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ORIGINAL RESEARCH ARTICLE

Age, growth rate, and otolith growth of polar cod (*Boreogadus saida*) in two fjords of Svalbard, Kongsfjorden and Rijpfjorden

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Summary This work presents biological information for polar cod (*Boreogadus saida*) collected with a Campelen 1800 shrimp bottom trawl in Kongsfjorden (two stations located in the inner part of the fjord adjacent to the glacier) and Rijpfjorden (one station at the entrance to the fjord) in September and October 2013. The otolith-based ages of polar cod collected in Kongsfjorden (6.1—24 cm total length TL; $n = 813$) ranged from 0 to 4 years. The growth rate was relatively constant at approximately 4.7 cm year^{-1} between years 1 and 4, which indicates that growth was fast in the glacier area. The ages of polar cod collected in Rijpfjorden (8.6—15.9 cm TL; $n = 64$) ranged from 2 to 3 years. The fish from Rijpfjorden were smaller at age than those from Kongsfjorden, and their growth rate between years 2 and 3 (no other age classes were available) was approximately 3.3 cm year^{-1}. In both fjords, males and females were of the same size-at-age and the same weight-at-TL. The small sampling area means that the results on growth rate are not representative of the entire fjords. Instead, the results can be discussed as presenting the possible growth rates of some populations. A strong relationship was identified between otolith size (length and weight) and fish size (TL and TW), with no differences between males and females or the fjords. A significant, strong relationship was also noted between fish and otolith growth rates.

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1. Introduction

Polar cod (*Boreogadus saida*) is both a pelagic and demersal gadoid species that plays a key role in the Arctic shelf seas (Hop and Gjøsæter, 2013). It is distributed in open and ice-covered waters, and it provides a link between the lower (mainly zooplankton) and higher (seabirds and mammals) trophic levels (Christiansen et al., 2012; Hop and Gjøsæter, 2013). Closer association with ice, however, occurs particularly during the larval and juvenile stages (Bouchard and Fortier, 2011), whereas adult fish are primarily distributed in open or deeper waters below the ice (Geoffroy et al., 2011, 2016). From the point of view of population ecology, polar cod as an abundant planktivorous species could be a significant food competitor for other species (Renaud et al., 2012) such as capelin (*Mallotus villosus*) (Hedeholm et al., 2012). The level of competition depends, of course, on polar cod life stages. Additionally, the poleward expansion of Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) observed in recent years (Fossheim et al., 2015; Haug et al., 2017; Misund et al., 2016; Szczucka et al., 2017) increases the risk of predation by these species on polar cod. Another potential risk involves increased food competition between the young stages of Atlantic cod and haddock and polar cod, even if competition currently seems still to be at a low level (Renaud et al., 2012).

As the temperature is predicted to rise in the Arctic, further changes in species composition, their requirements, and processes such as predation and food competition are expected in the future (Berge et al., 2015; Fossheim et al., 2015; Haug et al., 2017; Misund et al., 2016). In regions such as Svalbard, these changes are likely to have serious consequences for the polar cod population. Therefore, obtaining a good understanding of polar cod life history strategies, biology, and ecology, including, for example, information on size range, growth rate, and length-weight relationship, is crucial. The amount of information of this kind for polar cod remains insufficient.

Otoliths are a useful tool in research on fish ecology. Information on the relationship between somatic growth and otolith growth as well as between otolith size and fish size is important for many applications, such as back-calculating growth rates (Francis, 1990), size estimates of fish from the guts of predators (Dietrich et al., 2006; Fritts and Pearsons, 2006; Takasuka et al., 2004), and age prediction (Boehlert, 1985; Fey and Linkowski, 2006). Although literature data on otolith size-fish size are available for polar cod (Christiansen et al., 2005; Frost and Lowry, 1981; Lidster et al., 1994), no data on the somatic growth-otolith growth relationship are available for this species except in a publication by Bouchard and Fortier (2008), who show that otolith growth is a reliable estimator of somatic growth for age-0 polar cod. Validating this assumption is necessary if growth back-calculation from otoliths or relative growth estimates from annual ring widths are to be conducted. The above-mentioned applications make otoliths a useful tool in research on the ecology of polar cod especially in light of the processes occurring in the Arctic ecosystems — increasing temperature and changes in community structure of different groups of sea animals (Fossheim et al., 2015; Haug et al., 2017; Misund et al., 2016) including mammals (Haug et al., 2017) that prey on polar cod.

This study determines the sex-specific size frequency, growth rate, and weight at length relationship for polar cod collected in two fjords — Kongsfjorden and Rijpfjorden. Because of the small sampling areas, we cannot treat the growth rate results as representative of the entire fjords. Instead, the results can be considered as indicative of the possible growth of some populations in the fjords analyzed. Additionally, the otolith size-fish size relationship as well as the fish growth rate-otolith growth rate relationships were analyzed to verify the usefulness of polar cod otoliths for their size and growth back-calculation. Possible sex and fjord effects were considered in these relationships.

2. Material and methods

2.1. Study area

Kongsfjorden is approximately 25 km long and 5—10 km wide and is located on the northwest coast of Svalbard (79°N, 12°E) (Fig. 1). Because it is an open fjord with no sill at the entrance, the influence of warm, saline Atlantic waters carried with the North Atlantic Current makes it sub-Arctic rather than Arctic. However, at the head of the fjord is an active tidal glacier that causes marked environmental gradients in salinity, temperature, and sedimentation rates (Walkusz et al., 2009). Rijpfjorden is approximately 40 km long and 12 km wide and is located in the high-Arctic on the northern side of Nordaustlandet, Svalbard (80°N, 22°30′E) (Fig. 1). The fjord is open toward the Arctic Ocean, and, because of the limited influence of warm Atlantic waters, its environment is truly arctic (Walkusz et al., 2009). The fjord is ice-covered for six to eight months annually (Wallace et al., 2010).

2.2. Fish collection

Polar cod (*B. saida*) were collected in Kongsfjorden and Rijpfjorden (Svalbard, Norway) between September 29 and October 4, 2013 during a cruise of the R V^{-1} *Helmer Hanssen* using a Campelen 1800 shrimp bottom trawl. The horizontal and vertical openings were 17 m and 4—5 m, respectively, and the door spread was about 45—50 m. Mesh size was 80 mm in the front and 22 mm in the cod end. The gear was towed on the bottom for approximately 10—15 min at 3 knots/h. The fish were collected at two stations in Kongsfjorden (depth: 134 m and 52 m) and at one in Rijpfjorden (depth: 280 m) (Fig. 1). Random sub-samples of polar cod were collected, and a total of 813 fish from Kongsfjorden and 64 from Rijpfjorden were used for the biological analysis, which included determining total length (TL, ±0.1 cm), total wet weight (TW, ±0.1 g), and sex. The fish were stored frozen before the measurements were taken. All the fish from Rijpfjorden (n = 64) and a sub-sample (n = 358) of fish from Kongsfjorden were used for otolith extraction (Fig. 2).

2.3. Otolith analysis

The sagittal otoliths were extracted from each fish non-randomly to cover the size range and to represent the fish size frequency in a given sample. The otoliths were cleaned

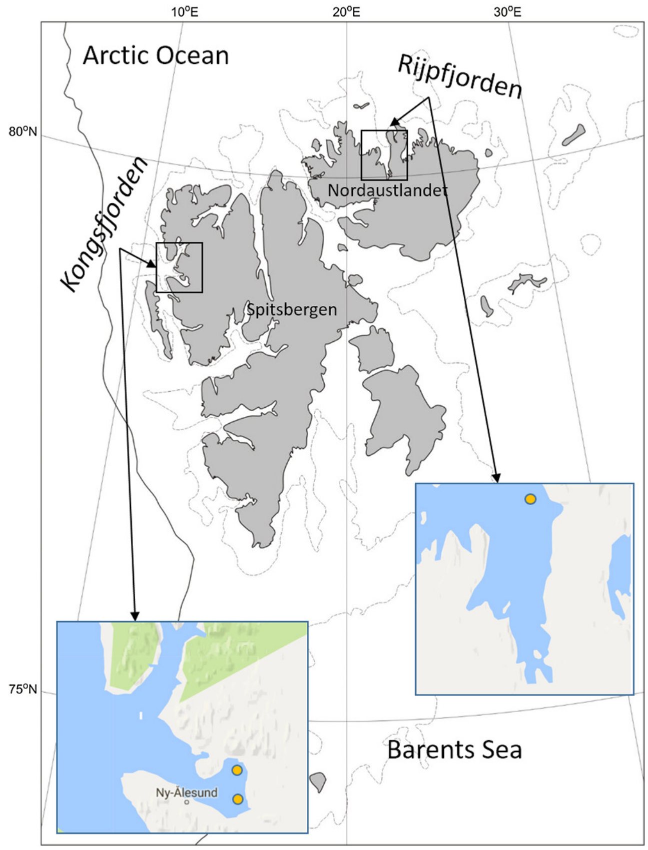

Figure 1 Map of sampling sites — Kongsfjorden and Rijpfjorden (Svalbard, Norway). The fish were collected at two stations in Kongsfjorden (depth: 134 m and 52 m, n = 813) and one station in Rijpfjorden (depth: 280 m, n = 64).

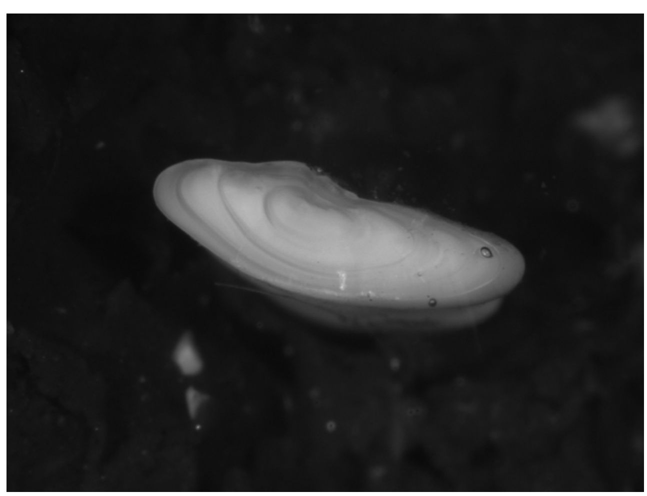

Figure 2 Annual rings in the sagittae of 13.4 cm TL polar cod.

in 96% ethanol, dried, and stored in paper envelopes for further analysis. Age was then estimated by counting the annual rings from broken otoliths. This was performed twice by the same person on different occasions using a compound microscope. The left or right sagitta was used for age estimation depending on the clarity of the increment pattern. No comparison of age estimates between the two otoliths were made. If the ages obtained from the two readings were different, the otolith was re-examined and another reader was consulted. If the two readers could not come to a decision about age, the otolith was excluded (13 of the 422 otoliths examined were excluded). Otolith length was measured for each fish from one of the sagittae with the Image Pro image analysis system (Media Cybernetics, USA). The same otolith was also weighed (±0.01 mg) on a Cahn C-31 microbalance (Thermo Orion, Beverly, MA).

2.4. Data analysis

The polar cod weight-at-length was described separately for males and females and fjord of origin with first order polynomial functions. The potential differences were evaluated with ANCOVAs after the data were log transformed to obtain linearity. The growth rate of cod was estimated from the length and weight at age data separately for the two fjords and for males and females. The age and sex effect as well as age and fjord effect on fish length and weight were evaluated for both locations with the application of two-way factorial ANOVAs.

The fish size (length and weight) and otolith size (length and weight) relationships were estimated with linear and polynomial functions, and potential differences between the sexes and fjords were evaluated with ANCOVAs. Data transformation (log) to obtain linear relationships was conducted if necessary.

Mean otolith growth rate was calculated for each specimen as otolith size divided by age, whereas the mean fish growth rate was calculated as fish size (TL and TW) divided by age. The size at hatch was omitted as insignificantly small for the analysis of adult fish growth. Fish age-0 were not included in this analysis. The significance of the otolith growth rate and fish growth rate relationship was then evaluated based on the coefficient of determination (r^2) of the first order polynomial functions fitted to the analyzed data within each age class separately. Eliminating the age effect permitted separating the somatic growth effect on otolith growth. Confirmation of the fish growth rate-otolith growth rate relationship is highly important, in addition to the otolith size-fish size relationship, if the fish growth rate is to be back-calculated or if the width of the otolith annual rings is to be interpreted as a proxy of fish growth in a corresponding year.

3. Results

3.1. Fish size and growth

The fish collected in Kongsfjorden ($n = 813$) ranged from 6.1 to 24 cm TL, and the dominant size-classes were 12—14 cm (Fig. 3). The fish collected in Rijpfjorden ($n = 64$) ranged from 8.6 to 15.9 cm TL and the dominant size-classes were 11—12 cm (Fig. 3). Males were generally more abundant among smaller fish and females among larger ones.

A significant relationship occurred between fish TL and TW ($TW = 0.0053TL^{3.042}$, $r^2 = 0.955$) (Fig. 4). The slope and intercept of the relationship were not affected by sex (ANCOVA, $n = 877$, $P > 0.05$) or fjord of origin (ANCOVA, $n = 877$, $P > 0.05$).

The otolith-based ages of the polar cod collected ranged from 0 to 4 years in Kongsfjorden and from 2 to 3 years in Rijpfjorden. TL-at-age and TW-at-age were not significantly affected by sex in either Kongsfjorden or Rijpfjorden (in all cases: two-way factorial ANOVA, $n = 409$, for age effect $P < 0.001$, for sex effect $P > 0.05$); therefore, the data were pooled for males and females (Fig. 5). Fish collected in Kongsfjorden were larger at age in comparison to those from Rijpfjorden for both size parameters — TL (two-way factorial ANOVA, $n = 409$, for fjord effect $P < 0.001$) and TW (two-way factorial ANOVA, $n = 409$, for fjord effect $P < 0.001$). The growth of polar cod in TL in Kongsfjorden was relatively

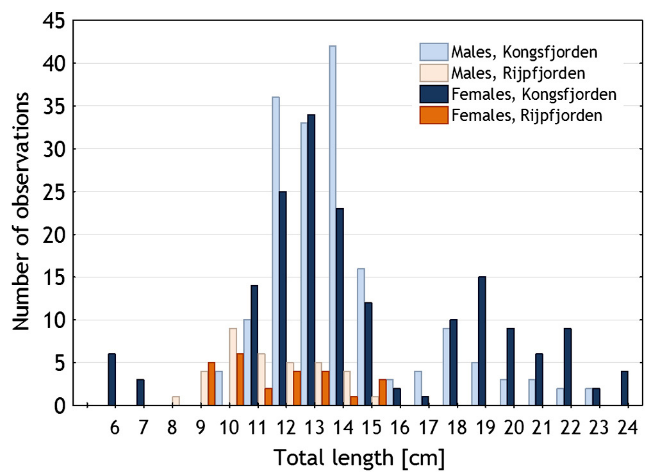

Figure 3 Total length frequency distribution of males and females collected at the Kongsfjorden and Rijpfjorden sites ($n = 877$).

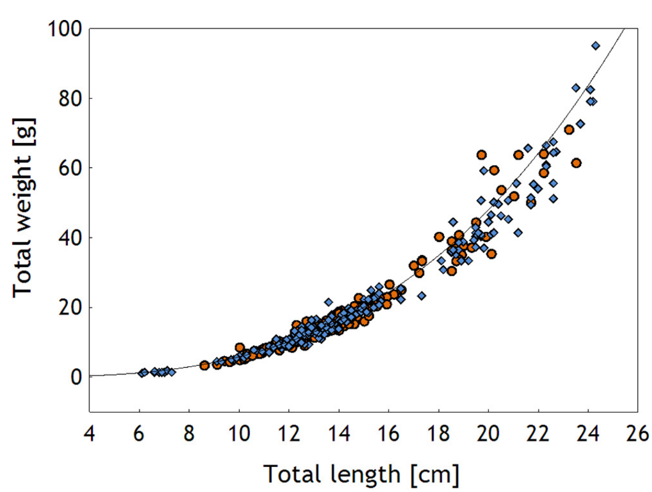

Figure 4 Relationship between total length and weight. Single function was fitted for males (circles) and females (diamonds) from Kongsfjorden and Rijpfjorden ($TW = 0.0053TL^{3.042}$, $n = 877$, $r^2 = 0.955$).

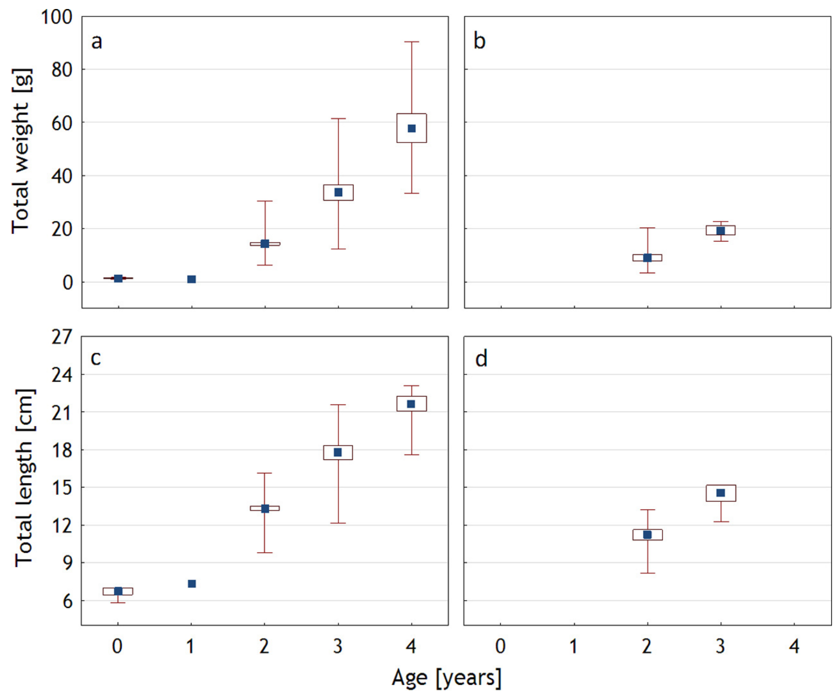

Figure 5 Total weight at age for Kongsfjorden (a) and Rijpfjorden (b), and total length at age for Kongsfjorden (c) and Rijpfjorden (d). Data for males and females are pooled. Square denotes mean, boxes 95% confidence intervals, and whiskers minimum and maximum. Number of data points for each age-group is given.

constant between years 1 and 4 at 4.7 cm year^{-1}. In Rijpfjorden, the growth between years 2 and 3 (no other year classes were available) was 3.3 cm year^{-1}.

3.2. Otolith size and growth

Both otolith size parameters (length and weight) expressed significant fish size-otolith size relationships. Because no differences in slope or intercept were recorded either between males and females or sampling locations (for all comparisons: ANCOVA, $n = 409$, $P > 0.05$), all the fish size-otolith size data were pooled for males and females and for Kongsfjorden and Rijpfjorden (Table 1, Fig. 6). Considering the high values of the coefficients of determination r^2 for these relationships that ranged from 0.861 to 0.947 (each r^2 was statistically significant, $P < 0.05$), both otolith length and weight can be used in the equation predicting fish TL and TW.

Fish growth rate-otolith growth rate relationships were significant for fish size expressed in both TL and TW ($P < 0.0001$) (Fig. 7). The r^2 of the polynomial equations fitted to these data ranged from 0.436 (age 4) to 0.884 (age 3) for TL, and from 0.401 (age 4) to 0.778 (age 3) for TW. The equations were developed just to show the strength of the relationships described. The exact formulas have no biological importance, and, as such, are not presented.

3.3. Discussion

The fish collected ranged from 6.1 to 24 cm TL. The dominant size classes were 11–14 cm with males more abundant among smaller fish and females among larger ones. This size structure and female/male ratio corresponds with other

Table 1 Functions describing the relationship between fish size (total length, TL; and weight, TW) and otolith size (length, OL; and weight, OW). Data pooled for males and females, and for Kongsfjord and Rijpfjorden ($n = 409$).

Function	r^2
$TL = 1.215 + 2.3297*OL$	0.947
$TL = 6.0655 + 0.7883 \cdot OW - 0.0159 \cdot OW^2 + 0.0001 \cdot OW^3$	0.916
$TW = 2.8226 - 3.558 \cdot OL + 1.1062 \cdot OL^2$	0.861
$TW = -2.4734 + 1.4402 \cdot OW$	0.935

publications reporting polar cod size range ratios in the Beaufort Sea (Benoit et al., 2010; Craig et al., 1982), the east coast of Newfoundland (Lidster et al., 1994), Allen Bay, Canada (Matley et al., 2013), and Svalbard (Nahrgang et al., 2014). It was suggested previously that the relatively high frequency of females in upper age classes in samples collected in fall is related to higher male mortality during summer (Bain and Sekerak, 1978) and faster growth rates in females (Hop et al., 1997). In the present work, however, no differences in growth rates were found between males and females. Considering the age range, the oldest fish in the present work were 4 years old. Even if older polar cod were described in other studies — for example, age 5 (Matley et al., 2013), age 6 (Craig et al., 1982) or age 7 (Hop et al., 1997; Nahrgang et al., 2014) — they were not numerous.

TL-at-age and TW-at-age were not significantly affected by sex either in Kongsfjorden or in Rijpfjorden. Similar results showing no difference between males and females in fish size-at-age are reported by other researchers (Craig et al., 1982; Matley et al., 2013; Nahrgang et al., 2014). The growth of polar cod in TL in Kongsfjorden was relatively constant at

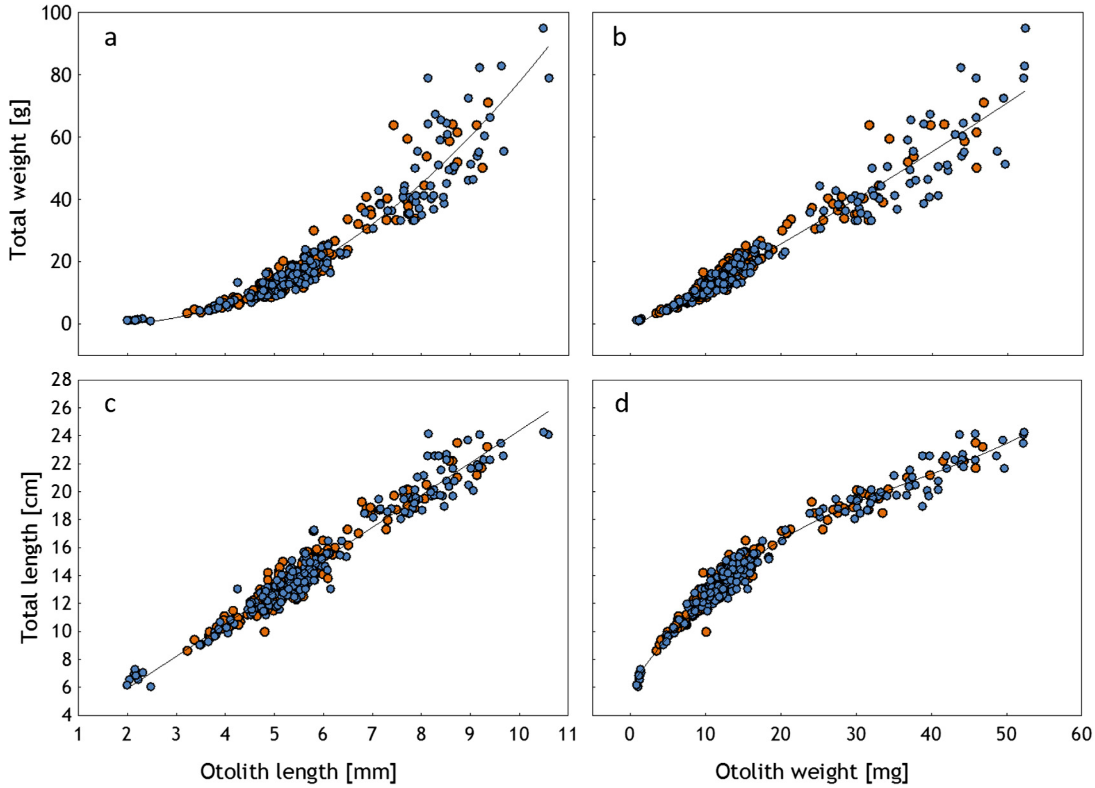

Figure 6 Relationship between: (a) total weight and otolith length, (b) total weight and otolith weight, (c) total length and otolith length, and (d) total length and otolith weight. Pooled data for males (orange points) and females (blue points) from Kongsfjorden and Rijpfjorden sites (n = 409). The formulas for these relationships are presented in Table 1. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

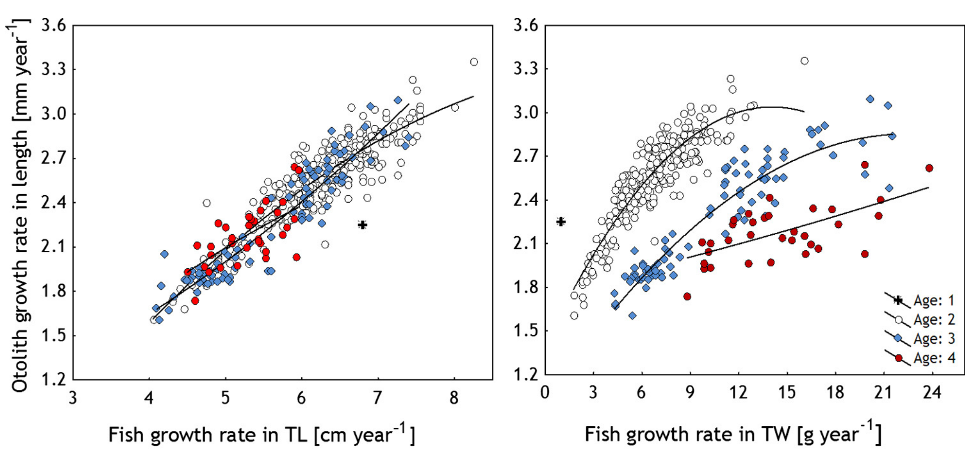

Figure 7 Relationships describing the dependence of otolith growth rates in length on fish growth rate in length (left panel) and weight (right panel) (n = 409 for both figures). The curves have no biological significance and were fitted just to exclude the potential age effect and to evaluate the significance of the relationships.

approximately 4.7 cm year^{-1} between years 1 and 4. The literature provides examples for polar cod of both relatively constant growth through the first four years of life (Nahrgang et al., 2014) and of slower growth after years 2 or 3 (Craig et al., 1982; Matley et al., 2013). To some extent this discrepancy could result from high variation in the reported size at age 4 since the number of fish of this age collected is usually low compared to the dominant age class 2 or even 3. 'This is why estimates for age 4 and higher are less accurate compared to those for younger age classes.

Generally, growth rate (size at age) variances related to geographical and latitudinal differences in the distribution of the fish analyzed are to be expected (Bain and Sekerak, 1978; Bradstreet et al., 1986). The growth rate of 4.7 cm year in the current study was higher than that reported for the same age classes by Craig et al. (1982) for polar cod from Alaska and Matley et al. (2013) for polar cod from Canada, who found that 4-year-old fish were 18 cm and 18.2 cm FL, respectively, compared to 21.5 cm TL in the present study. Lønne and Gulliksen (1989) reported slower polar cod growth in the western Barents Sea of 11 cm TL at age 2 (no older fish were caught) compared to 13.5 cm noted in the current work. Falk-Petersen et al. (1986) reported results that are similar (13 cm) to ours for age 2 polar cod from Spitzbergen coastal waters.

In addition to large-scale geographical and latitudinal differences in sample origin, differences in environmental conditions within the same fjord can result in growth differences. The size at age data presented in the current work indicate significantly faster growth in polar cod from the glacial area compared to results presented for the same species from the same fjord, but which was collected in the entrance to the fjord (Nahrgang et al., 2014): for example, age 2: 13.5/13; age 3: 18/14 cm; age 4: 21.5/15 cm (present work/Nahrgang et al., 2014). On the one hand, distinct differences were noted in fish collected at the same time (September 2013) and based on a relatively numerous sample of fish (345 — our study and 199 — Nahrgang et al., 2014), so the results are reliable and provide evidence for growth differences within the fjord with faster growth in the subpopulation located in the direct glacial area. On the other hand, the strength of this finding is reduced by the fact that the fish were only collected in one season (September) and at one (Nahrgang et al., 2014) and two stations (present work).

In the present study, the comparison of the growth of fish from the two fjords sampled indicated that the fish collected in Kongsfjorden were larger at age in comparison to those from Rijpfjorden for both of the size parameters — TL and TW. However, the fish from Rijpfjorden represented only year classes 2 and 3, and their number was low (64) compared to the number of analyzed fish from Kongsfjorden (345). The results for Rijpfjorden should, therefore, be treated with more caution. Nahrgang et al. (2014) reported opposite results — faster growth in Rijpfjorden compared to Kongsfjorden, and their results for Rijpfjorden also are based on a relatively small sample size (97) that was collected at one station only. This disagreement clearly shows not only the need for more research presenting polar cod size-at-age data from different geographical areas, but also the importance of sampling strategy based on appropriate spatial and temporal scales. Any comparison based on small samples from one point in time and space is questionable, as it is in the comparison of Rijpfjorden to Kongsfjorden described above.

Otoliths found in the stomachs of predators, such as fish, birds, and seals, can be used to identify fish species and to determine their size (Dietrich et al., 2006; Jobling and Breiby, 1986; Wigley et al., 2003). The otolith size-fish size relationship, however, must be clearly described and take into consideration variables that can affect this relationship, such as, sex or population origin. In this work, neither the sex nor the sampling location had an effect on the relationships analyzed. Because both otolith length and weight provided good relationships, the two otolith size dimensions can be used in equations predicting fish TL and TW. The regression describing the relationship between polar cod length and their otolith length presented here is in agreement (linear character and almost identical otolith size at fish size) with regressions presented for this species by other authors (Christiansen et al., 2005; Frost and Lowry, 1981; Lidster et al., 1994). Otolith morphometrics were used successfully, for example, by Short et al. (2006) to separate small walleye pollock from Arctic cod in mixed samples. However, if otolith size measurements are to be used to determine the size of individual specimens found in the stomachs of consumers, it must be remembered that the rate of otolith dissolution is very fast and, for example, it can be as high as several percents in seal stomachs just within the first hour (Christiansen et al., 2005).

One of the most useful methods in fish biology for employing otolith size analysis is in the back-calculation of growth rates (Francis, 1990). In the present work on polar cod, a very significant relationship was determined between the growth rates of fish and otolith growth within each of the analyzed age classes. Similar verification was performed for other fish species, for example, the round goby (*Neogobius melanostomus*) (Sokołowska and Fey, 2011) and Atlantic menhaden (*Brevoortia tyrannus*) (Fey and Hare, 2012), but not for polar cod. The width of annual rings formed at a given age can be used as an indication of fish growth in corresponding years. Unfortunately, growth back-calculation is frequently performed for different species without verifying the relationship between somatic and otolith growth. The estimation of the fish size-otolith size model itself permits performing back-calculations, because otolith size generally increases with age (Thorrold and Hare, 2002). It does not, however, automatically indicate that the otolith growth rate is significantly correlated with the fish growth rate. Thorrold and Hare (2002) demonstrated that otolith and somatic size can be positively correlated even if the relationship between otolith and somatic growth is negative. Moreover, as previously evidenced, otolith growth might be related more to temperature than to somatic growth (Fey, 2005). The latter issue, however, is not of great importance for cod inhabiting Arctic waters. Therefore, data presented here supporting the fish growth-otolith growth relationship are very important, because they provide the basis for future studies that can benefit from otolith analysis.

In conclusion, the present work provided, in addition to some basic biological information (e.g., size frequency distribution, male/female ratio, and the fish size-weight relationship), growth rate data that indicate the presence of a fast-growing subpopulation (approximately 4.7 cm year^{-1} between ages 1 and 4) located in the glacial area in one of the Spitzbergen fjords — Kongsfjorden. The results presented here on fish size at age, after comparing them with data available in the literature, indicate there is substantial variability in the growth rates reported for polar cod depending on both large-scale differences in geographical origin of the samples as well as small-scale differences at sampling locations within the fjord. The fact that most of the age-length data available in the literature are based on small sample sizes that were frequently obtained from one or two stations in a given geographical area underscores the need to improve sampling strategy in order to increase the value and strength of results. In addition to biological information, the existence of a significant somatic growth-otolith growth relationship was confirmed in polar cod, and no data of this kind have been available to date.

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