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The bigger they are, the faster they fall

Implications of size selective fishing on the spawning stock of *Pandalus borealis* in the Svartnes basin, (Balsfjord, northern Norway) as relates to size, age, growth, and abundance

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Abstract

The Svartnes basin stock of Pandalus borealis Krøyer, 1838 was investigated in the east Atlantic boreal zone of Balsfjord (northern Norway). The scope of the study spanned 12 years (March 2010 - October 2021), including two periods; prior to January 2017, with no commercial shrimp fishing; and after 2017, with commercial shrimp fishing. The study sought to determine the effects induced by size selective commercial shrimp fishing practices on the Svartnes basin stock dynamics of *P. borealis*, as relates to size (carapace length), age (years), growth (growth performance index), and abundance (sampled catch). There were no discernible indices of change between year classes of P. borealis with respect to age and growth during the study. More time is required to fully observe the development of year classes beginning in and after 2017. Catch per unit effort exhibited a notable decrease following the onset of commercial shrimp fishing, as did the number of females retained in each sample trawl haul. The carapace length of females within the 95th percentile of the spawning stock, depicted a significant decreasing trend (F= 19.1, n= 19, p< 0.001). A reduction in carapace length of large females indicates the size selective effects of fishing pressures exerted by the commercial shrimp fishery. The development of the Svartnes basin stock of *P. borealis* should continue to be monitored over time, in response to the fishery. Increased understanding of changes in the stock dynamics as induced by external pressures, will help to further improve management practices, and protect the identity of individual stocks.

Keywords: Pandalus borealis, size selectivity, commercial shrimp fishing, stock dynamics

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1.0 Introduction

Pandalus borealis has evolved as a lucrative, commercially exploited, shrimp species in the North Atlantic (Hansen et al., 2021). There is a strong correlation to size at harvest - larger individuals fetch higher market prices (Nilssen & Hopkins, 1992; Garcia, 2007; Koeller et al., 2007), and demand is largely driven by international markets (Garcia, 2007; Gillett, 2008). As such, understanding the implications of commercial shrimp fishing on the biological aspects of shrimp stocks is crucial.

Records of *P. borealis* predate the official scientific description provided by Krøyer in 1838 (Søndergaard & Schwach, 2009). Common species names are geographically dependant, colloquial, and frequently interchange the word "shrimp" for "prawn" (Shumway, 1985), such as "Northern shrimp/prawn", "Coldwater shrimp/prawn", "Deepsea shrimp/prawn", or "Pink shrimp/prawn" (Shumway, 1985; Bergstrom, 2000). Berkley (1930) identified most *Pandalid* species, including *P. borealis*, as being protandric hermaphrodites, meaning that individuals transition from mature males to spawning females (Berenboim, 1989; Anon, 1994). Growth and maturation are strongly influenced by localised environmental parameters (Fuentes-Yaco et al., 2007). A thermal tolerance from -1.6 °C to 12 °C, and a population abundance between 0 °C and 5 °C, has limited the latitudinal distribution of *P. borealis* to the boreal waters of the northern hemisphere (Fig. 1) (Shumway, 1985; Nedreaas & Øynes, 1987; Bergstrom, 2000; Fuentes-Yaco et al., 2007).

Traditionally thought to be distributed throughout both the Pacific and Atlantic oceans (Fig. 1), debate exists as to the speciation of Pacific *P. borealis* stocks (Bergström, 2000). Genetic differences have been identified between locations (Hansen et al., 2021), while Rasmussen & Aschan (2011) found differences in the larval development of Pacific and Atlantic stocks, and Squires (1992) argued for speciation, recognising *P. eous*. A maximum age of 11 years for *P. borealis* has been recorded at the northernmost distributions off Jan Mayan (northern Norway) (Nilssen & Aschan, 2009). The maximum age/size are reduced when descending in latitude from the northern to southern ranges (Koeller et al., 2007). *P. borealis* inhabits water depths from 9m to 1450m, showing a preference for soft substrates (Shumway, 1985; Bergström, 2000). Feeding occurs in both the pelagic and demersal zones of the marine

environment, exhibiting patters of diurnal migration (Barr, 1970; Apollonio et al., 1986). As an opportunistic, carnivorous feeder, *P. borealis* regularly consumes polychaetes, molluscs, crustaceans, and detritus (Hopkins et al., 1989; Hopkins et al., 1993; Aschan et al., 2004). *P. borealis* is an integral component of the respective ecosystems and vital to the local food-web (Hopkins et al., 1989; Parsons, 2005). Cod fishes (*Gadidae spp.*) are a major consumer of *P. borealis* (Hopkins et al., 1989; Parsons, 2005), with modeling by Hvingel & Kingsley (2006) suggesting that, in certain instances, the consumption of *P. borealis* by *Gadidae. spp* could rival that of the biomass removed by the commercial fishery.



Figure 1. Overlapping distribution of *Pandalus borealis* and *Pandalus eous* throughout the Pacific and Atlantic ranges. *P. borealis* is prominently established within the Atlantic, while *P. eous* remains in the Pacific. Similarities exist between the two species, though the differences presented by Squires (1992); Bergström (2000); Rasmussen & Aschan (2011); and Hansen et al. (2021), are supportive of speciation (image from Bergström (2000)).

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Norway has an established history of commercial shrimp fishing (Garcia, 2007; Søndergaard & Schwach, 2009). In the early 1840's, traditional fishing practices in southern Norway were mainly comprised of trapping techniques (Søndergaard & Schwach, 2009) but, as the demand for shrimp increased through expansion into global markets, trawling practices specific to *P. borealis* were developed. 1899 saw the installment of 10 permanent commercial shrimp fishing vessels within the fishery (Hjort and Ruud, 1938). Since then, the Norwegian shrimp fishery has continued to evolve and in 2019, generated a landed value estimated at ~ US\$108 million (SSB, 2020). Total landed biomass for the Norwegian *P. borealis* has fluctuated on an annual basis (SSB, 2018) with peak landings of 91,163 tonnes in 1985 (SSB, 2018). In contrast, 2017 recorded the lowest levels of retention, producing a total landed biomass of 13,313 tonnes (SSB, 2018).

The commercial shrimp fishery in Norway is governed by license restrictions controlling both allotments and provisions (Aschan et al., 2004). Catch restrictions are based on both the quantities of retained bycatch and members of *P. borealis* below the minimum catch size (Aschan et al., 2004). Currently, there is no total allowable catch (TAC) issued in Norway (Hansen & Aschan, 2000; Aschan et al., 2004), representing the sole northeast Atlantic fishery participant not to adopt the TAC system (Drengstig et al., 2000). Area closures are used to manage instances of excessive amounts of bycatch and undersized shrimp.

Despite the identification of genetically unique stocks of *P. borealis* by Jorde et al. (2015) and Hansen et al. (2021) throughout Norway, management continues to be regulated by geopolitical boundaries that may overshadow the requirements of specific ecosystems. Such instances persist in the management of *P. borealis* due to limited availability of information surrounding the direct effects of commercial shrimp fishing on stock dynamics. As noted by Allendorf & Leary (1988), the preservation of genetic identity throughout a population is crucial.

A shift in focus from a broad managerial view, by refining the scope of management zones to those of stock specific localities, can help to accumulate a conclusive understanding of the relationships exhibited by commercial shrimp fishing practices and the individualised dynamism of *P. borealis* stocks.

The *P. borealis* stock within the Svartnes basin, of Balsfjord (northern Norway) has been studied extensively, with an extensive compilation of existing data (Hopkins & Nilssen, 1990). Until the mid 1980's the Svartnes basin stock was sampled at monthly intervals within the fjord, before being reduced to intervals of two to five times a year. Balsfjord, and the Svartnes basin stock of *P. borealis*, were fished extensively prior to 1983/1984. From 1983/1984 until 2017, a change in regulation banned trawling at depths shallower than 200m, closing the commercial shrimp fishery within the fjord. New regulations introduced in 2017 reduced the minimum depth of shrimp trawling from 200m to 170m and made many fjords (including Balsfjord) again accessible to the commercial shrimp fishery.

The objective of this thesis is to investigate the pressures exerted by commercial shrimp fishing on the Svartnes basin stock of *P. borealis*. The use of size selective fishing practices and their influence on the stock, in conjunction with growth patterns, will be explored. The 2017 reduction in minimum trawling depths yields a unique opportunity to explore stock dynamics over a linear progression of time. Data pertaining to the Svartnes basin *P. borealis* stock are held by the University of Tromsø (UiT), and have been supplemented by physical descriptions of individual shrimp collected through systematic trawling transects from research vessels between 1979 and the present. The end goal is to provide a more comprehensive understanding of the dynamics of *P. borealis* (size, age, growth, and abundance, with of focus on the spawning stock) and the influences of commercial shrimp fishing. Fostering a deeper sense of knowledge allows for unbiased and scientific approaches to managerial decisions within specific zones.

2.0 Material and Methods

2.1 Study area

Balsfjord is situated north of the Arctic circle (Hopkins et al., 1989) within the eastern Atlantic boreal region (Fig. 2) (Ekman, 1953; Briggs, 1974). Restricted by three sounds (Tromsøsundet, Sandnessundet and Rystaumen) with sill depths of 8, 9, and 30m respectively (Eilertsen et al., 1981), there is little exchange of deep water between Balsfjord and the outside environment (Eilertsen et al., 1981). At depths greater than 100m in the fjord, yearly temperatures remain stable, rarely exceeding 5° C and are thus within the optimal population abundance range for P. borealis (Shumway, 1985; Nedreaas & Øynes, 1987; Bergstrom, 2000; Fuentes-Yaco et al., 2007). Deep areas remain coldest during the spring, with elevated temperatures in the winter months (Eilertsen et al., 1981). Balsfjord is occupied by 20 different observed species of fish, including an indigenous capelin stock and a genetically distinct population of herring (Hopkins et al., 1989). Balsfjord supports a unique ecosystem of marine flora and fauna, ranging in structure from primary producers to apex predators (Hopkins et al., 1989). Located at 69°21'N 19°06'E (Fig. 2), the Svartnes basin represents the deepest portion of the fjord, reaching a maximum depth of 195m. Variable depths exist elsewhere in the Svartnes basin, predominantly ranging from 180m to 190m (Hopkins & Nilssen, 1990). Composed of soft, muddy substrate, the Svartnes basin is separated from other locations in the fjord by uneven seabed (Hopkins & Nilssen, 1990). The scope of this study was restricted to the trawling ground located within the Svartnes basin.



Figure 2. The location of Balsfjord in relation to Norway. Located above the Artic Circle at a latitude of 69°N, Balsfjord extends south from the city of Tromsø. The Svartnes basin is found at the center of the fjord, and, at a maximum depth of 195m, represents the deepest portion (image from Hopkins & Nilssen (1990)).

2.2 Field work

Data available for this study was collected from the Svartnes basin (Fig. 2) two to five times a year between 2010 and 2021. Most of the sampling was conducted by the R/V Johan Ruud (vessel length 30.5m; March 2010 until January 2020) and the R/V Helmer Hansen (vessel length 63.8m; September 2020 until October 2021). Two surveys were undertaken from the smaller R/V Hyas (12.2m; April and May of 2021). While at sea, sampling events followed similar practices to those outlined by Hopkins & Nilssen (1990). The R/V Johan Ruud employed a Skjervøy 1600 trawl with a 35mm codend and a 8-14mm inner mesh size, while the R/V Helmer Hansen employed a Campelen 1800 bottom trawl with a codend of 40mm and a 15mm cover to collect samples. The R/V Hyas employed a ~1000 trawl. Sampling occurred at a speed of ~2 nautical miles per hour (knots; ~3.7km/hr) for a period of 20

minutes with the R/V Johan Ruud, and ~3 knots (~ 5.6km/hr) for a period of 15min with the R/V Helmer Hansen. The R/V Hyas sampled at a speed of ~1.5 knots for a period of 30min. Trawl times were registered from when contact was made with the seabed, until the start of hauling. Information was recorded by a Scanmar sensor attached to the trawl. Trawling times, distances, and locations were recorded in the ships' log.

At the end of each trawling period, upon removal, the contents of the trawl were sorted and identified as to species. Whenever possible, the entire population of *P. borealis* was fully separated from the other sample materials before being weighed. When the trawl contents were heavily mixed, and the complete removal of *P. borealis* was unfeasible, a subsample of the catch was removed and fully sorted. The proportion of *P. borealis* in the subsample, in comparison to the remnants of the mixed sample, were then used to calculate the total sampled biomass.

After each sorting event, a small subsample of *P. borealis* representing approximately 1-3kgs was removed, placed in 2-3 plastic bags, and stored in the onboard freezer, where they remained until the end of each outing. All sample bags of *P. borealis* were transported to laboratory facilities at UiT, where they remained frozen until processing and further analysis. Sorting, sampling, and storage methods while at sea are explained in greater detail by Hopkins & Nilssen (1990).

The author participated in four sample trawls conducted from the R/V Helmer Hansen (February, June, and October 2021, and February 2022) and the subsequent sample analysis. Samples of *P. borealis* collected prior to the author's involvement were gathered by staff and students at UiT as part of their ongoing investigation into several shrimp stocks along the Norwegian coast.

2.3 Laboratory work

Plastic sample bags of *P. borealis* were removed from the UiT freezer and defrosted overnight in a refrigerator, or for several hours at room temperature. The contents were carefully placed in water to remove the remanent of any frozen materials, clean any debris from the sample, and allow complete separation of the shrimp. Water was then strained from the sample, and the remaining material placed onto a tray. The total weight of the entire shrimp sample was manually recorded to an accuracy of 0.01g using an electronic scale. Any bycatch that had not been previously sorted at sea was removed and weighed. A final weight for *P. borealis* was recorded after subtracting the weight of the bycatch from the initial sample weight.

P. borealis were then individually sorted into the respective stage of maturation. Pelagic larval stages were not sampled, and thus individuals were classified into one of eight maturation stages (Appendix Fig. 1). Males occupy stages 1-3, where stage 1 represents immature males, stage 2 the mature males, and stage 3 the early sex-changing males. Females were sorted to maturation stages 4-8, where stage 4 represents early maturing females with sternal spines, stage 5 females with eggs, stage 6 females that have recently spawned, and stage 7 resting females with no sternal spines and no headroe. Stage 8 represents second time female spawners with headroe and no sternal spines. Sorting of each individual by maturation group followed the parameters described by Hansen and Aschcan (2001) (Appendix Fig. 1).

Sex changing males (stage 3) were differentiated from mature males (stage 2) by manually removing and checking the first two pleopods on the right ventral side of the anterior. Under the microscope, the correct stage of maturation was identified by investigating the endopoditt on the first pleopod (Fig. 3A) and both the appendix masculina and the appendix interna of the second pleopod (Fig. 3A). Late stage 3, identifiable by the presence of headroe, were identified as stage 4 "females" due to the onset of egg production and hence, first time female spawners.



Figure 3 (A & B). (A). Location of and identifiable features of the first two pleopods on *P. borealis*, used for determining the sex and stage of sexual maturation (image adapted from Hansen and Aschcan (2001)). (B). Placement of the calipers to measure carapace length of *P. borealis*. Measurements were taken from the solid structure directly behind the eye, and the back of the carapace. The carapace was used as a point of measure due to a lack of solid structures, and the changes in body dimensions which can occur when molting (image adapted from Rasmussen (1953)).

After sorting the individuals by maturation group, carapace length (Fig. 3B) was measured to an accuracy of 0.01mm with the use of an electronic caliper. Carapace length was used as the standard form of measurement due to a lack of hard structures on *P. borealis*. Using the methods outlined by Rasmussen (1953) the calipers were placed behind the eye, and the centre of the posterior dorsal ridge of the carapace (Fig. 3B). The carapace length was then recorded electronically, with reference to the individual's stage of maturation. All measurement were recorded and placed into a database for future analysis. The occurrence of parasites were included with respect to the host when present.

2.4 Statistical interpretations

2.4.1 Software and environment

Statistical and visual analyses were performed through the R environment within R studios version 4.0.4 (R Core Team, 2021). Ggplot2 version 3.3.5 (Wickham, 2016), was used as the template to create a visual representation of all findings. The FSA version 0.9.3 (Ogle et al., 2022), MIX version 1.0-10 (Shafer, 2017), and Mixdist version 0.5-5 (MacDonald et al., 2018) packages were used to calculate mean carapace length, and growth, while creating visuals to identify the year class and age of each modal group.

2.4.2 Length distribution and year class identification

Carapace length was used as the variable by which to plot the length distribution of *P*. *borealis* from each sample throughout the scope of the study. Kernel density plots were employed to visualise the distribution of the length data. Plots were created for each sample date and identified male (stage 1-2), transitional (stage 3) and female (stage 4-8) groups. The progression and composition of each modal group, as presented in the density plots, were then used to identify individual year classes (Hopkins & Nilssen, 1990; Bergström, 1992; Yamaguchi et al., 2014). Year classes were identified by combining size and maturity distributions over a set period of time. With the exception of slow-growing male and fast-growing sex changing individuals generating multiple modal groups (see Appendix Fig. 2; and Rasmussen, 1965), each modal group within the respective density plot was assumed to be representative of individuals pertinent to the same year class mode. Year classes were systematically identified for each sample plot by following a chronological progression of development. When fast and slow growing parts of a year classes were identified, the respective groups were noted within the data.

MIX analyses (Macdonald & Green, 1985) were used to calculate the proportion of individuals within each modal group, the mean carapace length, and the standard deviation. Normal modal groups were fit to the length distributions through one of three constraints on the standard deviation, "Free", "SEQ" and "SFX". Initially, under the characteristics of a

"Free" fit, there were no constraints placed on the standard deviation of the modal group. "SEQ" created equal standard deviation across modal groups, and "SFX" distributed self selected fixed values to the standard deviation of each modal group (Macdonald et al., 2018). Modal groups were first fit with a "Free" approach to reduce additional constraints on the standard deviation. "SEQ" was then used if no good fit could be reached, before employing "SFX". Outliers were removed from the sample when present to avoid inconsistencies with the best fit. Individual outliers were completely excluded. Small clusters of outliers were removed and formed into a separate modal group, calculated without constraints. Results procured from the mix-analysis included the number and proportion of individuals within each mode, standard deviation of the modal groups, and mean carapace length of each mode (see Appendix Fig. 3). The results from the mix analysis were registered within a database. The final age associated to each modal year class as identified by the length distributions and mix analysis was calculated under the assumption of a consistent hatch date on April 1st every year.

2.4.3 Growth

Growth was calculated for each year class as a function of carapace length. The standard von Bertalanffy growth function (VBGF) (Lackey & Hubert, 1982; Bergström, 1992) was applied, when:

carapace length =
$$L_{\infty} \cdot [1 - exp^{-k \cdot (age - t_0)}]$$

where the parameter L_{∞} = the theoretical mean maximum carapace length, K = the speed at which L_{∞} is reached, and t_0 = the age when length is equal to 0. While calculating the VBGF, t_0 was assumed to be constant due to a lack of juvenile individuals in the samples. Therefore, t_0 was fixed at -0.25, reducing variability within the equation. After performing the initial VBGF calculation as per the size and age of individuals in each modal group across a year class or year classes, statistical weights were added, and the analysis repeated. Weighted values were produced in response to the separation of groups which could occur in a given year class or year classes. Weights were further used to mitigate the possible effects of a change in sample proportions, and to balance the overall proportion of individuals with respect to age and mean carapace length. Confidence intervals of 95% were then produced for each weighted and unweighted parameter.

To limit the correlation of L_{∞} and *K* within the VBGF (Hordyk et al., 2015) (Appendix Fig. 4) the growth performance index (GPI) was calculated (Pauly, 1978). The GPI was calculated by employing the L_{∞} and *K* values obtained from the VBGF:

$$GPI = Log_{10} \cdot K + 2Log_{10} \cdot L_{\infty}$$

as emphasised by Moreau et al., (1986). The GPI with a 95% confidence interval was estimated for all available year classes and combination of year classes. The process was completed for both the weighted and unweighted values.

2.4.4 Catch per Unit Effort (CPUE)

Catch per unit effort (CPUE) was calculated for the total retained biomass of *P. borealis* in a 20min sample trawl and the total number of females present in a sample catch after 20min. The total CPUE:

$$CPUE_{Total} = \frac{Kilograms of P.borealis}{20 minutes}$$

was calculated from the sample data collected by the trawl hauls. The catch per unit effort in relation to the number of females caught:

$$CPUE_{Number of females} = \frac{Number of females present}{20 minutes}$$

was calculated from the proportion of females in each sample, in relation to sampling time. Catch data from the commercial shrimp fishery could not be incorporated due to inaccuracies in the data.

3.0 Results

3.1 Length distributions and age

Sampling occurred at intermittent intervals on an annual basis between March 2010 and October 2021, resulting in the collection of 41 samples over a 12 year period. Samples were collected a minimum of two and a maximum of five times each year. Sampling events varied with regards to the month in which sampling took place (from, January - July, September, and October). All 41 length distributions generated for *P. borealis* between March 2010 and October 2021 are presented in Appendix Fig. 2. The number of modal peaks, subsequently associated with age, varied throughout the sampled period. October was the most sampled month, and thus presents insight into the progression of the stock (Fig. 4). Two dominant modes of males were frequently identified over time, with some degree of variability, reflecting the relative year class strength. A single dominant mode of females was most commonly identified, yet indicators of two modes did occur.



Figure 4. Size distribution as Kernel density plots of *P. borealis* males (blue - maturity stages 1-2), females (red - maturity stages 4-8) and transition individuals (green - maturity stage 3) in the Svartnes basin, Balsfjord (northern Norway). Annual sampling was undertaken during the month of October from 2010 to 2021 (excluding 2019). No sex-changing (transitional) individuals were present during any of the October sampling periods, as reflected by the lack of green traces on these Kernel plots.

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Difficulties did persist in identifying the progression of year classes for both fast and slow growing modal groups, however, a total of 16 year classes were identified in response to the respective modal groups. The earliest year class originated in 2005, with the most recent occurring as of 2020. New year classes, were identified for each consecutive year on an annual basis between 2005 and 2020. Large variations within the length distributions and the relative proportion of different modes were noted.

Over the course of the sampling period there were few immature males recovered (stage 1), and therefore the possibility of creating mean length estimates of young age groups was limited (and unattainable for unsettled larval stages). Despite variations across modal groups, modes could be tracked over a given period of time. Age was assigned to each modal group through the interpretation of associated size and maturity distributions. The age of modal groups was distributed from males in the first year of development, to mature second time female spawners having reached a sixth year (Appendix Table. 1).

Observed ages for the year classes identified throughout the study ranged from a minimum age of 0.8 years to a maximum age of 6.2 years (Appendix Table. 1). The mean carapace length displayed by the modal peaks ranged from a minimum length of 7.7mm to a maximum length of 26.4mm (Appendix Table. 1).

3.2 Size at age and growth

Size at age was investigated with respect to each year class found in the scope of the study. The progression of the mean carapace length for each year class in relation to age is displayed by Figure 5. The development and change in mean carapace length display the general trends in growth for each year class (Fig. 5).

Using a fixed t_0 in the VBGF allowed for individual growth parameters to be calculated. When calculating the growth parameters relevant to each year class, data deficient old (\leq 2009) and new (\geq 2017) year classes were combined to provide the working data. Both weighted and unweighted values for L_{∞} and *K* (95% confidence interval) are displayed in Appendix Table. 2. The largest weighted and unweighted L_{∞} values were 34.6mm and 32.8mm, respectively (Appendix Table. 2). In contrast, the smallest weighted and unweighted L_{∞} values were 25.4mm and 27.1mm, respectively (Appendix Table. 2). The largest weighted and unweighted *K* values were 0.47 and 0.41, while the smallest weighted and unweighted values were 0.25 and 0.26 respectively (Appendix Table. 2). The inverse relationship represented by the L_{∞} and *K* variables (Appendix Fig. 4) was notable throughout the VBGF. No trends could be observed with respect to the growth parameters produced from the VBGF, and each year class/year class group. A comparison of growth as relates to carapace length at age for all modal groups before and after January 2017, showed no identifiable changes in growth (Appendix Fig 5).



Figure 5. The mean carapace length at age for each year class of *P. borealis*, in Svartnes, Balsfjord (northern Norway) as identified throughout the scope of this study.

Using the GPI, weighted and unweighted values were derived from the L_{∞} and *K* variables of the VBGF. The largest weighted and unweighted values within the GPI were both 2.49 (Fig. 6). In contrast, the lowest values for the weighted and unweighted GPI were respectively, 2.41 and 2.43 (Fig. 6). Growth performance revealed little change between the largest and smallest weighted and unweighted values (Fig. 6). No notable trends were observed apart from a slight increase in the GPI until the 2016 year class, following a low in the 2011 year class (Fig. 6). In most instances, weighted values provided a narrower confidence interval when compared with unweighted values (Fig. 6).



Figure 6. Growth performance index (GPI) for *P. borealis* in the Svartnes basin, Balsfjord (northern Norway) with a 95% confidence limit for year classes between 2005 and 2020. Year classes prior to and including 2009 (\leq 2009) and those following and including 2017 (\geq 2017) were grouped.

3.3 Catch per unit effort (CPUE)

CPUE produced values relevant to population abundance. CPUE was only calculated for samples retrieved by the R/V Johan Ruud. A total of 27 samples collected from March 2010 until January of 2020 were analysed. Samples taken after January of 2020 by the R/V Helmer Hansen and R/V Hyas were not included due to a change in effort between the sampling techniques. Calculations pertaining to the total CPUE of P. borealis retained within each trawl haul of the R/V Johan Ruud are represented by Figure 7A. The largest CPUE occurred in April of 2013, with a total retention of 308.5 (kg/20min) of P. borealis (Fig. 7A). The lowest recorded CPUE took place in October of 2010, with a total of 2.3 (kg/20min) (Fig. 7A). Mean total CPUE over all sample years with the R/V Johan Ruud was 62.3 (kg/20min). Changes in the level of CPUE are evident throughout the sample trawl hauls (Fig. 7A), depicting notable drops in both 2010 and 2018. Drops in the CPUE were frequently followed by an instance of quick recovery, with the exception of 2018 (Fig. 7A and Appendix Fig. 6A). 2017 marks the onset of commercial shrimp fishing in the Svartnes basin, and as such, acts as a point of reference for changes within the CPUE across time and space. The drop after 2017 can be explained by the opening of the fishery, while the drop in 2010 remains difficult to interpret.



B

A



Figure 7 (A & B). Regulatory changes reopening the shrimp fishery are marked by the vertical dashed line. (A). Catch per unit effort (CPUE) for sample dates occurring between March of 2010 and January of 2020 by the R/V Johan Ruud. (B). Fluctuations in the number of females for each sampling event.

CPUE in relation to the total number of females at a maturity stage of 4-8 for each sample date are displayed in Figure 7B. The largest number of females retained was 11,445 individuals in April of 2013 (Fig. 7B). The lowest abundance of females present was found to be 56 individuals in March of 2018 (Fig. 7B). The mean number of females retained per trawl haul during the sampling period between March 2010 and January 2020 was 2,689 individuals. Fluctuations were observed throughout the sampling months (Fig. 7B), with sharp troughs occurring in 2010 and throughout 2018. Drops in 2018 were more severe and presented a slower recovery (in response to the fishery) than those in 2010 (difficult to interpret) (Fig. 7B and Appendix Fig. 6B). With the exception of a low CPUE in 2010, the effect of the fishery after 2017 is clearly illustrated by Figure 7A and 7B. The number of females in the catch are dependent on the CPUE of the entire catch (Appendix Fig. 7).

3.4 Size of females

The median carapace length for females sampled between March 2010 and October 2021 was plotted, and the 95th and 5th percentiles calculated (Fig. 8). Values were separated in January at the beginning of the 2017 calendar year to present a period before and after commercial shrimp fishing. Separate linear trendlines were added to the data before and after 2017 (Fig. 8). Trends for the median (F= 0.28, n= 23, p= 0.61), 95th (F= 2.59, n= 23, p= 0.12) and 5th (F= 1.29, n= 23, p= 1.29) percentile before 2017 represented no significance. After the onset of commercial fishing (2017), significance was not noted in the median (F= 1.88, n= 19, p= 0.19) or the 5th percentile (F= 1.73, n= 19, p= 0.21). A significant decreasing trend was noted for the 95th percentile length (F= 19.1, n= 19, p< 0.001) in the years after 2017 (Fig. 8). A size reduction in the largest individuals over the course of the sampling period after 2017, present a decreasing trend in carapace length.



Figure 8. The development of the median, 95th and 5th percentile carapace length of females in the Svartnes basin, Balsfjord (northern Norway) before and after the opening of the fishery in 2017 (marked by the vertical dashed line). The trends in size are illustrated by linear lines before and after 2017.

4.0 Discussion

Commercial shrimp trawling in Norway exhibits size selective practices which directly target the spawning stock of *P. borealis* (Garcia, 2007). The effort exerted by fishers can directly and indirectly impact abundance through the addition of fishing pressures (Shin et al., 2005; Garcia, 2007). Total abundance of the stock can be reduced through the direct removal of females. Due to the development of *P. borealis* as protandric hermaphrodites (Shumway, 1985; Bergström, 2000), females are proportionally larger than males (Rasmussen, 1953). Therefore, when exposed to size selective commercial shrimp fishing practices, they are directly removed by the fishery. Representing the spawning stock, females are essential to future recruitment (Rasmussen, 1953; Shumway, 1985; Bergström, 2000; Koeller et al., 2007) and by targeting a later stage of maturation, the fishery can indirectly affect recruitment of the stock.

Through a reduction in the spawning stock, impairments to the production and recruitment of juvenile individuals can occur (Koeller et al., 2007). In response to increased pressures, *P. borealis* will begin to reduce the maximum size of mature individuals (Koeller et al., 2007). A reduction in the individual size of females is suggestive of a shift towards early maturation and a smaller size of development (Koeller et al., 2007). The size of individuals at spawning is correlated with fecundity. Larger individuals hold a greater spawning potential, with more reproductive output (Chang et al., 2021). The degree to which the stock will respond is subjective to the level of severity brought about by added pressures.

P. borealis is also responsive to a range of pressures outside the scope of commercial shrimp fishing. Biotic and abiotic events within the respective ecosystem can present challenges to the stock, shifting the dynamics (Clarke et al., 1991; Koeller et al., 2007; Wieland & Siegstad 2012; Chang et al., 2021). Events of biotic and abiotic change should not be neglected when investigating stocks of *P. borealis*, and remain under consideration. Water temperature is a limiting factor in the latitudinal distribution of the species (Shumway, 1985; Nilssen & Hopkins, 1991; Bergström, 2000) and thus affected by climate shifts. Records of rapid and latent temperature change have been recorded to produce events of mass mortality for *P. borealis* (Nedreaas & Øynes, 1987).

Further consideration should be given to the impacts of predation on a given stock of *P*. *borealis*. Instances of predation have been considered to rival the effects of commercial shrimp fishing (Hvingel & Kingsley, 2006). Yet, the exertion of biotic and abiotic pressures throughout an environment are rarely as selective as those induced by human activities.

Confined by the scope of this study, an initial investigation into the population structure of the Svartnes basin stock was produced. The development of year classes over time, as presented by the analysis of length distribution data in full, is observed in Appendix Fig. 2. Visual representations for the progression of each year class (modal peak) helps to understand the unique changes occurring in the stock over a set period of time.

Stages of maturation between and including 1-8 were observed at different intervals within year classes throughout the study. Males (stage 1-3) and females (stage 4-8), were found at different densities on a per sample basis. The distribution and abundance of males and females within the stock revealed several instances of note. Initially, the distribution of individuals in the stock displayed a level of semblance to those expressed by Hopkins (1988) and Hopkins & Nilssen (1990). Berried females were present throughout the Svartnes basin from ~September until the onset of spawning in ~April (Appendix Fig. 2). After which, the transitional stage (3) in the development of males to females began in May and lasted until June, as noted in the sample data (Appendix Fig. 2). The recruitment of males to the catch was emphasised by the onset of large peaks, becoming most apparent in October. Slow and fast growing, sex changing groups within year classes as previously identified in Balsfjord (Hopkins and Nilssen, 1990), continued to be present throughout this study. Recruitment and mortality of the stock were not calculated at this stage, though should be investigated at a later date to better understand the stock.

The maximum ages reached by each individual year class ranged from 4 to 6 years, while the maximum mean carapace length was observed at 26.4mm (Appendix Table. 1). Year classes originating after 2017 (the restart of commercial fishing), did not conclusively reach a maximum age and therefore could not be fully assessed. More time is required to quantify any effects caused by the fishery with regards to growth and maturation of year classes, including and after 2017.

Historical results procured from Hopkins and Nilssen (1990) at a time of intensive fishing practices presented differences in observed carapace length and maximum age. From 1979 until 1983 Hopkins and Nilssen (1990) did not observe ages greater than 4, and retained few individuals larger than 22.0 mm in carapace length. A change in the maximum age and size of individual members within the Svatnes basin stock of *P. borealis* between studies, relates to the effect of high fishing mortality. With the early onset of commercial fishing in the current study, results suggest the stock has since recovered from the intensive practices prior to 1983/1984. This further suggests the impact of commercial shrimp fishing on the size and age of individuals within the stock, and should in turn, be more closely investigated.

An understanding of year class growth was first formulated by employing the VBGF. Age at length = 0 (t_0) was fixed at -0.25, to reduce variability in response to a lack of juvenile individuals. To reduce the correlation of L_{∞} and *K* (Appendix Fig. 4) the GPI was employed as described by Moreau et al., (1986). The GPI indicates a value associated to the overall growth of an individual year class and presents a better indication of growth than the parameters L_{∞} and *K* in the VBGF (Moreau et al., 1986). With a maximum weighted and unweighted GPI of 2.486 and a minimum of 2.412 and 2.430 respectively, there were limited fluctuations between each year class/year class group (Fig. 6). Growth performance appeared to rise and fall, with a single noticeable performance drop pertaining to the 2011 year class. A combination of all year classes yielded a weighted and unweighted GPI for the stock of 2.459 and 2.461 (Fig. 6). There were no observed impacts to the GPI, and consequentially growth performance of the stock throughout the scope of the study (with the exception of small fluctuations) when comparing year classes and year class groups before and after 2017 (Fig. 6 and Appendix Table. 2).

With respect to the exertion of fishing pressures on the stock, commercial activities targeting *P. borealis* began with the onset of the 2017 calendar year. From this point forward, the Svartnes basin stock was once again accessible to commercial fishers. Upon further investigation of the length distribution data, trends indicated a drop in the number of sampled females following 2017. When investigating carapace length at age for all modal groups prior to and after 2017, no differences as to the implications of the fishery could be observed

(Appendix Fig. 5). Similarly, growth performance across all the grouped and ungrouped year classes remained relatively unchanged. A low GPI was indicated for the 2011 year class, climbing slightly until the 2016 year class (Fig. 6). Commercial fishing practices cannot explain the poor growth performance presented by the 2011 year class. The 2011 year class reached a maximum age of 5, disappearing after October 2016. Having reached an age of 5, the impacts of commercial fishing on the growth of the 2011 year class after 2017 are improbable. Despite a drop in the GPI from the 2016 year class to the \geq 2017 year classes, the potential implications of commercial shrimp fishing towards growth, remain difficult to quantify. The combined \geq 2017 year class though treated as one in this study, should, in the future, be separated. When considered on an individual basis, the effect of accelerated growth within younger individuals would be negated and year classes would be able to reach a maximum age. Continuing to follow separate year classes after 2017 would allow for a more comprehensive understanding of the GPI during a period of active fishing. The GPI could then be compared to a period of inactivity to present any indications of change between year classes.

To visualise the effects of commercial shrimp fishing on the Svartnes basin stock of *P. borealis*, CPUE was used to represent changes in the sample catch volume, acting as an indicator of stock size (Fig. 7A). Total CPUE ranged from 2.26(kg/20min) - 308.48(kg/20min) presenting poor performance at the end of 2010 and through all of 2018, with a peak in 2013 (Fig. 7A). Trends in total CPUE vary on a yearly basis, though a prolonged drop and slow recovery is observed after 2017 (Fig. 7A). The drop in total CPUE suggests that commercial fishing practices have influenced the biomass of the stock. CPUE for the number of individual females present in each trawl haul, emphasises the impacts of commercial fishing (Fig. 7B). The size selectivity of the fishing gear used, present sharp drops in the number of females retained in the sample trawl haul after 2017 (Fig. 7B). With the removal of females from the system, the results solidify the implications of commercial fishing. The number of individual females present in the catch, in conjunction with the total CPUE (Fig. 7A & 7B) emphasises the selectivity. 2018 shows an excessive drop in the number of females with respect to the total composition of the sample. The number of females is shown to diverge from the total CPUE found during that time period. In contrast, the drop

in CPUE from 2010, shows a limited decrease in the number of females as they relate to the sample catch, matching the CPUE more closely (Fig. 7A & 7B).

Factors contributing to the changes in stock abundance during 2010 remain difficult to determine and could be representative of an outlier within the sample data. 2010 has the potential to be a function of sampling error, unknown stock behaviour, or as yet unrecognized environmental events. Ultimately, the drop in the number of females with respect to the total CPUE highlights the selectivity of the commercial fishing gear, as exhibited by pressure directed towards the number of females within the stock. Though CPUE offers a valuable reflection of the total stock abundance, information relating to the commercial fishing effort is severely lacking. There currently continues to be a gap in the availability of accurate, and location specific catch data for the stock. In future studies CPUE can be correlated to the GPI for each year class, presenting a measure of stock density. This would present a better estimate of stock abundance when there is a lack of commercial CPUE data.

Since selective fishing practices were reapplied to the Svartnes basin stock, a statistically significant drop in the median carapace length of females within the 95th percentile occurred (Fig. 8). The observed drop in the length of females within the 95th percentile (Fig. 8) can be hypothesised to originate in response to selective fishing pressures (Koeller et al., 2007). Figure 8 clearly shows a decreasing linear trend following the onset of 2017. Some caution should be applied when speculating as to the decline in carapace length of the female stock. More time is required to observe the full and lasting effects of the current selective pressures being exerted by the commercial shrimp fishery on the female stock. Furthermore, more statistical trends should be noted before deriving a conclusive decision as to the exact effects of commercial shrimp fishing on the Svartnes stock of P. borealis. Future investigation should closely consider the evolution of environmental trends within the Svatnes basin, as they relate to biotic and abiotic factors. Yet, the current trends should still be considered and the potential effects of commercial shrimp fishing pressure on the stock understood. Impacts on the number of individuals, size and age at spawning, fecundity, and population success through recruitment, can be altered. Negative changes to the stock dynamics can extend beyond the scope of the stock and incorporate the entire ecosystem. A reduction in P. borealis can also affect known predatory species such as cod fishes (Gadidae spp.). The social and

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economic impacts from such, could present challenges for the Norwegian shrimp fishery as a whole.

The close correlation between market value, and the size of landed *P. borealis*, relates to global consumer demand (Hopkins & Nilssen, 1990; Garcia, 2007). Landed value is directly affected by decreased size within the exploited stock of *P. borealis* (Nilssen & Hopkins, 1992; Garcia, 2007; Koeller et al., 2007). A lower market value can be detrimental to fishers, requiring larger catches and higher fishing effort to maintain income levels. When coupled with a low abundance of large female individuals, the consequences are amplified.

The unique aquatic biodiversity of the fjord systems along the Norwegian coast are well known (Hopkins et al., 1989). From genetic to morphological differences, an abundance of species inhabiting these ecosystems are on display (Hopkins et al., 1989; MNCE, 2014; Hansen et al., 2021). The same can be said for *P. borealis*, and with a lack of knowledge surrounding the species (Aschan & Ingvaldsen, 2009), more must be done. Current management approaches for *P. borealis* are antiquated and do not seem to consider them with the same importance as other commercially exploited species. Stocks of *P. borealis* have the potential to face shortfalls when presented with the onset of new challenges. With ongoing approaches to fisheries management continuing to centre themselves around political and economic incentives, the unique biological aspects of the stocks within are often negated (Hansen et al., 2021).

The scale of the Norwegian shrimp fishery, and the size of the active vessels, are unlikely to be impacted by incremental changes occurring throughout individual fjord systems. For the Balsfjord shrimp fishery, a reduction in individual size at time of catch would have little effect. Vessels can easily travel to other fishing grounds distributing fishing pressure to other systems. A general lack of understanding as relates to the specific stock dynamics of *P. borealis* along the Norwegian coast, presents challenges in comprehending the continued shifts in fishing pressure. Historical records from Balsfjord serve as a cautionary example as to why understanding the dynamics of local stocks, and how they can shift in response to traceable pressures, is so important. Therefore, from a managerial perspective, initiatives must be made so as to understand, and analyse the different stocks of *P. borealis*. In doing so, the

sustainability of the species and the fishery can be improved. One such goal would be to create a more accurate system for reporting catch data from commercial shrimp trawling vessels, with respect to space and time. In doing so, a deeper understanding as to the abundance of individual stocks could be established.

Svatrnes Blasfjord was recently re-exposed to commercial shrimp fishing following a 34 year hiatus, since the closure of all locations above a depth of 200m in 1983/1984 (Hopkins & Nilssen, 1990). As of 2017, vessels were once again able to fish within the fjord, thus reapplying size selective fishing pressures on the local stock of *P. borealis*. Throughout the course of this study, no notable changes to growth were observed over the year classes/year class groups, apart from a slight increase following the 2011 year class. CPUE was seen to decrease in conjunction with the reopening of the fishery, as did the number of sampled females. During that time, a significant decreasing trend in the carapace length of the spawning stock in the 95th percentile was depicted in response to commercial shrimp fishing. Notably, changes were observed between the current study, and past investigations by Hopkins and Nilssen (1990) as they relate to age and size. An increase in age and size within this study suggest the rehabilitation of the stock following the exertion of past intensive fishing practices. Implying that, over time, commercial fishing activities have the potential to pressure the stock, resulting in a decreased age and size.

Data for *P. borealis* in the Svartnes basin, is available from 1979 until the present, spanning three distinct periods of fishing activity; an open fishery from 1979 - 1983/1984; a closed fishery from 1984 - 2016; and a re-opened fishery starting from 2017 - present. Recommendations for future work would be to compare the changes throughout the stock in response to the fishery over the three periods of time. A preliminary look at the 1984 - 1990 data, immediately following the first closure, indicated a dramatic 20-fold increase in the spawning stock, and an increase in the mean female carapace length (E.M. Nilssen, personal communication, 2022). Future studies should also seek to continue following the changes occurring within the Svartnes basin stock (Blasfjord, northern Norway) of *P. borealis*, create catch curves for from the length distribution data, and give priority to developing an understanding of mortality factors affecting the stock.

5.0 Summary

- Past commercial shrimp fishing in the Svartnes basin (Balsfjord, northern Norway), ended in 1983/1984, reopening in 2017.
- Changes in CPUE and number of females fluctuated throughout the sampling period (with the R/V Johan Ruud) from March 2010 until January 2020. Yet, following 2017, a notable decrease in both the CPUE and number of sampled females is observed in 2018, with an instance of prolonged recovery. The drop is attributed to pressures induced by the commercial shrimp fishery. Suggesting that commercial endeavours have affected the stocks biomass.
- A drop in CPUE and number of sampled females in 2010 remains difficult to quantify.
 The effects inducing the drop in 2010 are either influenced by unknown environmental parameters, or sampling error, and could present an outlier in the data set.
- A significant decreasing trend in carapace length was noted for females in the 95th percentile length (F=19.1, n= 19, P<0.001) after January 2017. A decrease in the size of the largest individuals within the spawning stock can be attributed to the size selectivity of the commercial shrimp fishing gears.
- Small shifts in the growth performance were observed throughout the individual and grouped year classes. When combined together, all 16 year classes from 2005 until 2020 presented a weighted and unweighted GPI of 2.459 and 2.461. The 2011 year class showed the lowest growth performance, following which, the possibility of a small upward trend in the GPI until the 2016 year classes can be observed.
- Implications as to changes occurring in the GPI with respect to commercial shrimp fishing cannot be drawn conclusively. More time is required to allow for the year classes originating in and after 2017 to fully develop.

- Management initiatives should encourage better spatial definitions for zoning, shifting away from geopolitical boundaries. Thus, offering the possibility to create a more conclusive set of location specific catch data, as relates to the commercial shrimp fishery.
- Studies should continue to follow the progression of the Svartnes basin stock, and further investigate attributes relating to the stock's dynamics (catch curves and mortality). Data for the Svartnes basin exists from 1979 until the present, covering three distinct periods; commercial fishing prior to 1983/1984; closed fishery 1984 2016; open fishery 2017 present. Therefore, a comparison between the stock dynamics of each time period should be investigated.

6.0 References

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7.0 Appendix

7.1 Appendix Figures



Appendix Figure 1. Dichotomous key used for the interpretation and identification of seven maturity stages (2-8) within the sampled population, as presented by Hansen & Aschcan (2001).



Appendix Figure 2. Size distribution of *P. borealis* at Svartnes, Balsfjord (northern Norway) as sampled from March 2010 until June 2021. The distribution of males (blue - maturity stage 1-2) and females (red - maturity stage 4-8) are noted throughout all samples. Maturing/transitional sex changing stage 3 males (green) are present, with the development of both fast and slow growing modal groups apparent in May and June of 2021. Figure continues below.

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Appendix Figure 2. Continued.



Appendix Figure 2. Continued.



Appendix Figure 2. Continued.



Parameters: pi mu sigma 1 0.2829 16.11 0.7053 2 0.7171 19.33 0.9829

Standard Errors: pi.se mu.se sigma.se 1 0.02153 0.07306 0.05541 2 0.02153 0.05745 0.04485

Analysis of Variance Table

Df Chisq Pr(>Chisq) Residuals 23 22.216 0.5072

Appendix Figure 3. Example of fitting a modal group from this study through the MIX analysis. Data represents the male (stage 2) portion of a *P. borealis* sample taken March 8th, 2010 from the Svartnes basin (Balsfjord, northern Norway). Note: Mature males (stage 2) from the sample, are fit with no constraints to the standard deviation under the "Free" fitting approach. Males (stage 2) were separated from the female maturation stages (6 and 8) within the sample before being analysed. Males (stages 1-3) and females (stages 4-8) were split, during the MIX analyses.



Appendix Figure 4 (A & B). (A). *P. borealis* from Svartnes, Balsfjord (northern Norway) when t_0 is fixed (from unweighted "No" and weighted "Yes" estimates), depicting the relationship between L_{∞} and *K*. (B). The relationship between the von Bertalanffy growth parameters (unweighted "No" and weighted "Yes") L_{∞} and *K* for different year classes/grouped year classes with a free t_0 .

Linf

0.2

20,11

V



Appendix Figure 5. Comparison of *P. borealis* modal groups from Svartnes (Balsfjord, northern Norway) in relation to carapace length and age over the course of the study, shown before and after the onset of commercial shrimp fishing in 2017. No clear differences can be observed between the displayed patterns of growth for each period of time. Trendlines were added for illustration purposes.



Appendix Figure 6. (A & B). (A). Total CPUE for samples taken between March 2010 and January 2020 of *P. borealis* at Svartnes, Balsfjord (northern Norway). Large drops with a slow recovery in the CPUE are observed following 2017. (B). Total number of females retrieved per sample between March 2010 and January 2020. A drop in the number of sampled females after 2017 is evident, paired with a prologued recovery.



Appendix Figure 7. Linear relationship between the CPUE and the number of females retained during the sampling period from March 2010 until January 2020, with the R/V Johan Ruud.

7.2 Appendix Tables

Appendix Table. 1. Results from March 2010 - October 2021, as relates to, maturity stage, year class, age, and mean carapace length, of each modal group of *P. borealis* identified from the Svartnes basin (Balsfjord, northern Norway).

g g g k g k		ple date	urity stage	class		pace length	nple date	turity stage	ır class		apace length		nple date	turity stage	ır class		apace length
cbc.3200		Sam	Matı	Year	Age	Cara	Sar	Ma	Yea	Age	Car		San	Ma	Yea	Age	Car
0 0		08.03.2010	2	2008	1.934	16.11	27.10.2014 27.10.2014	2	2013	1.575 2.575	13.00 16.84	08.	10.2018	2	2017	1.523	14.00 18.20
Bit		08.03.2010 08.03.2010	2	2007	2.934	19.33 19.68	27.10.2014	2	2011	3.575	18.87	08.	10.2018	4+5+8	2016	2.523	17.31
010200 100 2000 134 191 1710204 1000 157 257 1001200 1001200 1200 158 158 1005200 1 2000 1134 9.87 2010 134 144 140 1005200 1 2000 1134 9.87 2010 134 144 140 3001200 1 2010 134 144 140 3001200 1 2010 134 144 140 3001200 1 2010 134 144 140 3001200 1 2010 134 144 140 140 144 140		08.03.2010	5+6	2006	3.934	21.92	27.10.2014	4+5+6+7+8 4+5+6+7+8	2011	3.575 4.575	21.49 23.84	08.1	10.2018	4+5+8	2015	3.523	20.07
19.9.2000 1 100.2000 2 100.2009 2 100.2009 2 100.2009 2 100.2009 2 100.2009 2 100.2009	-	08.03.2010	5+6	2005	4.934	23.28	27.10.2014	4+5+6+7+8	2009	5.575	25.87	08.	10.2018	4+5+8 4+5+8	2014	4.523 5.523	22.99
10.5.200 1 200 1.14 8.97 200.2013 1.4 8.85 300.2009 1.2 2.00 8.85 5.00 10.5200 1.4 2.00 1.53 1.8 2.00 1.84 2.55 1.84 2.55 1.84 2.55 1.84 2.55 1.95		19.05.2010	2	2005	2.134	16.34	22.01.2015	2	2014	0.814	7.71	30.	01.2019	2	2017	1.836	14.88
199 199 200 199 200 199 100 <td></td> <td>19.05.2010</td> <td>2</td> <td>2007</td> <td>3.134</td> <td>19.87</td> <td>22.01.2015</td> <td>2</td> <td>2013</td> <td>1.814 2.814</td> <td>14.50</td> <td>30.0</td> <td>01.2019</td> <td>2</td> <td>2016</td> <td>2.836</td> <td>19.57</td>		19.05.2010	2	2007	3.134	19.87	22.01.2015	2	2013	1.814 2.814	14.50	30.0	01.2019	2	2016	2.836	19.57
0.112200 1.2 2001 1.51 1.52 2.010.033 1.00 2.010.233 2.010 2.010.233 2.010 2.000 2.010 1.984 3.00 0.410.000 1 2.000 2.317 1.000.235 1.000 1.50 1.500 2.010 1.984 3.010 3.984 3.011 3.984 3.011 3.984 3.011 3.984 3.011 3.984 3.011 3.984 3.011 3.984 3.011 3.984 3.011 3.984 3.011 3.984 3.011 3.984 3.011 3.984 3.011 3.985 3.001 3.985 3.001 3.985 3.001 3.985 3.001 3.985 3.001 3.985 3.001 3.985 3.001 3.985 3.001 3.985 3.001 3.985 3.001 3.985 3.001 3.985 3.001 3.985 3.001 3.985 3.001 3.985 3.001 3.985 3.001 3.985 3.001 3.001 3.985 3.001		19.05.2010	6	2005	4.134 5.134	23.86	22.01.2015	2	2011	3.814	20.35	30.	01.2019	5+7	2013	4.836	23.72
Hall 2000 1.1 1.000 2.10 2.20 2.200 2.84 2.44 2.33 3.2 2.201 1.984 5.84 3.24 2.201 1.984 5.84 3.24 2.201 1.984 5.84 3.24 2.201 1.984 5.84 3.24 2.201 1.984 5.84 3.24 2.201 1.984 5.84 3.25 3.300 3 2.201 1.984 5.84 3.25 3.201 3.2 2.201 3.26 2.201 3.26 2.201 3.26 2.204 3.995 2.201 3.207 3.64 2.201 3.207 3.64 2.201 3.207 3.64 2.204 3.207 3.64 2.204 3.207 3.64 2.204 3.207 3.21 2.201 3.200 3.207 3.64 2.204 3.207 3.207 3.201 2.201 3.207 3.207 3.201 3.207 3.207 3.201 3.201 3.207 3.207 3.201 3.201 3.201 3.201		04.10.2010	2	2009	1.512	13.82	22.01.2015	5+7	2011 2010	3.814 4.814	21.12 22.69	25.	03.2019	2	2018	0.984	8.91
ch.12.020 i+		04.10.2010	2	2008	2.512 3.512	20.06	22.01.2015	5+7	2009	5.814	24.41	25.0	03.2019	2	2017	1.984	15.69 20.12
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18.0.2011 2 2000 844 9.56 101 9.99 1.23 200.4303 1 200.5 5.90 201.5 200.5 5.90 201.5 200.5 5.90 201.5 200.5 5.90 201.5 200.5		04.10.2010 04.10.2010	4+5 4+5	2007 2006	3.512 4.512	22.37 24.55	16.03.2015	1+2+3	2012	3.959	20.13	25.	03.2019	5	2015	3.995	22.73
240.2011 2 2009 1.64 1.60 1.60 1.60 2.00 <t< td=""><td>-</td><td>28.02.2011</td><td>2</td><td>2010</td><td>0.844</td><td>9.56</td><td>16.03.2015</td><td>5+6</td><td>2011</td><td>3.959</td><td>21.23</td><td>02.0</td><td>04.2019</td><td>2</td><td>2014</td><td>2.005</td><td>15.70</td></t<>	-	28.02.2011	2	2010	0.844	9.56	16.03.2015	5+6	2011	3.959	21.23	02.0	04.2019	2	2014	2.005	15.70
1 2 2007 1544 22.06 21.06 2003 21.07		28.02.2011	2	2009	1.844	16.49 20.15	16.03.2015	5+6 5+6	2010	4.959 5.959	23.06	02.	04.2019	2	2016	3.005	20.40
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BCRCC011 2003 218 10.2 2005 2105 2108 1.156 10.56 06G6.2011 2 2009 3.18 0.18 0.76 2206 2011 4.277 22.28 2705 2019 2 2017 2.141 6.77 06G6.2011 4 2003 3.148 0.18 1.256 22.052 74 2010 5.217 2.77 2.015 4.148 2.015 74 2010 5.217 2.017 2.018 1.156 1.056 0.066 2.011 4.2007 4.148 2.017 2.011 1.56 2.015 1.66 2.011 1.56 2.001 1.156 2.003 1.167 2.001 1.16 2.011 1.16 2.011 1.16 2.011 1.16 2.011 1.16 2.011 1.16 2.011 1.16 2.011 1.16 2.011 1.16 2.011 1.16 2.011 1.16 2.011 2.011 2.011 2.011 2.011 2.		28.02.2011	5	2007	3.844	22.46	22.06.2015	1+2+3+4	2013	2.277	16.64 20.91	02.0	04.2019	5+6	2014	6.005	26.38
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		06.06.2011	2	2009	2.184	17.46	22.06.2015	7+8	2011	4.227	22.16	27.	05.2019	2	2017	2.148	16.77 20.73
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666.6.2011 6+# 2007 4.144 2.20 1.21.0.2015 1:2 2013 2.534 1.7.08 1.7.08 2.018 1.24 0.2018 0.2118		06.06.2011	4	2007	4.184	23.37	12.10.2015	1+2	2014	1.534	13.50	27.	05.2019	7	2014	5.156	22.54
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24.10.2011 2 2009 2.567 18.08 12.10.2015 4+56 2011 4.534 23.15 7.066.209 2.44 2.006 3.267 13.26 2.10 2.10 2.006 3.267 13.86 12.10.2015 4+56 2001 4.58 2.10 7.066.209 2.44 2.006 3.26 2.10 7.066.209 2.44 2.006 2.2014 2.214 2.306 24.10.2011 4+6 20007 4.567 2.40 2.0017 2.60 2.0012 2.255 19.47 2.001	-	24.10.2011	2	2010	1.567	13.19	12.10.2015	4+5+6	2012	3.534	21.84	17.	06.2019	2+4	2017	2.214	17.04
24.14.011 1 10.02 3.09 1.10 11.10.101 1.400 10.00 1.400 <		24.10.2011	2	2009	2.567	18.08	12.10.2015	4+5+6	2011	4.534	23.15	17.	06.2019	2+4	2016	3.214	20.70
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		24.10.2011	4+5	2008	2.567	18.90	26.01.2015	4+5+6	2010	1.825	14.76	17.	06.2019	7+8	2010	4.214	21.00
24.10.2011 4:5 2007 4:50 24.00 4:50 2011 6.2.17 2012 3.825 1:40 20.01 7:40 2013 6.2.12 2013 6.2.12 2013 6.2.12 2015 6.68 3:3 27.02.2012 2 2009 2912 20.6 2005 2001 2001 8.68 3:0 27.02.2012 5:7 2003 2.912 2.06 2.001 2.001 2.001 2.001 8.89 2.001.1020 2 2.011 8.81 30.08.7020 2 2.011 8.08 8.93 2.010.1020 2 2.011 5.81 1.90 0.03.2006 5:46:7 2.013 3.03.9200 2 2.011 5.01 8.87 2.010.2012 5:7 2.003 3.81 2.66 0.03.2006 5:46:7 3.00.9.200 5:7.44 2.011 2.01 5.01 8.42 2.010.2012 5:7 2.003 3.023 1.02.00 5:01 8.42 <t< td=""><td></td><td>24.10.2011</td><td>4+5</td><td>2008</td><td>3.567</td><td>22.40</td><td>26.01.2016</td><td>2</td><td>2013</td><td>2.825</td><td>18.47</td><td>17.</td><td>06.2019</td><td>7+8</td><td>2014</td><td>5.214</td><td>23.06</td></t<>		24.10.2011	4+5	2008	3.567	22.40	26.01.2016	2	2013	2.825	18.47	17.	06.2019	7+8	2014	5.214	23.06
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$	-	24.10.2011	4+5	2007	4.567	24.44	26.01.2016	2	2012	3.825	21.03	20.	01.2020	7+8	2013	0.808	9.31
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		27.02.2012	2	2009	2.912	19.70	26.01.2016	5+7	2011	4.825	22.90	20.	01.2020	2	2018	1.808	15.60
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		27.02.2012	5+7	2009	2.912	20.06	26.01.2016	5+7	2010	5.825	25.92	20.	01.2020	2	2017	2.808	19.14
29.10.2012 2 2011 1.58 13.10 O7.03.2016 5 2012 2012 3.00.9.2000 2 2.01.82 2.01.82 2.01.82 2.01.82 2.01.82 2.01.82 2.01.82 2.01.82 2.01.82 2.01.82 2.01.82 2.01.73 2.01 3.00.9.200 2 2.01.82 2.01.73 2.01 3.00.9.200 2 2.01.82 2.01.73 2.01.73 2.01 3.00.9.200 5.77.48 2.016 4.501 2.67 29.10.2012 5.77 2008 4.581 2.3.8 2.00.6 2016 2 2.015 1.201 5.501 4.8.7 0.90.4 2013 2.23 2.01 2.020 2 2.01.9 2.10.7020 2 2.01.9 2.01.6 2.01.5<	_	27.02.2012	5+7	2007	4.912	23.84	07.03.2016	2	2013	1.934	15.42	30.0	09.2020	2	2010	1.501	14.45
22.30.2022 2 2000 2.33 19.38 30.09.2020 2 2.1017 3.501 20.64 29.10.2012 5*7 2009 3.581 22.00 7 3.501 20.64 29.10.2012 5*7 2008 4.581 2.5.41 20.06 20.06 5*6+7 2015 5.221 1.283 30.09.2020 5*7+48 20.16 2.017 3.501 2.064 09.04.2013 2*2 2012 1.025 5.68 20.06.2016 2 2013 3.222 1.12 21.0200 5*7+48 20.16 2.2013 3.222 1.02 2.017 3.562 2.015 5.562 2.016 2.013 3.222 1.0200 5*7 20.16 5.562 2.20 2.017 3.562 2.20 2.017 3.562 2.015 2.012 2.0017 3.562 2.20 2.017 3.562 2.018 2.018 2.018 2.018 2.018 2.018 2.018 2.018 2.018 2.018 2.01		29.10.2012	2	2011	1.581	13.10	07.03.2016	2	2013	2.934	19.04	30.	09.2020	2	2018	2.501	18.77
29.10.2012 5+7 2008 3.581 22.68 07.03.2016 5+6+7 2010 5.94 2015 1.222 11.28 30.09.2020 5+7+48 2015 5.10 2.01 99.04.2013 2+3 2011 2.025 5.03 2.006.2016 2 2.014 2.222 17.27 22.10.2020 5+7+48 2.015 1.222 1.128 30.09.2020 5+7+48 2.015 1.205 1.50 2.015 1.222 1.128 30.09.2020 5+7+48 2.015 1.52 2.014 1.222 1.128 30.09.2020 5+7+48 2.015 1.52 2.014 1.222 1.128 30.09.2020 5+7+48 2.015 1.522 2.014 2.211 2.21.0200 5+7 2.016 5.52 2.20 2.016 1.10 2.016 1.11 2.016 1.11 2.21 2.2019 1.55 5.50 2.25 2.55 5.50 2.2019 1.56 2.2018 2.017 2.2018 1.11 1.11 2.016 1.11 2.2018 3.52 1.11 1.2020 1.11 2.2018 3.52		29.10.2012	2	2010	3.581	20.70	07.03.2016	5+6+7 5+6+7	2012	3.934 4.934	19.98 22.67	30.0	09.2020	2	2017	3.501	20.64
29.00.012 307 2006 4.34 23.44 20.06.2016 2 2014 2.22 17.27 21.0200 2 2019 15.65 20.65 14.11 09.04.2013 2-33 2010 3.025 15.78 20.06.2016 2 2013 3.222 17.47 21.10200 2 2018 2.562 18.78 09.04.2013 2-34 2010 3.025 22.49 20.06.2016 47.44 2013 3.222 21.17 22.10.2000 5-7 2016 5.62 2.857 20.06.2016 47.44 2013 3.222 21.67 22.10.2000 5-7 2016 5.62 2.55 2.56 2.55 2.56 2.55 2.012 2.55 2.012 2.55 2.012		29.10.2012	5+7	2009	3.581	22.68	07.03.2016	5+6+7	2010	5.934	25.01	30.0	09.2020	5+7+48	2016	4.501	22.67
$\begin{array}{cccccccccccccccccccccccccccccccccccc$	-	09.04.2012	2	2008	1.025	9.68	20.06.2016	2	2015	1.222	11.28	30.	09.2020	5+7+48	2015	5.501	24.54
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		09.04.2013	2+3	2011	2.025	15.03	20.06.2016	2	2014	3.222	19.42	22.	10.2020	2	2019	2.562	14.21
$\begin{array}{c c c c c c c c c c c c c c c c c c c $		09.04.2013 09.04.2013	2+3	2010 2009	3.025 4.025	19.78 22.49	20.06.2016	2	2013	3.222	21.12	22.	10.2020	5+7	2017	3.562	22.10
$\begin{array}{cccccccccccccccccccccccccccccccccccc$		09.04.2013	5+6+7	2010	3.025	20.50	20.06.2016	4+7+8 4+7+8	2013	3.222 4.222	21.87	22.	10.2020	5+7	2016	4.562	23.55
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		09.04.2013	5+6+7	2009	4.025	22.65	20.06.2016	4+7+8	2011	5.222	25.63	12.	02.2021	2	2015	0.871	8.03
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	-	13.06.2013	2	2011	2.203	15.95	11.10.2016	2	2015	1.532	13.82 17.83	12.	02.2021	2	2019	1.871	15.28
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		13.06.2013	2	2010	3.203	20.09	11.10.2016	2	2014	3.532	19.89	12.	02.2021	5+7	2018	2.871	19.34
$\begin{array}{c c c c c c c c c c c c c c c c c c c $		13.06.2013	4+8	2011	2.203 3.203	20.51	11.10.2016	4+5+8	2013	3.532	21.86	12.	02.2021	5+7	2010	3.871	22.25
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	_	13.06.2013	4+8	2009	4.203	23.13	11.10.2016	4+5+8 4+5+8	2012	4.532 5.532	24.29 25.19	15.	04.2021	2	2019	2.041	16.07
$\begin{array}{c c c c c c c c c c c c c c c c c c c $		14.10.2013 14.10.2013	2	2012 2011	1.54 2.54	12.79 16.80	24.01.2017	2	2016	0.819	8.27	15.0	04.2021	2	2018	3.041 3.041	20.00
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		14.10.2013	2	2010	3.54	19.72	24.01.2017 24.01.2017	2	2015 2014	1.819 2.819	15.06 19.14	15.	04.2021	5+6	2018	3.041	19.91
$\begin{array}{c c c c c c c c c c c c c c c c c c c $		14.10.2013	4+5+7+8	2010	3.54	21.36	24.01.2017	2	2013	3.819	21.22	15.0	04.2021	5+6	2017	4.041	22.72
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $	_	14.10.2013	4+5+7+8	2008	5.54	25.03	24.01.2017	5+6	2013	3.819	22.00	04.0	05.2021	2+3	2019	3.093	20.94
$ \begin{array}{c c c c c c c c c c c c c c c c c c c $		23.01.2014	2	2013	0.816	7.98	27.02.2017	2	2012	1.912	15.67	04.	05.2021	7	2018	3.093	19.59
$\begin{array}{c c c c c c c c c c c c c c c c c c c $		23.01.2014	2	2012	2.816	17.45	27.02.2017	2	2014	2.912	19.23	04.0	05.2021	7	2017	4.093	11.39
$ \begin{array}{cccccccccccccccccccccccccccccccccccc$		23.01.2014	2	2010	3.816	20.04	27.02.2017 27.02.2017	2	2013	3.912	21.32	09.0	06.2021	2+3+4	2019	2.192	16.93
$\begin{array}{c c c c c c c c c c c c c c c c c c c $		23.01.2014	5+7	2011	2.816 3.816	18.36 21.23	27.02.2017	5+6	2012	4.912	24.16	09.0	06.2021	2+3+4	2018	3.192	20.87
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	_	23.01.2014	5+7	2009	4.816	23.36	03.07.2017	2+4	2016	1.258	12.56	09.0	06.2021	7+8	2018	3.192 4.192	21.99
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		10.03.2014	2	2012 2011	1.942 2.942	14.19 17.73	03.07.2017	2+4	2013	3.258	21.68	21.	10.2021	2	2020	1.559	13.38
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		10.03.2014	2	2010	3.942	20.64	03.07.2017	8	2013	4.258	23.15	21.	10.2021	2	2019	2.559	17.67
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		10.03.2014	5+6+7	2011	2.942	18.45	10.10.2017	8	2012	5.258 1.529	25.23	21.	10.2021	4+5+8	2019	3.559	22.51
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$		10.03.2014	5+6+7	2009	4.942	22.78	10.10.2017	2	2015	2.529	18.57						
$ \begin{array}{c ccccccccccccccccccccccccccccccccccc$	_	10.03.2014	5+6+7	2008	5.942	25.00	10.10.2017	4+5+8	2015	2.529	19.22						
$ \begin{array}{ccccccccccccccccccccccccc$		16.06.2014	2	2013	2.211	10.85	10.10.2017	4+5+8	2013	4.529	23.72						
		16.06.2014	2	2011	3.211	18.37	10.10.2017	4+5+8	2012	5.529	25.71						
16.06.2014 4+8 2010 4.211 22.49 12.03.2018 2 2015 2.948 20.39 16.06.2014 4+8 2009 5.211 24.19 12.03.2018 5+6 2014 3.948 22.48 12.03.2018 5+6 2013 4.948 22.48 12.03.2018 5+6 2013 4.948 24.41		16.06.2014 16.06.2014	2	2011	3.211	20.32	12.03.2018 12.03.2018	2	2017	0.948 1.948	10.83 17.14						
16.06.2014 4+8 2009 5.211 24.19 12.03.2018 5+6 2014 3.948 22.48 12.03.2018 5+6 2013 4.948 24.41		16.06.2014	4+8	2010	4.211	22.49	12.03.2018	2	2015	2.948	20.39						
	-	16.06.2014	4+8	2009	5.211	24.19	12.03.2018 12.03.2018	5+6 5+6	2014 2013	3.948 4.948	22.48 24.41						

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Appendix Table. 2. Results from the present study for the von Bertalanffy growth model fitting, giving estimates of L_{∞} and K parameters (with a 95% confidence limit) for individual and grouped year classes of *P. borealis* in the Svartnes basin, Balsfjord (northern Norway). The GPI is indicated with a 95% confidence limit.

YC	Number	Weight	t0_fixed	Linf	Linf_min	Linf_max	К	K_min	K_max	GP	GP_min	GP_max
<=2009	53	No	-0.25	27.1	26.41	. 28.01	0.413	0.382	0.445	2.486	2.474	2.498
<=2009	53	Yes	-0.25	26.99	25.99	27.99	0.421	0.387	0.455	2.486	2.478	2.495
2010) 23	No	-0.25	28.1	26.42	29.77	0.354	0.307	0.402	2.447	2.431	2.463
2010) 23	Yes	-0.25	27.22	25.89	28.56	0.382	0.343	0.422	2.452	2.443	2.462
2011	L 25	No	-0.25	29.29	26.4	32.17	0.314	0.253	0.374	2.43	2.414	2.445
2011	L 25	Yes	-0.25	27.88	25.22	30.54	0.332	0.273	0.392	2.412	2.398	2.426
2012	2 20	No	-0.25	32.79	28.76	36.82	0.263	0.206	0.32	2.451	2.43	2.472
2012	2 20	Yes	-0.25	34.62	30.32	38.93	0.246	i 0.195	0.296	2.469	2.446	2.493
2013	3 25	No	-0.25	29.51	27.92	31.09	0.329	0.292	0.365	2.456	2.444	2.469
2013	3 25	Yes	-0.25	29.25	27.12	31.39	0.333	0.29	0.376	2.454	2.442	2.466
2014	1 18	No	-0.25	27.75	25.67	29.83	0.374	0.313	0.435	2.459	2.438	2.48
2014	1 18	Yes	-0.25	26.9	25.14	28.66	0.398	0.347	0.448	2.459	2.446	2.472
2015	5 18	No	-0.25	26.58	23.84	29.31	0.398	0.308	0.489	2.449	2.42	2.479
2015	5 18	Yes	-0.25	25.39	22.93	27.84	0.455	0.363	0.548	2.468	2.447	2.488
2016	6 15	No	-0.25	27.32	24.71	. 29.93	0.41	0.328	0.491	2.486	2.466	2.505
2016	5 15	Yes	-0.25	25.89	24.25	27.53	0.469	0.409	0.529	2.497	2.484	2.511
>=2017	43	No	-0.25	28.96	26.83	31.09	0.356	i 0.31	0.402	2.475	2.462	2.488
>=2017	43	Yes	-0.25	30.03	27.74	32.33	0.337	0.297	0.378	2.483	2.468	2.499
All	239	No	-0.25	28.12	27.51	. 28.73	0.365	0.348	0.382	2.461	2.455	2.466
All	239	Yes	-0.25	26.84	26.12	27.55	0.4	0.379	0.42	2.459	2.454	2.464

