual.

The hepatosomatic index (HSI) indicates the proportion of the liver weight to the total fish weight, giving information about the energy reserve of each individual of the sample. If the energy reserve is low, the environment and circumstances of the fish appear to be poor. This in turn is reflected in a low HSI value (SAGEBAKKEN 2012). The index was calculated as follows:

$$HSI = \frac{W_{liver}\,(g)}{W\,(g)} * 100 \tag{14}$$

where W_{liver} is the weight of the liver and W is the total weight of the individual.

Growth performance index Φ was calculated for both fish species for different areas of the Antarctic waters. The growth performance index reflects the growth rate of a fish with respect to unit length. The slope value derives from the mean of the empirical relation between k and $L\infty$ (BREY 1999; RAGONESE *et al.* 2012). The higher the index values, the better the growth performance. The index enables the growth performance of different populations and species to be compared and was calculated by using of the following formula according to MUNRO & PAULY (1983):

$$\Phi = 2 * \log L\infty + \log k \tag{15}$$

where L_∞ is the asymptotic length and k is the growth coefficient of the von Bertalanffy growth function (2).

3.4.6 Energy Content

Extreme conditions of the Antarctic marine environment govern the energy budget of Antarctic fish (VANELLA *et al.* 2005). Energy budgets are used to examine theoretical functions and linkages of ecosystem components and structures of ecosystems or communities (STEIMLE & TERRANOVA 1985). Energy allocation is an important factor influencing fish growth. Increased capacity for storing of energy reserves may be advantageous in intermittent starvation. To get an idea of the energy contents of both species from the different areas of investigation, the carbon content and kilocalories (kcal) were estimated. This was done by given conversion factors. Dry weight (DW) was calculated from the wet weight (WW) of the individuals, whereby a DW/WW ratio of 25 % was used. A conversion factor of 0.11 g C/g WW was used to estimate the carbon content (PINKERTON *et al.* 2010). The kilocalorie content was determined by the wet weight of the fish as 1g WW equals approximately 1.15 kcal (PINKTERTON *et al.* 2010). 1 kcal equals 4.19 kJ (DONNELLY *et al.* 1990). Moreover, the lipid content was calculated for both species from all areas of investigation by a Lipid/DW ratio of 0.477 for adult individuals of both species (REINHARDT & VAN VLEET 1986; HAGEN 1988; FRIEDRICH & HAGEN 1994). For juvenile *P. antarcticum,* a Lipid/DW ratio of 28.4 % and for juvenile *T. eulepidotus* a ratio of 29.8 % was employed

(FRIEDRICH & HAGEN 1994). These factors were used for all conversions in this study to get a general overview about the energy contents of fish from different geographical areas.

3.4.7 Box-Whisker Plots

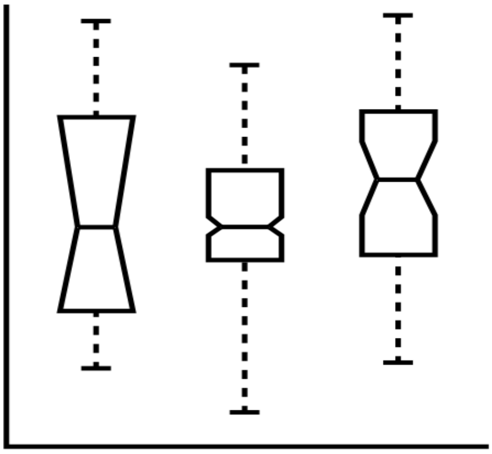


Figure 6: Notched box plot (POTTER 2006).

The Box-Whisker Plot was used in this study to illustrate medians and ranges of dataset dispersion. The Box-Whisker plot consists of the minimum and maximum range values (whiskers), the upper and lower quartiles, and the median to summarize the distribution of a dataset (POTTER 2006). The box itself contains 50 % of the observational data (HARTUNG *et al*. 2005). One special type of Box-Whisker plot is the notched Box-Whisker plot. The notched box plot (Fig. 6) does not only present the data descriptively, but also indicates if the data significantly differ from each other. The plots have been “notched” to show the 95% confidence intervals of the medians (SCHEINER & GUREVITCH 2001). Thus, this plot allows a pairwise comparison of the medians at the 95% confidence interval (SCHOONJANS *et al.* 1995). If the notches of two plots do not overlap, it indicates that the two median values are significantly different. As the notches just roughly indicate the significant differences (POTTER 2006) between the values additional significance tests (Student`s T-test or Mann-Whitney U test) were conducted to confirm possible significant differences.

4 RESULTS

4.1 Otolith Size and Shape

Otoliths of *P. antarcticum* from all areas of investigation were quite small in regard to their body length, with maximum diameters between 0.5 – 2.5 mm (Fig. 7A). The smallest otolith pair had a diameter of 0.46 mm and belonged to an individual in age class 1+ with a SL of 4.2 cm. Otoliths of the oldest individual in age class 13+ with a SL of 21.1 cm were about 2.5 mm in diameter. During ontogenesis of the individuals, the shape of the otoliths seemed to change. While otoliths of individuals with a SL of up to 15 cm appeared almost circular in shape, otoliths of larger individuals had a more oval and discoidal shape.

The weight of the otoliths of *P. antarcticum* was between 0.01 – 4.9 mg (Fig. 7B). This takes into account the reliable measuring limit of the used scale, since 0.01 mg is the smallest value it can detect. Hence, some otoliths may have weighed less than 0.01 mg.

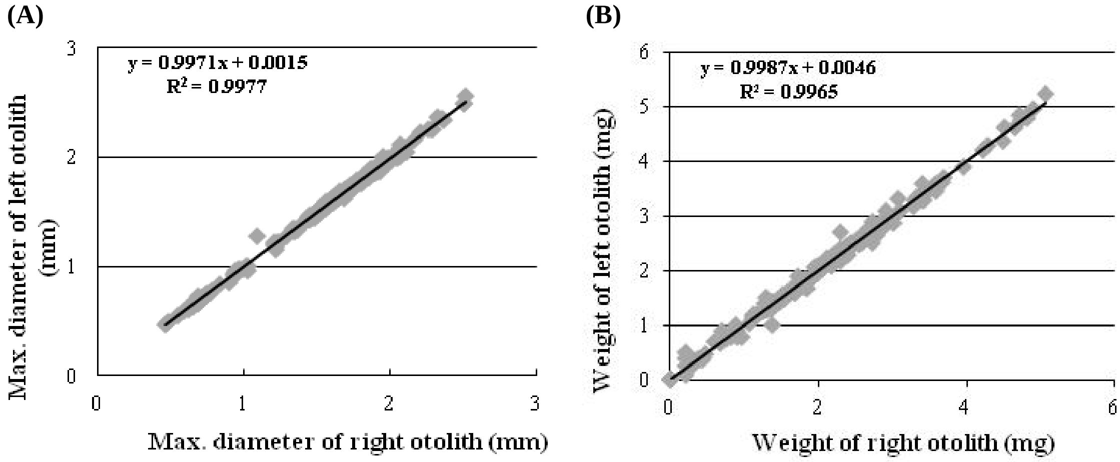


Figure 7: Relation between (A) the maximum diameter and (B) the weight of the right and left sagittal otoliths of *P. antarcticum*.

Statistical analyses via the KS-test of the left and right sagittal otoliths showed that the respective data pairs of the diameters and weights were not normally distributed. When the Wilcoxon singed-rank test (significance level $\alpha = 0.05$) for matched samples was conducted afterwards, it was revealed that there was no significant difference ($p = 0.91$) between the data pairs of the diameters of the left and right otoliths. The same applied to the weights of the otolith pairs. Here, no significant difference (p = 0.98) was observed between left and right otoliths either.

Otoliths of *T. eulepidotus* were relatively thin but overall distinctly larger than the otoliths of *P. antarcticum*. Moreover, the shape of the otoliths of *T. eulepidotus* was not as circular as the ones of *P. antarcticum*, but rather oblong instead. Otoliths had diameters of between 1.9 – 6.2 mm (Fig. 8A). The smallest otolith pair had a maximum diameter of 1.94 mm in an individual with a TL of 12 cm. This individual belonged in age class 4+. The largest otolith diameter of 5.42 mm belonged to an individual in age class 14+ with a TL of 25 cm.

The weight of the sagittal otoliths varied between 2.9 – 32.7 mg (Fig. 8B). The otoliths with the lowest weight of 2.93 mg belonged to an individual in age class 4+ with a TL of 12 cm. It is the same individual that also had the smallest otolith diameter. The heaviest otolith with a weight of 32.73 mg belonged to an individual in age class 14+ with a TL of 25 cm, which was the same individual that also had the largest otolith diameter.

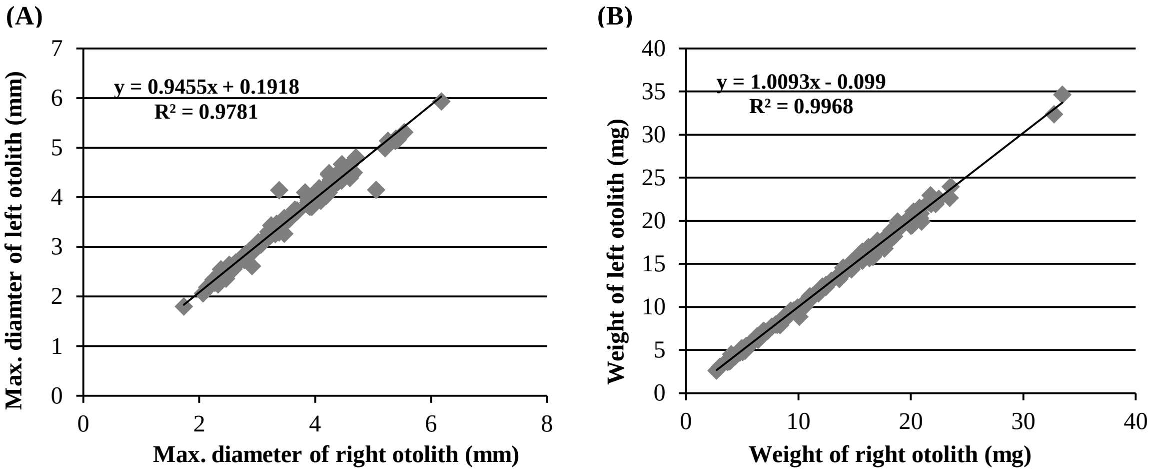


Figure 8: Relation between (A) the maximum diameter and (B) the weight of the right and left sagittal otoliths of *T. eulepidotus*.

The KS test showed that the data pairs of the left and right otolith diameters and weights of *T. eulepidotus* were not normally distributed. The subsequently applied Wilcoxon signed-rank test indicated that neither the diameter (p = 0.95) nor the weight (p = 0.99) were significantly different between the left and right otolith pairs of *T. eulepidotus*.

Hence, left and right otoliths of both species, *P. antarcticum* and *T. eulepidotus*, exhibited uniform growth.

4.2 Age and Growth

Altogether, age determination was performed on a total of 433 individuals via otolith increment analysis. 274 of them belonged to the species *P. antarcticum* and the remaining 159 individuals to *T. eulepidotus*. Fig. 9 and Fig. 10 show the number of analysed individuals per age class of the respective areas for *P. antarcticum* and *T. eulepidotus*. In the case of *P. antarcticum,* most individuals were caught at the Larsen Shelf (n = 153), while the fewest individuals originated from the South Orkneys (n = 20). Most of the individuals of *P. antarcticum* pertained to age classes from 2 – 8 years. Individuals in age classes ≤ 4 and ≥ 10 were only found at the eastern Weddell Sea and at the Larsen Shelf.

Most individuals of *T. eulepidotus* – 100 individuals - were caught at the South Shetland Islands (King George Island and Elephant Island), while 43 individuals were caught in the eastern Weddell Sea at Austasen and only 16 individuals at the Larsen Shelf. Most individuals of *T. eulepidotus* pertained to higher age classes of 7 – 14 years, while most individuals of *P. antarcticum* were in age classes of 2 – 8 years. Individuals ≥ 11 years were only present at Austasen and the South Shetland Islands. At the Larsen Shelf, the age of the individuals ranged from 4 – 10 years.

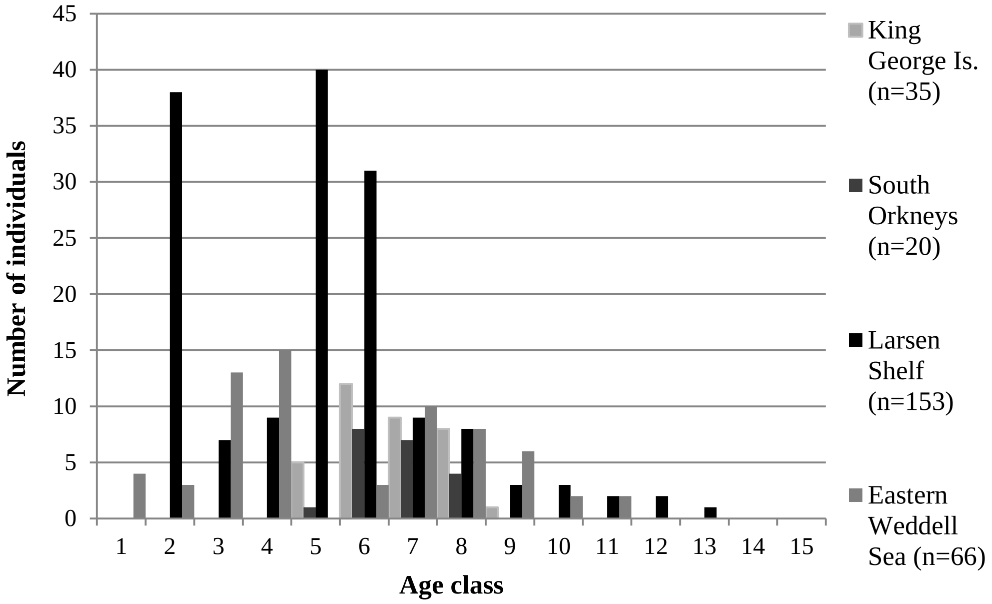


Figure 9: Analysed number of *P. antarcticum*-individuals (total n = 274) per age class from the respective investigated areas.

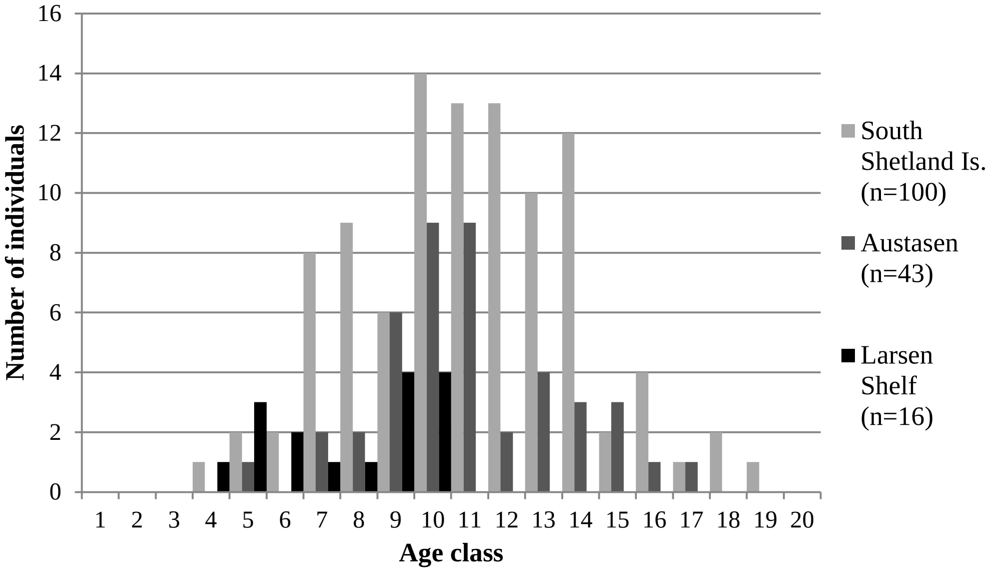


Figure 10: Analysed number of *T. eulepidotus*-individuals (total n = 159) per age class from the respective investigated areas.

Growth curves for both species were created by applying the von Bertalanffy growth function to the estimated age and length data of the single individuals. The corresponding parameter of the von Bertalanffy growth curves are listed in Tab. 3.

P. antarcticum individuals had a SL between 13.9 – 16.5 cm at the South Orkneys, 10.1 – 17.0 cm at King George Island, 4.2 – 18.2 cm at the eastern Weddell Sea, and 5.8 – 19.6 cm at the Larsen Shelf. The maximum weight of an individual observed from all investigated areas was 68.3 g from the Larsen Shelf, whereas the individual with the smallest weight of 0.3 g was from the eastern Weddell Sea. The obtained length-weight relationship is shown in Fig. 11.

Age determination of *P. antarcticum* revealed an age range of 5 - 8 years at the South Orkneys, 5 – 9 years at King George Island, 1 - 11 years at the eastern Weddell Sea, and 2 – 13 years at the Larsen Shelf. Fig. 12 presents the von Bertalanffy growth curves for all four areas.

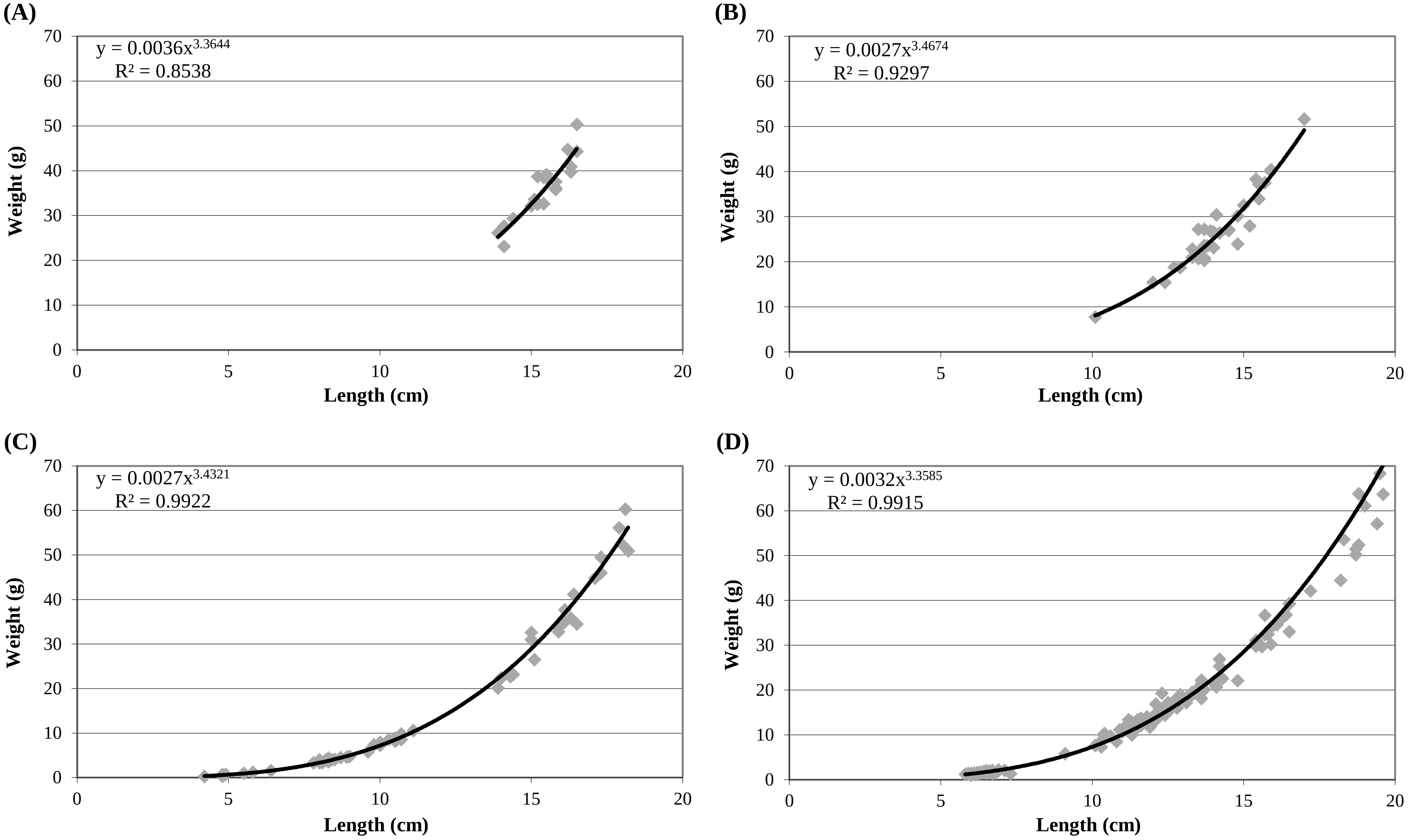

(A)
y = 0.0036x^3.3644
R² = 0.8538
Weight (g)
Length (cm)
0
10
20
30
40
50
60
70
0
5
10
15
20
(B)
y = 0.0027x^3.4674
R² = 0.9297
Weight (g)
Length (cm)
(C)
y = 0.0027x^3.4321
R² = 0.9922
Weight (g)
Length (cm)
(D)
y = 0.0032x^3.3585
R² = 0.9915
Weight (g)
Length (cm)

Figure 11: Length-weight relationship of *P. antarcticum* at (A) the South Orkneys (n = 20), (B) King George Island (n = 35), (C) the eastern Weddell Sea (n = 66), and (D) the Larsen Shelf (n = 153).

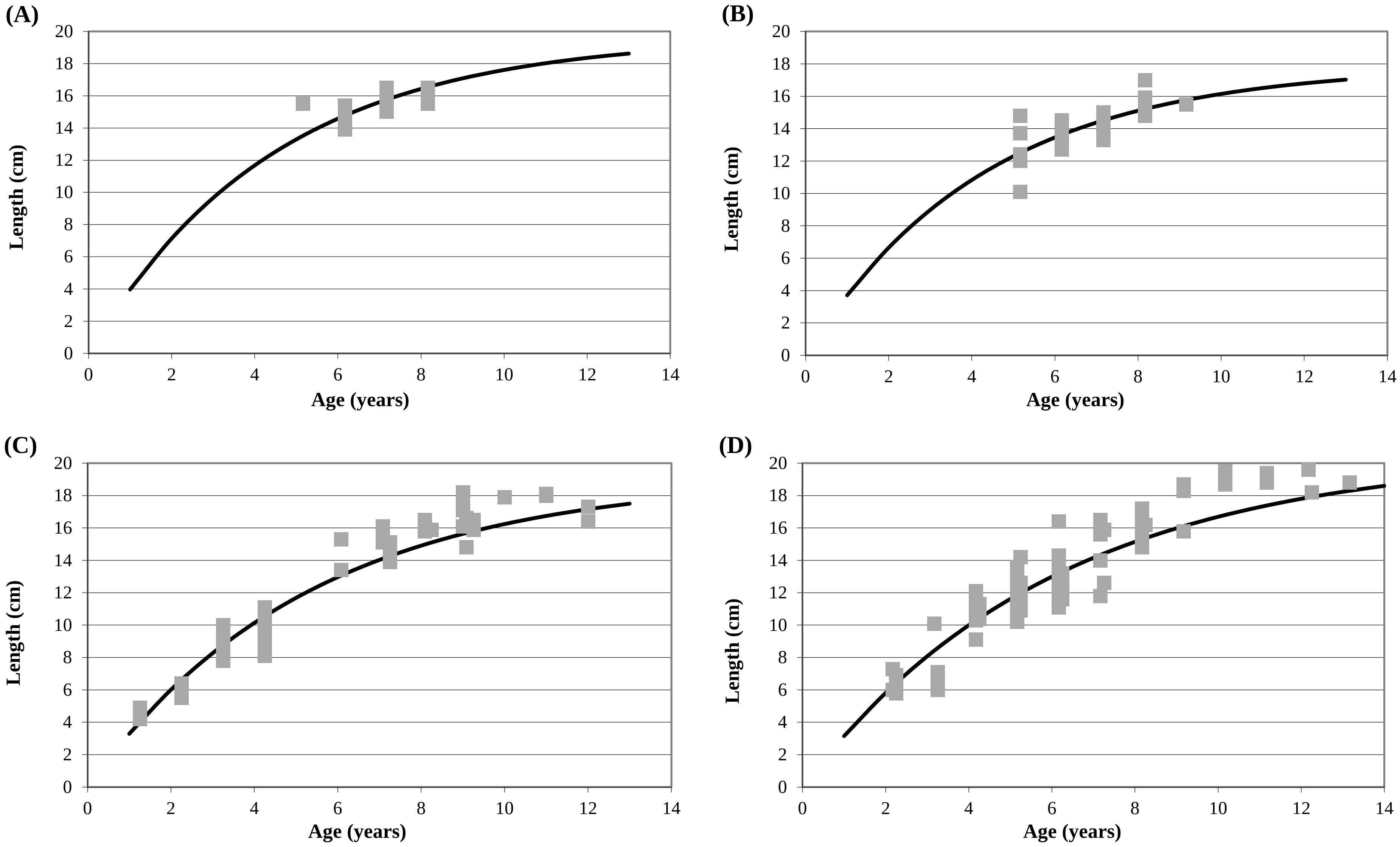

(A)
(B)
(C)
(D)
Length (cm)
Age (years)
0
2
4
6
8
10
12
14
16
18
20

Figure 12: Von Bertalanffy growth curves of *P. antarcticum* at (A) the South Orkneys (n = 20), (B) King George Island (n = 35), (C) the eastern Weddell Sea (n = 66), and (D) the Larsen Shelf (n = 153).

The *T. eulepidotus* individuals that were examined ranged from 14.0 – 29.0 cm in length at the South Shetland Islands, 12.0 – 24.6 cm in the area of Austasen, and 11.8 – 16.0 cm at the Larsen Shelf. The maximum weight of an individual was 327.8 g from the South Shetland Islands, 156.0 g at Austasen, and 33.5 g at the Larsen Shelf. The obtained length-weight relationship is shown in Fig. 13.

Age determination for *T. eulepidotus* revealed an age range from 4 - 19 years at the Shetland Islands, 4 – 17 years at Austasen, and 4 – 10 years at the Larsen Shelf. No individuals in an age class ≤ 3 were present within the areas of investigation. Fig. 14 shows the von Bertalanffy growth curves for all three areas. Overall, fish showed larger lengths for the same age classes at the South Shetland Islands than at the other two areas. Individuals in age class 10+ had an average length of 22.7 cm at the South Shetland Islands, 16.8 cm at Austasen, and 15.0 cm at the Larsen Shelf.

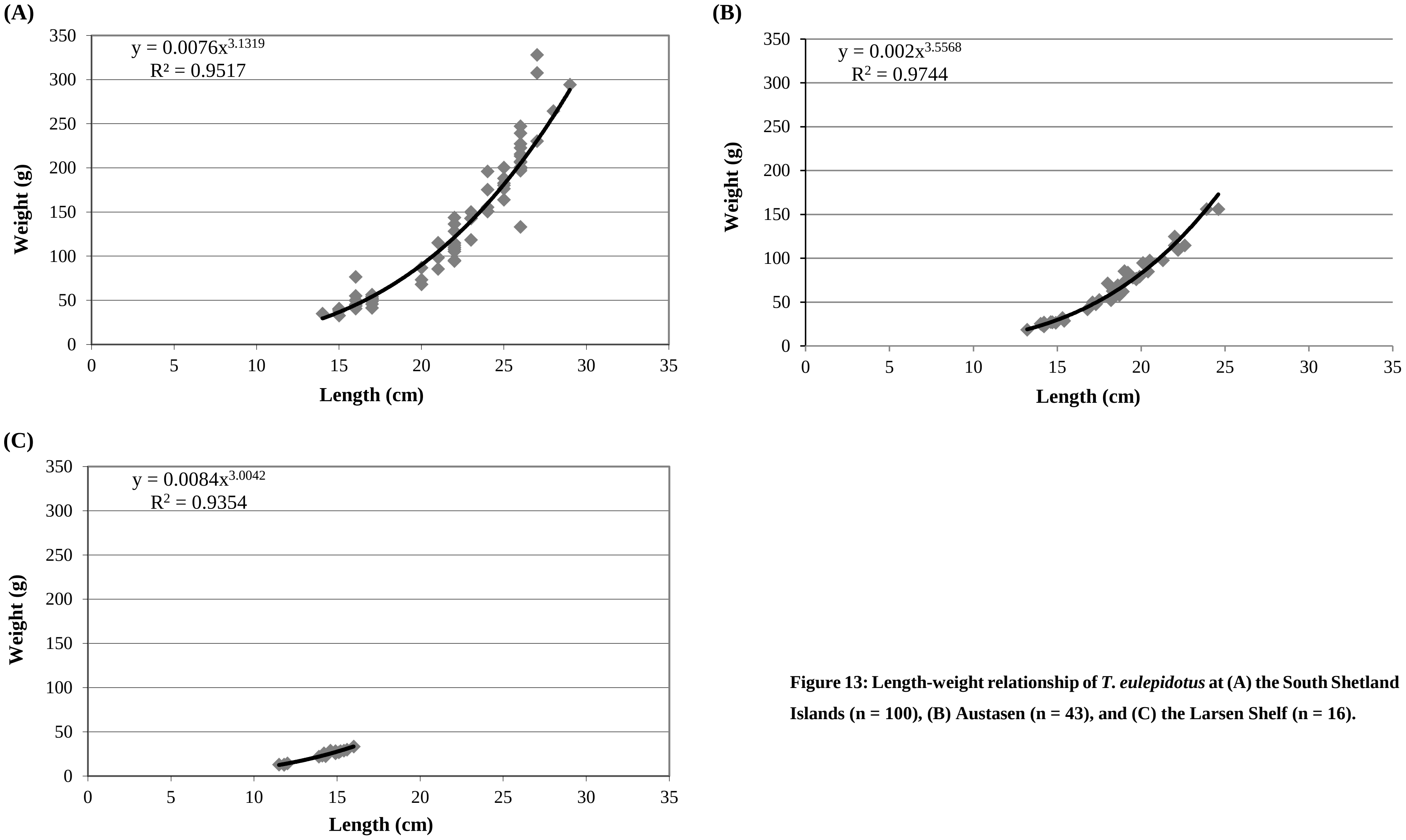


Figure 13: Length-weight relationship of *T. eulepidotus* at (A) the South Shetland Islands (n = 100), (B) Austasen (n = 43), and (C) the Larsen Shelf (n = 16).

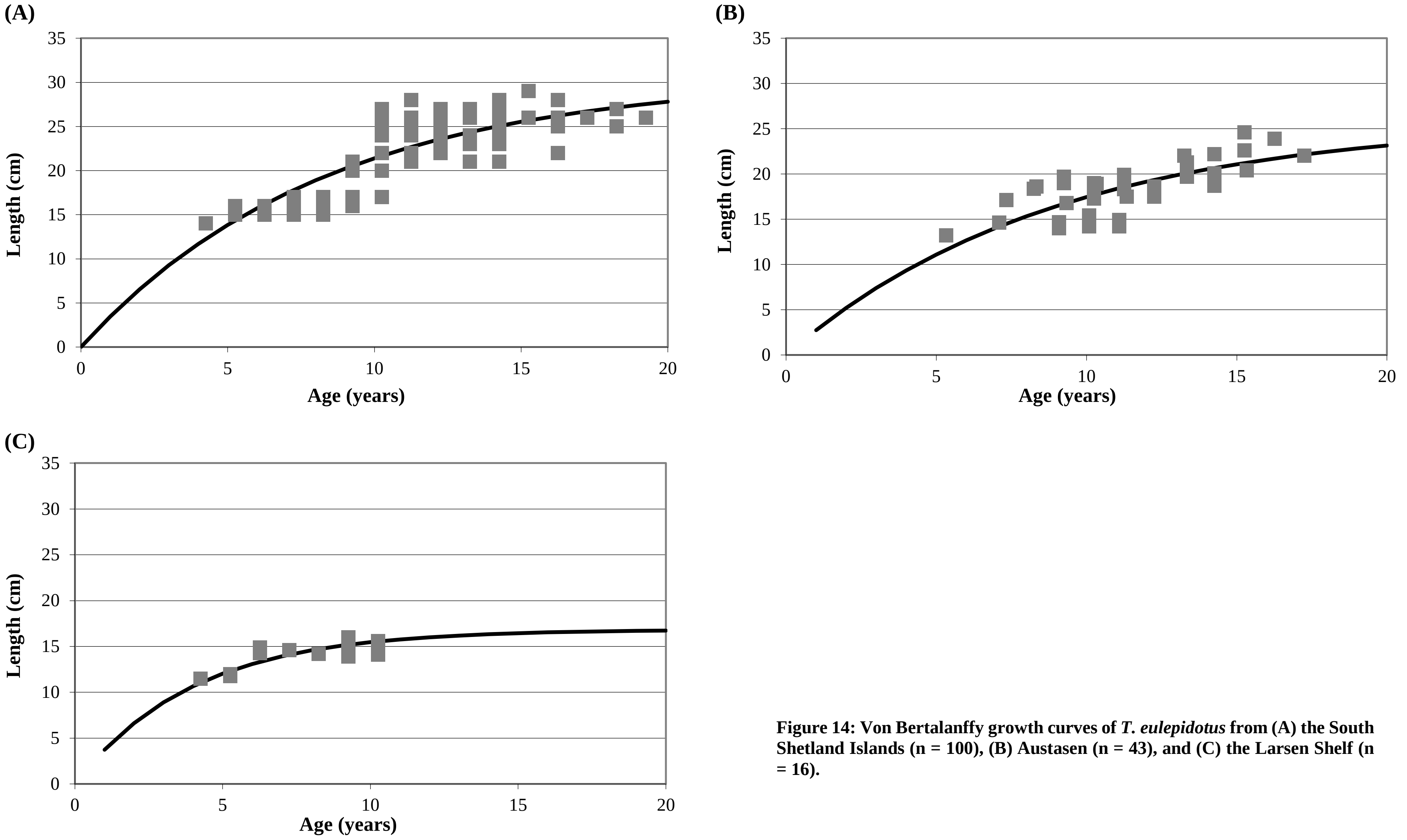


Figure 14: Von Bertalanffy growth curves of *T. eulepidotus* from (A) the South Shetland Islands (n = 100), (B) Austasen (n = 43), and (C) the Larsen Shelf (n = 16).

Statistical analysis of the growth curves via the test according to KAPPENMAN (1981) showed that growth for both investigated species differed among the different geographical regions of Antarctica (Tab. 2). Both species examined exhibited higher growth coefficients and therefore slightly faster growth in the areas of lower latitudes, such as the South Orkneys and the South Shetland Islands, than in the eastern Weddell Sea (Tab. 3). Only the comparison of the growth curves of *P. antarcticum* between the Larsen Shelf and King George Island and between King George Island and the eastern Weddell Sea did not show significant differences. Their estimated values for D_1 and D_2 were still relatively close to each other (Tab. 2).

Table 2: Statistical analysis of the growth curves from different areas of investigation according to KAPPENMAN 1981; D_1 = sum of the combined data sets; D_2 = sum of distinct data sets; + = significant difference; - = no significant difference.

Species	**Area**	**D_1**	**D_2**	**Significant difference**
P. antarcticum	Larsen Shelf - South Orkneys	279.68	242.23	+
	Larsen Shelf - King George Island	255.46	257.71	-
	Larsen Shelf - Eastern Weddell Sea	319.66	294.00	+
	South Orkneys - Eastern Weddell Sea	104.37	72.45	+
	South Orkneys - King George Island	62.33	36.16	+
	King George Island - Eastern Weddell Sea	85.30	87.93	-
T. eulepidotus	Austasen - Larsen Shelf	215.45	176.24	+
	Austasen - South Shetland Islands	1232.26	741.61	+
	South Shetland Islands - Larsen Shelf	898.51	587.46	+

Growth performance index Φ for *P. antarcticum* ranged from 1.84 - 1.94 for all investigated areas. The highest index values for *P. antarcticum* were observed at the South Orkneys with an overall growth performance index of Φ = 1.94. The eastern Weddell Sea had the lowest value at 1.84. In the other areas, growth performance values were in between those of the South Orkneys and the eastern Weddell Sea, with values of 1.87 for King George Island and 1.85 for the Larsen Shelf (Tab. 3).

Growth coefficients *k* of *P. antarcticum* varied between 0.166 – 0.232 within the different areas of investigation. Individuals grew faster in the more northern areas of King George Island and the South Orkneys than in the higher latitudes in the eastern Weddell Sea and at the Larsen Shelf. *P. antarcticum* did not show great differences in growth between females and males within one area. At the eastern Weddell Sea, a growth coefficient of $k = 0.220$ for both sexes and a growth performance index of $\Phi = 1.90$ for females and $\Phi = 1.91$ for males was calculated. In the area of the South Orkneys the growth coefficient was slightly higher for the females ($k = 0.324$) than for the males (0.322). Nevertheless, the growth performance index was the same for both sexes ($\Phi = 1.99$).

Table 3: Von Bertalanffy growth parameters ($L\infty$ = asymptotic length, k = growth coefficient, t_0 = time of hatching, R^2 = coefficient of correlation) and growth performance index Φ of *P. antarcticum* and *T. eulepidotus* from different investigated areas.

Species	Area	$L\infty$ (cm)	k	t_0	Age_{max} (years)	R^2	Φ	n
P. antarcticum	King Geroge Island	17.90	0.232	0	9	0.53	1.87	35
	South Orkneys	19.68	0.225	0	8	0.24	1.94	20
	Larsen Shelf	20.63	0.166	0	13	0.90	1.85	153
	Eastern Weddell Sea	19.16	0.188	0	12	0.94	1.84	66
T. eulepidotus	South Shetland Islands	30.53	0.121	0	19	0.68	2.05	100
	Larsen Shelf	16.84	0.250	0	10	0.71	1.85	16
	Eastern Weddell Sea	25.90	0.112	0	17	0.53	1.88	43

The difference in the growth performance index of *T. eulepidotus* was greater between the different areas of investigation compared to the values obtained for *P. antarcticum*. Whereas the growth performance index was almost the same for the Larsen Shelf ($\Phi = 1.85$) and the eastern Weddell Sea ($\Phi = 1.88$), the value for the South Shetland Islands, where a growth performance index of $\Phi = 2.05$ was observed, was markedly higher.

The estimated growth coefficients for *T. eulepidotus* varied between 0.112 – 0.250 within all areas investigated in this study. Growth seemed to be faster in the area of the Larsen Shelf ($k = 0.250$) than at the South Shetland Islands ($k = 0.121$) and at Austasen ($k = 0.122$). The growth of the sexes of *T. eulepidotus* differed only slightly from each other. Females at the eastern Weddell Sea had a slightly lower k-value (0.110) than the males (0.128) but a higher index of growth performance (1.87) than the males (1.86). On the other hand, *T. eulepidotus* had a higher growth coefficient for females ($k = 0.262$) than for males ($k = 0.260$) at the Larsen Shelf.

4.3 Production

P. antarcticum exhibited differences in annual length growth and weight increase within different areas. In the area of the South Orkneys, the fastest length increase took place during the first life stages as illustrated in Fig. 15. From the first to the second year, individuals grew 3.17 cm on average at the South Orkneys, whereas individuals from the Larsen Shelf grew 2.67 cm on average in the same year. Length growth seemed to be faster in the first years of life in the areas of the South Orkneys and King George Island, but also decreased faster in later years. In the age classes of 13 - 15 years, individuals still grew a bit more at the more southern areas of the Larsen Shelf (0.26 - 0.36 cm / year) and the eastern Weddell Sea (0.20 - 0.29 cm / year) compared to the South Orkneys (0.14 - 0.21 cm / year) and King George Island (0.11 - 0.18 cm / year).

T. eulepidotus had the fastest length growth within the first few years at the South Shetland Islands (Fig. 16). Here, individuals grew 3.08 cm on average from the first to the second year. Length growth seemed to decrease the fastest at the Larsen Shelf. At higher ages (age classes of 17 - 20) individuals only grew 0.03 - 0.05 cm per year. This may be due to the fact that individuals from this area had a small asymptotic length of 16.84 cm but a relatively high growth coefficient of k = 0.25 (Tab. 3). In the same age classes of 17 – 20 years, individuals from the South Shetland Islands still grew about 0.35 – 0.45 cm per year, and 0.33 – 0.41 cm per year at Austasen.

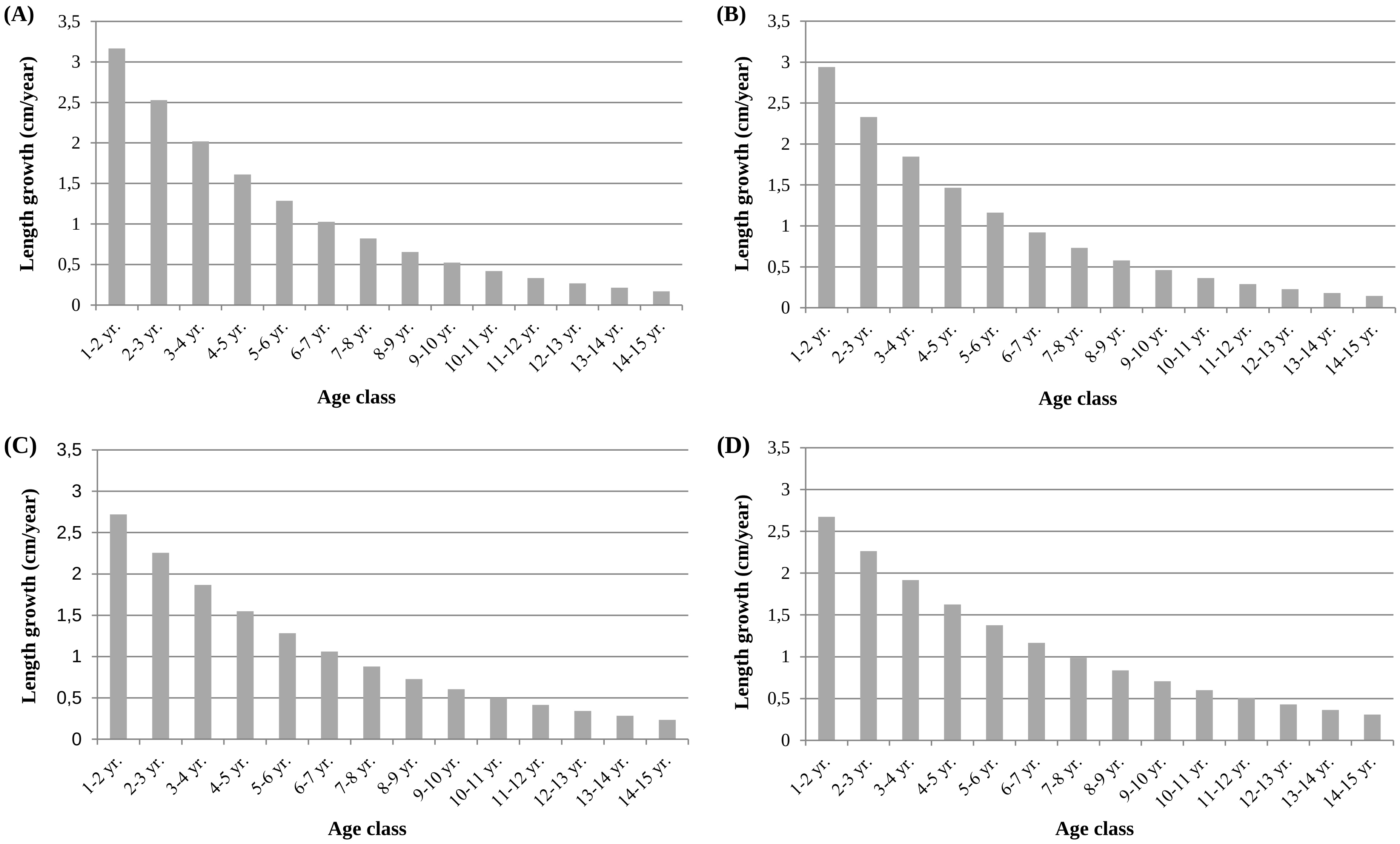
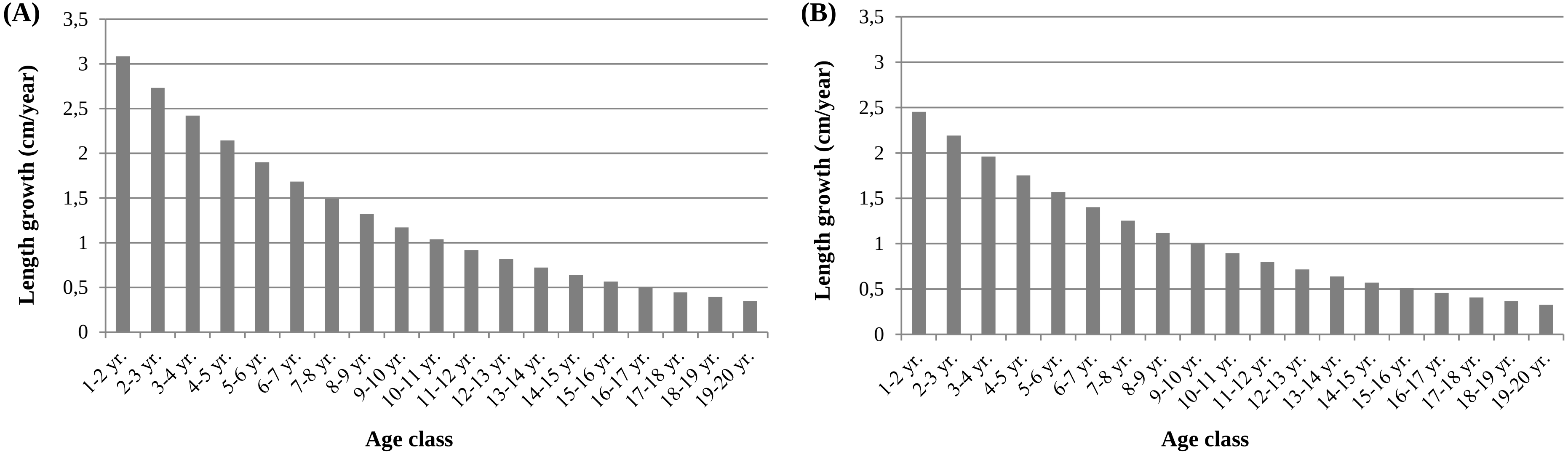

(A)
Length growth (cm/year)
0
0,5
1
1,5
2
2,5
3
3,5
1-2 yr.
2-3 yr.
3-4 yr.
4-5 yr.
5-6 yr.
6-7 yr.
7-8 yr.
8-9 yr.
9-10 yr.
10-11 yr.
11-12 yr.
12-13 yr.
13-14 yr.
14-15 yr.
Age class
(B)
Length growth (cm/year)
Age class
(C)
Length growth (cm/year)
Age class
(D)
Length growth (cm/year)
Age class

Figure 15: Comparison of the increase in length of *P. antarcticum* at (A) the South Orkneys, (B) King George Island, (C) the eastern Weddell Sea, and (D) the Larsen Shelf for the different age classes. Production is shown for each year, beginning with the increment between the first and second year.



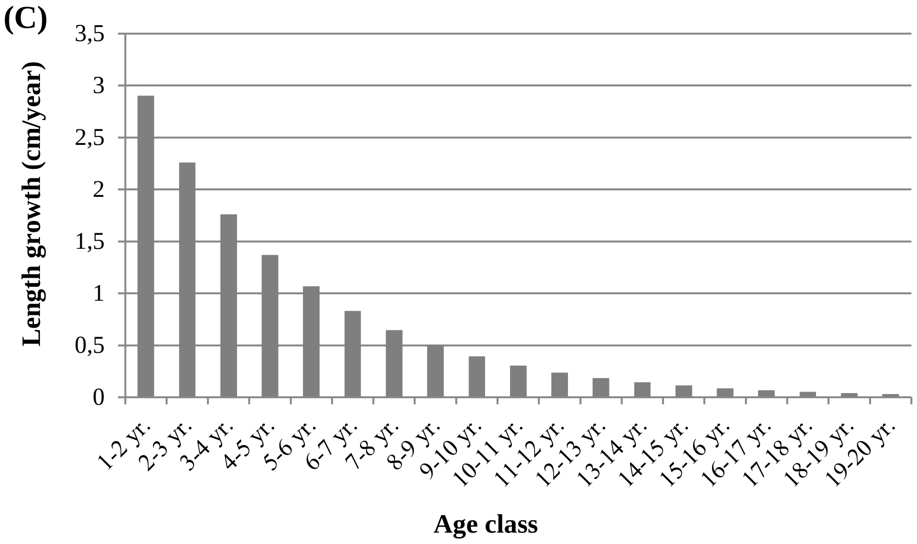


Figure 16: Comparison of the increase in length of *T. eulepidotus* at (A) the South Shetland Islands (B) Austasen, and (C) the Larsen Shelf for the different age classes. Production is shown for each year, beginning with the increment between the first and second year.

Annual production in weight for *P. antarcticum* revealed little variations within the different areas of investigation. In the graphs of Fig. 17, it can be seen that the production of the individuals concerned slightly faster at the South Orkneys and King George Island than at the eastern Weddell Sea or the Larsen Shelf. Whereas annual weight production at the South Orkneys and King George Island was about 0.5 g in the age classes of 19 to 20 years, production at the eastern Weddell Sea was still 1.0 g / year for the same age range and at the Larsen Shelf even 1.5 g / year. The maximum weight increase took place at an age between 5 – 8 years for *P. antarcticum*. At the South Orkneys individuals had a maximum weight increase of 7.93 g / year between the 5th and 6th year, whereby the maximum increase at the eastern Weddell Sea was just 5.20 g / year from the 6th to the 7th year.

The annual weight increase of *T. eulepidotus* showed larger variability within the different areas than with *P. antarcticum*. The increase in weight for the individuals investigated appeared to be the greatest at the South Shetland Islands (Fig. 18). Here, the maximum increase in weight was exhibited by the age classes of 8 - 11 years at 17 - 18 g per year. The annual weight increase was lowest at the Larsen Shelf with a maximum of 4.50 g / year in the years between age class 4 and 5. In the age classes of 19 – 20 years, *T. eulepidotus* exhibited a weight increase of 9.83 – 11.78 g / year at the South Shetland Islands and 7.03 – 8.09 g / year at Austasen, but only an increase of 0.23 – 0.38 g / year at the Larsen Shelf.

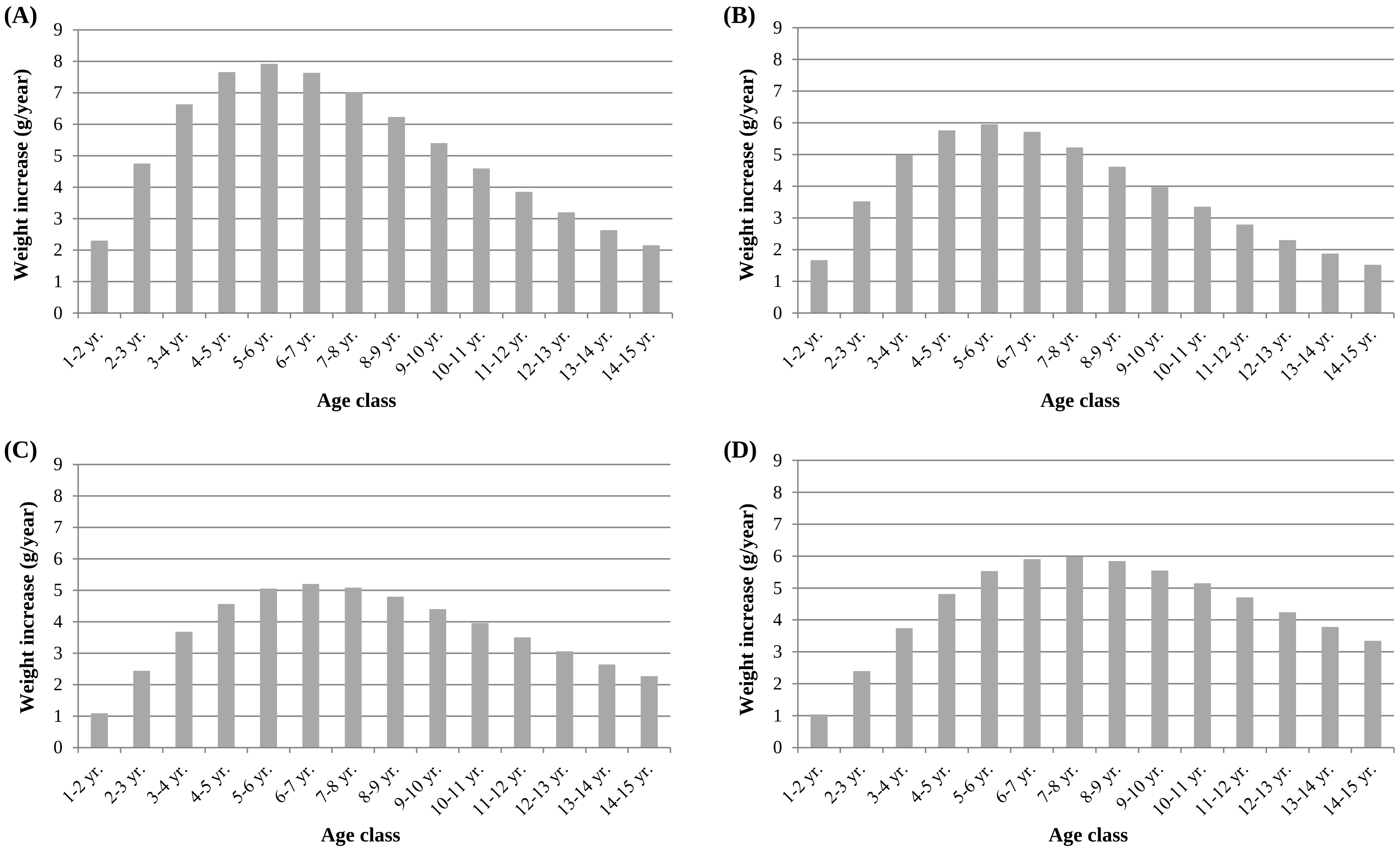
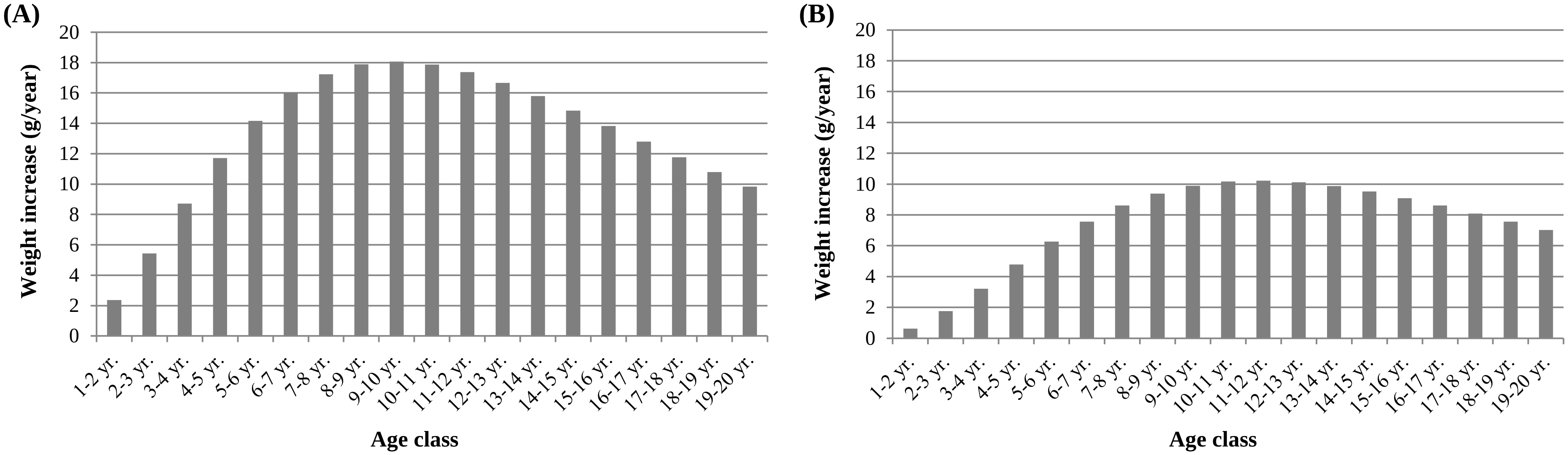

(A)
(B)
(C)
(D)
Weight increase (g/year)
0
1
2
3
4
5
6
7
8
9
Age class
1-2 yr.
2-3 yr.
3-4 yr.
4-5 yr.
5-6 yr.
6-7 yr.
7-8 yr.
8-9 yr.
9-10 yr.
10-11 yr.
11-12 yr.
12-13 yr.
13-14 yr.
14-15 yr.

Figure 17: Comparison of the annual weight increase of *P. antarcticum* at (A) the South Orkneys, (B) King George Island, (C) the eastern Weddell Sea, and (D) the Larsen Shelf for the different age classes. Production is shown for each year, beginning with the increment between the first and second year.



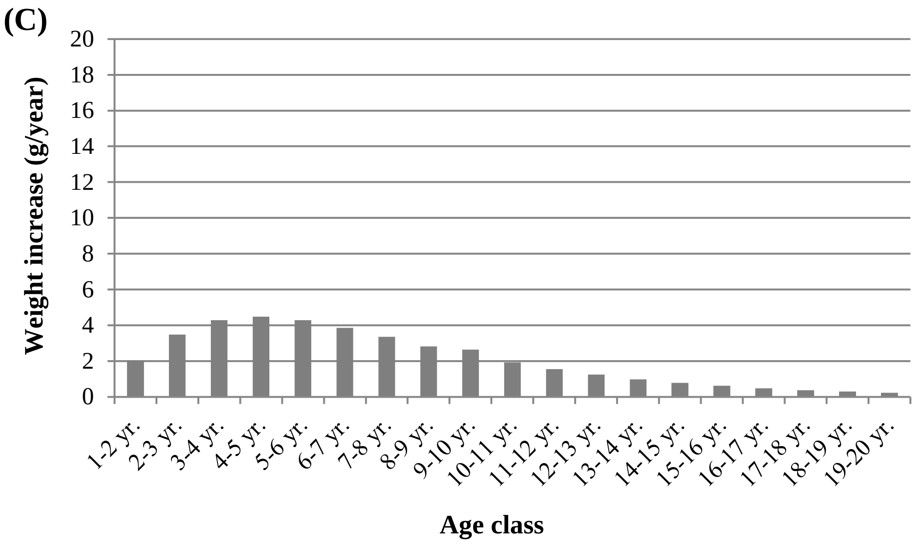


Figure 18: Comparison of the annual weight increase of *T. eulepidotus* at (A) the South Shetland Islands (B) Austasen and, (C) the Larsen Shelf for the different age classes. The production is shown for each year, beginning with the increment between the first and second year.

Abundance and biomass data were used to point out the population dynamics of the populations of both species from different regions. Via these data, provided by KNUST (personal communication, October 2012), the production of the populations of both species were calculated for the different areas under investigation. Hence, production does not say something about the growth of single individuals but rather about the annual production of whole populations and therefore, provides an understanding of the trophic ecology and sets the limit on food/energy availability for higher trophic levels (MERTZ & MYERS 1998). *P. antarcticum* appeared to be most abundant in the area of King George Island with 0.004 n / m². The abundance of *P. antarcticum* decreased from King George Island to the south. This was also evident from comparing the biomass and mortality of *P. antarcticum* for the different areas of investigation (Tab. 4). Both were higher in the more northern areas of the South Orkneys and King George Island compared to the areas of the eastern Weddell Sea and the Larsen Shelf. As annual production is a consequence of biomass and mortality, it provides evidence of the ecological success of the populations. Results of annual production showed the same trend as observed for the biomass. So production (quantity of tissue elaborated per year) was by far the highest at King George Island (0.04 - 0.06 g / m² per year), whereas production seemed to lower towards the south. The lowest production values were obtained at the eastern Weddell Sea, with an annual production of 0.0005 - 0.0009 g / m².

In contrast, *T. eulepidotus* exhibited the greatest abundance in the most southern investigated area, the eastern Weddell Sea (Tab. 4). Here, an abundance of 0.0007 n / m² was calculated. In the more northern areas of the Larsen Shelf and the South Shetland Islands, abundance appeared to decrease. The estimated mortality values of *T. eulepidotus* were, in comparison to *P. antarcticum,* lower in the areas of the South Shetland Islands and Austasen. Only at the Larsen Shelf did mortality seem to be quite high, with values between 0.352 – 0.571 yr^{-1}. Biomass and annaul production was highest at Austasen. Here, annual production ranged between 0.001 – 0.002 g / m².

Table 4: Abundance, average annual temperature (T), biomass (B), production (P) and mortality of *P. antarcticum* and *T. eulepidotus* from different investigated areas. Abundance and biomass data from POLARSTERN cruises in the years 1996 – 2011 according to KNUST (personal communication, October 2012). Mortality *M* was calculated by

the formula according to Hewitt & Hoenig 2005; Mortality expressed as $ZW\infty$ and $ZL\infty$ was calculated by the formula according to Pauly 1980.

Species	Area	Abundance (n/1000 m^2)	T (°C)	B (g/1000 m^2)	P (g/1000 m^2)	M	$ZW\infty$	$ZL\infty$
P. antarcticum	South Orkneys	0.458	- 0.158	14.12	4.48 - 7.22	0.317	0.499	0.511
	King George Island	4.920	- 0.452	118.55	38.77 - 63.19	0.327	0.514	0.533
	Eastern Weddell Sea	0.050	- 1.559	1.90	0.50 - 0.85	0.265	0.430	0.445
	Larsen Shelf	0.338	- 1.789	7.41	1.73 - 2.99	0.233	0.393	0.404
T. eulepidotus	South Shetland Islands	0.018	- 0.332	1.17	0.20 - 0.35	0.170	0.284	0.298
	Austasen	0.722	- 1.599	71.62	11.32 - 21.20	0.158	0.285	0.296
	Larsen Shelf	0.078	- 1.789	2.59	0.91 - 1.48	0.352	0.563	0.571

4.4 Condition

The estimated condition factors (*Cf*) of *P. antarcticum* were significantly different among the investigated areas. The average condition factor was highest at the South Orkneys, whereas it was lower in the more southern regions of the Larsen Shelf and the eastern Weddell Sea (Fig. 19A). At the South Orkneys highest *Cf*-value was observed with 1.12. Whereas *Cf*-values were mainly lower than 0.85 at the eastern Weddell Sea and the Larsen Shelf, values at the South Orkneys and King George Island were mainly higher than 0.90. The *Cf*-values obtained differed significantly among almost all four areas. Applying the Student`s t-test (significance level $\alpha = 0.05$) confirmed these significant differences statistically. Only between the areas of the eastern Weddell Sea and the Larsen Shelf no significant differences were estimated in the *Cf*-values ($p = 0.29$).

The condition factor of *T. eulepidotus* was highest at the South Shetland Islands (Fig. 19B), with values greater than 2, whereas the lowest values were obtained at the Larsen Shelf. Here, *Cf*-values varied between 1.10 – 1.45. *Cf*-values differed significantly between the Larsen Shelf and the South Shetland Islands and the Larsen Shelf and Austasen. No significant difference was found between Austasen and the South Shetland Islands ($p = 0.14$).

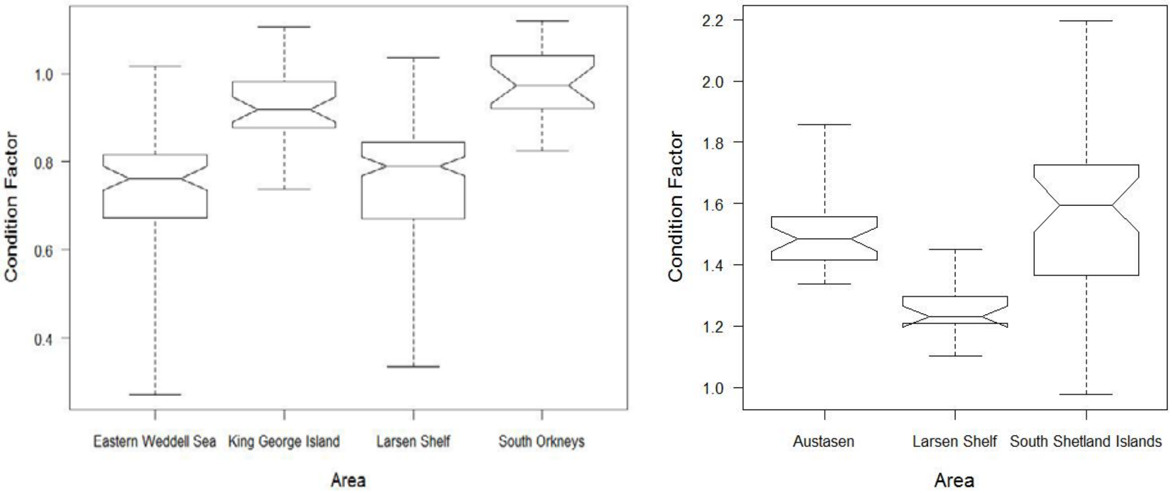


Figure 19: (A) Condition factor (*Cf*) of *P. antarcticum* at the South Orkneys (n = 20), King George Island (n = 35), the Larsen Shelf (n = 152), and the eastern Weddell Sea (n = 66); and (B) the condition factor (*Cf*) of *T. eulepidotus* at Austasen (n = 33), the South Shetland Islands (n = 40), and the Larsen Shelf (n = 16).

The gonadosomatic index (GSI) of *P. antarcticum* was fairly low in all investigated areas. Fish were caught during spring and summer. At this time, the weight of the gonads is generally quite low, as gonads are still not mature and still in a “resting stage”. GSI values were not greater than 2.76 within all areas (Fig. 20A). Statistical analyses via the Mann-Whitney U test (significance level $\alpha = 0.05$) confirmed that the GSI were significantly different between almost all of the four areas. It was only between the South Orkneys and King George Island ($p = 0.055$) that no significant difference was determined.

The GSI of *T. eulepidotus* was quite low as well, with a maximum value of 3.80 being reached at the South Shetland Islands. At Austasen and the Larsen Shelf, the GSI values were considerably lower than at the South Shetland Islands (Fig. 20B), where the maximum values of 2.99 (Austasen) and 0.93 (Larsen Shelf) were observed. Statistical comparison showed that the GSI values of *T. eulepidotus* differed significantly among all areas of investigation with p-values equal to zero ($p < 0.05$).

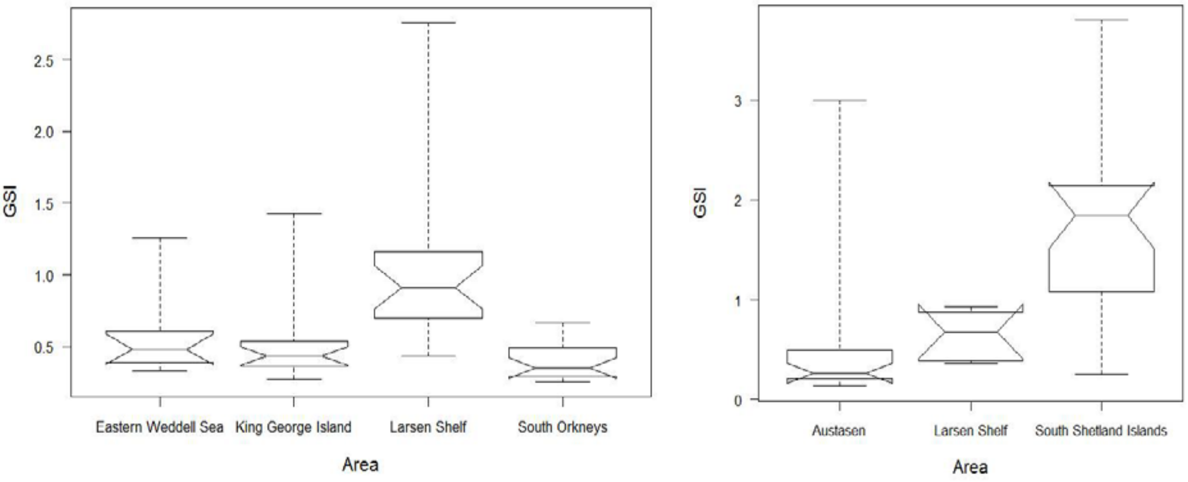


Figure 20: (A) Gonadosomatic index (GSI) of *P. antarcticum* at the eastern Weddell Sea (n = 11), King George Island (n = 19), Larsen Shelf (n = 24), and South Orkneys (n = 20); and (B) the gonadosomatic index (GSI) of *T. eulepidotus* at Austasen (n = 21), the Larsen Shelf (n = 8), and the South Shetland Islands (n = 25).

The hepatosomatic index (HSI) indicated significant differences between the investigated areas as well. Individuals of *P. antarcticum* had the highest HSI value at the Larsen Shelf (HSI = 9.09), whereas the lowest values were calculated at King George Island (HSI = 0.69). On average the HSI was slightly higher at the more northern areas than the more southern areas, of the eastern Weddell Sea and the Larsen Shelf (Fig. 21A).

(A) **(B)**

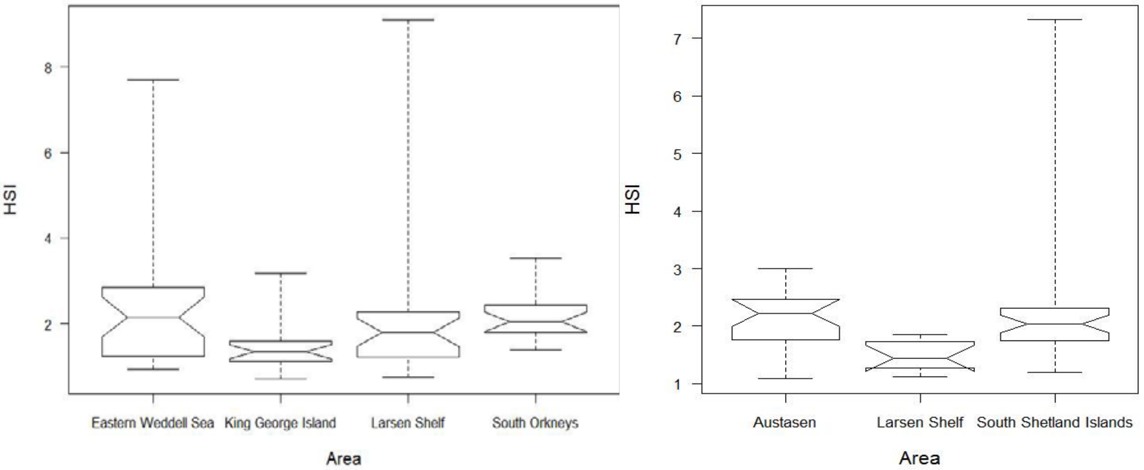


Figure 21: (A) Hepatosomatic index (HSI) of *P. antarcticum* at the eastern Weddell Sea (n = 30), King George Island (n = 20), Larsen Shelf (n = 25), and the South Orkneys (n = 20); and (B) the hepatosomatic index (HSI) of *T. eulepidotus* at Austasen (n = 21), Larsen Shelf (n = 10), and South Shetland Islands (n = 33).

Statistical analyses verified significant differences between all areas (p-values < 0.05) except between the areas of the Larsen Shelf and South Orkneys, where the p-value was estimated to be exactly 0.05.

The HSI of *T. eulepidotus* had nearly the same distribution as the values of *P. antarcticum*. The values of the South Shetland Islands and Austasen were higher than those of the Larsen Shelf (Fig. 21B). The highest value of 7.32 was discovered at the South Shetland Islands. But here as well, values of 1.19 occurred. Thus, the range of HIS values for *T. eulepidotus* was quite high in this area. At Austasen, values varied between 1.08 – 3.00, and at the Larsen Shelf between 1.12 – 1.85. Statistical analyses revealed that the HSI were significantly different among all three investigated areas as the estimated p-values equal to zero.

4.5 Energy Content

Tab. 5 and 6 display the total carbon contents, the kilocalories, and the lipid contents for *P. antarcticum* and *T. eulepidotus* in juveniles and adults from the different areas of investigation. Actual carbon contents were between 2.90 – 3.97 g on average for adult *P. antarcticum*, showing a mean wet weight between 26.80 – 36.05 g within all areas of investigation. Carbon contents of juveniles varied between 0.52 – 0.65 g in the areas of the eastern Weddell Sea and the Larsen Shelf. The lipid content of adults varied with an average range of 3.20 – 4.14 g, whereas juveniles showed a distinctly lower lipid content with an average range of 0.34 – 0.42 g.

Table 5: Energy content of *P. antarcticum* distinguishing between juvenile and adult individuals from the areas of investigation. TL = total length; SL = standard length; WW = wet weight; DW = dry weight; kcal = kilocalories.

P. antarcticum		**South Orkneys**	**King George Is.**	**Eastern Weddell Sea**		**Larsen Shelf**	
		Adults	**Adults**	**Juveniles**	**Adults**	**Juveniles**	**Adults**
TL	Mean	17.30	16.26	9.12	18.31	9.58	16.20
	Range	15.7 - 18.7	14.2 - 19.9	4.8 - 12.2	17.4 - 20.6	6.3 - 13.6	13.7 - 22.2
	n	20	35	26	9	75	68
SL	Mean	15.40	14.24	8.35	15.93	8.50	14.40
	Range	13.9 - 16.5	12.0 - 17.0	4.2 - 11.1	13.4 - 18.2	5.8 - 11.9	12.1 - 19.6
	n	20	35	35	31	79	74
WW (g)	Mean	36.05	27.40	4.75	34.72	5.94	26.80
	Range	23.1 - 50.3	15.4 - 51.6	0.3 - 10.6	14.9 - 60.3	1.0 - 14.0	13.3 - 68.3
	n	20	35	35	31	79	73
DW (g)	Mean	9.01	6.85	1.19	8.68	1.49	6.70
	Range	5.8 - 12.6	3.9 - 12.9	0.1 - 2.7	3.7 - 15.1	0.3 - 3.5	3.3 - 17.1
	n	20	35	35	31	79	73
Carbon (g)	Mean	3.97	3.01	0.52	3.82	0.65	2.90
	Range	2.5 - 5.5	1.7 - 5.7	0.03 - 1.2	1.6 - 6.6	0.1 - 1.54	1.5 - 7.5
	n	20	35	35	31	79	73
kcal	Mean	41.45	31.51	5.46	39.92	6.83	30.80
	Range	26.6 - 57.9	17.7 - 59.3	0.4 - 12.2	17.1 - 69.3	1.2 - 16.1	15.3 - 78.5
	n	20	35	35	31	79	73
Lipid (g)	Mean	4.03	3.27	0.34	4.14	0.42	3.20
	Range	2.6 - 5.6	1.8 - 6.2	0.02 - 0.8	1.8 - 7.2	0.1 - 1.0	1.6 - 8.1
	n	20	35	35	31	79	73

T. eulepidotus had higher carbon content values than did *P. antarcticum* (Tab. 6). The carbon content of adult *T. eulepidotus* varied between 9.56 – 18.54 g on average, and even juveniles had a carbon content of 2.59 – 5.15 g on average within the different investigated areas. However, it should be duly considered that the individuals of *T. eulepidotus* exhibited distinctly higher wet weights, ranging between 23.57 – 168.28 g on average, whereas *P. antarcticum* had wet weights measuring between 4.75 – 36.05 g on average. The lipid content of juvenile *T. eulepidotus* varied between 1.76 – 3.49 g on average. Adults had a lipid content of 10.36 g on average at the eastern Weddell Sea and 20.07 g on average at the South Shetland Islands.

Table 6: Energy content of *T. eulepidotus* distinguishing between juvenile and adult individuals from the areas of investigation. TL = total length; SL = standard length; WW = wet weight; DW = dry weight; kcal = kilocalories.

T. eulepidotus		**South Shetland Island**		**Eastern Weddell Sea**		**Larsen Shelf**
		Juveniles	**Adults**	**Juveniles**	**Adults**	**Adults**
TL	Mean	16.08	24.06	15.34	20.04	14.08
	Range	14.0 - 17.0	20.0 - 29.0	13.2 - 17.5	18.0 - 24.6	11.5 - 16.0
	n	25	48	16	27	16
SL	Mean	14.68	21.81	14.33	17.69	12.26
	Range	13.4 - 15.2	18.5 - 25.3	11.1 - 15.4	15.6 - 21.9	9.9 - 13.7
	n	8	32	6	27	16
WW (g)	Mean	46.78	168.28	32.98	86.87	23.57
	Range	32.6 -76.5	68 - 327.8	18.4 - 52.3	52.2 - 156.0	12.7 - 33.5
	n	25	48	16	27	16
DW (g)	Mean	11.72	42.07	8.25	21.72	5.89
	Range	8.2 - 19.1	17.0 - 82.0	4.6 - 13.1	13.1 - 39.0	3.18 - 8.38
	n	25	48	16	27	16
Carbon (g)	Mean	5.15	18.54	3.63	9.56	2.59
	Range	3.6 - 8.4	7.5 - 36.1	2.0 - 5.8	5.7 - 17.2	1.4 - 3.7
	n	25	48	16	27	16
kcal	Mean	53.90	193.53	37.93	99.91	27.10
	Range	37.5 - 88.0	78.2 - 377.0	21.2 - 60.2	60.0 - 179.4	14.6 -38.5
	n	25	48	16	27	16
Lipid (g)	Mean	3.49	20.07	2.46	10.36	1.76
	Range	2.4 - 5.7	8.1 - 39.1	1.4 - 3.9	6.2 - 18.6	1.0 - 2.5
	n	25	48	16	27	16

The annual enrichment of energy reserves in *P. antarcticum* was highest at lower latitudes in the areas of the South Orkneys and King George Island (Tab. 7). Especially at King George Island, carbon (6.95 g / 1000 m²) and lipid (7.54 g / 1000 m²) contents were considerably higher than at higher latitudes. At the eastern Weddell Sea, the annual carbon and lipid enrichment were the lowest with values of 0.09 g / 1000 m² and 0.10 g / 1000 m².

Contradicted values of the annual enrichment of energy reserves were observed for *T. eulepidotus*. This is the same for biomass, mortality, and production estimates in Tab. 4.

Considerably higher enrichments of carbon and lipids were determined at the eastern Weddell Sea in the area of Austasen. Here, annual carbon and lipid production were 2.33 g / 1000 m^2 and 2.53 g / 1000 m^2. The lowest values were calculated for the South Shetland Islands. Whereas *P. antarcticum* exhibited annaul production values of 6.95 g / 1000 m^2 in carbon at the South Shetland Islands, *T. eulepidotus* showed markedly lower values of 0.04 g / 1000 m^2.

Table 7: Maximum annual production of wet weight (WW), dry weight (DW), carbon, kilocalories (kcal), kilojoules (kJ), and total lipid of *P. antarcticum* and *T. eulepidotus* from different areas of investigation.

Species	Area	WW (g/1000 m^2)	DW (g/1000 m^2)	Carbon (g/1000 m^2)	kcal	kJ	Lipid (g/1000 m^2)
P. antarcticum	South Orkneys	7.22	1.81	0.79	8.30	34.78	0.86
	King George Island	63.19	15.80	6.95	72.67	304.49	7.54
	Eastern Weddell Sea	0.85	0.21	0.09	0.98	4.12	0.10
	Larsen Shelf	2.99	0.75	0.33	3.44	14.41	0.36
T. eulepidotus	South Shetland Islands	0.35	0.09	0.04	0.40	1.68	0.04
	Austasen	21.20	5.30	2.33	24.38	102.15	2.53
	Larsen Shelf	1.48	0.37	0.16	1.70	7.12	0.18

5 METHODOLOGICAL DISCUSSION

The age of fish was determined via otoliths as their growth is directly related to the growth of fish (PILLING *et al.* 2007). Age can also be determined by other hard structures such as scales or bones that form growth rings (GRÖGER 2000). Using scales has the advantage that the extraction method is not lethal for the fish (PANFILI 2002). However, bones and scales do not show growth if the body growth is reduced or the food intake stops (CAMPANA & THORROLD 2001). In contrast, otoliths show features that are not present in other hard structures. Otoliths are no skeletal structures and therefore, do not occupy a postural function. In otoliths material accretion also takes place if the somatic growth stops. Thus, otoliths are the only calcified hard structures in fish that grow throughout their life (HILDEBRANDT 2009). Even though the growth of the otoliths seems to be continuous it correlates with the growth of the fish, also in phases in which no body growth takes place (MAILLET & CHECKLEY 1990). Furthermore, otoliths are metabolically stable. Material that accreted once is not going to be resorbed again and the chemical composition of otoliths therefore remains persistent over time (WALTHER & THORROLD 2006). Resorption can take place in bones or scales due to starvation or other stressors (HILDEBRANDT 2009; CAMPANA & THORROLD 2001).

5.1 Otolith Preparation

Removed and cleaned otoliths can be stored dry but also in liquids such as water, ethanol, formalin or glycerin. However, these are known to brighten up the structures of the otoliths and reduce their clarity (SIGLER & SIGLER 1990). Therefore, it is recommended just to store them dried without any of these liquids. It is well known, that in some cases otoliths can brighten up to such a degree that the ring structures are no longer visible and consequently impractical for age determination. Hence, all otoliths for this study were simply stored dry in tubes or small bags for the later age determination.

5.2 Weight and Length Measurement

Different methods are possible for weighing otoliths. Mass can be directly determined by weighing as well as indirectly by applying morphometric methods. However, morphometric methods have the disadvantage that often an exact measurement of the volume is impossible due to the unequal and irregular forms of the otoliths. Here, the mass can only be estimated by setting off the assumed volume of the body against the specific weight. Direct weighing via scales gives a very accurate indication even though it is restricted by the precision of the used scale. Furthermore, for direct weighing all otoliths need to be isolated and available without any debris.

In both investigated species the maximum diameter of the otoliths was taken because it is more precise instead of measuring from rostrum to postrostrum. Measurements from rostrum to postrostrum are often not accurately definable, because otoliths have irregularities even if they show an almost circular shape (HUBOLD 1989).

5.3 Age Determination

The determination of age is mostly done via otoliths as it is the best known method (DUJMIC 1997) for showing the best correlation with the actual age of the fish (CASSELMAN 1987). Still, it also involves some difficulties such as the occurrence of rings in between the actual growth rings. These may develop due to extreme stress like spawning (MÄCK 2009) and make the age determination more difficult. These “false rings” can often lead to a wrong estimation of the actual fish age (GASSNER *et al*. 2002).

Otoliths show allometric growth (JANTSCHIK 2007) which leads to an asymmetric shape and makes the estimation of the annuli difficult. This may result in variations of number and width of the annuli within the different zones. Furthermore, margins between the increments may be difficult to see and may appear diffuse (BLACK *et al*. 2005). Moreover, the sometimes obscure formation of the increment structures can be interpreted differently by different readers. Even the same reader may come to different conclusions while reading one and the same otolith several times. Therefore, age determination via otoliths requires a certain period of vocational adjustment and experience. In addition, the reader needs to decide during the reading of the otoliths whether the age should be adjusted downward or upward. So a rounding process takes place, by which the age of fish becomes an integer size although it is a continuous feature. As a result, the aging of fish takes place in yearly intervals (GRÖGER 2000). For that reason the estimated age classes of the fish in this study were standardized and referred to the month of capture before they were used for the statistical analyses.

An explicit and confident estimation of the age of fish needs experience and a lot of practice. Quite reliable evidence can be given for most cases of age determination in young fish (age class of 1-7). In older fish the age determination is increasingly difficult because the body growth is decreasing with an increasing age so that the annuli appear to be closer to each other. Hence, single annuli are more difficult to distinguish (DÖNNI *et al*. 1996).

Teleosts have three pairs of otoliths. For this study the sagitta was used because in most fish they are the biggest pairs (MORALES-NIN 1992) and are therefore, in most cases best suited for age determination. Moreover, the sagitta from different species differ in shape and size which is not as distinctively the case for the other otoliths pairs (asterisci and lapilli). Because of the typical morphology of sagittae, wrongly defined individuals can be allocated clearly to their true species and be suspended from the analysis (LOMBARTE & LLEONART 1993).

According to the literature there are different approaches for the analysis of otoliths and the reading of their annuli. For otoliths which are quite big it is reasonable to polish the otoliths down to their nucleus to see the single annuli better. In the case of *P. antarcticum* the otoliths were quite small and the annuli were already visible without being polished. In this case polishing might only have damaged the quite small otoliths of *P. antarcticum*. The otoliths of *T. eulepidotus* were considerably larger than the ones of *P. antarcticum*. Here, the otoliths needed to be polished as the increments were not readable by just transferring them into glycerin.

To avoid as many error sources as possible it would be worthwhile for future age determinations and growth estimations of fish to carry out the increment analysis of otoliths by two or three readers if the time permits it. Another option would be to do the age determination not just via otoliths but additionally via scales or bones. Thus, two readers could work at the same time, the age determination would be more exact than with just one reader and, furthermore, it would be interesting to compare the different methods of investigation and their accuracy and adaptability.

5.4 Statistical Analysis

To compare the growth performance of *P. antarcticum* and *T. eulepidotus* from the different areas of the Antarctic waters all age-length data were fitted to a von Bertalanffy growth equation. This function is based on the antagonistic effects of anabolism and catabolism and is one of the most commonly used growth models in the ichthyology (FONTOURA & AGOSTINHO 1996). The von Bertalanffy growth curve is based on the fact that the growth rate of fish is decreasing with increasing age and increasing size (MOSS 1998).

For the estimation of all von Bertalanffy growth curves the values for the parameter t_o were set to zero ($t_o = 0$), as without setting $t_o = 0$ the growth curves seemed to be deviating and wrong from the biological point of view. Without setting $t_o = 0$ individuals of an age of two or three years would have a standard length of zero centimeters and their growth would just start at that point of time. Furthermore, a lack of young individuals in the calculation of the growth coefficients may also lead in an underestimation of the parameter k (PILLING *et al.* 1999). Therefore, other authors constrained t_0 = zero as well. Generally, values for t_0 are negative, so that individuals have reached positive lengths at the time of birth. That is, larvae already have a certain size when hatching and may also display a completely different growth curve than adults (KUUN 1998). To avoid the wrong illustration in the biologically meaning, the value for t_o was set to zero for all created growth curves.

Apart from the von Bertalanffy function some other functions exist that can be used for fitting the age-length data to a growth curve. Another function would be for example the Gompertz function (ROY & SARANGI 2008). However, the Gompertz function is used relatively rarely by now, as the determination of the single parameters seems to be quite difficult and therefore, the evaluation of the obtained values may be problematic. Hence, the practicability of a growth function is not only based on the quality of the repetition of data but also especially on the explanatory power of the single parameters (KRÜGER 1967).

Annual production of both species was calculated over the biomass and the mortality and is therefore the result of these estimated data. The biomass of both species in this study could only be estimated from bottom trawl catches. This still gives a good overview of the biomass of both species from different geographical regions. Nevertheless, it has to be kept in mind, that *P. antarcticum* is a pelagic species and therefore, its biomass might be slightly underestimated. Thus, it would be advisable in further studies to obtain the biomass of *P. antarcticum* also from pelagic nets to get a more precise estimate. As *T. eulepidotus* is a bentho-pelagic species the estimates via the bottom trawls will reflect quite accurate its actual biomass.

Mortality was determined via two different methods according to HEWITT & HOENIG (2005) and PAULY (1980). Mortality is a parameter generally extremely difficult to obtain but still needed to estimate the population dynamics of fish. With both methods, mortality was calculated indirectly, based on general ecological and physiological considerations. For both methods mortality is calculated among other parameters via the growth coefficient (*k*), as it shows the highest partial correlation with the mortality. However, PAULY (1980) perceived that also the environmental temperature has an effect on the mortality. Regarding temperature in the equation, same growth parameters produce different values of mortality when changing the temperature values from e.g. 5 °C to 20 °C. Therefore, the equation according to PAULY (1980) might be more accurate, whereas the formula according to HEWITT & HOENIG (2005) still gives a rough idea of the approximate mortality of a fish population. Still, other factors than temperature that are not integrated in both equations may probably also affect the growth and therefore, the mortality of fish (KOCK 1992).

6 DISCUSSION

6.1 Otolith Shape and Size

Otoliths of *P. antarcticum* were relatively small in relation to their body length. The largest observed otolith diameter was 2.5 mm of an individual with a SL of 19 cm. Not only the fish size but also the otolith size is influenced by the growth rate of the fish. PAWSON (1990) suggested that otolith growth is not synchronous with the body growth of fish but rather with an additional time-dependent rate which results in slow growing individuals having heavy otoliths for their body size. This could not be confirmed by analysing the otoliths of *P. antarcticum*, which had small maximum diameters and small weights between 0.01 – 4.90 mg. During ontogenesis the shape of the otoliths seems to alter. While otoliths of smaller individuals appear almost circular in shape, otoliths of adults were more oval and discoidal. Otoliths of *T. eulepidotus* were quite thin but larger (1.9 - 6.2 mm) than the otoliths of *P. antarcticum*. The shape of the otoliths was not as circular as the ones of *P. antarcticum* but more oblong. LOMBARTE *et al.* (2010) examined ecomorphological trends and phylogenic inertia of otoliths in different Antarctic and sub-Antarctic notothenioids. The analyses showed that the otoliths of *P. antarcticum* differed from all other species by their wider, discoidal shape. Moreover, the shape of otoliths relate to the habitat dwelling and on the lifestyle of the species. Hence, benthic species show more oblong and larger otoliths in relation to their body size whereas planctonic and pelagic species have smaller otoliths with a rounder and more discoidal shape. This also matches the results of this study. The pelagic *P. antarcticum* showed small, nearly circular otoliths while the otoliths of the epibenthic *T. eulepidotus* were larger, longer and more oblong. Thus, analyses of size and shape of otoliths are useful in ecomorphological studies since there is a clear correlation between relative size and shape and the trophic niche of fish (LOMBARTE *et al*. 2010).

6.2 Growth Production of *P. antarcticum* and *T. eulepidotus*

Antarctic fish show slow growth compared to most fish from lower latitudes. There are several attempts to explain the slow annual growth of fish from the Southern Ocean. CLARKE

& NORTH (1991) and PÖRTNER *et al.* (2005) describe the following causes, which will be discussed in the subsequent chapter, as the main effects influencing growth:

- Low temperature as a limiting factor
- Seasonal variability and food availability
- Costs of maintenance and energy allocation

Age, growth rate and mortality are the life history characteristics influencing and controlling the productivity of fish (CAMPANA & THORROLD 2001). Stock numbers are the result of birth rates, recruitment rates and mortality rates of fish. These in turn are controlled by factors such as density effects which include e.g. the competition for food and space and predator risks. Density-independent effects may include changes in water temperature, storms, adverse currents and other physical characteristics of the environment (KING 1995). Geographic isolation by distance, oceanographic isolation by currents and thermal isolation by subzero temperatures constitute the Antarctic environments (EASTMAN 2000). Stable low temperatures and large variations in primary production which are coupled to seasonal changes in the ice-cover and day–length are characteristic for Antarctic waters (JOHNSTON 1993).

Both investigated species grow relatively slow, also compared to other Antarctic fish. In general, fish from tropic regions may have the potential to grow faster due to the higher temperatures (VAL *et al.* 2005) as sufficient food may be available throughout the year. From tropical fish growth coefficients *(k)* up to 2 are known (HILDEBRANDT 2009). Antarctic fish show a reduction in feeding activity and mobilization of lipid reserves during winter months. Thus, lower growth rates may be a result of appetite suppression and of a possible food limitation during the winter months (CAMPBELL *et al.* 2008). However, differences in growth rates of fish are not only found between polar, temperate and tropical regions but also within them, e.g. between sub-Antarctic and high-Antarctic regions. Fig. 22 illustrates the relation between the environmental temperature and the growth coefficient of several fish species from polar to tropical regions. It is shown that the growth coefficient of fish appears to increase with increasing environmental temperatures. Hence, growth seems to depend on habitat temperatures and thus, on latitudinal distribution of a species. However, the mechanisms governing the distribution of Antarctic fish are still poorly understood as being driven by complex environmental physical and biological interactions (KOCK 1992). But slow growth rates are also reported from warmer waters, and Antarctic species of the family Channichthyidae show faster growth than species of the families Nototheniidae, Bathydraconidae and Artedidraconidae within the same habitats (HUBOLD 1992). Although temperature is an important parameter influencing chemical reactions and thus biological processes such as metabolism, growth, and fast-start performance, there are other factors influencing these processes (CLARKE & NORTH 1991). Under advantageous circumstances, when energy is primarily allocated to growth, some polar species can have almost the same growth performances as temperate or tropical species of related size and ecology (PÖRTNER *et al.* 2005). Therefore, growth of notothenioids is not simply referable to meridional temperature gradients. Growth also seems to be controlled by ecological requirements for the habitats and niches of single species (HUBOLD 1992).

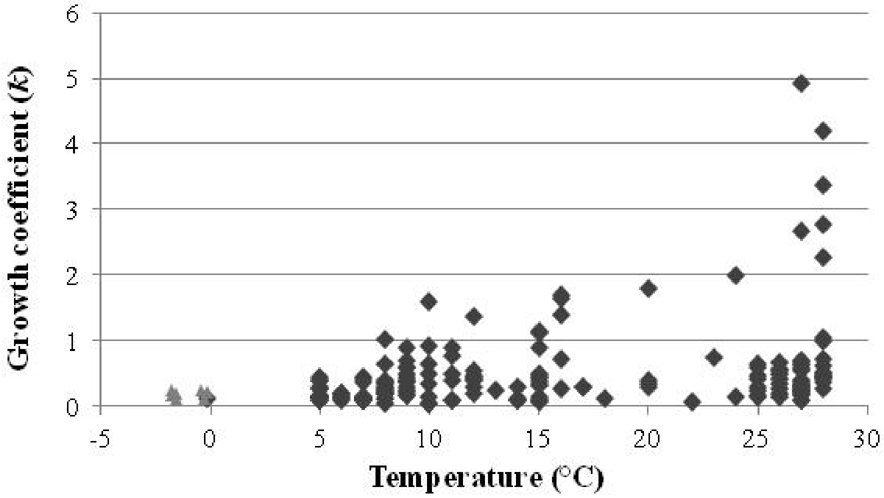


Figure 22: Relation between the environmental temperature (°C) and the growth coefficient (*k*) of the Bertalanffy growth function of different fish species ranging from polar to tropical waters. Black data points were estimated by PAULY (1980); grey data points are the estimated values for *P. antarcticum* and *T. eulepidotus* from this study.

Also within the Antarctic waters, fish exhibit different growth performances which might be attributed to the different life styles of different species. Pelagic species are fuelled by higher metabolic rates at the expense of reduced growth. Hence, growth performance increases from pelagic to benthic lifestyles (PÖRTNER *et al.* 2005). Fig. 23 shows differences in the growth performance (*P*) of several Antarctic fish species. Whereas *T. scotti* shows a growth performance of < 1, *D. mawsoni* grows much larger with a growth performance of nearly 4. Within Antarctic fish, *P. antarcticum* and *T. eulepidotus* show relatively low to moderate values of growth performance. These quite low values for *P. antarcticum* and *T. eulepidotus* are based on relatively slow growth rates and as well as small asymptotic lengths these species can reach.

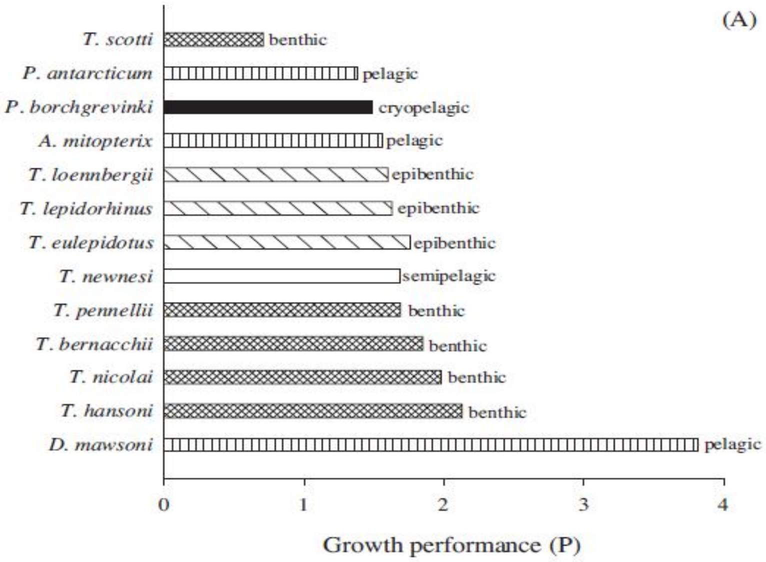


Figure 23: Overall growth performance (*P*) of several notothenioid fish species in relation to their mode of life in the high-Antarctic zone (PÖRTNER *et al* 2005). Growth performance is here defined as the growth rate at the inflection point of size (mass) of the growth curve estimated by $P = (\log k + \log M\infty)$.

The correlation between average annual environmental temperature and the growth performance (Φ) of the two investigated species *P. antarcticum* and *T. eulepidotus* is shown in Fig. 24. Even though just a few data sets are available, the growth performance index was higher in the lower latitudes where the average environmental temperature was higher. However, the growth performance of *T. eulepidotus* seemed to be more temperature sensitive than *P. antarcticum*. Also in other studies it was shown that notothenioids e.g. *T. hansoni* show higher growth performances in the warmer areas of the sub-Antarctic waters than in the high-Antarctic areas (HUBOLD 1992; KNOX 2007). Even though low temperatures possibly impose a general constraint on growth of Antarctic fish, there are other factors (e.g.

food availability, energy content, seasonal variability) which are more likely to affect the growth performance (KNOX 2007).

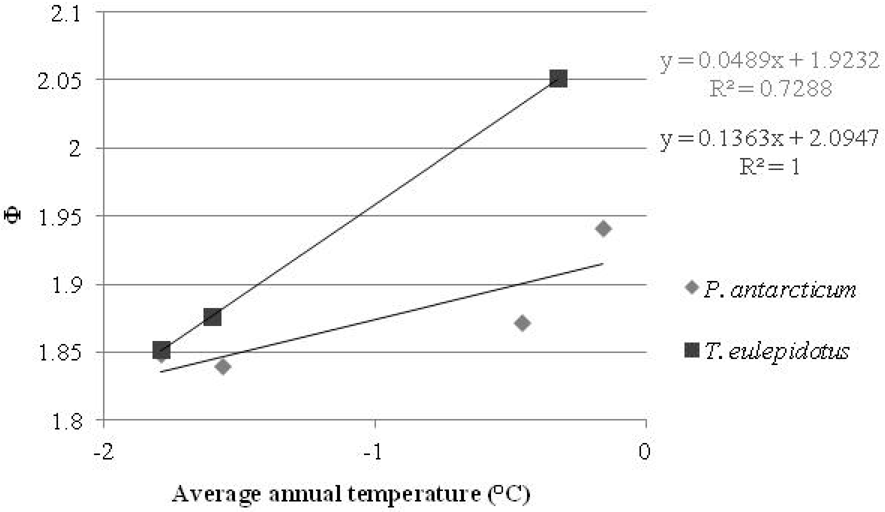


Figure 24: Relation between the average annual temperature (°C) and the growth performance index (Φ) of *P. antarcticum* and *T. eulepidotus*. Growth performance index was calculated by $\Phi = 2 * \log L\infty + \log k$.

At the first sight rapid growth and therefore high growth rates seem to be advantageous to avoid predation by bigger fish and to increase the potential of survival (METCALFE & MONAGHAN 2003). But fish showing rapid growth have a higher food uptake and therefore in turn higher predation risk (FIKSEN & JØRGENSEN 2011) as they may become victims of predatory species near the ground (HUBOLD 1992) while searching actively for food. Thus, another important factor being involved in growth is the food availability. In Antarctic waters the lower growth rates may be due to the seasonal food scarcity. Sufficient light for the growth of phytoplankton is only available during the short period of polar spring and summer (HILDEBRANDT *et al.* 2011). Hence, the available food for Antarctic fish can be very low during autumn and winter. The condition factors of the individuals correlate with the temperatures of the respective areas. For both species, *P. antarcticum* and *T. eulepidotus*, higher condition factors were verified for higher water temperatures (Fig. 25). Therefore, condition was slightly better in the more northern areas of the South Shetland Islands and the South Orkneys, where food availability might be sufficient.

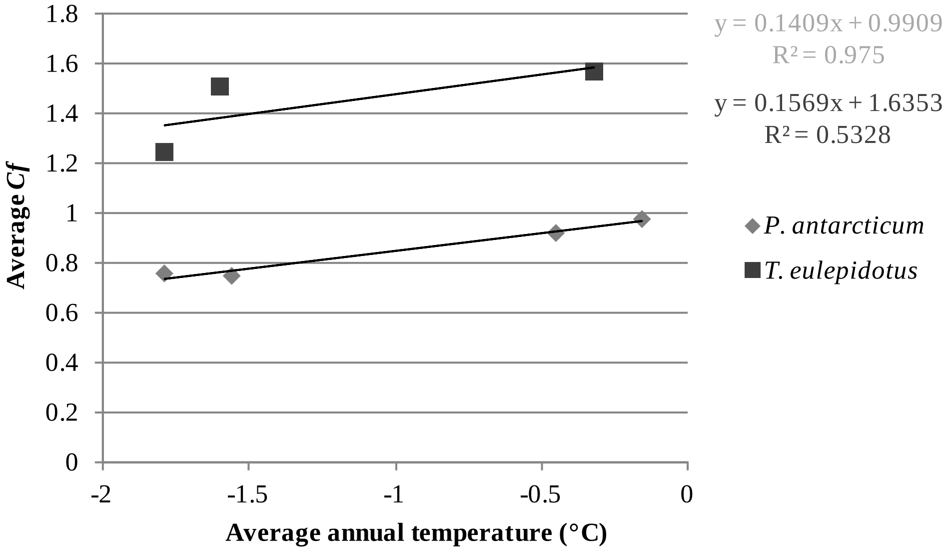


Figure 25: Relation between the average annual temperature (°C) and the average of the condition factor (*Cf*) of *P. antarcticum* and *T. eulepidotus*.

Condition factors, especially the ones of *P. antarcticum*, were lower in areas where the growth rates of the fish were lower as well. In the more northern areas of the South Orkneys and King George Island the *Cf*-values were predominantly higher. In these areas food does not appear to be a limiting factor and may be beneficial for the fish in terms of growth. But still it needs to be analysed in detail how fish use the available food to convert it into energy, as the energy for growth is only available after the requirements for maintenance covered. Some studies showed that *T. eulepidotus* from the Weddell Sea was able to hunger for 361 days in tanks without showing distinct differences in lipid, protein or water contents compared to directly caught individuals (WÖHRMANN 1988 cited in HUBOLD 1992). Thus, some fish species seem to be adapted quite well to the seasonal food scarcity and do not suffer that much while waiting for krill or fish schools and seasonal deep living zooplankton (HUBOLD 1992). Still, both species, *P. antarcticum* and *T. eulepidotus,* showed slightly faster growth rates and higher growth performance indices in the more northern regions of the South Orkneys and the South Shetland Islands where fish were in better condition. In the more northern regions krill is more abundant in the pelagic zone, which may explain the faster growth (SOLTWEDEL *et al.* 2009; HILDEBRANDT *et al.* 2011) and higher densities of *P. antarcticum* in these areas. However, benthos such as sponges, polychaetes and asterioids are a seasonally stable resource but of low energy content and hardly utilized by fish. In addition, amphipods comprise only small forms in the benthic zone (KOCK 1992). Condition of fish seems to be influenced not only by the food quantity but also by the food quality. Larval *P. antarcticum* off Terre Adélie were in better condition when feeding on copepods than others feeding on diatoms. Therefore, prey quality is an important factor affecting the condition of fish (MINTENBECK *et al.* 2012). In addition, *P. antarcticum* and especially larvae and juveniles seem to be highly vulnerable to alterations in the food web (MINTENBECK *et al.* 2012). Most fish from the Weddell Sea make a less marked dormancy than fish from boreal areas. Also in the winter months diet composition and filling level of the stomach seemed to be comparable to the summer months of fish. Presumably, fish follow the zooplankton into deeper water layers (HUBOLD 1992) and is therefore known to feed year round. Hence, it is uncertain if the seasonality in primary production may be a limiting factor influencing the growth to such an extent. Antarctic fish may show a slower annual growth compared to species from other latitudes as somatic growth mainly takes place during the summer months when sufficient food of high quality is available. In the Weddell Sea (70 – 78° S) phytoplankton growth is mainly limited to December through March and the life cycles of herbivorous zooplankton is closely related to the phytoplankton production. Abundance of copepods is five times greater in summer than in winter (NORTH 1998). So it may be the length of the growing season that allows tropical fish to grow faster, rather than the maximum daily growth rate (VAL *et al.* 2005). Seasonality in solar radiation and food availability/quality in the Antarctic waters may influence the growth of fish. Therefore it might be the lower energy transfer through the food web in winter (CAMPBELL *et al.* 2008) which affects the growth, as within the summer months some Antarctic fish can show a growth production similar to temperate fish (PÖRTNER *et al.* 2005).

The results of growth performances of the respective areas of investigation fit to the life history of *P. antarcticum*. In the investigated areas of the South Orkneys and King George Island no larvae and juveniles (age group 1 - 4) were found as larvae and young individuals mainly occur in colder waters at the shelf areas. They are carried to the innershelf depressions and banks as they increase in size (KOUBBI *et al.* 2011). After a few years juveniles move to warmer waters until they migrate back to the colder spawning grounds of Cape Norvegia and Vestkapp in eastern Weddell Sea (HUBOLD 1992; JARRE-TEICHMANN *et al.* 2009). *P. antarcticum* is mature at an age of about 7 - 9 years (KOCK & KELLERMANN 1991). This may be a reason, why no individuals of age group < 4 or >10 were caught at the South Orkneys and King George Island. DUCKLOW *et al.* (2007) also assessed that larvae were rarely to be found in the northern parts of the Antarctic waters. The different stages of life of *P. antarcticum* depend on latitudinal and seasonal temperature variations and are therefore related to geographical distribution (PÖRTNER *et al.* 2005). Furthermore, *P. antarcticum* is known to have a vertical separation of age classes. With depth mean body length of *P. antarcticum* seems to increase (WHITE & PIATKOWSKI 1993). The subsequent spatial and trophic segregation between different life stages prevent the exposure of larvae to predation and to competition for food between juveniles and adults (KOUBBI *et al.* 2011). Juveniles ≤ 5 cm feed especially on copepods e.g. of the genus *Oncaea, Ctenocalanus* and *Microcalanus*, whereas older individuals ≥ 8 cm mostly feed on krill and copepods such as *Calanus propinquu* and *Rhincalanus gigas* (HUBOLD & HAGEN 2009). This shows that *P. antarcticum* is adapted quite well to the pelagic environment in the cold, which might be a reason for their high dominance in the Antarctic shelf waters (LA MESA *et al.* 2010).

P. antarcticum did not show body lengths larger than 20 cm. The largest individual with a SL of 19.6 cm was found at the Larsen Shelf. However, largest individual of *T. eulepidotus* was found at the South Shetland Islands with a TL of 29 cm. Maximum length for *P. antarcticum* is supposed to be 26 cm and over 30 cm for *T. eulepidotus*. Notothenioids of the seasonal pack-ice zone and around the islands north of it attain larger sizes of more than 45 cm, whereas 90 % of the high-Antarctic species are reported not to grow larger than 45 cm and about 65 % do not even reach sizes of > 30 cm (KOCK 1992). In the Weddell Sea larger fish constitute an exception (e.g. *D. mawsoni*) as the Weddell Sea is generally populated by small species e.g. of the family Nototheniidae and Channichtthyidae. But at this point it should be taken into account that the number of examined individuals varied within the investigated areas. Whereas 153 individuals of *P. antarcticum* were examined from the Larsen Shelf and 66 individuals from the eastern Weddell Sea, just 20 and 35 individuals were analysed from the South Orkneys and King George Island. This also applies for the individuals of *T. eulepidotus* as 100 individuals came from the South Shetland Islands but only 43 individuals from Austasen and 16 individuals from the Larsen Shelf.

The values for the asymptotic length (L_∞) of just above 20 cm were quite low for *P. antarcticum* for all areas of investigation. The relatively low asymptotic lengths are due to the low L_{max}-values for the single regions. But even RADTKE *et al.* (1993) estimated an L_∞-value of 21.1 cm for *P. antarcticum* in the Weddell Sea which is not considerably higher than the 19.16 cm estimated in this study. As *P. antarcticum* is known to reach total lengths of up to 24 - 26 cm (HUBOLD & TOMO 1989), values of > 30 cm for the asymptotic length may also be possibly estimated. But to obtain such a high L_∞-value, fish must show quite high L_{max}-values which are only reached in very old fish and must be regarded as rare exceptions (HUBOLD & TOMO 1989).

The asymptotic length (L_∞) and the growth coefficient (k) showed a clear negative correlation (Fig. 26). The growth coefficient of the von Bertalanffy growth function is a parameter for the rate of growth and indicates how fast an individual will reach its specific asymptotic length. The faster the fish grows, the smaller is the asymptotic length it will reach. Therefore, higher growth coefficients go in hand with reduced expectancy. Fish with lower *k*-values, such as in the Weddell Sea, grow slowly but will therefore reach larger sizes. Consequently, long-lived individuals simply have more time to reach larger body lengths.

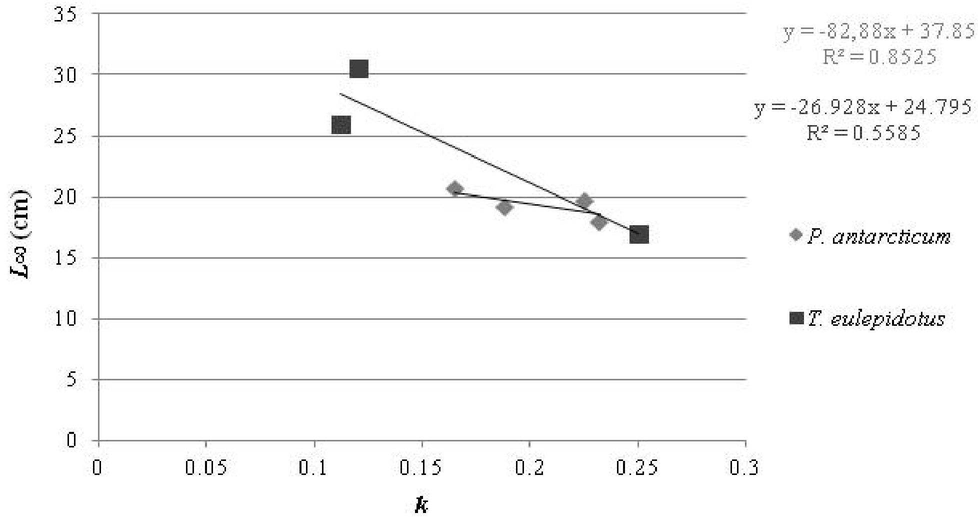


Figure 26: Relation between the growth coefficient (*k*) and the asymptotic length (L_∞) of *P. antarcticum* and *T. eulepidotus*.

For notothenioid fish growth coefficients of $k = 0.04 – 0.360$ are common (LA MESA & VACCHI 2001). For *P. antarcticum* values varied between $k = 0.166 – 0.232$ in this study.

Other authors estimated *k*-values between 0.052 – 0.32 for *P. antarcticum* from different Antarctic regions (SUTTON & HORN 2011). While HUBOLD & TOMO (1989) observed a growth coefficient of 0.07 for *P. antarcticum* from the Weddell Sea and Antarctic Peninsula (combined), a growth coefficient of 0.167 was observed at the Ross Sea (SUTTON & HORN 2011) and $k = 0.17$ for the Mawson Sea (GHERACIMCHOOK 1987 cited in HUBOLD 1992). Estimated growth rates of this study were slightly higher for *P. antarcticum* in the eastern Weddell Sea than the estimated values of HUBOLD & TOMO (1989) for the Weddell Sea and Antarctic Peninsula (Fig. 27). However, more recent studies suppose that the growth rates of high-Antarctic notothenioids from the Weddell Sea were underestimated in earlier studies and may be comparable to those of notothenioids and channichthyids from the seasonal pack-ice zone and from islands north of it (KOCK 1992).

Some Antarctic fish species show differences in growth between females and males. Females of some nototheniids exhibit larger values of growth performance and higher growth rates than males. These might be explained by physiological factors e.g. lower catabolic rates in females rather than intraspecific competition for food (LA MESA & VACCHI 2001). In this study no obvious differences in growth could be estimated between females and males of *P. antarcticum*. For example, at the eastern Weddell Sea a growth coefficient of $k = 0.220$ for both sexes and a growth performance index of $\Phi = 1.90$ for females and $\Phi = 1.91$ for males was calculated. Other authors found greater differences between the growth coefficients of females and males. For the Mawson Sea *k*-values of 0.32 for males and 0.21 for females were estimated and *k*-values of 0.26 for males and 0.20 for females at the Cosmonaut Sea (GERASIMCHUK 1992 cited in LA MESA & VACCHI 2001).

For *T. eulepidotus* growth coefficients varied from 0.121 - 0.250 in this study which are also within the typical range of $k = 0.04 - 0.36$ for notothenioids. MORALES-NIN *et al.* (2000) calculated for the Weddell Sea almost the same growth coefficient of 0.115 as in this study for the area of Austasen. However, EKAU (1988) calculated a slightly higher *k*-value of 0.124 for *T. eulepidotus* in a more southern area of the Weddell Sea, the Vestkapp (Fig. 28). The different estimated growth coefficients within the different investigated areas might be referable to varying environmental conditions between the habitats, e.g. temperature increases to the north whereas food availability increases within the Weddell Sea to the south. Furthermore, the stability of the temperature and predictability of hydrographic features increase to high-Antarctic areas (WÖHRMANN *et al.* 1997).

Females of *T. eulepidotus* had a slightly lower *k*-value (0.110) than the males (0.128) at the eastern Weddell Sea but a higher growth performance index (1.87) than the males (1.86). At the Larsen Shelf *T. eulepidotus* had a higher growth coefficient for females (k = 0.262) than for males (k = 0.260). EKAU (1988) found slightly greater variations between the growth coefficients of males and females with values of 0.094 for females and 0.154 for males at the eastern Weddell Sea. LA MESA & VACCHI (2001) estimated *k*-values of 0.16 for males and 0.11 for females at the eastern Weddell Sea.

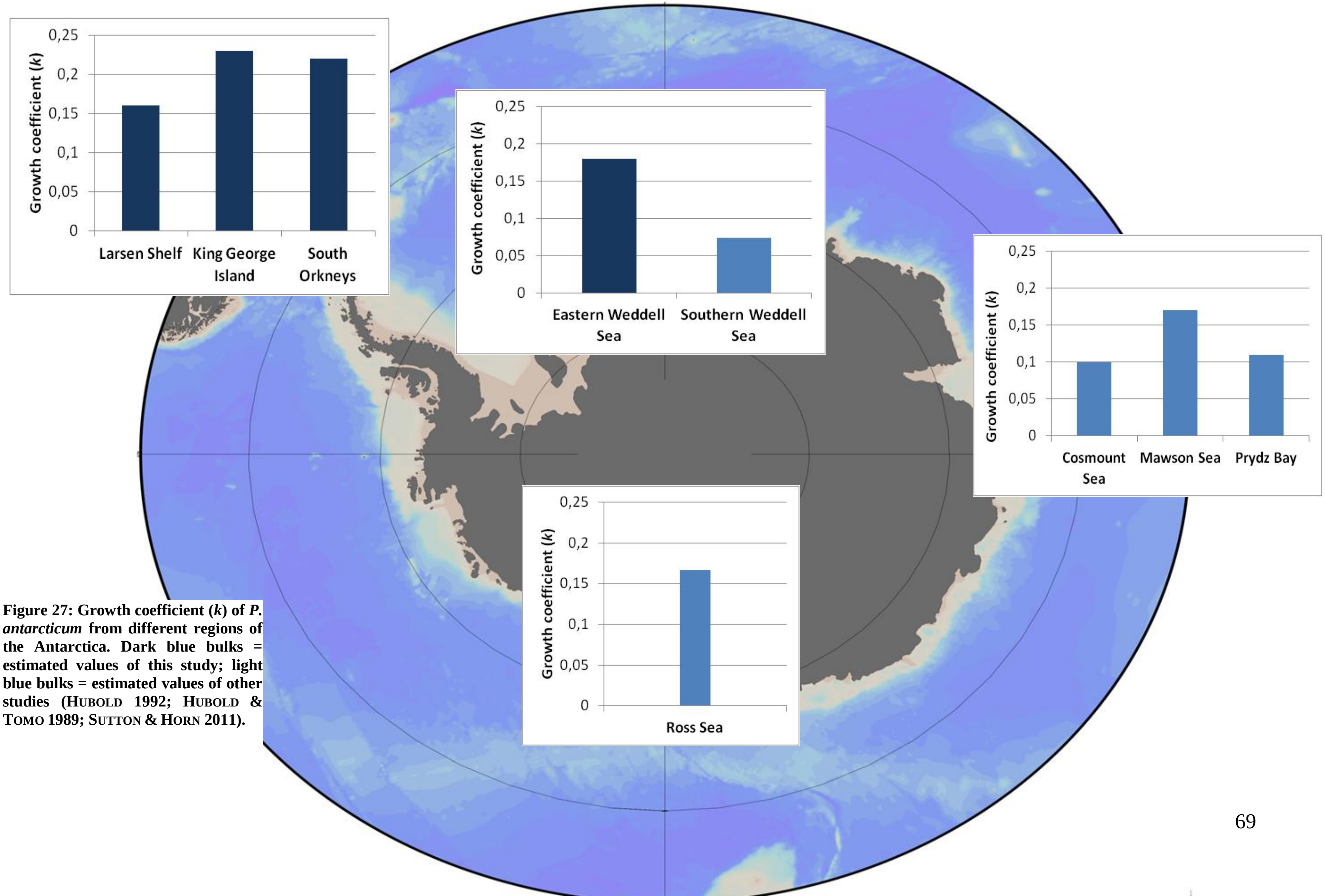
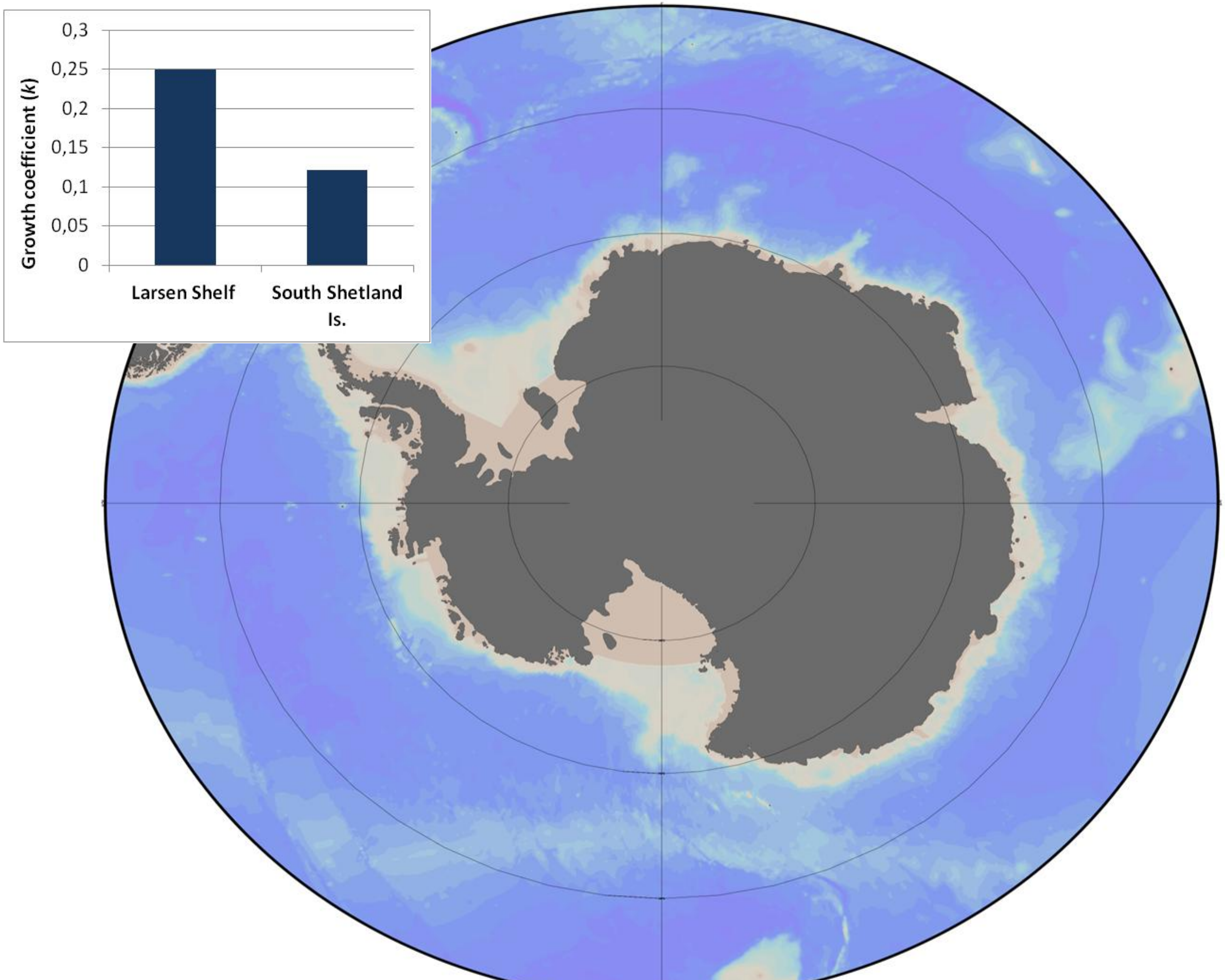


Figure 27: Growth coefficient (*k*) of *P. antarcticum* from different regions of the Antarctica. Dark blue bulks = estimated values of this study; light blue bulks = estimated values of other studies (HUBOLD 1992; HUBOLD & TOMO 1989; SUTTON & HORN 2011).


0,3
0,25
0,2
0,15
0,1
0,05
0
Growth coefficient (*k*)
Larsen Shelf
South Shetland Is.

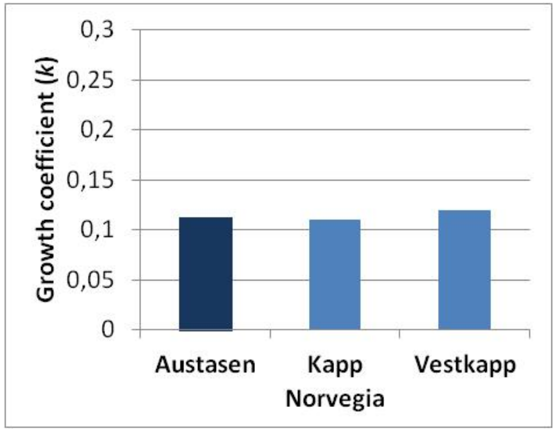

Growth coefficient (k)
0,3
0,25
0,2
0,15
0,1
0,05
0
Austasen
Kapp Norvegia
Vestkapp

Figure 28: Growth coefficient (*k*) of *T. eulepidotus* from different regions of the Antarctica. Dark blue bulks = estimated values of this study; light blue bulks = estimated values of other studies (EKAU 1988; LA MESA & VACCHI 2001.

All in all *P. antarcticum* showed an annual length growth between 0.05 – 3.17 cm and *T. eulepidotus* of 0.03 – 3.08 cm. These values match quite well with the ones from LA MESA & VACCHI (2001). They obtained values of 0.01 – 3.59 cm for *P. antarcticum* from different regions and 0.02 – 2.03 cm for *T. eulepidotus* in the Weddell Sea. In this study, annaul length growth of *T. eulepidotus* was between 0.32 – 2.45 cm for the eastern Weddell Sea and is therefore exiguously higher than the values estimated by LA MESA & VACCHI (2001).

Living conditions of the sub-Antarctic areas and the high-Antarctic areas differ particularly in terms of temperature, seasonality and therefore, also the structure of the food web. The high-Antarctic shelf areas show constantly water temperatures between 0 and -2 °C, lower krill abundances as well as a lower overall secondary production (HUBOLD 1992). Abundance, biomass and production estimates of *P. antarcticum* were the lowest in the eastern Weddell Sea and increased to the areas of King George Island and the South Orkneys (Tab. 4). For the eastern Weddell Sea, the highest annual production determined was 0.85 g / 1000 m². However, HUBOLD (1992) estimated an annual production of 20 g / 1000 m² for the southern Weddell Sea. This distinctly higher estimate might be due to the fact, that in the study of HUBOLD (1992) *P. antarcticum* was also caught with pelagic nets and not just with bottom trawls used in this study. As *P. antarcticum* is a pelagic species, this may lead to a higher fishing quota in the study of HUBOLD (1992). Furthermore, the biomass of *P. antarcticum* is known to increase within the Weddell Sea to the south, as they just migrate to the eastern Weddell Sea during the winter months for spawning. Hatching performance of *P. antarcticum* depends on the ice conditions. Stable and cold temperatures are needed for about 2 - 9 months to ensure successful hatching (VACCHI *et al.* 2004). Therefore, abundance and biomass estimates of *P. antarcticum* may vary between seasons and can be occasionally higher in the winter months than in the summer months in the eastern Weddell Sea due to migration and spawning events. In addition, food availability is known to be greater in the southern areas as a large cyclonic gyre with a central upwelling was found over the Filchner Depression. In the region of the Filchner Ice Shelf productivity values were twice as high as in the eastern Weddell Sea (EL-SAYED & MANDELLI 1965). This may foster intense phytoplankton blooms in this area (HUBOLD 1984). The higher biomass (119 g / 1000 m²) and production (63 g / 1000 m²) estimates in the lower latitudes are still unclear, as *P. antarcticum* is adapted to the cold temperatures in the high-Antarctic region. The estimates may result from the occasional higher primary production, the greater food availability and, possibly a better energy supply in the some sub-Antarctic areas compared to the eastern Weddell Sea and the Larsen Shelf. Compared to the Drake Passage, a substantial increase of concentrations of chlorophyll and carbon fixation was found in the more northern areas between the South Orkneys and the South Sandwich Islands. Also densest standing crops of phytoplankton were found in these regions (EL-SAYED & MANDELLI 1965). *P. antarcticum* seems to migrate to the more northern areas for feeding and energy supply and migrates back to the eastern Weddell Sea for spawning later. Abundance, and therefore also the biomass of particular species is often influenced by large single catches. This underscores the natural variation of fish assembles and may reflect real preferences by species in terms of to local hydrographic, habitat and trophic conditions (EKAU 1990; DONNELLY *et al.* 2004).

HUBOLD (1992) estimated in the southern Weddell Sea a lower mortality of M = 0.2 for *P. antarcticum* compared to this study. Here, values for mortality varied between 0.2 – 0.5 yr^{-1} depending on the investigated area. However, PINKERTON *et al.* (2010) estimated quite high P/B ratios for *P. antarcticum* in the Ross Sea. In balanced ecosystems the P/B ratio in known to equal the mortality of fish. For adults PINKERTON *et al.* (2010) give a P/B ratio and therefore, a value for the mortality of 0.63 yr^{-1} on average and for larva and juveniles even a higher P/B ratio of 2.1 yr^{-1} on average. Mortality values vary within different studies as the mortality estimates highly depend on the growth coefficient (*k*) which may vary between different regions and different studies. Mortality seems to be higher for larvae and juveniles than for adults as they show a reduced tolerance to low temperatures (KOUBBI *et al.* 2011). Increased growth rates and a better food supply in seasonal pack-ice zone may result in reduced mortality in these areas at least for postlarvae (KELLERMANN 1986).

For *T. eulepidotus* the estimates of abundance, biomass and production were converse to the ones for *P. antarcticum*. Biomass and annual production (0.02 g / m²) was highest at Austasen and decreased to the lower latitudes. Production estimated by HUBOLD (1992) for the southern Weddell Sea was slightly higher with 0.03 g / m². *T. eulepidotus* is a high-Antarctic fish species whose main distribution area is in the Weddell Sea and nearby islands. Abundance might be lower in the sub-Antarctic areas due to its temperature and distribution limits in the north. Also KOCK (2000) found that *T. eulepidotus* was of little significance and accounted for only small values at Elephant Island and the South Orkney Islands in terms of all species that were caught. The biomass of demersal fish is quite stable during the course of the year, as they do not perform spawning migrations like the pelagic *P. antarcticum*. Furthermore, *T. eulepidotus* inhabits preferably shallow waters at the continental shelves and areas beneath the sea-ice in. At the continental shelf of the Weddell Sea many larvae of *T. eulepidotus* were found (EKAU 1988) which may indicate that *T. eulepidotus* spawn in these areas.

Slow growth of Antarctic fish may also be a result of adaptation mechanisms to the cold environment. Fish developed physiological antifreeze mechanisms (ROESSIG *et al.* 2004), e.g. the “*Pleuragramma*-antifreeze-gylcopeptide” (PAGP), which are regulated by the ambient water temperature (WÖHRMANN 1995) and protect body fluids from freezing. Other important modifications are the absence of a swim bladder in all notothenioids (ZANE *et al.* 2006), natural buoyancy, increased enzyme activities, structural and functional modifications in oxygen transport and aerobic energy production. All these modifications display key innovations for cold adaptation (PATARNELLO *et al.* 2011). Therefore, most of the energy may be needed for the production and regulation of these adaptation mechanisms and less energy will be invested in growth (FONSECA & CABRAL 2007). So the available energy will be allocated to the respective needs of the environment (Hubold 1992). The effort of living at subzero temperatures is higher in Antarctic fish. Even in a resting stage an increased respiration and energy turnover is needed to maintain anti-freeze capacity, reactivity and the potential of activity (HUBOLD 1992). SCHOLANDER (1953) WOHLSCHLAG (1960) found remarkably higher metabolic rates in polar fish species at low temperatures than in tropical fish species that were extrapolated to the same low temperatures (cited in MARK 2004). This lead to the assumption of a metabolic cold adaptation (MCA) of Antarctic fish, that offered a good explanation for slow growth rates of the few investigated species at that time (KOCK 1992). In the meantime other studies on Antarctic fish have failed to demonstrate MCA and therefore, it has been doubtful if MCA really exists. It is more likely that the elevated metabolic rate is not an adaptation to low temperatures but rather a consequence of increased energy requirements associated with other adaptive changes (KOCK 1992). Energy expenditure for locomotion in Antarctic fish is higher than in fish from boreal areas due to the higher viscosity of the water. Therefore, energy consumption in Antarctic fish is kept down by a sluggish life style (HUBOLD 1992). Furthermore, in most Antarctic fish an increased energy input is needed for the reproduction efforts. The more energy is needed for the metabolism, the less energy can be invested in the growth. These anatomical, ecological, physiological and biochemical adaptations may also represent insuperable limitations for surviving in warming environments (PATARNELLO *et al.* 2011).

Growth also depends on the energy budget and the lifestyle of fish. Antarctic fish show massive energy reserves, mainly lipid stores that are advantageous in times of food scarcity and also play an important role in buoyancy. Pelagic species, like *P. antarcticum* and *A. mitopteryx*, tend to reduce heavy components such as bones and scales and show a stronger tendency to accumulate lipids (Fig. 29) than benthic species (FRIEDRICH & HAGEN 1994). Furthermore, the capacity of oxygen provision by ventilation and circulation is higher in active (pelagic) fish then in more sluggish (benthic) fish species. Reducing maintenance costs allows to invest more energy in growth. Such savings are maximised in Antarctic fish living at permanently low temperatures (PÖRTNER *et al.* 2005). Insufficient food supply would lead to lipid depletion and this would have in turn a negative effect on buoyancy and further energetic demands. The ingested food during the short times of primary production will be stored as lipids and serve as energy reserves (HAGEN 1988), also for the gonad development of Antarctic fish (FRIEDRICH & HAGEN 1994). Reproductive effort (expressed by GSI) is higher in most Antarctic fish species compared to e.g. gadoids or clupeids in the North Atlantic that exhibit typical GSI values of about 10 (KOCK 1992). GSI values ranged from 0.25 – 2.76 for *P. antarcticum* and 0.13 – 3.80 for *T. eulepidotus* in this study. These values were quite low, especially for *T. eulepidotus* as DUHAMEL *et al.* 1993 estimated values of 11.70 – 19.90 for *T. eulepidotus*. Fish were caught during spring in this study. At this time, the weight of the gonads is generally quite low, as gonads may not be mature and still in a “resting stage”. Generally, energy loss during spawning is substantially in Antarctic fish (KOCK 1992). For *N. rossii* energy loss was 50 – 60 % at South Georgia (KOZLOV 1980 cited in KOCK 1992). Therefore, energy expenditure needs to be partitioned between growth and reproduction in the lifespan of species (KOCK & KELLERMANN 1991).

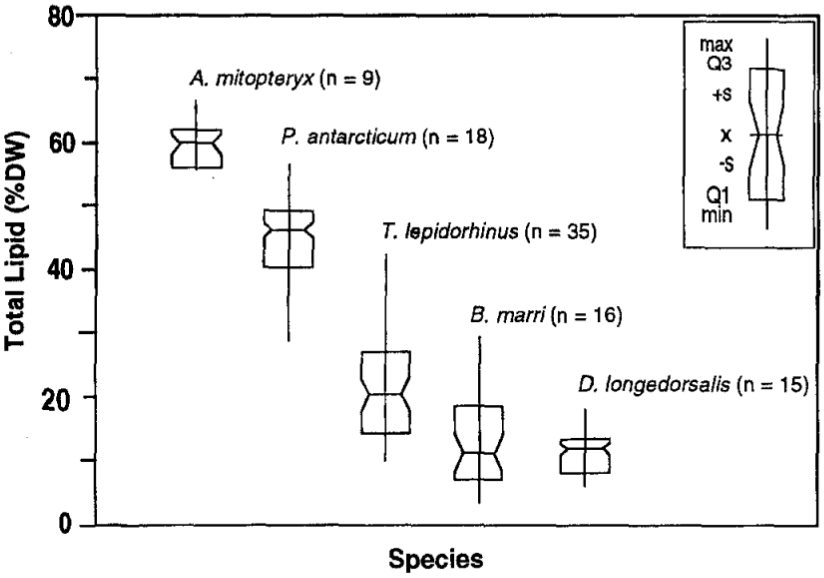


Figure 29: Lipid content (% DW) of adult *Aethotaxis mitopteryx* (pelagic), *Pleuragramma antarcticum* (pelagic), *Trematomus lepidorhinus* (demersal), *Bathydraco marri* (demersal) and *Dolloidraco longedorsalis* (demersal) (FRIEDRICH & HAGEN 1994).

Slight changes in the Antarctic environment may cause a shift in migratory patterns (CLARKE *et al.* 2007) and geographical ranges of fish populations; e.g. fish need to seek deeper waters for colder temperatures (ROESSIG *et al.* 2004) or fish need to migrate to other regions to find new suitable spawning grounds. As a response to global warming plasticity in fish`s diet would be adventurous to ensure survival (GIRALDO *et al.* 2011). Changing ice conditions due to global warming may lead to a loss of reproductive success and could endanger the population (HUBOLD 1984). Especially larvae and small fish will be hindered due to their high metabolic rates, lower energy reserves, and lower capability to migrate towards new suitable habitats. This increases the risk of mortality in periods of adverse environmental living conditions (RIJNSDORP *et al.* 2009). Despite that most Antarctic fish are highly stenothermal; EVANS *et al.* (2012) recently determined a surprisingly high average acute temperature tolerance range of > 17 °C for larvae of *P. antarcticum*. Such a thermal tolerance is strikingly high for a species living at subzero temperatures. But still, it has to be kept in mind that these investigations were from short-term measurements. PÖRTNER *et al.* (2001) showed that global warming causes a northward shift of populations of the Atlantic cod and the common eelpout. Furthermore, the growth performance of the Atlantic cod seems to decrease with higher latitudes. These findings suggest that a cold-induced shift in energy budgets may occur which has a disadvantageous effect on growth and fecundity (PÖRTNER *et al.* 2001).

Both investigated species show high abundances in the Antarctic waters. *T. eulepidotus* is the second most dominant species (11 % of the biomass) in the Weddell Sea (EKAU 1990) and also within benthic species the most abundant one in the Ross Sea (DONNELLY *et al.* 2004). *P. antarcticum* is the most dominant species in the pelagic zone (EKAU 1988) and is a major link between lower and higher trophic levels and between surface waters of the Antarctic convergence of the open waters and the coastal waters of the Antarctic continent. It occupies an ecological position similar to the clupeids in temperate regions (RADTKE *et al.* 1993). Therefore, it is important to expand the knowledge of how species growth is interrelated through feeding in different regions of Antarctica considering the seasonal, spatial and interannual variations. This knowledge is also required to get an understanding of how these species are being affected by climate change and to imagine possible future prospects. A reduction in sea ice due to global warming will particularly affect the life stages of *P. antarcticum* and other Antarctic fish species that are closely associated with the sea ice (MINTENBECK *et al.* 2012). A reduction in the population of *P. antarcticum* would have an impact on the whole Antarctic food web and on life in the Antarctic ecosystem. This may for example be the case for warm-blooded predators as they depend on the pelagic organisms of the food web (MINTENBECK 2008). The recent onset of global warming causes an increase in temperatures for most regions of the Antarctic waters and will certainly affect Antarctic fish through increased physiological stress, reduced ice sources, and declining phytoplankton and krill populations that comprise the basis of the food webs for several fish species (KOCK & KELLERMANN 1991). As poikilotherms, the body temperature of fish is analogous to the environmental temperature. Therefore, metabolism of Antarctic fish is adapted quite well to the cold. However, the ability to life in the cold goes in hand with sensitivities to warmer temperatures. Thus, sensitive fish species of the high-Antarctic shelf will have a low change of survival when temperature rises by just a few degrees. However, sub-polar species and those inhabiting warmer deep-sea layers of the Antarctic waters have the possibility to migrate to higher latitudes (LANNIG *et al.* 2005). Rising temperatures may also lead to an invasion of non-indigenous species which may in turn result in changes in the trophic structures and alterations in the composition and population density of prey and predator communities (WOODWARD *et al.* 2010; MINTENBECK *et al.* 2012). Still, precise effects of increasing temperatures in the Southern Ocean on Antarctic fish are unknown (NEAR *et al.* 2012). But especially for an environment whose species are characterized by special adaptations to manage life in such cold environments, the ongoing climate change may constitute a serious threat on the long run.

7 CONCLUSION

The impact of environmental conditions, such as temperature and food availability, are crucial factors influencing not only the growth, but also the reproduction, abundance, distribution, and entire population structures of fish. Reasons for differences in growth production in different regions may be caused by ecological (food limitations) as well as physiological (metabolic rates) determinants. Growth performance of both investigated species, *P. antarcticum* and *T. eulepidotus*, depend on geographical distribution. The higher the environmental temperature, the higher was the growth performance of both species. In addition, even the condition of the fish was better in the warmer waters of the lower latitudes than in the colder waters of the Weddell Sea. In this study, it was not possible to solve which factors (temperature, food availability, energy allocation) affect growth production the most, as they depend on the specific physiological plasticity of species or even single individuals. But inter- and intraspecific latitudinal differences as well as seasonal differences in growth probably depend most on variations of food availability, food quality, and the feeding intensity. Further research will be needed to confirm this assumption. This is especially true now, since climate change has become an important topic, and thus the assessment of the changing environmental conditions and their effects on key species is of particular concern and should be taken into account for future research. As fish are a key link between different trophic levels, it is important to know how they cope with varying conditions. Particularly *P. antarcticum* seems to be a suitable and relevant model organism, since this species fulfills some of the most important functions in the Antarctic food web and is one of the most frequent species in the high-Antarctic waters. It is necessary to know the life histories of key and indicator species in their natural environment to get a clear understanding of the relationships between the climate regime and the reaction of these species to changing environments. As *P. antarcticum* is known to migrate and to change its diet during different life stages, it would also be important to observe these seasonal and ontogenetic changes in more detail to better understand the production dynamics of *P. antarcticum* as a key species in the Antarctic waters.

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9 APPENDIX

Table I: Age–length key of *T. eulepidotus* from the South Shetland Islands.

Length (cm)	**Age class**																				**n**
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	
5																					0
6																					0
7																					0
8																					0
9																					0
10																					0
11																					0
12																					0
13																					0
14				1																	1
15					1	1	3	2													7
16					1	1	2	2	2												8
17							3	5	1	1											10
18																					0
19																					0
20									2	2											4
21									1		1		1	1							4
22										6	2	1				1					10
23												4	1	1							6
24										1	2	1	4	2							10
25										1	1	3		3		1		1			10
26										1	6	2	3	2	1	1	1		1		18
27										2		2	1	1				1			7
28											1			2		1					4
29															1						1
30																					0
n	0	0	0	1	2	2	8	9	6	14	13	13	10	12	2	4	1	2	1	0	100

Table II: Age-length key of *T. eulepidotus* from Austasen.

Length (cm)	Age class																				n
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	
5																					0
6																					0
7																					0
8																					0
9																					0
10																					0
11																					0
12																					0
13					1																1
14									2	1	1										4
15							1		1	3	1										6
16																					0
17							1		1	1											3
18								1		2	2	1									6
19								1	1	2	3	1		1							9
20									1		2		1	1	1						6
21													2								2
22													1	1			1				3
23															1						1
24																1					1
25															1						1
26																					0
27																					0
28																					0
29																					0
30																					0
n	0	0	0	0	1	0	2	2	6	9	9	2	4	3	3	1	1	0	0	0	43

Table III: Age-length key of *T. eulepidotus* from the Larsen Shelf.

Length (cm)	**Age class**																				**n**
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	
5																					0
6																					0
7																					0
8																					0
9																					0
10																					0
11																					0
12				1	3	1															5
13						1															1
14								1	1	1											3
15							1		2	2											5
16									1	1											2
17																					0
18																					0
19																					0
20																					0
21																					0
22																					0
23																					0
24																					0
25																					0
26																					0
27																					0
28																					0
29																					0
30																					0
n	0	0	0	1	3	2	1	1	4	4	0	0	0	0	0	0	0	0	0	0	16

Table IV: Age-length key of *P. antarcticum* from the South Orkneys.

Length (cm)	**Age class**															**n**
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	
4																0
5																0
6																0
7																0
8																0
9																0
10																0
11																0
12																0
13																0
14						4										4
15						4	2									6
16					1		4	3								8
17							1	1								2
18																0
19																0
20																0
n	0	0	0	0	1	8	7	4	0	0	0	0	0	0	0	20

Table V: Age-length key of *P. antarcticum* from King George Island.

Length (cm)	**Age class**															**n**
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	
4																0
5																0
6																0
7																0
8																0
9																0
10					1											1
11																0
12					2											2
13						3	1									4
14					1	7	6									14
15					1	2	2	3								8
16								4	1							5
17								1								1
18																0
19																0
20																0
n	0	0	0	0	5	12	9	8	1	0	0	0	0	0	0	35

Table VI: Age-length key of *P. antarcticum* from the Larsen Shelf.

Length (cm)	**Age class**															**n**
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	
4																0
5																0
6		24	3													27
7		14	3													17
8																0
9				1												1
10			1	3	1											5
11				3	11	1										15
12				2	19	7	1									29
13					7	12	1									20
14					2	10	1									13
15								3								3
16						1	4	3	1							9
17							2	2								4
18									1			1				2
19									1	2	2		1			6
20										1		1				2
n	0	38	7	9	40	31	9	8	3	3	2	2	1	0	0	153

Table VII: Age-length key of *P. antarcticum* from the eastern Weddell Sea.

Length (cm)	Age class															n
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	
4	1															1
5	3															3
6		3														3
7																0
8			8	4												12
9			3	2												5
10			2	3												5
11				6												6
12																0
13						1										1
14							4									4
15						2	4		1							7
16							2	4	2		1					9
17								3	2		1					6
18								1	1	2						4
19																0
20																0
n	4	3	13	15	0	3	10	8	6	2	2	0	0	0	0	66

Table VIII: Investigated individuals of *T. eulepidotus* from the South Shetland Island. TL = total length; SL = standard length; Diameter 1 and 2 = Maximum diameter of the right and left otolith; Weight 1 and 2 = Weight of the right and left otolith.

ID	TL (cm)	SL (cm)	Total weight (g)	Sex	Age (years)	Diameter 1 (mm)	Diameter 2 (mm)	Weight 1 (mg)	Weight 2 (mg)
1	26	23.2	222.6	F	11	4.60	4.66	20.25	21.08
2	27	24.1	307.6	F	13	4.36	4.31	20.79	21.50
3	25	22.3	200.2	M	11	4.33	4.33	18.29	18.86
4	27	25.0	327.8	F	14	4.45	4.48	21.98	22.48
5	16	14.5	40.5	F	7	broken	2.53	5.06	4.79
6	21	18.7	98.1	M	14	3.38	4.14	10.09	8.88
7	17	14.7	48.8	M	8	3.19	3.31	5.69	5.58
8	17	15.2	45.7	M	10	2.59	2.55	5.56	5.45
9	24	21.2	155.4	M	13	4.19	4.03	17.65	16.79
10	23	20.7	142.5	F	12	4.51	4.47	16.98	16.45
11	26	23.5	227.3	F	11	4.63	4.45	20.79	21.41
12	21	19.3	115.1	F	13	4.17	4.21	14.72	14.37
13	27	23.8	230.3	F	10	4.38	broken	21.58	17.04 (broken)
14	26	23.2	213.2	F	11	4.46	4.36	20.13	19.52
15	26	23.0	206.2	F	13	4.36	4.29	19.02	19.39
16	16	14.6	43.4	F	7	2.56	2.52	5.58	5.60
17	26	23.2	198.6	F	13	4.10	4.11	17.04	17.67
18	23	20.5	150.0	F	12	3.99	3.89	13.81	13.81
19	26	23.2	200.7	F	13	4.27	4.35	19.08	19.55
20	24	21.3	150.6	F	14	4.33	4.33	17.14	16.88
21	22	19.3	109.9	F	10	3.36	3.44	10.55	10.06
22	17	15.0	41.2	F	8	2.44	2.49	5.41	5.35
23	17	15.2	50.0	M	7	2.58	2.63	6.26	6.34
24	26	24.0	247.2	F	10	4.44	4.47	17.94	18.31
25	26	22.4	239.1	F	17	4.30	4.25	19.20	19.50

Continuation of Table IX: Investigated individuals of *T. eulepidotus* from the South Shetland Island. TL = total length; SL = standard length; Diameter 1 and 2 = Maximum diameter of the right and left otolith; Weight 1 and 2 = Weight of the right and left otolith.

ID	TL (cm)	SL (cm)	Total weight (g)	Sex	Age (years)	Diameter 1 (mm)	Diameter 2 (mm)	Weight 1 (mg)	Weight 2 (mg)
26	29	25.3	294.1	F	15	4.52	4.54	20.35	20.36
27	22	19.7	128.1	M	11	4.02	4.10	14.23	14.45
29	24	21.8	196.0	F	11	missing	4.64	missing	20.98
30	22	19.9	94.3	M	16	5.26	5.14	22.21	22.30
31	16	14.8	49.5	F	9	2.63	2.68	6.44	6.47
32	15	13.4	32.6	F	7	2.39	2.48	4.54	4.56
33	26	23.5	133.0	F	14	4.23	4.46	18.81	19.91
34	28	25.1	264.1	F	11	5.39	5.19	23.54	23.98
34 a	20	\N	\N	\N	10	4.56	4.56	22.21	21.94
35	20	19.1	68.0	M	9	4.35	4.44	18.37	18.09
36	25	\N	163.9	\N	14	4.07	4.07	14.00	13.96
37	20	\N	86.8	\N	9	4.21	4.21	13.93	14.10
38	22	\N	107.7	\N	12	3.40	3.34	11.78	11.60
39	25	\N	176.4	\N	12	4.07	4.18	14.78	15.28
40	26	\N	196.8	\N	16	4.32	4.41	16.35	16.88
41	25	\N	182.5	\N	18	missing	4.08	missing	14.82
42	26	\N	207.0	\N	19	3.82	4.10	14.74	14.74
43	26	\N	215.4	\N	11	4.23	4.15	17.18	17.23
44	24	\N	150.4	\N	12	4.02	3.98	16.23	16.95
45	25	\N	180.2	\N	16	3.99	3.95	15.68	16.43
46	23	\N	142.8	\N	14	3.88	3.84	12.94	13.02
47	22	\N	143.6	\N	10	5.05	4.15	12.46	12.55
48	22	\N	136.3	\N	10	4.21	4.23	16.08	16.30
49	22	\N	105.3	\N	11	3.94	3.81	14.08	13.98
50	24	\N	175.2	\N	11	4.21	broken	16.32	15.69
51	20	\N	73.1	\N	10	broken	5.63	21.57	22.16
52	21	18.5	85.5	F	11	5.21	4.99	18.43	18.16
53	22	19.8	112.3	F	10	5.54	5.31	22.50	22.55
54	23	20.5	118.3	\N	12	5.42	5.16	20.82	20.34
55	25	22.6	187.9	F	14	6.18	5.93	32.73	32.36
56	22	20.9	114.9	M	10	broken	5.47	21.74	22.96
57	22	19.3	95.3	F	10	5.81	broken	23.46	22.66
58	26	\N	\N	\N	15	4.42	4.42	19.43	19.78
59	23	\N	\N	\N	13	4.20	4.12	16.64	15.83
60	27	\N	\N	\N	10	4.40	4.40	20.14	20.40
61	27	\N	\N	\N	12	4.46	4.34	20.23	20.86
62	27	\N	\N	\N	12	4.50	4.40	20.95	19.90
63	24	\N	\N	\N	10	4.10	4.13	15.89	15.89
64	24	\N	\N	\N	14	4.11	4.14	15.69	15.39
65	26	\N	\N	\N	12	4.60	4.39	18.50	18.22
66	25	\N	\N	\N	14	4.50	4.44	20.10	20.18
67	25	\N	\N	\N	12	3.89	3.93	15.72	15.54
68	24	\N	\N	\N	13	4.10	3.93	16.14	16.00
69	27	\N	\N	\N	18	4.30	4.31	19.90	19.85
70	28	\N	\N	\N	14	4.46	4.66	20.87	20.83
71	26	\N	\N	\N	14	4.23	4.10	18.16	17.82
72	24	\N	\N	\N	13	4.15	4.12	16.16	16.14
73	28	\N	\N	\N	14	4.24	4.48	18.98	19.18
74	28	\N	\N	\N	16	4.39	4.30	20.02	19.43
75	23	\N	\N	\N	12	3.88	3.89	13.99	13.92
76	24	\N	\N	\N	13	missing	4.15	missing	17.65
77	25	\N	\N	\N	12	4.11	4.12	17.62	17.07
78	21	\N	\N	\N	9	3.47	3.27	11.32	11.31
79	26	\N	\N	\N	12	4.66	4.50	21.80	21.95
80	26	\N	\N	\N	11	4.19	4.15	17.39	17.27
81	26	\N	\N	\N	11	3.97	3.90	14.70	14.46
82	25	\N	\N	\N	10	3.89	4.00	15.51	16.21
83	16	\N	76.5	\N	8	2.68	2.70	5.55	5.54
84	17	\N	51.4	\N	8	2.67	2.67	6.91	6.82

Continuation of Table X: Investigated individuals of *T. eulepidotus* from the South Shetland Island. TL = total length; SL = standard length; Diameter 1 and 2 = Maximum diameter of the right and left otolith; Weight 1 and 2 = Weight of the right and left otolith.

ID	TL (cm)	SL (cm)	Total weight (g)	Sex	Age (years)	Diameter 1 (mm)	Diameter 2 (mm)	Weight 1 (mg)	Weight 2 (mg)
85	17	\N	56.4	\N	7	2.78	2.74	6.47	6.26
86	16	\N	54.8	\N	8	2.52	2.64	\N	\N
87	15	\N	\N	\N	7	2.74	2.79	5.66	5.75
88	16	\N	50.0	\N	6	2.78	2.78	6.76	6.63
89	17	\N	54.1	\N	7	2.66	2.71	6.32	6.62
90	17	\N	51.8	\N	9	2.80	2.86	6.72	6.90
91	15	\N	40.4	\N	8	2.43	2.50	5.00	5.15
92	16	\N	43.4	\N	9	2.68	2.71	5.85	5.86
93	17	\N	53.9	\N	8	missing	2.54	missing	5.46
94	15	\N	39.4	\N	8	2.48	2.54	5.64	5.53
95	15	\N	40.0	\N	6	2.48	2.47	5.44	5.41
96	17	\N	50.2	\N	8	2.63	missing	5.63	missing
97	15	\N	40.2	\N	5	2.54	2.61	5.35	5.49
98	14	\N	34.7	\N	4	2.59	2.59	4.93	4.98
99	16	\N	45.1	\N	5	2.65	missing	5.26	missing
100	15	\N	37.7	\N	7	2.91	2.62	4.92	5.18

Table XI: Investigated individuals of *T. eulepidotus* from Austasen. TL = total length; SL = standard length; Diameter 1 and 2 = Maximum diameter of the right and left otolith; Weight 1 and 2 = Weight of the right and left otolith.

ID	TL (cm)	SL (cm)	Total weight (g)	Sex	Age (years)	Diameter 1 (mm)	Diameter 2 (mm)	Weight 1 (mg)	Weight 2 (mg)
1	14.6	\N	27.1	F	7	2.35	missing	4.39	missing
2	14.7	\N	27.0	F	9	2.34	2.27	4.02	4.51
3	14.7	\N	26.9	F	10	2.45	2.42	4.21	4.34
4	15.4	\N	28.6	F	10	2.28	2.34	3.97	3.79
5	14.1	\N	24.0	M	9	2.27	2.33	3.62	3.71
6	15.3	\N	31.9	M	10	2.42	2.38	4.55	4.56
7	14.0	\N	25.2	M	9	2.14	2.19	3.70	3.63
8	14.2	\N	22.3	F	10	2.24	2.34	4.14	4.14
9	14.9	\N	26.4	F	11	2.29	2.30	4.09	4.05
10	14.2	\N	26.7	M	11	2.20	2.23	3.87	3.69
11	24.6	21.9	156.0	F	15	4.71	4.80	18.41	18.80
12	19.7	17.4	76.9	F	9	3.55	3.60	10.58	10.54
13	18.0	16.6	71.2	F	10	3.56	3.57	9.94	9.90
14	18.3	15.8	62.5	F	11	3.11	3.11	8.75	8.63
15	19.0	17.0	85.2	\N	11	missing	3.35	missing	10.05
16	20.1	17.2	94.5	F	14	broken	3.60	9.42 (broken)	9.84
17	22.0	19.5	124.7	\N	17	3.69	3.74	12.13	12.36
18	18.4	15.9	62.0	F	8	3.10	3.13	7.24	7.19
19	18.6	16.5	69.0	M	12	3.23	3.23	7.98	7.98
20	17.5	15.4	52.3	M	12	2.93	2.91	6.52	6.44
21	18.7	16.3	57.9	F	14	broken	3.38	7.42 (broken)	7.69
22	19.0	17.3	73.3	\N	9	3.38	3.29	9.33	9.56
23	19.9	17.5	79.0	M	11	3.91	3.81	10.90	10.69
24	18.2	15.6	52.2	M	10	3.18	3.19	8.12	7.95
25	23.9	20.8	155.8	F	16	4.27	4.27	13.99	14.56
26	22.2	19.6	109.3	F	14	3.47	3.58	10.50	10.32
27	22.6	19.6	114.7	M	15	4.15	4.17	13.64	13.27
28	17.3	15.0	47.4	F	10	3.09	3.13	8.38	7.90
29	19.2	17.1	83.6	\N	11	3.31	3.26	9.07	8.92
30	19.0	17.5	85.0	\N	10	3.69	3.72	9.83	9.55
31	18.9	16.5	62.1	M	11	3.02	3.10	6.93	7.23
32	19.5	17.2	77.8	\N	11	3.34	3.46	9.59	9.60
33	22.0	19.8	114.7	\N	13	4.14	4.14	13.55	13.68
34	18.6	16.2	60.2	M	8	3.07	3.05	7.63	7.73
35	17.1	14.9	49.6	M	7	3.41	3.39	9.91	9.93
36	21.3	18.8	97.7	F	13	3.88	3.98	12.41	12.30
37	16.8	14.4	41.8	M	9	2.93	2.99	6.42	6.18
38	17.5	15.2	52.1	M	11	2.91	broken	7.90	7.74 (broken)
39	19.7	17.0	76.0	M	13	3.30	3.33	8.82	8.99
40	13.2	11.1	18.4	J	5	2.06	2.06	3.04	3.06
41	18.9	16.4	62.1	M	10	2.87	2.93	6.83	7.15
42	20.4	18.1	84.8	M	15	3.39	3.34	10.11	9.76
43	20.5	18.4	97.4	\N	13	3.65	3.75	11.03	11.24

Table XII: Investigated individuals of *T. eulepidotus* from the Larsen Shelf. TL = total length; SL = standard length; Diameter 1 and 2 = Maximum diameter of the right and left otolith; Weight 1 and 2 = Weight of the right and left otolith.

ID	TL (cm)	SL (cm)	Total weight (g)	Sex	Age (years)	Diameter 1 (mm)	Diameter 2 (mm)	Weight 1 (mg)	Weight 2 (mg)
1	16.0	13.7	33.5	J	9	2.46	2.36	5.40	5.31
2	14.9	12.8	25.8	F	9	2.33	2.42	4.69	4.71
3	15.1	13.3	26.9	F	10	2.37	2.55	5.07	5.18
4	15.6	13.5	30.0	F	10	2.38	2.46	5.24	4.92
5	13.9	12.2	22.1	F	9	2.32	2.25	4.00	4.16
6	14.1	12.2	23.1	M	10	2.35	2.35	4.40	4.31
7	15.4	13.1	28.9	M	9	2.43	2.49	4.84	4.92
8	11.5	9.9	13.0	M	4	missing	1.81	missing	2.63
9	11.8	10.2	13.0	M	5	1.74	1.80	2.72	2.63
10	11.8	10.1	12.7	M	5	2.44	missing	2.64	missing
11	15.2	13.6	28.2	\N	10	2.37	2.41	5.07	5.03
12	14.2	12.6	25.8	\N	8	2.27	2.28	5.09	5.10
13	14.3	12.7	22.6	\N	6	2.30	2.35	5.29	4.99
14	14.6	13.0	28.7	\N	7	2.26	2.33	4.78	4.69
15	14.9	13.3	28.3	\N	6	2.38	2.41	5.15	5.14
16	12.0	10.0	14.5	\N	5	missing	1.94	missing	2.93

Table XIII: Investigated individuals of *P. antarcticum* from the South Orkneys. TL = total length; SL = standard length; Diameter 1 and 2 = Maximum diameter of the right and left otolith; Weight 1 and 2 = Weight of the right and left otolith.

ID	TL (cm)	SL (cm)	Total weight (g)	Sex	Age (years)	Diameter 1 (mm)	Diameter 2 (mm)	Weight 1 (mg)	Weight 2 (mg)
1	17.7	15.8	35.8	M	7	1.85	1.86	2.80	2.66
2	18.7	16.5	44.3	M	7	1.88	1.86	2.91	3.10
3	18.4	16.3	39.7	M	8	1.86	1.86	2.93	2.87
4	15.7	14.1	23.1	M	6	1.57	1.56	2.20	2.14
5	18.5	16.3	40.9	F	8	1.72	1.70	2.40	2.28
6	17.1	15	32.1	M	7	1.73	1.75	2.72	2.51
7	17.4	15.5	39.1	M	8	1.82	1.82	2.85	2.91
8	15.9	13.9	26.1	F	6	1.78	1.77	2.74	2.72
9	15.9	14.1	27.6	F	6	1.69	1.62	1.81	1.50 (broken)
10	17.6	15.8	36.1	M	7	1.90	1.87	2.66	2.60
11	18.5	16.5	50.3	F	8	1.97	1.94	3.29	3.19
12	16.6	15.2	38.7	M	6	1.76	1.77	2.67	2.73
13	17.3	15.1	33.6	M	6	1.69	1.70	2.11	2.23
14	17.5	15.5	38.4	F	5	1.81	1.81	2.50	2.54
15	18.4	16.2	44.7	F	7	1.92	1.92	2.98	2.95
16	17	15.2	32.5	F	6	1.82	1.83	2.55	2.58
17	16.5	14.4	29.3	F	6	1.67	1.66	2.30	2.70
18	17	15.4	32.6	M	6	1.74	1.72	2.30	2.41
19	17.6	15.4	38.5	M	7	1.83	1.84	2.38	2.45
20	16.7	15.8	37.5	M	7	1.87	broken	3.24	3.17 (broken)

Table XII: Investigated individuals of *P. antarcticum* from King George Island. TL = total length; SL = standard length; Diameter 1 and 2 = Maximum diameter of the right and left otolith; Weight 1 and 2 = Weight of the right and left otolith.

ID	TL (cm)	SL (cm)	Total weight (g)	Sex	Age (years)	Diameter 1 (mm)	Diameter 2 (mm)	Weight 1 (mg)	Weight 2 (mg)
1	12.2	15.9	40.4	F	8	1.89	1.87	3.41	3.30
2	16.4	14.8	30.1	F	7	1.81	1.80	3.02	2.97
3	19.9	17	51.6	F	8	2.03	2.02	3.60	3.52
4	15.5	13.7	20.3	F	6	1.62	1.60	1.82	1.75
5	16.2	14.2	26.4	M	6	1.64	1.64	2.02	2.05
6	17.2	15.2	27.9	M	8	1.81	1.80	2.59	2.50
7	16.2	14	26.6	F	7	1.83	1.84	2.72	2.90
8	17.8	15.5	37.2	M	8	1.86	1.90	2.23	2.22
9	16.5	14.5	27.1	M	6	1.78	1.78	2.47	2.47
10	15.4	13.6	22.7	F	7	1.72	1.70	2.22	2.22
11	16.8	14.8	30.1	F	8	1.82	1.80	2.18	2.09
12	15.5	13.7	23.6	F	6	1.64	1.62	1.73	1.90
13	15.4	13.5	20.7	M	7	1.76	1.77	2.26	2.25
14	14.2	12	15.4	M	5	1.54	missing	1.66	missing
15	15.9	14	23.1	F	6	1.74	1.73	2.25 (broken)	2.27
16	17.6	15.5	33.9	F	9	1.93	1.87	2.90	2.81
17	17	15	32.5	F	7	1.91	1.93	3.07	3.32
18	17.9	15.9	40	F	8	1.87	1.85	2.66	2.77
19	11.7	10.1	7.7	J	5	1.36	1.35	1.07	1.03
20	14.3	12.9	18.7	M	6	1.43 (broken)	1.51	1.60 (broken)	1.66
21	17.7	15.4	38.3	\N	8	1.86	1.81	3.01	2.99
22	15.5	13.6	22.7	\N	6	1.74	1.74	2.30	2.19
23	15.7	13.9	26.8	\N	7	1.77	1.79	2.54	2.47
24	15.8	13.8	23.5	\N	7	1.74	1.73	2.45	2.42
25	16.5	14.5	26.9	\N	6	1.88	1.86	3.02	2.88
26	15.9	13.7	20.8	\N	5	1.89	1.86	2.73	2.81
27	14.2	12.4	15.4	\N	5	1.64	1.61	1.66	1.66
28	18.9	15.7	37.5	\N	8	1.90	1.86	2.87	2.87
29	14.5	12.7	18.8	\N	6	1.66	1.66	2.05	2.03
30	15.3	13.3	21	\N	6	1.94	1.94	2.36	2.35
31	15.3	13.3	22.8	\N	7	1.81	1.79	2.34	2.29
32	16.3	14.1	30.4	\N	6	1.70	1.72	2.63	2.63
33	16.8	14.8	23.9	\N	5	1.61	1.62	2.11	2.13
34	15.9	13.7	27.2	\N	7	1.83	1.80	2.27	2.31
35	15.5	13.5	27.2	\N	6	1.75	1.76	2.56	2.57

Table XIII: Investigated individuals of *P. antarcticum* from the Larsen Shelf. TL = total length; SL = standard length; Diameter 1 and 2 = Maximum diameter of the right and left otolith; Weight 1 and 2 = Weight of the right and left otolith.

ID	TL (cm)	SL (cm)	Total weight (g)	Sex	Age (years)	Diameter 1 (mm)	Diameter 2 (mm)	Weight 1 (mg)	Weight 2 (mg)
1	19.1	17.2	42.1	M	8	1.95	1.94	3.32	3.34
2	15.6	13.6	18.1	J	6	1.77	1.79	2.38	2.39
3	13.5	11.8	13.1	F	7	1.55	1.54	1.51	1.57
4	12.6	11.1	11.8	J	6	1.44	1.46	1.36	1.29
5	13.9	12.2	14.5	F	5	1.49	1.49	1.41	1.40
6	18.5	16.4	36.8	\N	6	1.84	1.82	2.44	2.52
7	12.4	11.3	10.0	\N	5	1.33	1.35	1.11	1.18
8	13.0	11.4	11.8	\N	5	1.51	missing	1.40	missing
9	14.1	12.3	19.3	\N	5	1.69	1.70	1.96	2.07
10	13.2	11.5	13.4	\N	5	1.45	1.45	1.37	1.35
11	11.9	10.4	10.3	\N	4	1.36	1.33	1.15	1.14
12	13.1	11.3	12.9	\N	5	1.51	1.51	1.32	1.30
13	14.0	12.1	16.9	\N	4	missing	1.54	missing	1.78
14	14.1	12.2	15.5	\N	5	1.60	1.58	1.81	1.71
15	14.0	12.6	15.8	\N	5	1.54	1.53	1.60	1.61
16	16.0	14.0	21.5	\N	7	1.64	1.63	2.42	2.45
17	16.9	14.8	22.1	\N	8	missing	1.87	missing	2.89
18	14.1	12.4	16.4	\N	5	1.54	1.53	1.62	1.62
19	15.4	13.5	19.8	\N	6	1.59	1.59	5.06	5.23
20	6.8	7.3	1.3	J	2	0.68	0.68	0.20	0.26
21	6.9	6.0	1.4	J	2	0.71	0.71	0.01	0.00
22	6.3	6.0	1.0	J	2	0.66	0.63	0.31	0.30
23	12.5	10.8	8.5	\N	5	1.35	1.35	1.28	1.40
24	18.5	16.5	33.0	\N	7	1.98	1.94	3.96	3.90
25	13.6	11.9	12.0	\N	5	1.51	1.50	1.83	1.84
26	11.6	10.1	7.6	\N	3	1.41	1.41	0.96	0.80
27	12.8	11.0	10.7	\N	4	1.46	1.45	1.38	1.44
28	13.3	11.5	11.7	\N	5	1.58	1.58	1.62	1.62
29	13.5	11.9	11.7	\N	5	1.47	1.45	1.53	1.48
30	\N	10.2	8.0	\N	5	1.48	1.48	1.36	1.39
31	\N	9.1	5.8	\N	4	1.20	1.20	0.89	0.95
32	21.0	18.7	51.5	\N	9	2.29	2.26	4.49	4.37
33	18.1	15.7	36.7	32.70	7	1.95	2.00	2.67	2.61
34	21.1	18.8	63.8	56.60	13	2.51	2.56	4.91	4.96
35	21.1	19.0	61.1	54.50	10	2.50	2.48	4.82	4.80
36	22.2	19.5	68.3	60.50	10	2.37	2.34	4.79	4.81
37	13.5	11.9	13.5	12.20	6	missing	1.55	missing	1.37
38	21.3	18.8	52.4	47.80	11	2.26	2.26	4.66	4.61
39	14.5	12.5	16.4	14.80	6	1.62	1.61	1.26	1.25
40	14.8	12.9	19.0	16.00	6	1.61	1.63	1.40	1.37
41	13.4	11.7	13.2	11.70	5	1.52	1.53	1.30	1.30
42	13.8	12.2	14.4	12.70	5	1.51	1.51	1.28	1.28
43	14.7	12.9	18.6	16.70	6	1.68	1.68	1.39	1.34
44	16.0	14.1	20.7	18.90	6	1.69	1.71	2.01	2.03
45	\N	18.7	50.2	41.00	10	2.17	2.16	3.67	3.61
46	18.9	16.5	39.2	35.80	7	1.81	1.80	2.70	2.78
47	15.6	13.6	21.4	18.40	5	1.72	1.72	1.57	1.57
48	\N	18.3	53.6	48.00	9	2.36	2.36	4.28	4.28
49	16.3	14.2	26.9	24.30	6	1.79	1.77	2.74	2.72
50	22.0	19.4	57.1	52.40	11	2.33	2.37	4.51	4.62
51	15.0	13.1	18.3	\N	5	1.55	1.59	1.70	1.71
52	13.7	12.1	14.3	\N	5	1.45	1.43	1.45	1.44
53	14.3	12.5	16.8	\N	5	1.55	1.53	1.63	1.59
54	15.5	13.6	22.2	\N	6	1.56	1.59	1.99	2.10
55	17.7	15.8	32.5	\N	9	2.07	2.04	2.34	2.32

Continuation of Table XIII: Investigated individuals of *P. antarcticum* from the Larsen Shelf. TL = total length; SL = standard length; Diameter 1 and 2 = Maximum diameter of the right and left otolith; Weight 1 and 2 = Weight of the right and left otolith.

ID	TL (cm)	SL (cm)	Total weight (g)	Sex	Age (years)	Diameter 1 (mm)	Diameter 2 (mm)	Weight 1 (mg)	Weight 2 (mg)
56	17.8	15.4	29.8	\N	8	2.06	2.08	3.42	3.42
57	17.7	15.4	31.1	\N	8	1.94	1.96	3.53	3.50
58	17.6	15.7	32.4	\N	8	1.94	1.94	2.90	2.94
59	18.6	16.1	34.6	\N	8	2.06	2.07	2.87	2.89
60	15.2	13.3	19.5	\N	6	1.63	1.65	1.78	1.81
61	14.3	12.5	15.8	\N	5	1.56	1.57	1.68	1.72
62	14.5	12.8	17.7	\N	6	1.55	1.55	1.66	1.65
63	13.8	12.1	13.3	\N	6	1.58	1.60	1.47	1.43
64	13.6	11.9	13.3	\N	5	1.52	1.53	1.51	1.51
65	15.5	13.6	20.8	\N	6	1.63	1.63	1.82	1.84
66	17.5	15.6	29.7	\N	7	1.81	1.81	3.32	3.28
67	\N	13.2	18.6	\N	6	1.55	1.55	1.71	1.66
68	\N	19.6	63.7	\N	12	2.50	2.48	4.74	4.76
69	\N	15.9	33.9	\N	7	2.06	2.05	2.77	2.69
70	16.0	14.1	22.0	\N	6	1.57	1.58	2.00	2.03
71	12.9	11.2	13.4	\N	5	1.50	missing	1.39	missing
72	15.1	13.1	17.2	\N	6	1.65	1.67	1.95	1.94
73	14.3	12.3	14.7	\N	5	1.47	1.47	1.38	1.42
74	16.5	14.3	22.6	\N	6	1.68	1.70	2.19	2.30
75	14.2	12.4	14.4	\N	6	1.51	1.53	1.68	1.59
76	15.5	13.5	19.5	\N	6	1.70	1.70	2.22	2.27
77	\N	11.5	12.6	\N	5	1.43	1.43	1.45	1.47
78	14.0	12.1	14.8	\N	5	1.49	1.49	1.51	1.50
79	14.7	12.7	17.6	\N	6	1.63	1.65	2.14	2.12
80	15.6	13.7	20.1	\N	6	1.70	1.69	1.76	1.81
81	12.8	11.1	11.6	\N	5	1.42	1.42	1.40	1.40
82	14.5	12.8	16.0	\N	5	1.44	1.44	1.62	1.59
83	14.4	12.5	17.2	\N	5	1.52	1.52	1.58	1.59
84	11.6	10.3	7.3	\N	4	1.45	broken	1.47	broken
85	13.3	11.6	13.7	\N	5	1.51	1.52	1.67	1.67
86	13.3	11.6	12.1	\N	4	1.53	1.53	1.65	1.65
87	15.1	13.3	19.2	\N	6	1.57	1.58	2.18	2.10
88	14.2	12.4	15.6	\N	6	1.59	1.61	1.68	1.69
89	15.2	13.4	19.8	\N	6	1.69	1.68	2.27	2.24
90	18.9	16.5	39.3	\N	8	2.07	2.11	3.10	3.10
91	14.8	12.8	17.2	F	6	1.57	1.57	1.17	1.20
92	11.9	10.4	9.8	F	4	1.31	missing	1.22	missing
93	12.8	11.2	12.3	M	5	1.47	missing	1.13	missing
94	13.9	12.6	16.8	M	5	1.68	1.68	1.71	1.66
95	12.7	11.3	12.7	F	4	1.60	1.60	1.26	1.26
96	20.2	18.2	44.5	F	12	2.10	2.04	3.90	3.67 (broken)
97	14.5	12.3	15.7	M	5	1.60	1.63	2.23	2.18
98	\N	14.2	25.3	F	5	1.65	1.69	1.84	1.79
99	13.1	11.6	12.3	M	6	1.45	1.47	1.13	1.21
100	12.7	11.1	12.0	M	5	1.53	missing	0.76	missing
101	14.3	12.6	16.5	M	7	1.48	1.45	1.40	1.43
102	14.1	12.2	14.7	M	6	1.57	1.57	1.68	1.59
103	13.4	11.8	14.0	M	5	1.44	1.44	1.38	1.42
104	13.6	11.8	12.9	M	6	1.64	1.65	1.37	1.00
105	14.2	12.4	\N	M	5	1.70	1.69	1.62	1.60
106	12.2	10.6	9.7	M	4	1.50	1.48	0.89	1.00
107	12.6	11.0	10.7	M	5	1.43	1.43	1.12	1.11
108	12.4	10.9	11.1	M	5	missing	1.45	missing	0.98
109	15.0	13.2	18.3	M	6	1.78	1.76	2.37	2.34
110	13.1	11.4	12.7	M	5	1.51	1.49	1.29	1.51

Continuation of Table XIII: Investigated individuals of *P. antarcticum* from the Larsen Shelf. TL = total length; SL = standard length; Diameter 1 and 2 = Maximum diameter of the right and left otolith; Weight 1 and 2 = Weight of the right and left otolith.

ID	TL (cm)	SL (cm)	Total weight (g)	Sex	Age (years)	Diameter 1 (mm)	Diameter 2 (mm)	Weight 1 (mg)	Weight 2 (mg)
111	7.5	6.7	1.4	J	2	0.68	0.66	0.00	0.00
112	6.8	6.1	1.3	J	2	0.63	0.62	0.00	0.00
113	6.7	5.9	1.4	J	2	0.64	0.63	0.00	0.00
114	7.2	6.4	1.7	J	3	0.70	0.69	0.00	0.00
115	6.9	6.2	1.2	J	2	0.69	0.66	0.00	0.00
116	7.0	6.3	1.5	J	2	0.71	0.71	0.00	0.00
117	6.8	6.0	1.3	J	3	0.70	0.70	0.00	0.00
118	7.0	6.3	1.5	J	2	0.66	0.68	0.00	0.00
119	7.5	6.7	1.7	J	2	0.72	0.71	0.00	0.00
120	7.3	6.5	1.7	J	2	0.74	0.73	0.00	0.00
121	7.1	6.4	1.6	J	2	0.72	0.71	0.00	0.00
122	7.1	6.3	1.7	J	2	0.75	0.75	0.00	0.00
123	6.7	6.0	1.4	J	2	0.69	0.69	0.00	0.00
124	7.0	6.2	1.5	J	2	0.64	0.64	0.00	0.00
125	7.2	6.4	1.7	J	2	0.67	0.68	0.00	0.00
126	7.1	6.5	1.7	J	3	0.70	0.69	0.00	0.00
127	7.3	6.1	1.5	J	2	0.61	0.62	0.00	0.00
128	7.7	6.9	2.0	J	2	0.79	missing	0.00	missing
129	7.0	6.2	1.6	J	3	0.73	0.72	0.00	0.00
130	6.8	5.9	1.3	J	2	0.66	0.67	0.00	0.00
131	7.6	6.7	1.8	J	3	0.78	0.78	0.00	0.00
132	7.9	6.9	2.2	J	2	0.83	0.84	0.00	0.00
133	7.2	6.3	1.6	J	2	0.69	0.69	0.00	0.00
134	7.2	6.3	1.5	J	2	0.65	0.65	0.00	0.00
135	6.7	5.9	1.4	J	2	0.59	0.59	0.00	0.00
136	7.2	6.4	1.6	J	2	0.68	0.67	0.00	0.00
137	7.3	6.5	1.7	J	2	0.71	0.69	0.00	0.00
138	6.6	5.8	1.2	J	2	0.66	0.66	0.00	0.00
139	7.0	6.2	1.4	J	2	0.69	0.69	0.00	0.00
140	7.2	6.4	1.8	J	2	0.66	0.66	0.00	0.00
141	7.3	6.5	2.0	J	2	0.73	0.74	0.00	0.00
142	7.4	6.6	1.7	J	2	0.69	0.70	0.00	0.00
143	7.0	6.1	1.3	J	2	0.63	0.63	0.00	0.00
144	\N	6.6	1.9	J	2	0.72	missing	0.00	missing
145	8.0	7.1	2.1	J	3	0.83	missing	0.00	missing
146	6.9	6.3	1.6	J	2	0.68	0.73	0.00	0.00
147	7.4	6.6	1.7	J	2	missing	0.76	missing	0.00
148	7.6	6.7	2.1	J	2	0.73	0.72	0.00	0.00
149	18.4	16.2	35.6	M	8	1.91	1.93	3.42	3.42
150	18.3	15.9	30.2	F	7	1.89	1.85	3.42	3.28
151	7.2	6.5	1.5	J	2	0.74	0.73	0.00	0.00
152	7.7	6.8	1.5	J	2	0.77	0.76	0.00	0.00
153	6.7	6.1	1.2	J	2	0.75	0.74	0.00	0.00

Table XIV: Investigated individuals of *P. antarcticum* from the eastern Weddell Sea. TL = total length; SL = standard length; Diameter 1 and 2 = Maximum diameter of the right and left otolith; Weight 1 and 2 = Weight of the right and left otolith.

ID	TL (cm)	SL (cm)	Total weight (g)	Sex	Age (years)	Diameter 1 (mm)	Diameter 2 (mm)	Weight 1 (mg)	Weight 2 (mg)
1	5.5	4.9	0.7	J	1	0.48	0.49	0.00	0.00
2	6.2	5.5	1.0	J	2	0.55	0.54	0.00	0.00
3	6.5	5.8	1.2	J	2	0.62	0.60	0.00	0.00
4	7.2	6.4	1.6	J	2	0.63	0.63	0.00	0.00
5	5.4	4.8	0.7	J	1	broken	0.48	0.00	0.00
6	5.5	4.8	0.3	J	1	0.47	0.48	0.00	0.00
7	4.8	4.2	0.3	J	1	0.46	0.47	0.00	0.00
8	\N	9.0	4.8	J	4	1.09	1.27	0.20	0.40
9	\N	8.4	4.0	J	4	1.03	1.00	0.36	0.35
10	\N	8.9	4.6	J	3	1.01	1.01	0.45	0.43
11	9.9	8.7	4.5	J	3	broken	1.03	0.48	0.47
12	9.2	8.2	3.9	J	3	0.89	0.85	0.20	0.10
13	9.4	8.3	4.2	J	3	1.02	0.96	0.43	0.38
14	11.3	10.0	7.3	J	3	1.22	1.18	0.76	0.76
15	9.2	8.0	4.0	J	3	1.00	0.97	0.33	0.34
16	9.2	8.0	3.4	J	3	0.93	0.92	0.40	0.40
17	\N	8.5	4.1	J	3	0.96	0.98	0.33	0.35
18	\N	8.4	4.1	J	3	0.97	0.98	0.36	0.36
19	\N	8.3	4.0	J	4	0.95	0.94	0.32	0.33
20	\N	11.1	10.6	J	4	1.34	1.32	1.20	1.20
21	\N	10.0	7.9	J	4	broken	1.23	0.90	0.80
22	9.3	8.2	3.9	J	3	0.98	missing	1.50	missing
23	\N	15.0	32.6	F	7	1.82	1.80	0.70	0.90
24	12.2	10.6	9.1	J	4	1.23	1.23	0.68	0.68
25	11.7	10.3	8.6	J	4	missing	1.32	missing	0.97
26	9.5	8.3	4.4	J	3	0.54 (broken)	0.987 (broken)	broken	broken
27	10.4	9.6	5.8	\N	3	missing	1.04	missing	0.51
28	12.1	10.7	9.8	\N	4	1.21	1.15	0.60	0.70
29	12.0	10.5	8.9	\N	4	1.29	1.27	0.83	0.80
30	11.8	10.7	8.6	\N	4	1.21	1.22	0.91	0.91
31	11.9	10.5	8.2	\N	4	1.21	1.20	0.89	0.88
32	9.3	8.3	3.6	\N	4	0.98	broken	0.32	0.30
33	9.1	8.1	3.4	\N	4	0.92	0.93	0.31	0.29
34	8.8	7.8	3.3	\N	3	0.94	0.94	0.30	0.28
35	9.6	8.5	4.1	\N	4	0.94	0.96	0.40	0.38
36	10.9	9.8	7.4	\N	4	1.24	1.23	0.20	0.50
37	\N	15.0	31.0	M	7	1.80	1.76	1.91	1.91
38	\N	15.9	33.7	F	9	1.90	1.87	2.30	2.30
39	\N	16.5	34.5	F	9	1.86	1.86	2.45	2.47
40	\N	15.1	26.5	F	7	1.72	1.72	2.38	2.43
41	\N	16.3	35.8	F	9	2.04	2.00	2.87	2.92
42	\N	15.9	32.8	M	8	1.83	1.83	2.24	2.31
43	\N	14.3	22.7	M	7	1.64	1.62	2.00	1.95
44	\N	14.0	22.4	M	7	1.73	1.68	1.73	1.73
45	\N	13.9	20.1	F	7	missing	1.61	missing	1.98
46	\N	14.4	23.2	M	7	1.69	1.68	1.84	1.69
47	\N	18.0	52.4	F	10	2.06	2.07	3.40	3.60
48	20.6	18.2	50.9	M	8	2.07	2.09	3.70	3.70
49	20.6	18.1	60.3	F	10	2.28	2.26	4.72	4.85
50	19.5	17.1	44.8	M	8	1.95	1.94	3.38	3.40
51	\N	17.3	49.5	F	8	2.10	2.10	4.22	4.20
52	19.5	17.9	56.1	F	9	2.01	2.01	3.31	3.28
53	18.3	16.4	41.2	F	11	2.09	2.05	2.88	2.91
54	18.3	16.1	35.0	F	8	1.99	1.99	3.59	3.46
55	18.2	16.1	37.7	M	8	1.93	1.91	2.94	2.90

Continuation of Table XIV: Investigated individuals of *P. antarcticum* from the eastern Weddell Sea. TL = total length; SL = standard length; Diameter 1 and 2 = Maximum diameter of the right and left otolith; Weight 1 and 2 = Weight of the right and left otolith.

ID	TL (cm)	SL (cm)	Total weight (g)	Sex	Age (years)	Diameter 1 (mm)	Diameter 2 (mm)	Weight 1 (mg)	Weight 2 (mg)
56	19.8	17.3	46.0	M	11	2.19	missing	4.11	missing
57	\N	15.3	25.1	F	6	1.87	1.86	2.27	2.26
58	\N	16.5	33.3	M	8	1.97	1.95	3.38	3.34
59	\N	15.1	24.8	M	7	1.88	1.89	2.38	2.39
60	\N	16.6	41.4	F	9	missing	2.09	missing	3.72
61	\N	13.4	14.9	J	6	missing	1.66	missing	1.49
62	17.4	15.3	28.9	M	6	1.87	1.90	2.41	2.43
63	\N	15.8	32.7	F	8	broken	1.99	broken	3.40
64	\N	14.8	21.8	M	9	2.07	2.01	3.56	3.56
65	\N	16.1	32.9	M	7	1.95	1.94	3.44	3.41
66	\N	16.0	31.2	M	7	1.98	1.99	3.58	3.60

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DECLARATION

Hereby, I declare that this master thesis “Growth production of two notothenioid fish species from different geographical regions of the Antarctic waters” is my own work, and not to have used other sources than stated before.

Date..Signature..