



Midtrophic fish feeding modes at the poles: an ecomorphological comparison of polar cod (*Boreogadus saida*) and Antarctic silverfish (*Pleuragramma antarctica*)

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Abstract

The polar cod (*Boreogadus saida*) and the Antarctic silverfish (*Pleuragramma antarctica*) are pelagic fish endemic to the Arctic and Antarctica sea, respectively. Both species are abundant and play a central role as midtrophic wasp-waist species in polar ecosystems. Due to their biological and ecological characteristics (small size, complex life histories, relatively short generation cycles, movement capability, planktivorous diet, and importance as prey), the polar cod and the Antarctic silverfish are potentially good sentinels of ecosystem change. Changes in polar zooplankton communities are well documented. How changes impact ecosystems as a whole largely depend on the degree of diet specialization and feeding flexibility of midtrophic species. Here, we provide the ecomorphological characterization of polar cod and Antarctic silverfish feeding performances. A comparative functional ecology approach, based on the analysis of morpho-anatomical traits, including calculation of suction index and mechanical advantage in jaw closing, was applied to profile the feeding modes and flexibility of the two species. Ecomorphological evidence supports differences in food acquisition: the polar cod appears able to alternate particulate ram-suction feeding to a pump filter feeding, and the Antarctic silverfish results be both a particulate ram and a tow-net filter feeder. Both species exhibit opportunistic feeding strategies and appear able to switch feeding mode according to the abundance and size of the available prey, which is a clue of potential resilience to a changing environment.

Keywords Antarctic silverfish · Polar cod · Ecomorphology · Jaw mechanics · Gill rakers · Feeding strategy

Introduction

Most pelagic ecosystems worldwide, including those of the Polar Regions, rely on a wasp-waist trophic structure. Such a structure is characterized by a few, small-sized, pelagic, planktivorous, and midtrophic species that exert both up and down control of the trophic dynamics (Bakun et al. 2006). These midtrophic species often have complex life histories coupled with relatively short generation cycles, potentially allowing for large fluctuations in population size. Further, they are highly motile, and so potentially able to rapidly change their geographical distribution. Such dynamics in abundance and dispersal have potential to generate dramatic changes in the trophic flow of energy. Due to their ecological role, and sensitivity to change, midtrophic level species are sentinels of the changes of the pelagic ecosystems (Lehodey et al. 2010; Koubbi et al. 2017) and hold potential to provide early warnings on the effects of climate change on the marine ecosystems.

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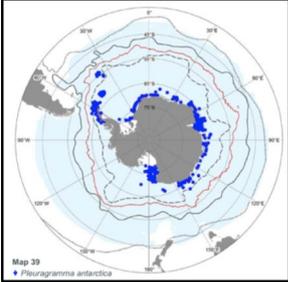
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In polar oceans, only a few midtrophic fishes dominate the pelagic energy flows: the polar cod (*Boreogadus saida*) in the Arctic and the Antarctic silverfish (*Pleuragramma antarctica*) in Antarctica are the major plankton feeders linking zooplankton and predators (Christiansen et al. 2012; Vacchi et al. 2012a; Duhamel et al. 2014). Both species are known to primarily feed on copepods, euphausiids, and amphipods (summarized in Table 1), and in turn, they are prey for a suite of predators, from mammals to birds and other fish (Christiansen 2017; Pinkerton 2017).

Polar cod is a gadid species with a circumpolar distribution, mainly at latitudes above the Arctic Circle (Cohen et al. 1990; Mecklenburg et al. 2018). It is abundant in the

northern Barents Sea (Ajiad et al. 2011), Svalbard Archipelago (Falk-Petersen et al. 1986; Renaud et al. 2012), Greenland waters (Christiansen et al. 2012), Canadian Arctic Archipelago, Beaufort, and Chuckchi Seas (Crawford et al. 2012). On the Arctic shelves, it dominates in both inshore and offshore waters and throughout the central Arctic Ocean from surface to ~1000 m depth (Geoffroy et al. 2016; Christiansen 2017; Mecklenburg et al. 2018). The polar cod can reach up to 460 mm in total length (TL) (Mecklenburg et al. 2018), but TL is generally <250 mm (Cohen et al. 1990). With an average 7–8 years life span, it becomes sexually mature between the age of 2–3 years (Hop and Gjørseter 2013; Mueter et al. 2016; Nahrgang et al. 2016) and is the

Table 1 Comparative ecology and life history aspects of the Antarctic silverfish (*Pleuragramma antarctica*) and the polar cod (*Boreogadus saida*)

	<i>Pleuragramma antarctica</i>	<i>Boreogadus saida</i>
		
Taxonomy	Order: Perciformes Family: Nototheniidae	Order: Gadiformes Family: Gadidae
Distribution	Circumpolar—Antarctic  (Map from Duhamel et al. 2014)	Circumpolar—Arctic  (Map from Mecklenburg et al. 2018)
Life mode	Pelagic	Pelagic
Migration, movements	Diel vertical migrations with fish moving shallower depths at night and deeper during the day (Plötz et al. 2001; Fuiman et al. 2002; Robison 2003; Lancraft et al. 2004) Spawning migrations are believed to take place from open waters to the coastal ice shelves (Koubbi et al. 2011; Ghigliotti et al. 2017; O’Driscoll et al. 2018)	Adults perform diel vertical migrations under the ice. Seasonal vertical migrations toward the bottom prior to winter are observed in juveniles and adults (Benoit et al. 2010; Geoffroy et al. 2016) The species may undertake extensive migrations (Ponomarenko 1968; Hop and Gjørseter 2013; Kessel et al. 2017)
Adult size (average)	15 cm (Fischer and Hureau 1985)	25 cm (Cohen et al. 1990)
Maximum age	14 years (Hubold and Tomo 1989; Sutton and Horn 2011)	8 years (Gillespie et al. 1997)
Trophic level	3.6–4 (Pinkerton 2017)	3.3–3.5 (Christiansen et al. 2012)
Diet	Generalist (Pinkerton 2017; Tavernier and Giraldo, 2017) Opportunistic feeding habit (Pinkerton 2017; Carlig et al. 2019) Ontogenic shifts in prey consumption (Kellermann 1987; Giraldo et al. 2011; Tavernier and Giraldo 2017) The diet in adults is dominated by euphausiids and copepods; a number of other invertebrates are taken by adults; piscivory is uncommon but can be relevant at the local level (Pinkerton 2017)	Generalist (Walkusz et al. 2013; Gray et al. 2016; Steiner et al. 2019) Opportunistic feeding habit (Mueter et al. 2016) Ontogenic shifts in prey consumption (Matley et al. 2013; Geoffroy et al. 2016) The diet in adults is dominated by amphipods, copepods, and young fishes (Matley et al. 2013); appendicularians have occasionally been found to have relevance at the local level (Nakano et al. 2016)

most short lived among the codfishes in the Arctic region (Gillespie et al. 1997; Nahrgang et al. 2014). The polar cod life cycle is complex and includes ontogenetic shifts in habitat: eggs develop under the sea ice, and larvae/juveniles remain associated with the sea ice, while sub-adults and adults are found in the water column under the sea ice, in open waters, and also close to the bottom (Christiansen 2017).

Antarctic silverfish is a nototheniid species widely distributed in the shelf waters around the Antarctic continent, including the Scotia Arc and adjacent islands (Gerasimchuk 1986; DeWitt et al. 1990; Knox 1994). Despite its ancestral benthic origin shared with all other notothenioid fishes, this species has evolved an exclusively pelagic life history, with a suite of relevant morphological and physiological adaptations, acquired during the Antarctic notothenioid diversification (DeVries and Eastman 1978; Wöhrmann et al. 1997; Voskoboinikova et al. 2017). The Antarctic silverfish is the only holopelagic notothenioid species (Vacchi et al. 2012b). Its ability to live in the water column has required extensive evolutionary adjustments centered on buoyancy, including deposition of lipids in subcutaneous and intramuscular sacs (Eastman 1988), partial or total reduction of bony elements, and other skeletal trait modifications (Voskoboinikova et al. 2017). Like the polar cod, its life cycle is complex, eggs develop under the fast ice (Vacchi et al. 2012a), larvae and juveniles disperse over the continental shelves (La Mesa et al. 2010), and adults live in the water column (De Witt et al. 1990; Vacchi et al. 2012b) from surface to 900 m depth (Gerasimchuk 1986; DeWitt et al. 1990; Knox 1994; Fuiman et al. 2002). The Antarctic silverfish may attain a maximum TL of 245 mm (Hubold and Tomo 1989), but TL is generally around 150 mm (Fischer and Hureau 1985). A relatively slow growth and long life were reported for this species that becomes sexually mature between the age of 4–7 years (La Mesa and Eastmann 2012) and lives up to 14 years (Hubold and Tomo 1989; Sutton and Horn 2011).

Although phylogenetically and geographically distant, the polar cod and Antarctic silverfish have been subjected to similar ecological drivers during their independent evolutionary histories in the Polar Regions. They show comparable biological and ecological adaptations, and currently occupy a similar position in their respective food webs. Their abundance and distribution affect the food-web structure, and any fluctuation of those parameters might lead to alternative pathways of energy flow, with repercussions for the whole ecosystem (Bradstreet et al. 1986; Murphy et al. 2016; Aune et al. 2021).

For both the Southern Ocean and Arctic waters, alterations in the physical environment drive the distribution of species, including those of the zooplankton community, leading to change in densities, size, and energetic value of the potential prey of midtrophic level fishes (Brodeur et al.

1999; Beaugrand et al. 2003; Mintenbeck et al. 2012; Henson et al. 2016; Mintenbeck and Torres 2017; Rogers et al. 2020). Such alterations might lead to changes in the distribution and abundance of midtrophic species, as well as on their body condition and energetic value for the upper trophic level, in which extent and relevance largely depend upon each species' degree of diet specialization and feeding flexibility.

Three broad methods of prey capture are known in fishes: suction feeding, ram feeding, and manipulation (Liem 1980). In suction feeding, the predator expands the buccal cavity creating a pressure gradient that forces the prey to move towards the mouth opening. In ram feeding, the predator ingests free-swimming prey by forward movement of the body and protruding jaws. Manipulation is a less common method, where the jaws are directly applied to the prey and used to remove it from the substratum (Wainwright and Bellwood 2002). Pure suction and pure ram feeding are relatively rare, the combination of both modes seems to be the most used. Suction and ram feeding represent ends of a continuum with in which many species fall, and in most of cases, the appropriate definition of their feeding mode would rather be ram-suction feeding (Norton and Brainerd 1993). Two distinct feeding modes are typical of planktivorous species, such as the species considered herein, particulate feeding, and filter feeding (reviewed in Lazzaro 1987). Particulate feeders attack single individual planktonic prey which they visually select from the water column. By contrast, filter feeders do not visually detect individual prey and engulf a volume of water containing the planktonic prey which are retained by entrapment structures, such as gill rakers. Furthermore, filter feeding may be sub-divided into two modes: the tow-net filter feeders which surround the prey with their open mouths while swimming rapidly and the pump filter feeders which use rhythmic suction to capture prey while swimming slowly (Lazzaro 1987).

The feeding ability and flexibility of fish are largely determined by the functional morphology of the feeding apparatus (Wainwright 1988; Sonnefeld et al. 2014; Gidmark et al. 2019). The anatomical and mechanical features of the muscle-skeleton systems involved in the feeding activities determine how fishes detect, pursue, capture, and successfully handle the prey (Wainwright 1988) and, ultimately, provide insights into the ecological roles of species (Motta et al. 1995; Westneat 2006).

The suction index (SI) and the jaw-closing mechanical advantage (MA) are often used to infer the feeding strategies of fish (Wainwright and Bellwood 2002; Gidmark et al. 2019).

The SI evaluates the suction feeding capability based on transmission of muscular force to the buccal cavity (Collar and Wainwright 2006). High SI values imply capability of rapid movements of the jaws, whereas a low SI indicates

slow movements of the jaws (Bansode et al. 2014). The MA, on the other hand, is the capability to produce force with jaws, and it is inversely proportional to the speed of the lower jaw movements (Westneat 2006). A low MA indicates great velocity transfer and typifies species with weak, rapidly closing jaws. A high MA is typical of species with great force transmission due to strong, slowly closing jaws (Bansode et al. 2014). As such, SI and MA measures can be used to infer the mechanism by which the fish uses jaws to catch the prey, i.e. the main feeding mode.

Considerable advances in our understanding of the mechanical basis of feeding performance in fishes have been made with the increase of ecomorphological studies offering insights on diversified ecological roles of the species by highlighting their potential prey usage, providing information on their feeding flexibility, and investigating their capability to adapt to changes in the prey availability (Wainwright and Bellwood 2002; Barnett et al. 2006). However, despite its high potential value, the actual role of the head and jaw morphology in shaping food habits of fishes living in polar environments is poorly known (Klingenberg and Ekau 1996; Bansode et al. 2014). A morphometric analysis of the feeding structures and biomechanics of three Antarctic notothenioids, including the Antarctic silverfish, was recently performed leading to a better definition of their degree of feeding specialization (Carlig et al. 2018).

Here, the feeding performance and potential for resource usage of the polar cod and the Antarctic silverfish were evaluated through an ecomorphological analysis. Key morphological traits of the head and jaw regions were measured to estimate the suction index (SI) and the mechanical advantage (MA). Since gill raker morphology is known to play an important role in food particle retention in planktivorous fishes (Gerking 1994; Tanaka et al. 2006), such structures were also considered.

The foraging flexibility of the polar cod and the Antarctic silverfish, as inferred from the ecomorphological analyses, is compared and discussed in context of ongoing climate

change. This information is particularly relevant because it provides clues about how species modify the feeding mode in response to change in environment and prey availability.

Materials and methods

Sampling

Polar cod *Boreogadus saida* ($n = 15$) were sampled in September 2017 during the TUNU-VII Expedition as part of the international TUNU-Programme (Christiansen 2012). Fish were collected from the RV *Helmer Hanssen* by bottom trawl at a depth of 392 m in Isfjorden (Spitsbergen), frozen, and preserved at $-20\text{ }^{\circ}\text{C}$ for later analyses.

Antarctic silverfish *Pleuragramma antarctica* ($n = 15$) were caught in February 2015 during a New Zealand survey onboard of the RV *Tangaroa*. Specimens were collected by midwater trawl at a depth of 540 m (O’Driscoll and Double 2015).

In order to minimize bias in this study, at the intra-specific level related to ontogeny, only adult specimens were analysed. To compare individuals and species of different total length, morphological measurements were standardized to the standard length of each individual (Barnett et al. 2006).

Species were of similar body size and standard lengths (SL) ranged: *B. saida* 114–166 mm; *P. antarctica* 151–198 mm, attributable to adult body sizes for both species (Cohen et al. 1990; La Mesa and Eastmann 2012).

Ecomorphological analyses

Calculations of morphological metrics of mouth structures and muscles of the head were conducted after dissecting the connection between muscles and bones. Measures were taken in mm to the nearest 0.01 mm.

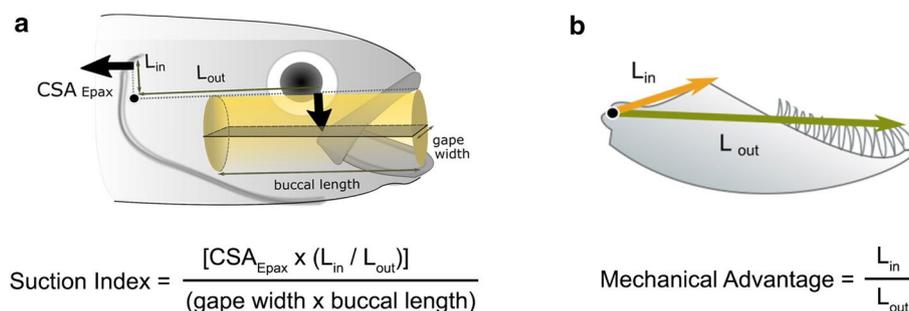


Fig. 1 **a** Scheme of the traits and levers involved in the mechanism of rotation of the neurocranium for the mouth opening to create the pressure gradient of the suction index (modified from Carroll and

Wainwright 2006). **b** Lower jaw-closing lever mechanism for the calculation of the mechanical advantage (modified from Wainwright and Bellwood 2002)

The relationship between mouth morphology and suction feeding performance was estimated by the Suction Index (SI) (Collar and Wainwright 2006; Bansode et al. 2014). The model for SI (Fig. 1a) is based on the transmission of force from the epaxialis muscle to the buccal cavity, generating negative pressure that allows the predator to engulf its prey.

Following Carroll et al. (2004), SI was calculated as follows:

$$SI = \frac{\left[CSA_{\text{epax}} \left(\frac{L_{\text{in}}}{L_{\text{out}}} \right) \right]}{\text{gape width} \times \text{buccal length}}$$

where CSA_{epax} is the cross-sectional area of the epaxialis, L_{in} is the moment arm of the epaxialis, and L_{out} is the moment arm of the buccal cavity. The cross-sectional areas of the ellipse-shaped epaxialis were calculated by the measurements of their axes. The major axis was measured from the supracleithrum-posttemporal (S-PT) joint to the dorsal margin of the epaxialis; the minor as the lateral width of the epaxialis. The L_{in} ($L_{\text{in}}SI$) was calculated as the vertical distance between the centroid of the epaxialis muscles' cross section and the S-PT, and L_{out} ($L_{\text{out}}SI$) was measured from the S-PT joint to the middle of the buccal cavity (see Collar and Wainwright 2006). Gape width (measured as the distance between the left and right coronoid processes of the mandible) and buccal length (measured as the distance between the anterior tip of the mandible and the depression in the sternohyoideus) were calculated to estimate the volume of the buccal cavity.

The capability of the fish to produce force during the closing of the lower jaw was evaluated from the Mechanical Advantage (MA) in jaw closing (Fig. 1b). We measured the lever arms associated with jaw-closing systems (Bansode et al. 2014). The MA was calculated as the ratio of the jaw closing in-lever ($L_{\text{in}}MA$) to the jaw-closing out-lever ($L_{\text{out}}MA$). $L_{\text{in}}MA$ was measured as the distance from the quadrate-articular joint to the point of insertion of the adductor mandibulae muscle on the lower jaw, $L_{\text{out}}MA$ as the distance from the quadrate-articular joint to the anterior-most tooth of the lower jaw (Westneat 2004; Bansode et al. 2014).

For the gill raker morphological analysis, the first left branchial arch was cut off from the gill. The gill arches were mounted with the gill rakers perpendicular to the base of the arch (Amundsen et al. 2004) and were observed under an Olympus SZX7 stereo microscope. Gill rakers were photographed by a Nikon "DS-L3" digital camera mounted on the microscope, and measurements taken to the nearest 0.01 mm. For each specimen, the length of the gill arch (LA) was measured, and the number of the gill rakers (NG) were counted; the length of gill rakers (LG), the spacing between subsequent gill rakers (SG), and the width of gill rakers

(WG) were measured for five gill rakers from the midsection of the gill arch (Tanaka et al. 2006). The filtering area, i.e. by approximating the set of gill rakers and gill arch as a rectangle (Magnuson and Heitz 1971), was calculated as the product of LG and LA.

Statistical analyses

The suction index (SI), the mechanical advantage (MA), and the surface area of gill rakers (standardized by SL^2) for polar cod vs. Antarctic silverfish were tested. Data were transformed in $\arcsin \sqrt{p}$. After testing normality and homoscedasticity of the distributions with Shapiro-Wilk and Levene tests, t tests were conducted for each variable. Statistical significance was determined at $\alpha = 0.05$.

To investigate which morphometric features explain the greatest variations between the two polar species, a principal component analysis (PCA) involving 13 morphological traits was developed. The variables considered were the morphological traits used for the SI and MA metrics, the lengths of the head and mouth, and gill rakers and gill arch metrics. The morphological measurements were standardized relative to the body size (SL) of each individual (Barnett et al. 2006). The 13 morphological traits were compared with t tests. The non-parametric Wilcoxon test was used when the assumptions of normality and homogeneity of variance of the data were not respected.

Statistical analyses were performed using the software R 3.2.2 (R Development Core Team 2015).

Results

The SI mean value was higher in polar cod than in Antarctic silverfish (0.070 ± 0.014 SD and 0.060 ± 0.011 SD, respectively; Fig. 2a). Conversely, the mean MA index was higher in Antarctic silverfish than in polar cod (0.253 ± 0.019 SD and 0.223 ± 0.025 SD, respectively; Fig. 2b). Both SI and MA significantly differed between the two species ($t = 2.22$; $p = 0.0351$ and $t = -2.96$; $p = 0.0066$, respectively).

The filtering surface was significantly larger for polar cod (0.0060 ± 0.0006 SD) compared to Antarctic silverfish (0.0047 ± 0.0006 SD; t test, $t = 5.75$, $p < 0.0001$; Fig. 2c).

The head length and buccal length of Antarctic silverfish were significantly longer than those of polar cod, but polar cod had a larger gape width (Table 2). When calculating the suction index (SI) and the mechanical advantage (MA), significant differences were detected between $L_{\text{out}}SI$ and $L_{\text{out}}MA$. All the measures of gill rakers were significantly different between the two species (Table 2). Polar cod had longer and more numerous gill rakers than Antarctic silverfish. In Antarctic silverfish, the gills arches were significantly longer and the gill rakers resulted more spaced and

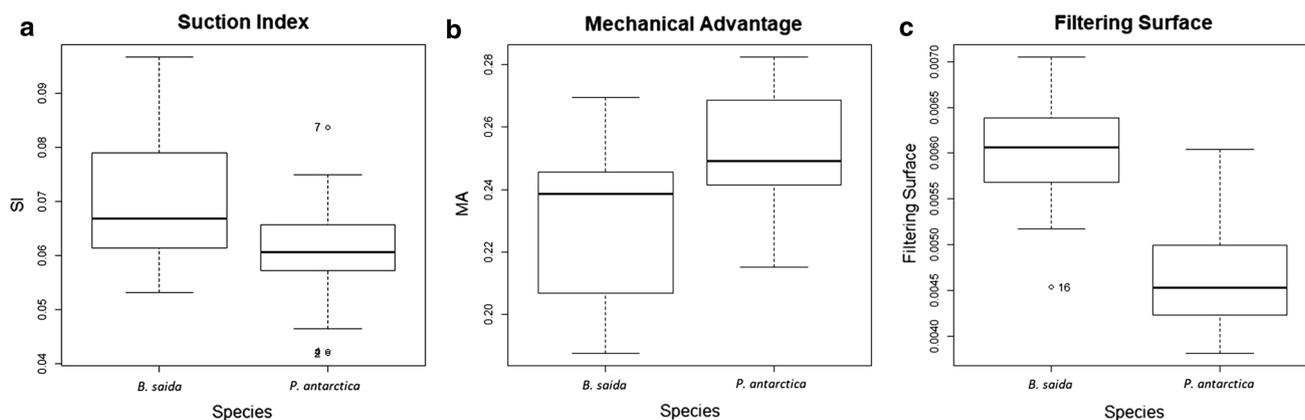


Fig. 2 Boxplots of the values of **a** suction index (SI), **b** mechanical advantage (MA), and **c** filtering surface calculated on the two polar species

Table 2 Mean values and standard deviation of the 13 morphological traits. Measures were standardized by SL

Trait	<i>Boreogadus saida</i> (n = 15) mean ± SD	<i>Pleuragramma antarctica</i> (n = 15) mean ± SD	<i>P</i> value
Head length (HL)	0.2351 ± 0.0065	0.2740 ± 0.0087	<i>p</i> < 0.0001
Gape width (GW)	0.0773 ± 0.0032	0.0679 ± 0.0044	<i>p</i> < 0.0001
Buccal length (BL)	0.0941 ± 0.0134	0.1453 ± 0.0063	<i>p</i> < 0.0001*
Cross-sectional area (CSA _{epaxialis})	0.0538 ± 0.0040	0.0550 ± 0.0028	<i>p</i> = 0.3518
In-lever suction Index (L _{in} SI)	0.0200 ± 0.0020	0.0213 ± 0.0016	<i>p</i> = 0.0674
Out-lever suction Index (L _{out} SI)	0.1154 ± 0.0061	0.1099 ± 0.0037	<i>p</i> = 0.0069
In-lever mechanical advantage (L _{in} MA)	0.0307 ± 0.0034	0.0347 ± 0.0028	<i>p</i> = 0.0017
Out-lever mechanical advantage (L _{out} MA)	0.1339 ± 0.0048	0.1369 ± 0.0052	<i>p</i> = 0.1136
Gill raker length (LG)	0.0322 ± 0.0027	0.0235 ± 0.0025	<i>p</i> < 0.0001
Gill raker spacing (SG)	0.0031 ± 0.0002	0.0034 ± 0.0004	<i>p</i> = 0.0391
Gill raker width (WG)	0.0020 ± 0.0002	0.0029 ± 0.0002	<i>p</i> < 0.0001
Gill arch length (LA)	0.1861 ± 0.0124	0.1980 ± 0.0119	<i>p</i> = 0.0125
Gill raker number (NG)	40.07 ± 2.91	27.67 ± 2.92	<i>p</i> < 0.0001

*Wilcoxon test

thicker (Fig. 3; Table 2). According to the PCA, 75.64% of the variance was explained on the first three axes (Table 3). The two species appear well distinct along the PC1 axis, which ordination is driven by head and buccal length, which are directly involved both in MA and SI, and by features of the filtration system of the gill rakers (Fig. 4).

Discussion

Following a functional ecology approach (sensu Villéger et al. 2017) to better understand the ecological processes that operate in nature (McGill et al. 2006; Luiz et al. 2019), we profiled the food acquisition of the polar cod and the Antarctic silverfish from key morpho-anatomical

traits, and calculation of jaw-closing force transmission (MA) and suction index (SI).

The biomechanics of feeding in the two species resulted differed significantly, with the polar cod having lower MA and higher SI than the Antarctic silverfish (Fig. 2a, b). In the frame of the available information on fish species, and based on the classification of suction feeders below 0.23 MA and biters above 0.27 MA (Wainwright and Richard 1995), this places the polar cod at the upper end of the MA range of suction feeders, while the Antarctic silverfish lies in between the suction feeders and the biters (Table 4).

Datasets from literature about jaw closing in polar and non-polar fishes show a wide range of MA values (Table 4). A high MA value defines fishes that are manipulators, i.e. species that bite or crush hard body prey, e.g. crustaceans or bivalves. The blue-striped grunt (*Haemulon sciurus*),

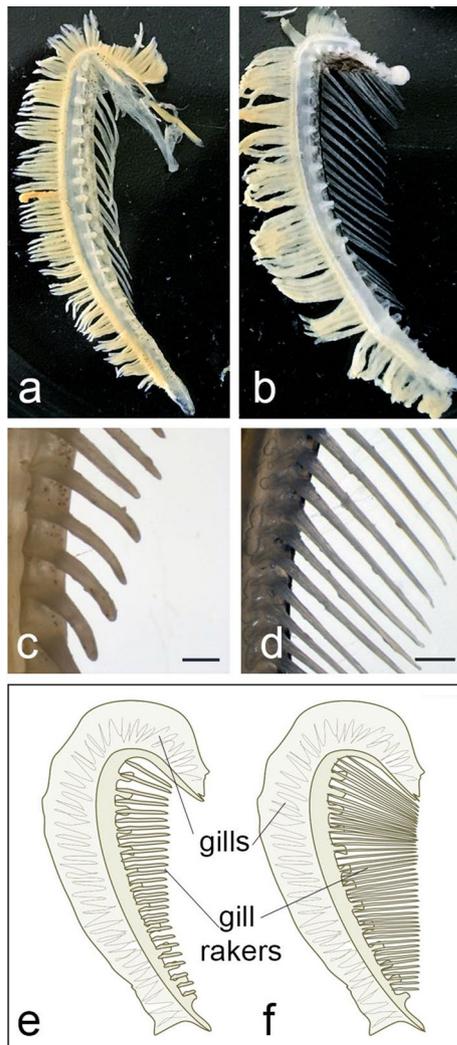


Fig. 3 Gill arch morphology of *Pleuragramma antarctica* (a, e) and *Boreogadus saida* (b, f). Detail of gill rakers of *Pleuragramma antarctica* (c) and *Boreogadus saida* (d). Scale bar 1 mm

feeding exclusively on benthic prey as brachyuran crabs and polychaetes, is an example of this group. The feeding performance of the blue-striped grunt is optimized by the presence of robust oral jaws, small gape, high MA of jaw closing, and powerful force-generating capability of the adductor mandibulae (Liem 1980; Wainwright and Bellwood 2002). The highest MA value is found in species which feeds on epilithic and endolithic autotrophic microorganisms, like the scarrid daisy parrotfish (*Chlorurus sordidus*) that crops, scrapes, or bites the calcareous substrate of the coral reef surface with their beak-like and extremely powerful jaws (Lange et al. 2020). For the large pelagic fishes, such as Atlantic Spanish mackerel (*Scomberomorus maculatus*), greater amberjack (*Seriola dumerili*) and common dolphinfish (*Coryphaena hippurus*), high MA values relate to ram feeding as the capability to produce force with jaws allows

Table 3 Coefficients of the 13 traits selected to describe differences in the feeding apparatus of *Boreogadus saida* and *Pleuragramma antarctica* as resulting from the PCA after standardization by SL

	PC1	PC2	PC3
Variance	6.167	2.454	1.213
% of variance	47.417	18.877	9.331
Cumulative % of variance	47.440	66.313	75.644
Traits			
Head length (HL)	0.948	-0.039	0.115
Gape width (GW)	-0.767	-0.138	0.225
Buccal length (BL)	0.931	-0.257	0.036
Cross-sectional area (CSA _{epaxialis})	0.143	- 0.864	0.408
In-lever suction index (L _{in} SI)	0.317	- 0.841	0.374
Out-lever suction index (L _{out} SI)	-0.463	0.421	0.496
In-lever mechanical advantage (L _{in} MA)	0.671	0.266	-0.119
Out-lever mechanical advantage (L _{out} MA)	0.384	0.591	0.492
Gill raker length (LG)	- 0.879	-0.103	0.218
Gill raker spacing (SG)	0.487	-0.369	-0.025
Gill raker width (WG)	0.937	0.148	0.092
Gill arch length (LA)	0.427	0.385	0.513
Gill raker number (NG)	- 0.900	0.013	0.141

In each component, highest and lowest (relative of driving variables) coefficients are in bold

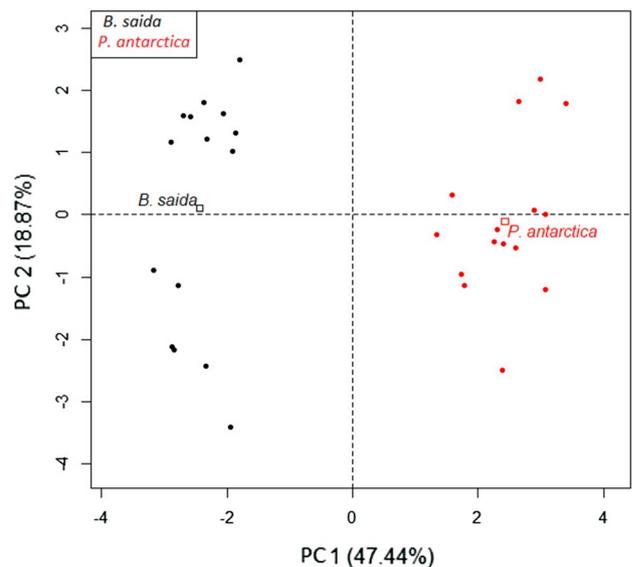


Fig. 4 Principal component analysis plot developed on 13 morphological traits of feeding apparatus of *Boreogadus saida* and *Pleuragramma antarctica*

to grab nekton such as fishes and large pelagic invertebrates (e.g. squid) during rapid swimming. In the case of the grey snapper (*Lutjanus griseus*), with varied diet, a high MA

Table 4 Mean SI and MA values of the Antarctic silverfish (*Pleuragramma antarctica*) and polar cod (*Boreogadus saida*) are compared to the values found in literature for other fish species

Species	Family	Max length	Habitat	Food habits	SI
<i>Opsanus tau</i>	Batrachoididae	43.2 cm TL [1]	Demersal	BI [2]	0.02
<i>Dissostichus mawsoni</i>	Nototheniidae	200 cm TL [3]	Demersal	F; NI [4]	0.03
<i>Scomberomorus maculatus</i>	Scombridae	91 cm FL [5]	Pelagic	F; NI [6]	0.04
<i>Micropterus salmoides</i>	Centrarchidae	97 cm TL [7]	Demersal	F; BI; V [7]	0.05
<i>Coryphaena hippurus</i>	Coryphaenidae	210 cm TL [8]	Pelagic	F; NI [9]	0.06
<i>Pleuragramma antarctica</i>	Nototheniidae	25 cm TL [10]	Pelagic	MZ; Z [11]	0.06
<i>Epinephelus drummonhayi</i>	Serranidae	110 cm TL [12]	Demersal	BI; F [2]	0.06
<i>Boreogadus saida</i>	Gadidae	30 cm TL [13]	Pelagic	MZ; Z; F; BI [14]	0.07
<i>Ambloplites ariommus</i>	Centrarchidae	30.5 cm TL [1]	Demersal	F; BI; NI [7]	0.07
<i>Seriola dumerili</i>	Carangidae	190 cm TL [15]	Pelagic	F; NI [15]	0.08
<i>Lutjanus griseus</i>	Lutjanidae	89 cm TL [16]	Demersal	F; BI; NI; MZ [17]	0.12
<i>Haemulon sciurus</i>	Haemulidae	46 cm TL [18]	Demersal	BI; F [18]	0.16
<i>Enneacanthus obesus</i>	Centrarchidae	9.5 cm TL [7]	Demersal	BI; NI [7]	0.22
<i>Lepomis punctatus</i>	Centrarchidae	20 cm TL [7]	Demersal	BI; NI; MZ; Z [7]	0.22
<i>Lycodichthys dearboni</i>	Zoarcidae	23 cm TL [19]	Demersal	MZ; BI [19]	0.23
<i>Trematomus bernacchii</i>	Nototheniidae	28 cm TL [10]	Demersal	MZ; BI; F [20]	0.27
<i>Pagrus pagrus</i>	Sparidae	91 cm TL [1]	Demersal	BI; F [21]	0.28
<i>Lepomis gibbosus</i>	Centrarchidae	40 cm TL [7]	Demersal	F; V [7]	0.33
<i>Lepomis macrochirus</i>	Centrarchidae	41 cm TL [7]	Demersal	BI; F; NI [7]	0.40
Species	Family	Max length	Habitat	Food habits	MA
<i>Hiodon alosoides</i>	Hiodontidae	52 cm FL [1]	Pelagic	BI; NI; F; V [22]	0.12
<i>Clepticus parrae</i>	Labridae	30 cm TL [23]	Demersal	MZ; Z [17]	0.19
<i>Atherinomorus lacunosus</i>	Atherinidae	25 cm TL [24]	Pelagic	Z [24]	0.21
<i>Elops saurus</i>	Elopidae	100 cm TL [23]	Pelagic	NI; F [25]	0.21
<i>Boreogadus saida</i>	Gadidae	30 cm TL [13]	Pelagic	MZ; Z; F; BI [14]	0.22
<i>Halichoeres pictus</i>	Labridae	13 cm TL [23]	Demersal	BI; MZ [23]	0.23
<i>Oncorhynchus tshawytscha</i>	Salmonidae	150 cm TL [26]	Demersal	BI; F; NI [26]	0.23
<i>Pleuragramma antarctica</i>	Nototheniidae	25 cm TL [10]	Pelagic	MZ; Z [11]	0.25
<i>Micropterus salmoides</i>	Centrarchidae	97 cm TL [7]	Demersal	F; BI; V [7]	0.25
<i>Gadus morhua</i>	Gadidae	200 cm TL [14]	Demersal	BI; F [14]	0.25
<i>Lycodichthys dearboni</i>	Zoarcidae	23 cm TL [19]	Demersal	MZ; BI [19]	0.25
<i>Opsanus tau</i>	Batrachoididae	43.2 cm TL [1]	Demersal	BI [2]	0.25
<i>Scomber scombrus</i>	Scombridae	60 cm FL [5]	Pelagic	MZ; Z; F [27]	0.27
<i>Dissostichus mawsoni</i>	Nototheniidae	200 cm TL [3]	Demersal	F; NI [4]	0.28
<i>Trematomus bernacchii</i>	Nototheniidae	28 cm TL [10]	Demersal	MZ; BI; F [20]	0.28
<i>Sardinella aurita</i>	Clupeidae	41 cm TL [28]	Pelagic	Z [28]	0.31
<i>Pagrus pagrus</i>	Sparidae	91 cm TL [1]	Demersal	BI; F [21]	0.36
<i>Haemulon sciurus</i>	Haemulidae	46 cm TL [18]	Demersal	BI; F [18]	0.47
<i>Lutjanus griseus</i>	Lutjanidae	89 cm TL [16]	Demersal	F; BI; NI; MZ [17]	0.50
<i>Scomberomorus maculatus</i>	Scombridae	91 cm FL [5]	Pelagic	F; NI [6]	0.51
<i>Coryphaena hippurus</i>	Coryphaenidae	210 cm TL [8]	Pelagic	F; NI [9]	0.56
<i>Epinephelus drummonhayi</i>	Serranidae	110 cm TL [12]	Demersal	BI; F [2]	0.56
<i>Seriola dumerili</i>	Carangidae	190 cm TL [15]	Pelagic	F; NI [15]	0.62
<i>Chlorurus sordidus</i>	Scaridae	40 cm TL [29]	Demersal	A [29]	0.68

Fishes (F); Nectonic invertebrates (NI); Benthic invertebrates (BI); Zooplankton (Z); Macrozooplankton (MZ); Algae (A); Other vertebrates (V)
 Values calculated for the species in this study are in bold. (Data of other species from Collar and Wainwright 2006; Bansode et al. 2014 and Sonnefeld et al. 2014)

References: [1] Froese and Pauly (2020); [2] Sonnefeld et al. (2014); [3] Eastman and De Vries (2000); [4] Stevens et al. (2014); [5] Muus et al. (1999); [6] Bowman et al. (2000); [7] Page and Burr (2011); [8] Collette (1999); [9] Eschmeyer and Herald (1999); [10] Dewitt et al. (1990); [11] Pinkerton (2017); [12] Heemstra and Randall (1993); [13] Nahrgang et al. (2014); [14] Matley et al. (2013); [15] Smith-Vaniz (1986); [16] Allen (1985); [17] Randall (1996); [18] Courtenay and Sahlman (1978); [19] Anderson (1990); [20] Bansode et al. (2014); [21] Papaconstantinou and Caragitsou (1989); [22] Donald and Kooyman (1977); [23] Robins and Ray (1986); [24] Kimura et al. (2007); [25] McBride et al.

Table 4 (continued)

(2010); [26] Morrow (1980); [27] Collette (1986); [28] Whitehead (1988); [29] Lange et al. (2020)

value corresponds to the double functions to crush benthic organisms (e.g. crabs, mussels, and other invertebrates) and to grab nektonic fishes (Yeager et al. 2014).

A combination of medium to low MA values and medium to high SI values is found among suction and ram-suction feeders, respectively. In the centrarchid bluegill (*Lepomis macrochirus*), a pure suction feeder, the high SI derived from the large buccal cavity and cross-sectional area of the epaxialis, allows feeding on soft, substrate-attached or elusive prey such as shrimp, small crabs, and fishes (Sonnefeld et al. 2014).

However, pure suction feeding is rare, in most cases suction is associated to ram activity and enacted by rapid bursts of swimming speed coupled to a powerful suction force (Wainwright and Richard 1995). The suction force (SI value) may adjust according to the prey of interest because feeding on prey suspended in the pelagic zone requires a lower suction force compared to feeding on sessile prey fixed to the substratum. Based on the biomechanics of suction, suction feeding is also supported by the capability to produce force with jaws, resulting in medium MA values (Westneat 2004; Collar and Wainwright 2006).

Polar cod has a medium to high SI value for a planktivore fish and jaw-closing MA values attributable to ram-suction feeding. Similar MA values are indeed found in the ram-suction midwater zooplanktivore wrasses (Labridae) *Hali-choeres pictus* and *Clepticus parrae* (Wainwright and Richard 1995). Despite having a slightly higher MA value and slightly lower SI value, Antarctic silverfish falls outside the range of suction feeders (following Wainwright and Richard 1995). Whatever the strategy, both the polar species of our study have the typical characteristics of zooplanktivore fishes, such as high visual acuity (i.e. large eye lenses, Jönsson et al. 2014) and the specialized structure for retaining zooplankton (i.e. elongated gill rakers) (Schmitz and Wainwright 2011).

Based on the biomechanical characteristics, Carlig et al. (2018) concluded that particulate feeding was likely the prevalent planktivory foraging mode in the Antarctic silverfish. This foraging strategy, which seems based on ram activity, is also supported by a good vision (Eastman and Lannoo 2011; La Mesa and Eastman 2012) which allows it to select single planktonic prey in the water column (Lazzaro 1987). This is also supported by the dentition of the Antarctic silverfish, with enlarged teeth about midway in length of lower jaw (DeWitt et al. 1990) and moderately protractile jaws (DeWitt and Hopkins 1977) that allows the Antarctic silverfish to grab relatively large agile pelagic prey items such as euphausiids.

The jaw metrics for polar cod and Antarctic silverfish reinforce the difference between those two species. In the polar cod, a short head and short buccal length support the capability for fast movements of the jaws underlying a suction feeding strategy to capture small motile prey (Wainwright and Bellwood 2002), widespread among midwater predators (Motta 1982, 1988). Compared to Antarctic silverfish, the polar cod would more effectively use suction and particulate ram-suction as the main feeding mode (suggested also by Cusa et al. 2019) also allowed by polar cod lens plasticity (Jönsson et al. 2014) to visually detect individual large prey. These ecomorphological traits are reflected in the diet of adult polar cod which consists of large agile prey such as euphausiids, amphipods, and young fishes (Orlova et al. 2009; Christiansen et al. 2012; Renaud et al. 2012; Matley et al. 2013; Hop and Gjørseter 2013) and gelatinous appendicularians (Nakano et al. 2016).

Based on the gill raker number, length, and breadth, our ecomorphological analysis highlighted also possible secondary feeding strategies for the studied species.

Gill raker morphology plays an important role in the feeding behaviour of planktivorous fishes, and it is often adopted to explain differences in the diets of planktivorous fishes (Gerking 1994; Castillo-Rivera et al. 1996; Tanaka et al. 2006). Gill raker number and morphology are strictly related to the trophic ecology of species and disclose differences in feeding behaviour at the inter- and intra-specific levels. In the polymorphic whitefish (*Coregonus lavaterus*), two morphs are known with different feeding habits: the sparsely raked morph (15–30 gill rakers in the first left arch) with shorter, thicker, and less densely packed rakers that feeds on zoobenthos, and the densely raked morph (28–42 gill rakers in the first left arch) whose diet is dominated by zooplankton and other pelagic prey (Amundsen et al. 2004).

Both the Antarctic silverfish and polar cod differ in the number, length, and breadth of gill rakers, indicative of a differentiated adaptation to planktivory. The morphology of gill rakers in the Antarctic silverfish suggests that this species relies on filter feeding as an alternative foraging mode (Carlig et al. 2018). Gill raker morphology of polar cod (numerous, longer, and narrower gill rakers than those of Antarctic silverfish) and its wider filtering surface, allows polar cod to have an even higher efficiency in retaining medium to small prey in the oral cavity than the Antarctic silverfish. Based on the biomechanical characteristics and gill raker morphology, polar cod may be defined as a pump filter feeder (sensu Lazzaro 1987), capable of rhythmic suction to capture prey items when prey items are small and/or present at high densities.

Compared to the extremely effective and complex filter apparatus of herrings (*Clupeiformes*) that are specialized to feed on small-sized zooplankton (Storm et al. 2020), the gill rakers of the polar cod and Antarctic silverfish are less dense, more spaced, and less numerous, supporting filter feeding as a possible alternative but not the main feeding mode of those species.

Overall, based on the ecomorphological characteristics, polar cod and Antarctic silverfish exhibit feeding plasticity. The Antarctic silverfish may prey on a wide size range of zooplankton owing to its large and strong mouth apparatus equipped with enlarged teeth about midway the length of lower jaw (DeWitt et al. 1990), but they may also rely on tow-net filter feeding, engulfing a volume of water by swimming bursts coupled with fully agape mouth, if small planktonic prey such as copepods are available (Carlig et al. 2018).

The polar cod, on the other hand, may be able to alternate particulate suction feeding and pump filter feeding to optimize energy intake in the presence of small prey. This feeding plasticity is supported also by diet studies that show a broad spectrum of pelagic and benthic prey of different size (Orlova et al. 2009; Christiansen et al. 2012; Renaud et al. 2012; Hop and Gjørseter 2013; Aune et al. 2021). Such a shift in the feeding mode may be ontogenetic but is also affected by prey density and prey size (Lazzaro 1987). Apparently particulate feeding is favoured when prey items are large and/or occur at low densities, whereas filter feeding prevails when prey are small and/or abundant (Gibson and Ezzi 1992).

The morpho-anatomical traits of the midtrophic Antarctic silverfish and polar cod support an opportunistic feeding strategy with a potential to switch from one feeding mode to another according to the prevailing abundance and size of the available prey. Such plasticity in feeding mode is supported by diet analyses that indicate different preys for both species based on area and seasons (Carlig et al. 2019; Cusa et al. 2019; Mueter 2016; Pinkerton 2017). In addition, planktivorous fishes such as Californian anchovy *Engraulis mordax* (O'Connell 1972), European pilchard *Sardina pilchardus* (Garrido et al. 2008), and Atlantic herring *Clupea harengus* (Gibson and Ezzi 1992) commonly switch between particulate and filter-feeding behaviour according to prey availability. This flexibility in feeding modes may counteract adverse changes in zooplankton communities.

The ongoing warming and sea-ice reduction at both poles lead to transformation of plankton communities, from assemblages dominated by large, lipid-rich copepods and euphasiids, to a more diverse community of smaller and less energy-rich zooplankton (Mintenbeck and Torres 2017). A switch in feeding mode may be advantageous for

the two midtrophic species under changing environmental conditions, but it does not necessarily translate into a higher resilience of the ecosystems as a whole or guarantee the maintenance of the energy flow. For example, prey that is low in energy, such as gelatinous zooplankton, may expand become abundant, as already described for some areas (see Rogers et al. 2020 for a review). Because the body conditions of fishes are linked to the availability and the quality of prey, changes in prey could lead to nutritional stress for individuals and populations with consequences across the entire food web (Moore and Gulland, 2014; Steiner et al. 2019). Moreover, in light of ocean warming, fish species spread from lower latitudes toward the Polar Regions, and they may outcompete the native polar fishes such as polar cod and Antarctic silverfish (Hunt et al. 2016; Christiansen 2017).

Further research integrating the functional ecology and adaptive capacity of key species in the context of ongoing change represents the necessary successive step to shed light on the food-web dynamics, address the range of potential ecosystems responses, and project the impact of change in these vulnerable polar ecosystems.

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Authors contribution EC, DDB, and LG conceived and designed the analysis. EC, LG, JSC, and RLO collected the samples. EC and DDB performed the analysis. EC wrote the manuscript. DDB, LG, JSC, RLO, MV, EP, and SF improved the manuscript with constructive criticisms. JSC and RLO revised the language.

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Data availability All datasets generated for this study are included in the manuscript.

Declarations

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Ethical approval (include appropriate approvals or waivers) All applicable international, national, and/or institutional guidelines for the care and use of animals were followed and all necessary approvals have been obtained. The sampling of Antarctic silverfish was carried out in accordance with permit AMLR14/04/Tangaroa/ZMFR issued by the

New Zealand government under the Antarctic Marine Living Resources (AMLR) Act 1981. The sampling of polar cod was conducted in compliance with the Government of Greenland and Norwegian authorities—TUNU document ID: C-17-129.

Consent to participate We declare all relevant parties consented to participate in this study.

Consent for publication We declare all relevant parties have consented to the publication of this work.

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