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Relation between habitat characteristics and abundance, diet and condition of 0-group cod in two northern Norwegian fjords



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Master's thesis in Biology
Mai 2013

Picture on the front page is from Porsangerfjord in August 2012

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In the present study the relation between habitat characteristics and abundance, diet and body condition of 0-group cod was investigated. The samples were obtained from two northern Norwegian fjords Balsfjord (69 °N and 25 °E) and Porsangerfjord (70 – 71 °N and 25 – 26 °E) in August 2012. The 0-group was sampled in shallow waters by beach seine and in the pelagic by pelagic trawl. The abundance in the beach seine hauls per station varied from one to 185 0-group cod, and from two to 992 0-group cod in the pelagic trawl. The highest density of 0-group cod appears to peak at between 50 – 70 % vegetation coverage in both fjords, implying that there is a nonlinear relation between the density of 0-group cod and the vegetation coverage. The diet diversity of the 0-group cod was significantly higher in the intertidal zones than in the pelagic. The diet of 0-group cod in the intertidal zones was fairly similar, with a mixture of pelagic and bottom dwelling prey categories, whereas the diet of the 0-group cod in the pelagic was dominated by pelagic prey categories. Body condition, expressed as weight at length, was estimated by simple linear regression. The height of the regression lines, i.e., and estimated dry weight was significantly different between habitats. 0-group cod from the intertidal zone in Balsfjord was significantly heavier at same length than in the intertidal zone in Porsangerfjord. Similarly in Porsangerfjord the 0-group cod from the pelagic was significantly heavier at same length than the 0-group cod in the intertidal zone.

Key words: 0-group cod, vegetation, diet, body condition, habitat.

Introduction

The two main populations of cod inhabiting the waters of northern Norway are the Norwegian coastal cod (NCC) and the Arcto-Norwegian cod (ANC). They can be distinguished by their life-history, the number of vertebrae, colour, growth, the pattern in the growth zones of the otoliths and also by the expressed genotype on the Pan I allele (Fevolden et al., 2012, Godø and Moksness, 1987, Jakobsen, 1987, Løken et al., 1994). Larvae and small juveniles of NCC and ANC are in some areas co-occurring before settlement (Fevolden et al., 2012). The juvenile Arcto-Norwegian- and Norwegian coastal cod can be distinguished from each other by different settling strategies (Løken et al., 1994). Juvenile cod that settles in shallow waters (0-20 m) are mostly the resident NCC whereas the deep-water settlers consists of the ANC. (Fevolden et al., 2012, Aglen et al., 2012). The different settling strategies is considered be essential for the maintenance of the population structure between the NCC and the ANC (Berg and Albert, 2003, Fevolden et al., 2012). An experimental study on life history traits of coastal cod from different fjords, at 60 °N and 70 °N, found that there also is a difference

in the growth potential of the juvenile coastal cod, suggesting that the coastal cod consists of several genetically different sub-populations.

North of 62° the populations of Norwegian coastal cod have been declining since 1994 to 2003 where they have remained at the same low level since. In 2011 the spawning stock of the Norwegian coastal cod was estimated to be one of the lowest (Aglen et al., 2012). The causes for the low recruitment of Norwegian coastal cod are not fully understood, and there is little knowledge of the population dynamics of northern juvenile coastal cod in their shallow water nursery habitats. For the 0-group Atlantic cod stocks that use shallow waters as a nursery habitat, the combination of aquatic vegetation and substrate has been shown to be of importance to age 0-group Atlantic cod. As it is seen to provide the juvenile fish with foraging grounds and protection against predators and reduced physical exposure (Gotceitas et al., 1997). Limited or lack of suitable habitat has been suggested to give poor annual year classes of cod and have a negative effect on the recruitment to the adult population (Fraser et al., 1996).

In Balsfjord (69 °N and 25 °E), northern Norway, one of the northernmost eelgrass habitats has been found, yet its importance, as nursing area for 0-group cod has not been investigated. Eelgrass beds are known to be very productive systems and complex habitats, that can sustain high abundances of potential prey for 0-group cod (Christie et al., 2012). In a previous study, Newfoundland, Canada, there has been shown a relation between eelgrass and the occurrence of 0-group cod (Gotceitas et al., 1997). In Langesund, Skagerrak, Norway, Tveite (1984) found that degradation and destruction of eelgrass beds due to anthropogenic pollution gave a rapid decline in density of 0-group cod.

In Porsangerfjord (70 – 71 °N and 25 – 26 °E), it has been observed that density of 0-group cod increases with increasing coverage of annual macro algae (Michaelsen, 2012). Kelp forest is also considered to be an important nursery ground for juvenile cod but have since the late 1970's been subjected to high grazing pressure by green sea urchins (*Strongylocentrotus droebachiensis*, O. F. Müller, 1776) along the Norwegian coast (Norderhaug and Christie, 2009). Norderhaug and Christie (2009) suggests that the reduction in kelp forests was initiated by overfishing commencing a process of self-reinforcement where reduced predation stimulated recruitment of sea urchins. The increased grazing pressure and subsequent loss of kelp forests caused a decrease in available nursing area for juvenile fish contributing to the reduction of the coastal cod populations (Norderhaug and Christie, 2009).

There is little knowledge about habitat suitability for 0-group cod. In a previous study by Copeman et al. (2009) on 0-group Atlantic cod found in eelgrass, within Newman Sound, Newfoundland, Canada indicated that the functional importance of the habitat was shelter and not nutrition, and that they were mainly feeding during the day on pelagic prey.

In previous diet studies of 0-group cod in northern Norway different groups of crustaceans were found to be the most numerous in both the intertidal and pelagic realm with copepods, decapods and amphipods as the most important groups (Wiborg, 1948b). Copepods were the most numerous prey and were dominated by harpacticids, but *Calanus finmarchicus* (Gunnerus, 1770) also occurred regularly (Wiborg, 1948b, Wiborg, 1949). Although crustaceans are the most common prey in both shallow and deep waters the composition of the diet in shallow waters differs from that of the deep (Wiborg, 1948a). The diet has also been found to vary with season and also be

dependent up on the size of the fish (Copeman et al., 2008).

In north-temperate regions the juvenile fish in their first growing season will try to maximize their somatic growth and energy storage to increase their potential for survival (Walters and Juanes, 1993, Post and Parkinson, 2001). Copeman et al. (2008) found the accumulated energy storage to decrease with increasing size in 0-group cod in Newman Sound, Canada. This suggests that an increase in size may be of greater importance than lipid storage due to gape-limited predation pressure. In their study of energy allocation strategy in 0-group trout, Post and Parkinson (2001), found that in lakes providing high growth rates the 0-group trout switched from somatic growth rate maximising strategy to a lipid storage maximising strategy at smaller size than in lakes that had less favourable conditions for growth. Small juvenile cod respond quickly to changes in quantity- and quality of food. Condition indices can therefore be used to assess long- and short-term changes in energy intake of small juvenile cod (Grant and Brown, 1999). The length of the fish inflicts constraints on what prey resources are available for the fish to forage on. Changes in lipid composition can be interpreted to reflect the trade-offs in growth, food availability and overwintering success (Copeman et al., 2008).

In this thesis, the main objective is to investigate if there is any effect of habitat variability on abundance, diet, condition measures and body size of 0-group coastal cod. The null hypotheses that have been tested are the following:

H₁: there is no relation between abundance of 0-group cod and vegetation coverage

H₂: there is no difference in diet between the different habitats

H₃: there is no difference in body condition between the habitats

The approach chosen to investigate habitats in two fjords, Balsfjord and Porsangerfjord, The three habitats investigated here, will provide the 0-group cod with different biotic and abiotic factors such as; vegetation coverage, food quality and quantity, shelter from predators and temperature regimes.

Methods

Study area

Samples were collected 07 – 09 August 2012 in Balsfjord and 14 – 18 August 2012 in Porsangerfjord (Figure 1). To collect the samples in shallow waters an inflatable rubber boat (Figure 2) were used, and to collect samples from the pelagic R/V “Johan Ruud” (100 ft) was used (Figure 3).

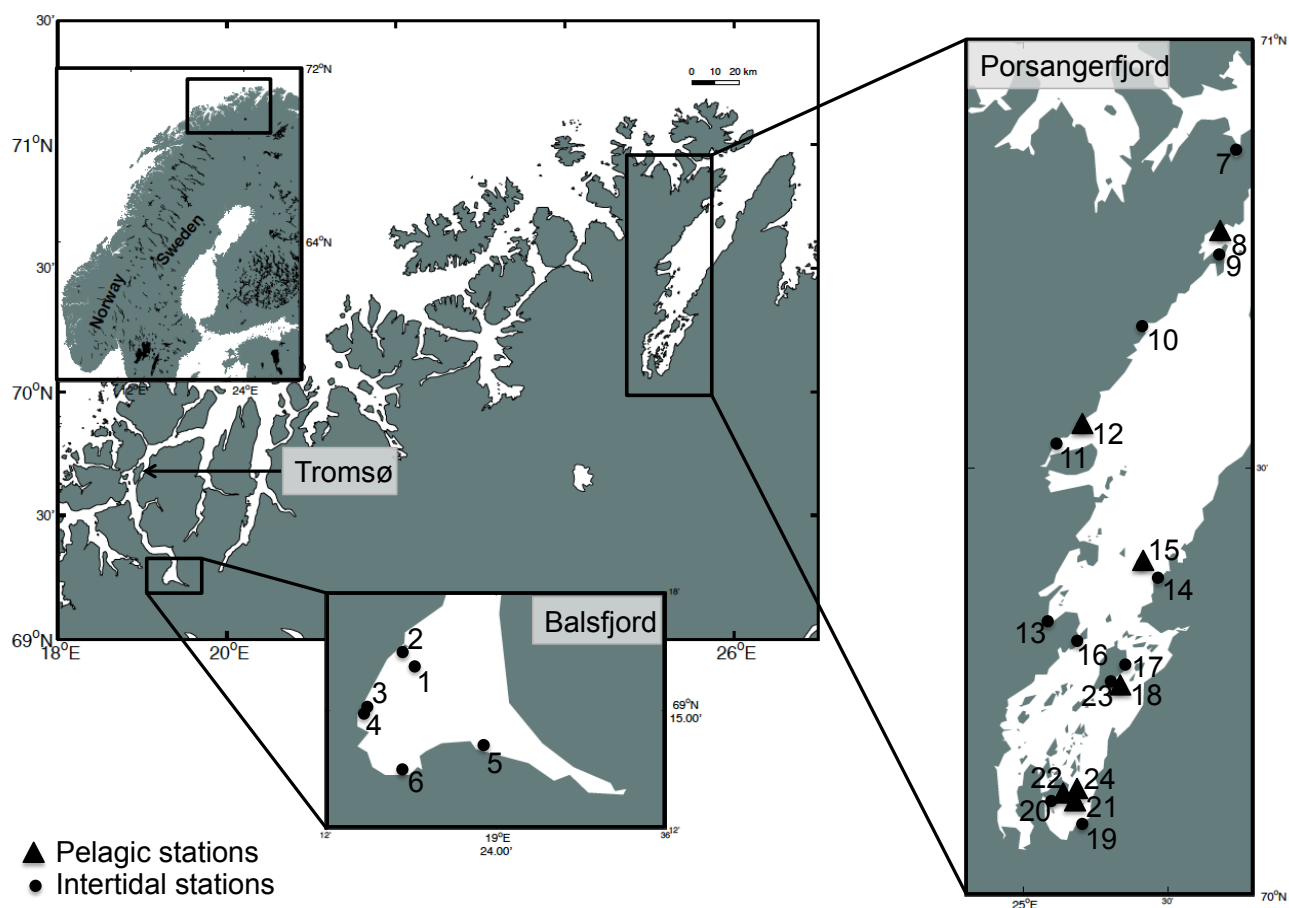


Figure 1. The different sampling locations in Balsfjord and Porsangerfjord. In Balsfjord there was six stations sampled by beach seine. In Porsangerfjord there was seven stations sampled by pelagic trawl and eleven stations where beach seine was used. For coordinates see Appendix B.



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Figure 2. To obtain samples from the intertidal zone a rubber boat was used to launch the beach seine.



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Figure 3. To obtain the samples from the pelagic zone the vessel R/V “Johan Ruud” was used for pelagic trawling.

Sampling area

Balsfjord is situated at 69 °N and 25 °E and has three shallow sills at 8, 9 and 30 m (Figure 4). These sills are limiting the influence of the outer coastal water on the inner basin waters. During the summer there is a high discharge of freshwater through river-runoff creating a typical estuarine circulation (Eilertsen and Skarðhamar, 2006), and Balsfjord contains one of the northernmost eelgrass habitats (pers. com N. M. Jørgensen). The dominating species of eelgrass in Balsfjord is the common eelgrass (*Zostera marina*) i. e., a vascular plant that forms meadows on muddy and sandy bottoms from lower tidal limit to between 5 and 10 m depth depending on the turbidity (Christie et al., 2012).

Porsangerfjord is situated further north than Balsfjord at 70 – 71 °N and 25 – 26 °E, and is the largest fjord in northern Norway, being approximately 100 km long and 15 – 20 km wide. Porsangerfjord has no shallow sills in the outer parts but has a several deep sills. One sill is located at 60 m depth in the inner part of the fjord, and creates a deep basin, Østerbotn (Fig. 4). Due to the lack of shallow sills Porsangerfjord are greatly influenced by the Norwegian coastal current (Wassmann et al., 1996, Eilertsen and Skarðhamar, 2006). The vegetation mainly consists of brown algae, i. e. *Chorda philum*, *Fucus* spp. and *Laminaria* spp., and some red algae species (Michaelsen, 2012).

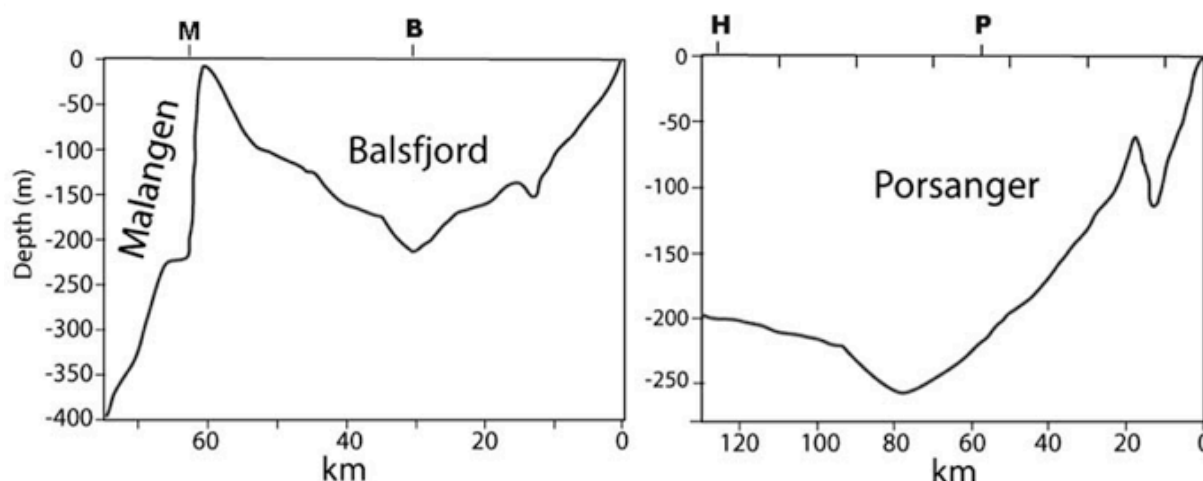


Figure 4. Bottom profile of Balsfjord and Porsangerfjord. The figures show the depth (m) and length (km) of the two fjords and where the sills are situated. M: Malangen, B: Balsfjord, H: Helines, P: Porsangerfjord. Modified from Eilertsen & Skarðhamar (2006).

Field sampling

To collect the samples in shallow waters, 3- 5 m depth, a beach seine (Figure 5), and an inflatable rubber boat was deployed. One person stood on the shoreline while the seine was launched. After which the seine was launched a second person moved ashore about 30 m apart from person one. This two person team then proceeded to haul the seine towards the beach at an even speed and at the same time decreasing the

distance so that the seine was landed as a bag. Two hauls were conducted per station.

In Balsfjord the beach seine was implemented at low tide only due to the morphology of long tidal flats present in this area. As a result of this tidal control factor, one station was sampled during the night. This was not necessary in Porsangerfjord and samples were therefore taken at any point of the tidal cycle.

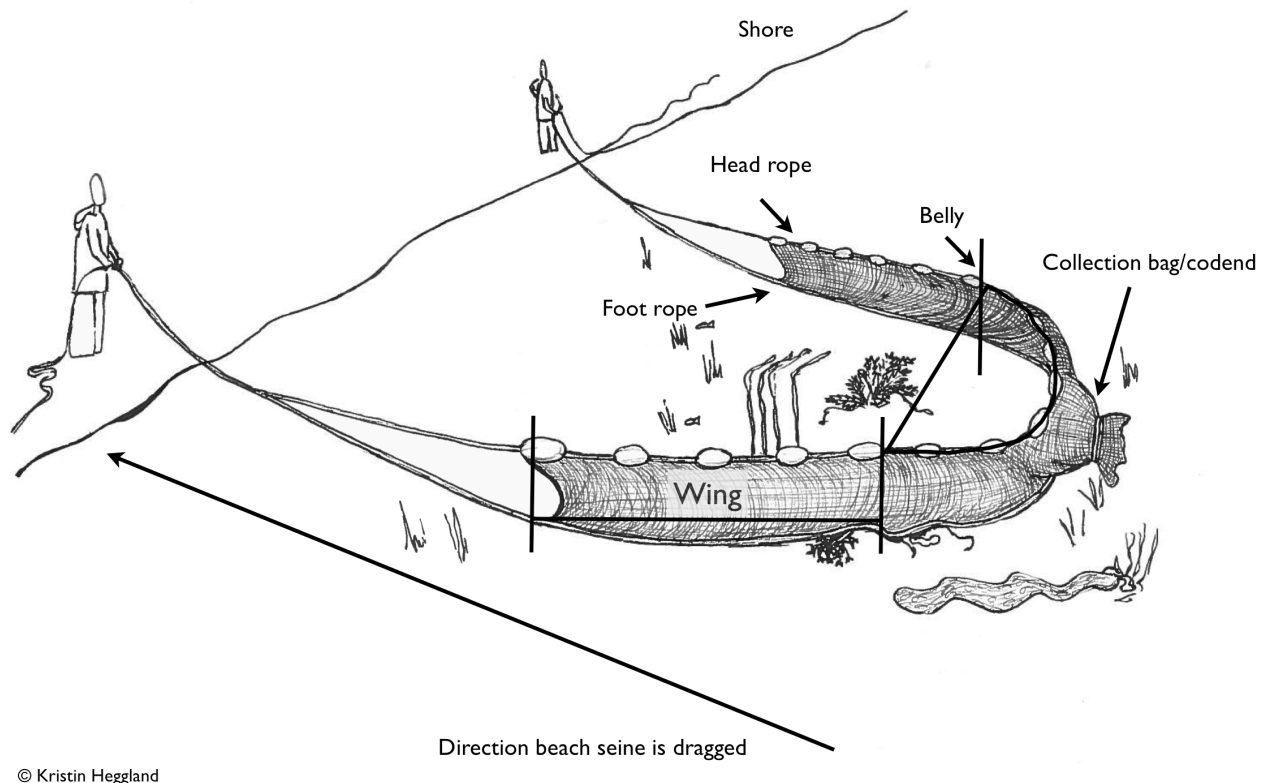


Figure 5. Schematic drawing of the beach seine. Each wing was 15 m, the belly was 9 m wide, and the beach seine had a total length of 39 m. Height of the beach seine at the collection bag was 2.8 m and at the attachment point of the ropes the height was 1 m in height. The rope attached to the seine was about 20 m. The stretched mesh size was 1 cm in the wing, 0.5 cm in the belly and 0.7 in the collection bag. The footrope had integrated led to prevent the footrope to float. The head rope had floaters attached to keep the head rope in the surface. The beach seine is constructed of nylon.

To collect samples from the pelagic a pelagic trawl with 12 x 12 m opening and an inner net with 4 mm mesh at the codend was used. The duration of the pelagic trawl hauls ranged from 12 – 26 minutes (Figure 6).

After landing of the catch, 10 individual 0-group cod, where present, were randomly selected from each haul and total length (TL, mm) were measured (Figure 7). The selected specimens were packed in individual zip lock bags, given unique ID and held in freezer storage at a temperature of -20°C , prior to laboratory analysis. The remaining trawl catch were sorted, identified to lowest possible taxa, then counted in the field before being frozen (-20°C).



Figure 6. The pelagic trawl in use on R/V "Johan Ruud".



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Figure 7. Handling of the 0-group cod after landing in the field.

The area where the beach seine was used was surveyed after the beach seine had been hauled, and information about the habitat at the beach seine stations was obtained using a water scope. This was done to quantify the proportions of the substrate covered by plants, sand, gravel and stones, (Figure 8 and 9, Appendix A).

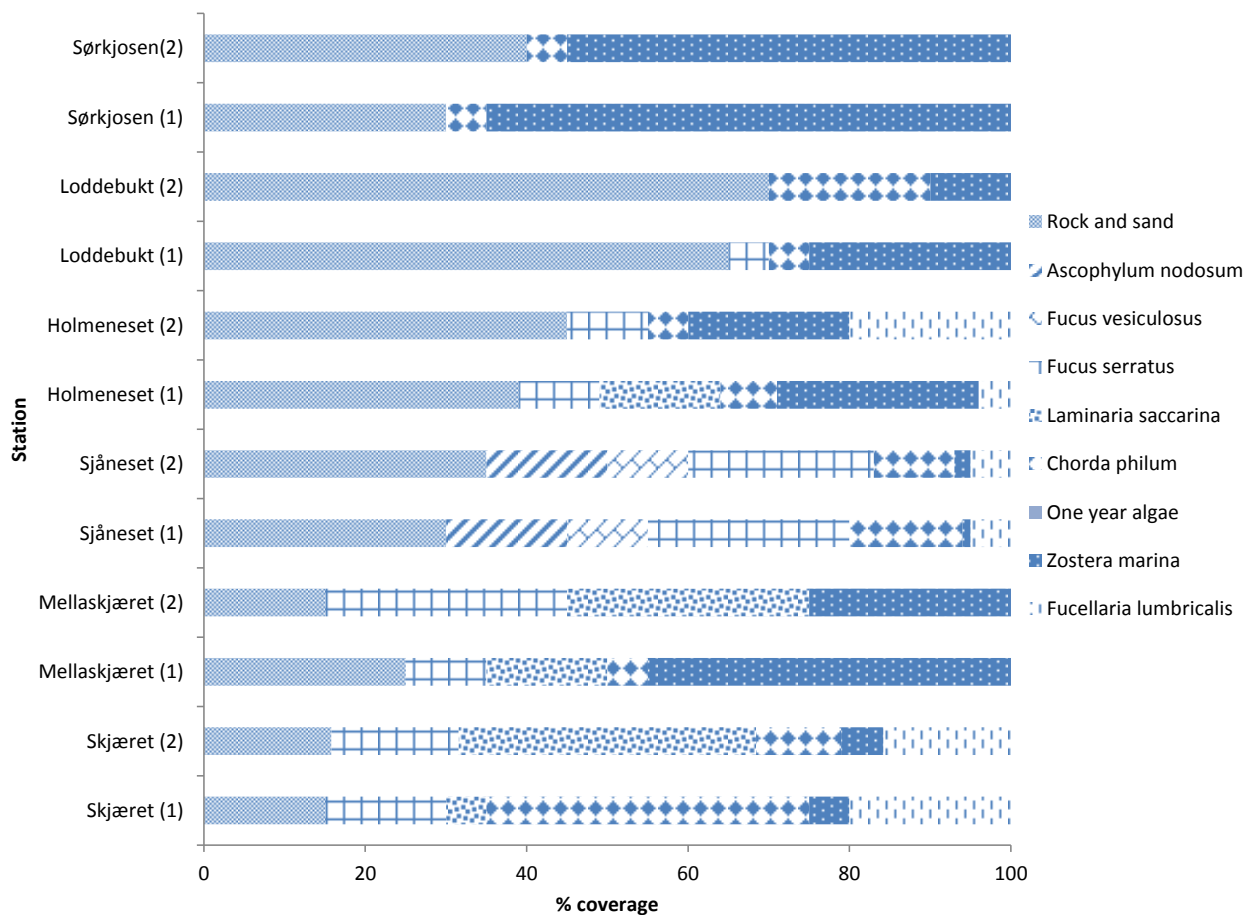


Figure 8. Percentage coverage of aquatic vegetation and rock and sand at beach seine stations in the intertidal zone in Balsfjord. Each station had two hauls taken side by side. Each haul is indicated with a number after the station name.

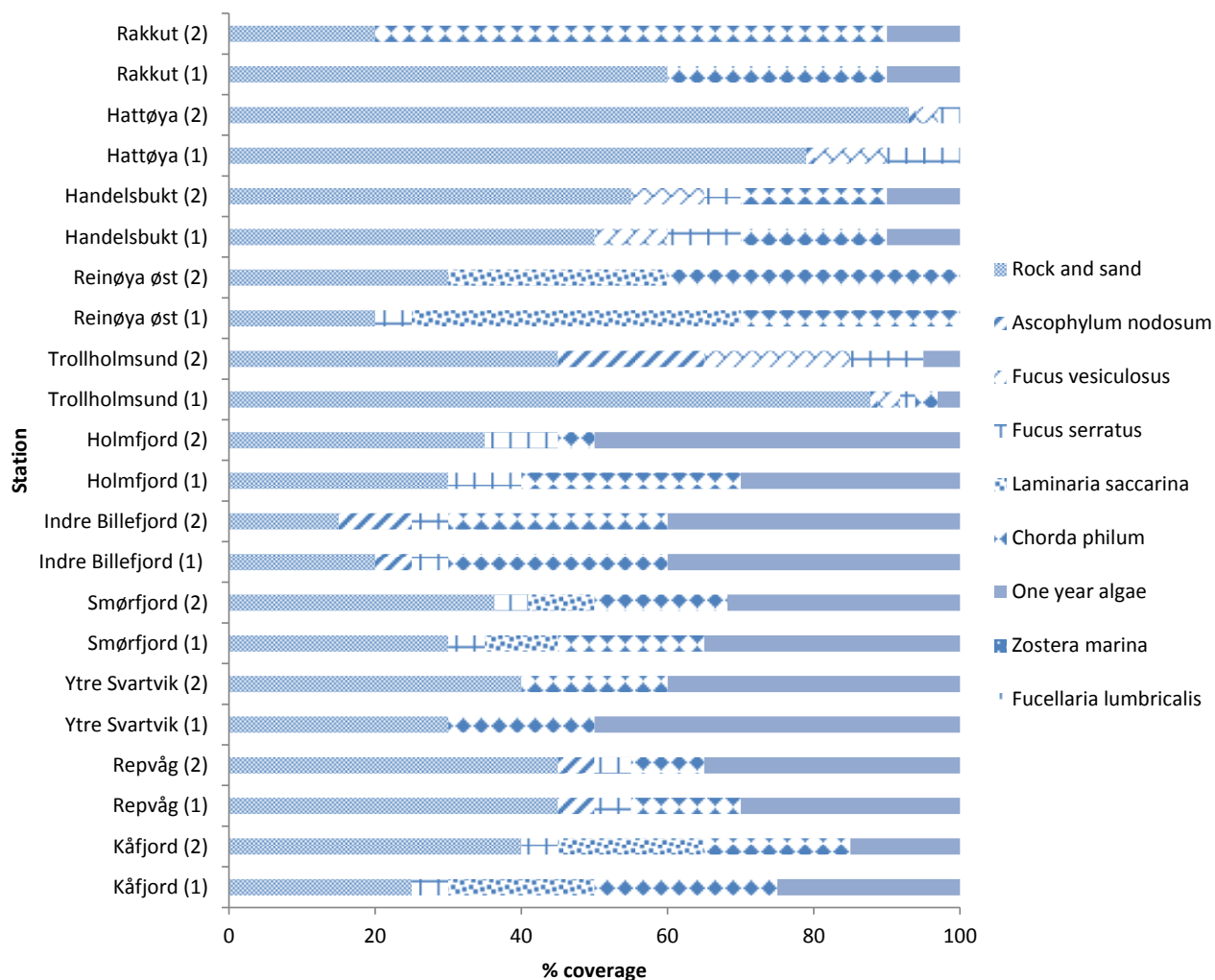


Figure 9. Percentage coverage of aquatic vegetation and rock and sand at stations in the intertidal zone in Porsangerfjord. Each station had two hauls taken side by side. Each haul is indicated with a number after the station name.

Laboratory analysis

In the laboratory 10 specimens from each station (5 from each haul the beach seine was used) was processed and dissected. Total fish length was measured again, stomach content analysed. After dissection the specimen was dried at a temperature of 60 °C until a constant weight and weighed (0.0000 g, brand: BP 110 S, KEBO Lab AS). The dry weight is derived from the gutted fish plus the liver and minus the otoliths.

The stomachs were retrieved during dissection of the specimens. The stomach content was immediately removed from the stomach and 40 %

ethanol was added to prevent further digestion and to coagulate the sample. The stomach contents of the individual fish have been sorted in to the lowest possible taxa (Enckell, 1980, Sars, 1903) and counted. Unidentified prey groups such as; stone and red algae were not included in further analysis due to low occurrence.

Following this process, the stomach content have been dried at a temperature of 60 °C until a constant weight and weighed (0.000 mg, brand: MX 5, METTLER-TOLEDO AS) to estimate the biomass of the different prey categories.

Data treatment

The complete dataset consists of 199 specimens from three different habitats, the intertidal zone in Balsfjord (n = 46), the intertidal zone in Porsangerfjord (n = 89) and from the pelagic in Porsangerfjord (n = 64).

Graphical presentations of the data have been made using R (version 2.12.1) or Microsoft Excel (2012). All statistical analysis is done in R (version 2.12.1), except the calculation of the X^2 , which has been conducted in Excel.

Spearman's Rank Order correlation coefficient (r_s)

This is a nonparametric correlation coefficient with no assumptions for the underlying distribution and no units. It determines the relationship between monotonic variables and is testing the null hypothesis of no correlation. The two variables are separately transformed to ranks and pairing is retained after ranking. The coefficients ranges between +1 and -1 (Quinn and Keough, 2003). To check for significance table in Zar (1999) was consulted.

Two tailed t-test

The `t-test` is a method of testing the hypothesis that the mean values of a variable from two groups are equal. The t-test assumes independence of the two groups and normal distribution. The t-test is however very robust and can be used even if the assumption of normal distribution is violated. By default in R if the variance between the groups is equal the pooled estimate of variance will be used, but if the variance of the variable is not equal in the groups the variance is estimated separately and Welch modification of the degrees of freedom is applied (R version 2.12.1).

Simple Linear Regression

A linear regression model was estimated to describe the length-weight relationship of the 0-group cod. The model describes how much of the variation in weight is explained by the length of the fish. The body condition (BC) is the residuals in the linear regression.

$$\ln(\text{dry weight}) = \alpha + \beta \ln(\text{total length})$$

Confidence interval for estimated weight ($S_{\hat{Y}_i}$)

The confidence intervals for \hat{Y}_i should be calculated from the mean of X_i (the natural logarithm of the total lengths) due to the standard error are at its lowest here (Zar, 1999).

$$S_{\hat{Y}_i} = \sqrt{s_{\hat{Y}*X}^2 \left[\frac{1}{n} + \frac{(X_i - \bar{X})^2}{\sum x^2} \right]}$$

$S_{\hat{Y}_i}$ is the standard error of \hat{Y}_i the expected $\ln(\text{dry weight})$ at X_i . $s_{\hat{Y}*X}^2$ is the residual mean square error. Confidence intervals (CI) for \hat{Y}_i are calculated as:

$$CI_i = \hat{Y}_i + t^* S_{\hat{Y}_i}$$

Where t is the student t-statistic.

Chi-square test (X^2)

The X^2 are testing the hypothesis of no difference in frequencies between groups. It is a measure of association for contingency tables. X^2 is comparing observations and theoretical frequencies in categories.

$$X^2 = \sum_{i=1}^n \frac{(o-e)^2}{e}$$

O is the observed frequencies, e is the theoretical expected frequencies. The degrees of freedom are a function of the number of categories (Quinn and Keough, 2002).

The R model of the NMDS

R-statistical software was used to create a Non-metric Multi Dimensional Scaling plot. The NMDS plot creates a visual presentation of a complex set of relationships. The MASS and vegan packages were used to calculate the dissimilarity matrix. The input data matrix was binary (i.e., 0, 1). Jaccard is the method used to create the dissimilarity matrix, and the plot has two dimensions. The stress values can be between 0 and one. The smaller the stress the better is the representation of the data.

Frequency of occurrence

To provide an overview of prey items found in the three main habitats defined, intertidal zone Balsfjord, intertidal zone Porsangerfjord and pelagic Porsangerfjord, frequency of occurrence (FO%) table and bar graph was made. The occurrence of the different prey groups were counted and divided by the total amount of stomach analysed in the respective habitat. The total number of 0-group cod stomachs analysed is; 25 in Balsfjord, 49 in the intertidal zone in Porsangerfjord and 29 in the pelagic in Porsangerfjord.

$$FO\% = \frac{\text{number of stomachs containing prey type } i}{\text{total number of stomach}}$$

Results

The data have been divided into three main groups, the intertidal zone in Balsfjord (IB), the intertidal zone in Porsangerfjord (IP) and the pelagic in Porsangerfjord (PP). These three groups will hereafter be referred to as habitat in the text. The seasurface temperature of the stations in Balsfjord was found to be on average 2.5°C warmer than those in Porsangerfjord (Appendix B).

There is a large variation in the number of 0-group cod caught at the different stations within the habitats. A total of 296 0-group cod were obtained from Balsfjord (IB), with a minimum of one and a maximum of 166 specimens per station (Figure 10). In Porsangerfjord a total of 2053 0-group were obtained, and 640 specimens were caught using the beach seine

(IP), with a minimum of two and a maximum of 185 specimens per station (Figure 10). In pelagic trawl hauls (PP) 1413 specimens have been caught, with a minimum of two and a maximum of 992 specimens being collected per station (Figure 11). Due to loss of a sample, the single cod caught by Skjæret is not included in any of the analysis.

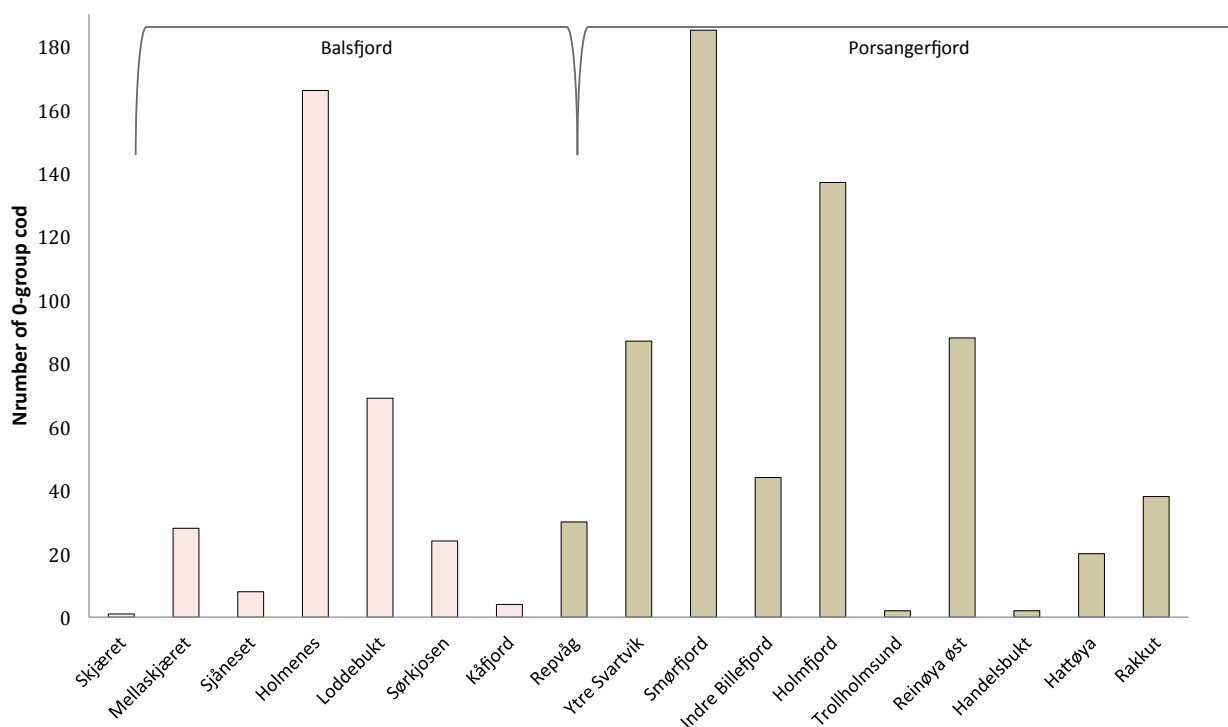


Figure 10. Total number of 0-group cod caught at each station in the intertidal zone in Balsfjord and Porsangerfjord. Two hauls were taken at each station and the number of 0-group cod from these has been combined.

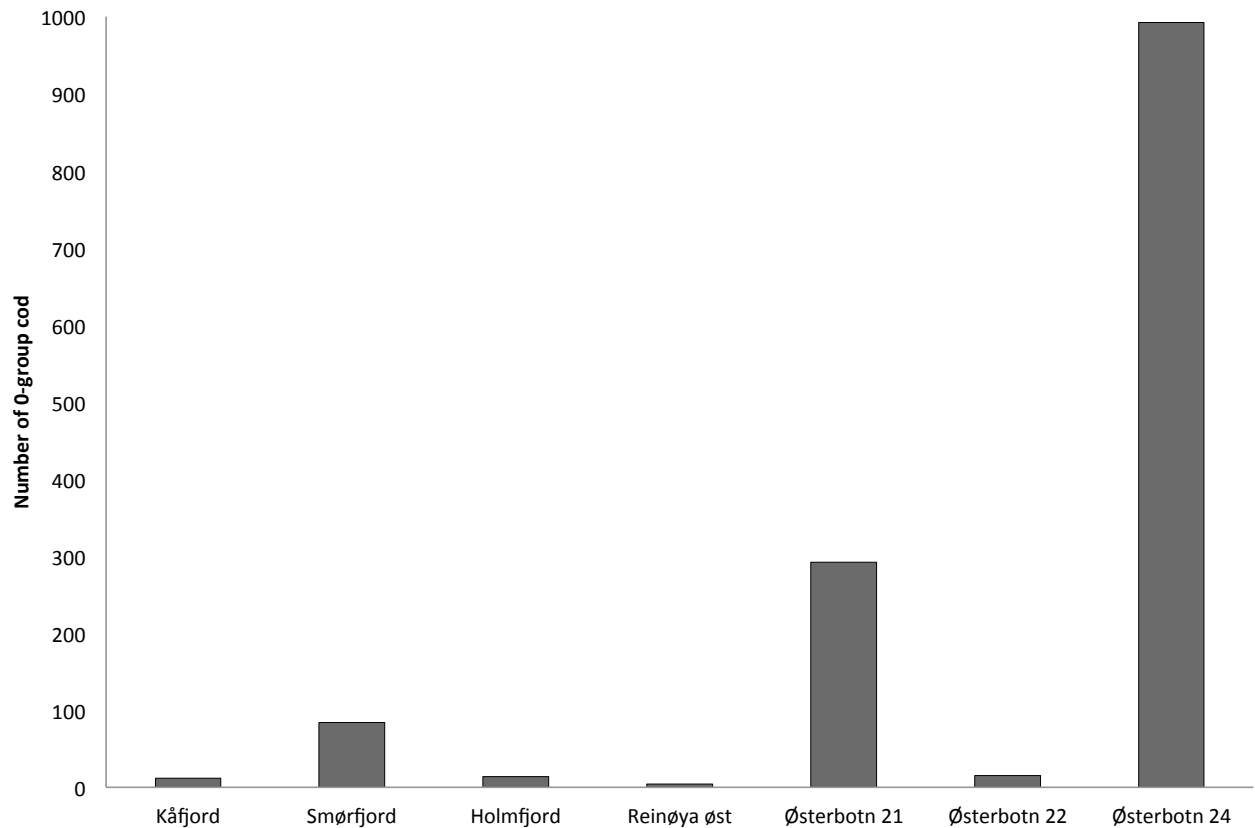


Figure 11. Total number of 0-group cod caught using a pelagic trawl in the pelagic in Porsangerfjord.

Vegetation and density of 0-group cod

To test if the strength and correlation between the vegetation coverage and the abundance of 0-group cod were correlated and a Spearman's Rank Order correlation (r_s) was estimated (Appendix C). In Balsfjord there was a negative correlation between the vegetation coverage and abundance of 0-group cod ($r_s = -0.70$, $n=12$, $0.01 < p < 0.02$), whereas in IP there is

seen to be a weaker but positive correlation between vegetation coverage and the number of 0-group cod obtained ($r_s = 0.38$, $n=22$, $0.05 < p < 0.10$). In both Balsfjord and Porsangerfjord, the highest abundance of 0-group cod was at 50 – 70 % vegetation coverage (Figure 12).

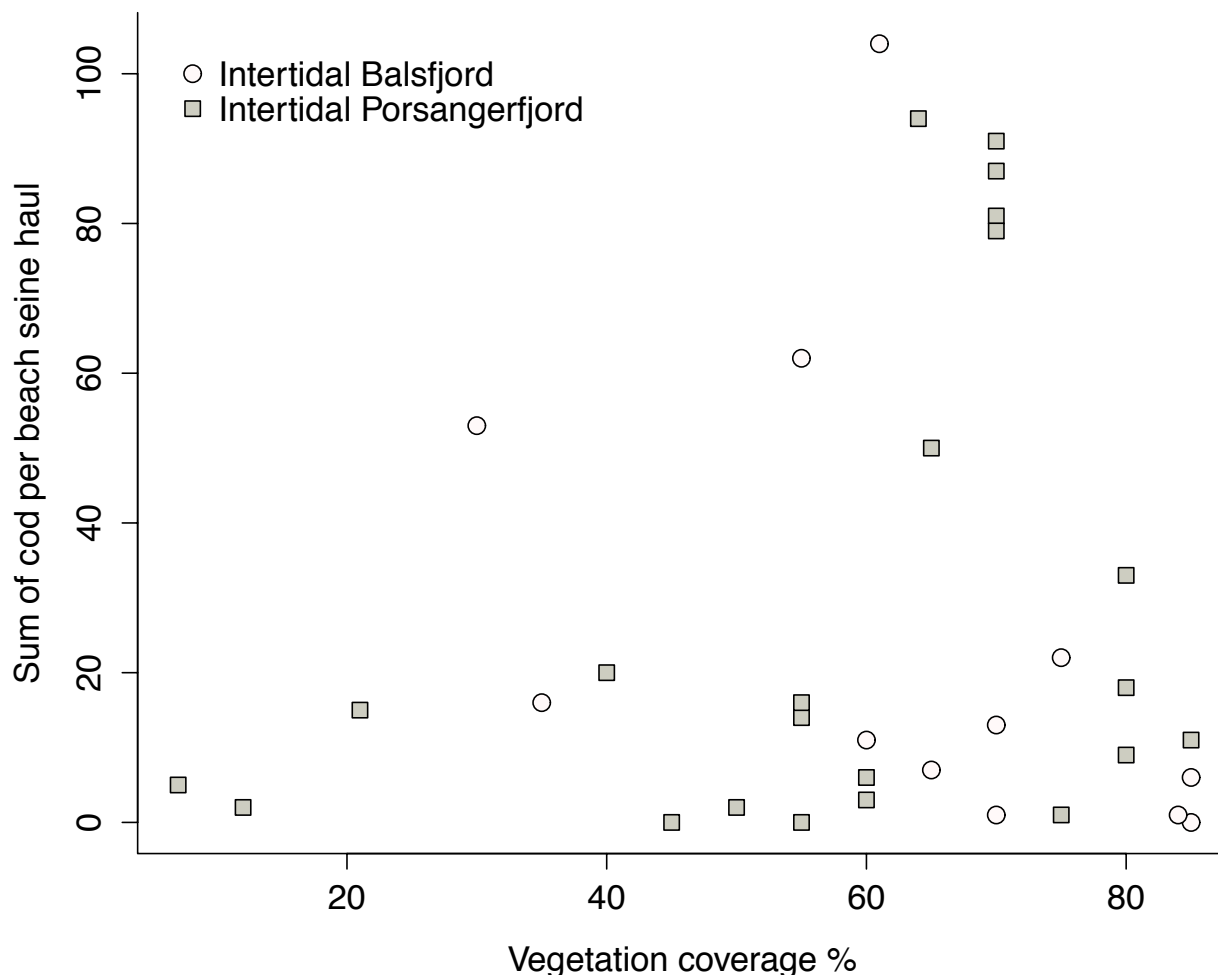


Figure 12. Relationship between vegetation coverage and number of 0-group cod per beach seine haul. Each station has two hauls, and each haul is represented by an own data point.

Diet

In total, 109 0-group cod stomachs were analysed, with only two stomachs being found to be empty. These two stomachs were excluded from the analysis. The stomach content was sorted into 18 different prey categories (Figure 13 and Appendix D, E and F). Copepods were divided into three different groups, harpacticoida, small pelagic copepods and large calanoida. Harpacticoida is mostly benthic and assumed to be locally produced but the pelagic *Microsetella norvegica*, was not found in any of the stomachs. The prey category small pelagic copepods

are merely containing small copepods, mostly *Acartia* sp.. The prey category large calanoida contains larger calanoid copepods of the genus *Calanus*. The smaller pelagic copepods and large calanoida are affected by advection of water masses, so their densities are not only dependent on the local conditions. Crustacea consists of prey that could be identified as crustacean, but were found to be in an overly digested condition to allow for further analysis. Examples of the 16 of the prey categories can be seen in Figure 13.

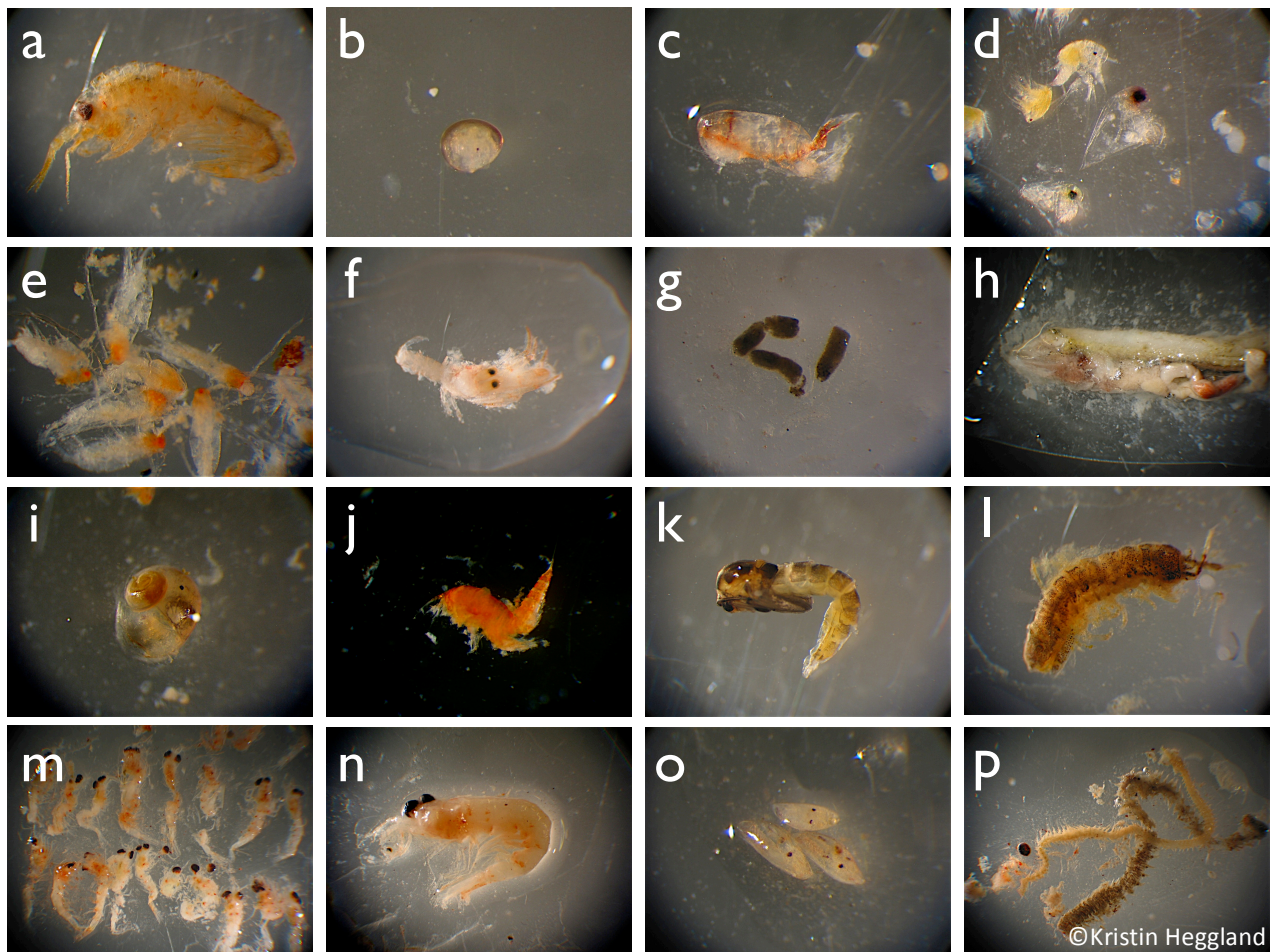


Figure 13. Pictures of 16 of the prey categories. a) amphipoda, b) bivalvia larvae, c) large calanoida, d) cladocera, e) small pelagic copepods, f) decapoda larvae, g) faecal pellet, h) fish, i) gastropoda, j) harpacticoida, k) insect, l) isopoda, m) krill, n) shrimp, o) ostracoda, p) polychaetae. Mysida and crustacea are not included since no picture was taken of them.

On average, the 0-group cod in IB had 4.8 (SE = 0.38) prey categories per fish, IP had 4.1 (SE = 0.47) prey categories per fish, and PP, had on average 2.4 (SE = 0.51) prey categories per fish (Figure 14). In PP, there was seen to be a significantly lower mean number of prey categories occurring in the individual 0-group cod's stomachs than in IB (t-test, $t = 4.70$, $df = 40.25$, $p = 0.023$) and in IP (t-test, $t = -4.45$, $df = 76.70$, $p = 0.019$). There is also no significant difference in mean number of prey categories consumed between IB and IP (t-test, $t = 1.23$, $df = 47.1$, $p = 0.23$) (Appendix D, E and F).

In the stomachs of the 0-group cod in IB 17 out of the 18 prey categories were found. The one prey category missing from IB was decapoda larvae that

were only found in PP. In IP 14 out of the 18 prey categories were be found, and the missing prey categories from IP are decapoda larvae, fish, krill and mysida. In PP 13 out of the 18 prey categories can be found, the missing prey categories are bivalvia larvae, faecal pellets, insect, isopoda and polychaetae.

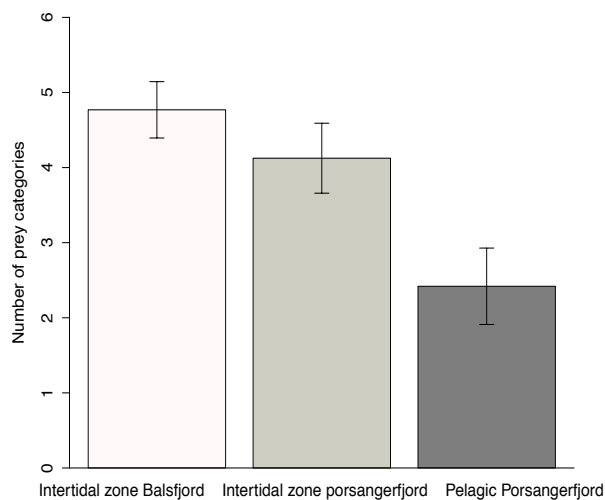


Figure 14. Mean number of prey categories occurring in the different habitats. Error bars show standard error of the mean values.

To express the distribution of prey categories between the habitats a Non-metric Multi Dimensional Scaling (NMDS) plot was made (Figure 15). The

points in the NMDS plot are representing the individual fish, and the lines are going towards the centroid of the individual fish's respective habitat. The centroid is the centre of a multivariate distribution; it is the mean of all the 0-group cod in the different habitats. The distance between the prey categories indicate how often prey categories are occurring in the same stomachs. The longer that distance the more rarely the prey categories were found in the same stomachs, whereas the shorter the distance between two prey categories the more frequent they were found in the same stomachs. The NMDS plot shows that the 0-group cod from IB and IP had similar diets consisting of a mixture of benthic (locally produced, e.g., harpacticoida) and pelagic prey categories (e.g., small pelagic copepods). In contrast, the diet in the pelagic in Porsangerfjord was characterised by prey categories that are affiliated with the pelagic. The only prey category that was unique to PP was the decapoda larvae. In the pelagic krill, shrimp and crustacean were typical prey categories found in the stomachs of the 0-group cod, whereas harpacticoida, isopoda, polychaetae and amphipods were the most typical prey found in the stomachs from the intertidal zones.

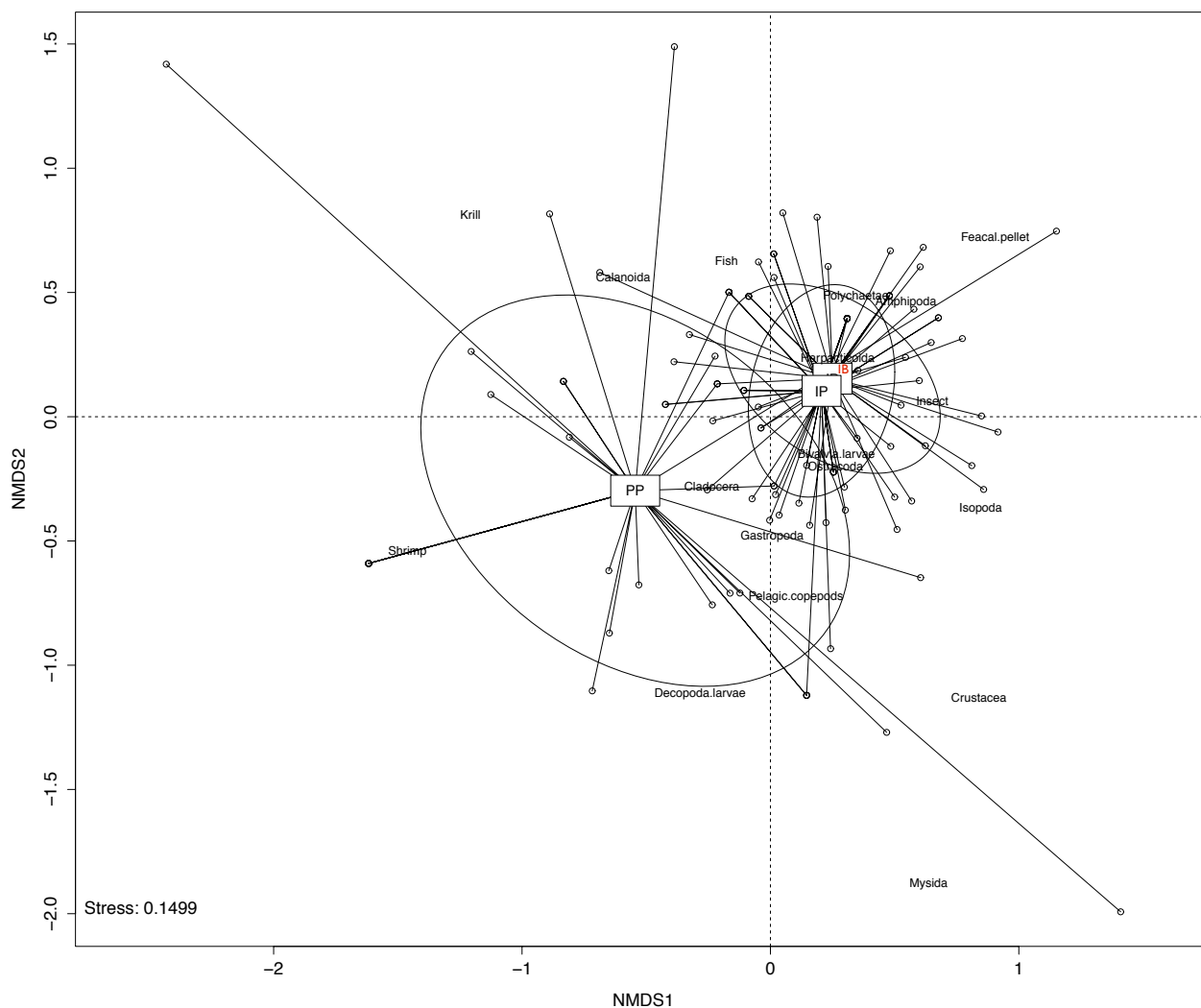


Figure 15. Kruskal’s Non-metric Multi Dimensional Scaling plot. Each point represents the combination of the diet of the individual fish. The ellipse is the standard deviations of the point scores of the weighed average scores. All the point has equal weight and the weighted correlation is defining the direction of the principal axis of the ellipse. The lines combine the individual observations from each habitat in to their respective centroid. The community data matrix is binary, to calculate the dissimilarity matrix the vegan package, and the metaMDS function in R was used. The distance is binary jaccard, and there are 2 dimensions. One outlier has been removed. IB: intertidal zone Balsfjord (n = 24), IP: intertidal zone Porsangerfjord (n = 49), PP: pelagic Porsangerfjord (n = 29).

The locally produced prey categories had the highest FO% in both IB and IP were harpacticoida, amphipoda, insect and polychaetae. IB had in addition; ostracoda, isopoda, bivalvia larvae and fish with a relatively high FO% (Figure 16 (a)). The pelagic prey categories with the highest FO% showed similar

patterns in all three habitats with cladocera, small pelagic copepods and large calanoida having the highest FO%. However FO%’s were higher for all pelagic prey categories in PP than in IB and IP. IB and IP had significant differences in FO% in 4 out of the 18 prey categories. IB and PP differ significantly in 6

out of 18 prey categories. IP and PP also differed significantly in 4 out of 18 prey categories (Appendix I). When comparing IB and IP, IB had significantly higher FO% of bivalvia larvae, fish, isopoda, krill ostracoda and polychaetae, whereas IP had significantly higher FO% of small pelagic copepods. Comparing IP and PP, PP had significantly higher FO% for large calanoida, krill and shrimp than IP. IP has significantly higher FO% of amphipoda, bivalvia larvae, harpacticoida, insect and polychaeta than PP. In general IP had more of the small prey categories than IB and PP. Table 1 and Appendix I provide a complete overview of all prey categories, which habitats that had a significant difference in FO%, accommodated by the χ^2 and p-values.

In terms of the estimated average biomass (mg) of the different prey categories per 0-group cod the heaviest prey groups were the most important one (Figure 19), the five most important species in terms of biomass in IB were fish (0.45 mg), krill (0.21 mg), harpacticoida (0.20 mg), isopoda (0.11 mg) and insect (0.08mg). In IP the five most important prey categories were harpacticoida (0.89 mg), insect (0.42 mg), shrimp (0.21 mg), amphipoda (0.15 mg) and pelagic copepods (0.12 mg). In PP the most important prey categories were shrimp (5.43 mg), fish (2.59 mg), pelagic copepods (1.72 mg), decapoda larvae (0.42 mg) and large calanoida (0.23 mg) (Figure 16(b)) and Appendix D, E and F).

Tab. 1 Overview of the prey categories that had significantly different frequency of occurrence in the various habitats. The plus (+) with abbreviation is the habitat with the highest occurrence. The minus (-) with is missing abbreviation tells from which of the habitats the prey category is missing. For complete list over all prey categories with χ^2 and p-values see Appendix I. IB: intertidal zone Balsfjord (n = 25), IP: intertidal zone Porsangerfjord (n = 49), PP: pelagic Porsangerfjord (n = 29).

Prey category	IB vs. IP	IB vs. PP	IP vs. PP
Amphipoda		+IB	+IP
Bivalvia larvae	+IB	-PP	-PP
Large calanoida			+PP
Small pelagic copepods	+IP	+PP	
Fish	-IP		-IP
Harpacticoida		+IB	+IP
Insect		-PP	-PP
Isopoda	+IB	+IB	
Krill	-IP		-IP
Ostracoda	+IB	+IB	
Polychaetae			-PP
Shrimp		+PP	+PP

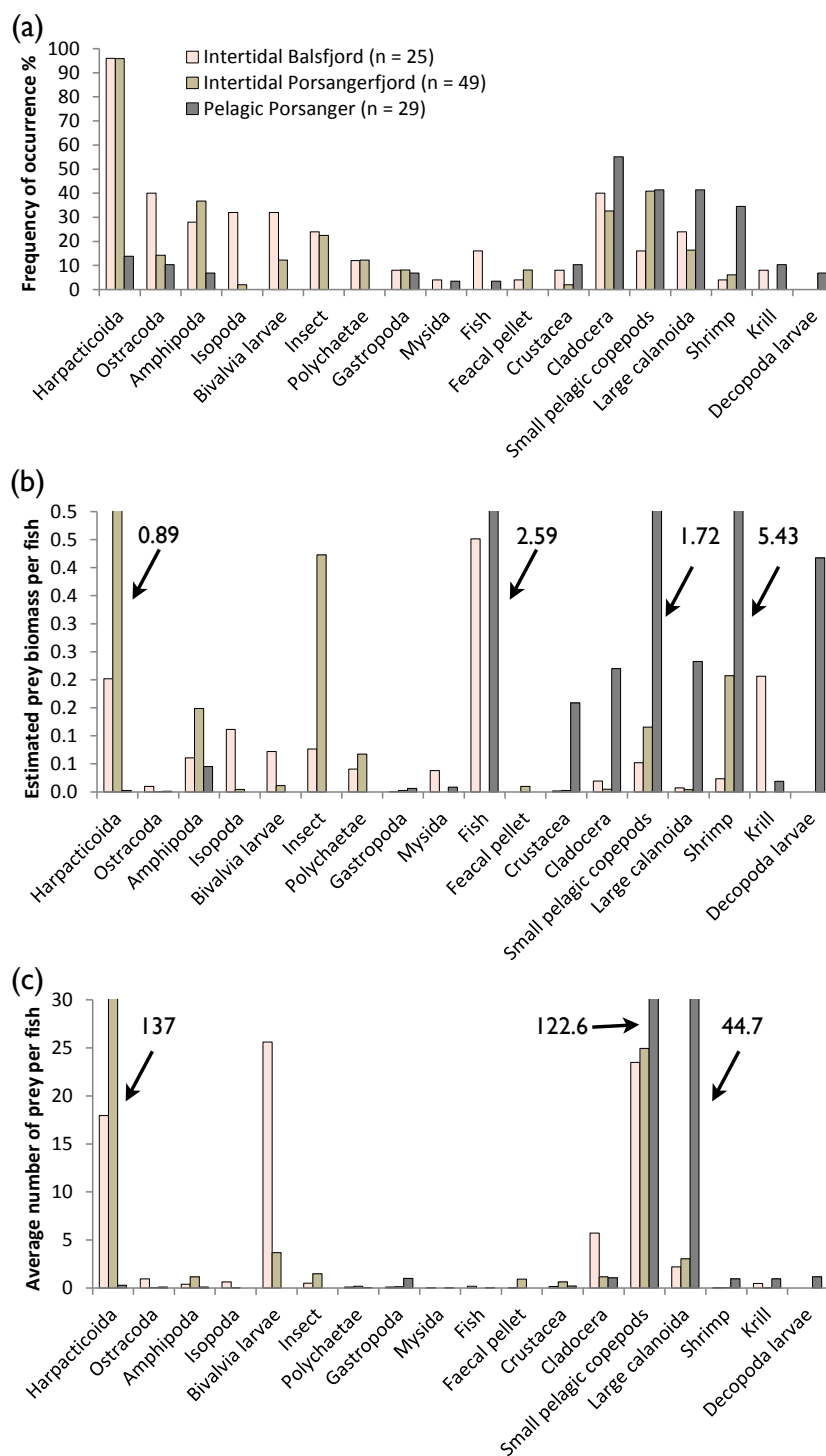


Figure 16. (a) Frequency of occurrence (FO%) of prey categories in the different habitats. The prey categories have been sorted descending from left to right, the most frequently occurring benthic prey categories (Harpacticoida – crustacea), and the most frequently occurring pelagic prey categories (Cladocera – decapoda larvae). (b) Estimated average prey weight per individual fish of the different prey categories in the three different habitats. The weight is in mg. (c) Average number of prey occurring per stomach in the three habitats.

Weight at length

To investigate if length-weight relationship was equal in the habitats a linear regression, with $\ln(\text{weight})$ as the dependent variable and $\ln(\text{fish length})$ as the independent variable was estimated (Figure 17). The analysis showed that all 0-group cod have a positive allometric growth ($\beta > 3$). The high multiple R^2 values, about 0.95 to 0.97, show that the models have a good fit to the data (Appendix J and K). There was no significant difference in the slopes (β) between the habitats, and a common slope of 3.19 have therefore been assigned to the regression to all habitats when testing for significance in intercept (α). The new model with common slope showed that there was a significant difference in intercept (α) between the habitats (Appendix N), where IB and PP have a significantly larger estimate for intercept than IP (IP vs. IB: $p = 0.007$, IP vs. PP: $p < 0.001$).

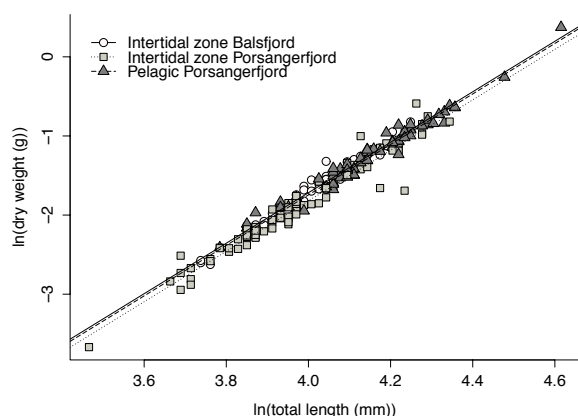


Figure 17. Linear regression between $\ln(\text{total length})$ and $\ln(\text{dry weight})$ for the intertidal zone in Balsfjord ($n = 46$), intertidal zone in Porsangerfjord ($n = 89$) and the pelagic in Porsangerfjord ($n = 64$). The regression lines have a common slope.

To illustrate the difference in height of the regression lines, the estimated dry weight at a given total length (mm) was found. The given length was the overall average total length for all habitats, which is 57 mm and $\ln(57)$ is 4.04. When comparing the estimated dry weights (g) of a 57 mm long fish in the three habitats, the 0-group cod from IP is 10.7 % lighter than a 0-group cod from IB, and 8.1 % lighter than a 0-group cod from PP (Figure 18 and Appendix P).

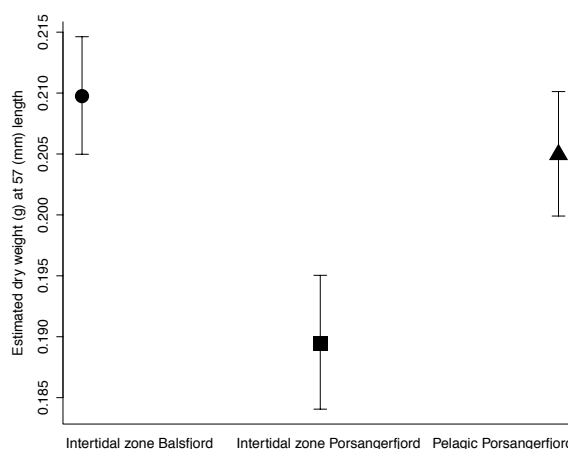


Figure 18. Estimated dry weight (g) at 57 (mm) length with 95 % confidence intervals. The estimates and confidence intervals have been back calculated (Appendix Q).

There was a significant difference in total length (mm) between IB and PP ($t = -5.18$, $df = 107.28$, $p = 0.007$), IP and PP ($t = -12.33$, $df = 133.47$, $p = 0.002$), with the 0-group cod from PP being larger than the fish from IB and IP. There was no significant difference in length between IB and IP ($t = 0.62$, $df = 123.32$, $p = 0.54$) (Appendix R and S).

Discussion

Vegetation and abundance of cod

In the present study the highest abundance of 0-group cod in the intertidal zone in Porsangerfjord were found at 60 – 80 % vegetation coverage. Abundance of juvenile fish have been found to be positively correlated with vegetation coverage, however this relation appears not to be linear but of parabolic nature (Michaelsen, 2012, Thistle et al., 2010, Carr, 1994). The parabolic relation between plant density and fish abundance has for kelp been explained by loss of complexity of the plant with increasing plant stem density (Carr, 1994). The loss of complexity may make the young fish more visible for visual predators, by which it may increase the rate of predation. In the present study the abundance of 0-group cod in the intertidal zone in Porsangerfjord was much higher than in previous years in the period 2008 - 2011. A further investigation of whether the relative high 0-group cod density can be explained by changes in presence of marcoalgae would be very interesting.

That there was a less pronounced high in density of 0-group cod in the intertidal zone of Balsfjord may be due to eelgrass being a habitat with

very high complexity. The height of the plants ranges from only a few cm to four meters and meadows may be patchy and the structure of the plants and the stem densities vary (Gotceitas et al., 1997, Williams and Heck Jr, 2001). Also when using the water scope to estimate the percent vegetation coverage it may be difficult to judge the structure and plants and the stem density of the eelgrass, it is therefore possible to question the accuracy of such a method to quantify the vegetation coverage. Gotceitas & Frasier (1997) found a relation between the plant stem density and the potential for an eelgrass patch as refuge from predators. If a location with low total vegetation coverage has patches with high stem densities and/or plants with high complexity, these areas may have the potential to support more or equal amounts of 0-group cod than an area with higher total vegetation coverage, but lower habitat complexity. This may explain the negative correlation between the density of 0-group cod and vegetation coverage in the intertidal zone in Balsfjord. Another plausible explanation for the negative correlation between density of 0-group cod and vegetation in Balsfjord may be the lack of stations which feature a low vegetation coverage. According to Thistle et al. (2010) there is a parabolic relationship between 0-group cod and vegetation coverage and that relationship is explained by predation pressure. In continuous eelgrass meadows the predation rate of 0-group cod will increase due to increased densities of predators as the vegetation coverage increases. Hence the density of 0-group cod will be reduced, relative to the intermediate eelgrass beds, which provides the parabolic relationship (Thistle et al., 2010). However, Gotceitas et al. (1997) found profound anti-predator avoidance behaviour in 0-group cod, it is therefore possible to suggest that the decline in smaller fish may be a combination of predator avoidance and increased predation pressure. The vegetation coverage in Balsfjord ranged from 35 - 85 %, where only one station has less than 50 % vegetation coverage. The theory of Thistle et al. (2010) that the predation rate and risk increases when the vegetation coverage goes above an intermediate level, this may explain the negative relation between density of 0-group cod and vegetation coverage observed in the intertidal zone in Balsfjord.

In addition to predation pressure, it is possible that abundance of available prey items may also have a regulatory effect the density of 0-group cod. A previous study has shown that in open sandy habitats, the density of potential prey will be lower, and the fish will be required to spend more time searching for food. Thus making habitats with no vegetation less profitable than habitats those with vegetation (Persson et al.,

2012). Vegetation is known to reduce the physical exposure of a site (Gotceitas et al., 1997), i.e., reducing the effect of currents and wave actions. If the vegetation coverage is very dense, there is potential for a reduction of current due to the presence of vegetation. This can have an inhibiting advection on pelagic zooplankton. Further, it can be speculated that at high reduction of currents the advection of zooplankton would be reduced to such a degree that it could lower the carrying capacity of an area. Also at areas of higher vegetative cover, the prey will have more structures to aid with concealment from potential predators and this may impact the foraging efficiency of a predator negatively. Adding the two scenarios together a similar parabolic relation as for predation pressure, may apply to the foraging efficiency of the 0-group cod.

When using the beach seine the area covered in each haul will not necessarily be the same between individual hauls, due to differences in slope of sampling locations. Due to the manual nature of hauling, the speed and duration of sampling with each haul will differ, thus resulting in a potential loss of samples by escape if hauled too slowly. The footrope of the beach seine has integrated led (as weight) to prevent it from floating to the surface. However, if the area morphology surveyed is complex, with high level of vegetation coverage the small fish may conceal themselves under the vegetation or disperse under rocks. 0-group cod has in a previous study been found to hide under stones to escape predators (Gotceitas et al., 1997) and the fish may also have the same reaction to the beach seine. Furthermore, the beach seine may be found to become immobilised due to snagging with rocks or other submerged objects whilst being hauled. In this instance the haul is paused for a short while, which can allow for fish to disperse away from the seine, resulting in loss of samples. All these factors may hamper the ability of the beach seine to give accurate estimates to the density of fish within the sampled area. A further limitation to the beach seine is that it has a depth limit of only 5 m depth. An alternative method that may be implemented in order to estimate densities of cod in relation to vegetation within the intertidal zone is that of video sampling. The advantage of this method is that is non-invasive, and can also be used at greater depth. In addition it can provide a more accurate estimate of the vegetation coverage than the water scope.

Although the correlations between vegetation coverage and density of 0-group cod in Balsfjord and Porsangerfjord differed, the underlying driving force behind the pattern observed may be the same. The difference in correlation may be caused by difference

in the distribution of percentage coverage between the two fjords.

Diet of 0-group cod in the different habitats

Cod is considered to be a generalist feeder (Norderhaug et al., 2005), and in the present study the observed differences in mean number of prey categories and frequency of occurrence of prey groups between the habitats are likely to reflect the available food resources in the habitats. Fish size will inflict constraints on the accessible prey in which to feed upon (Copeman et al., 2008), and diet will therefore also depend on fish size. However, 0-group cod from the intertidal zones in Balsfjord and Porsangerfjord were not significantly different in mean length, and thus the diet can be compared. Another potential source of error related to the difference in the rate of digestibility of the prey items. Soft-bodied prey items will dissolve faster than prey with hard exoskeleton and this may give underestimation of the quantity of certain prey items. Due to different sampling method the 0-group cod from the pelagic in Porsangerfjord and the intertidal in Balsfjord will not be compared.

The main difference in diet between the habitats could be seen most prominently between the pelagic and the intertidal zones. The 0-group cod from the pelagic zone were observed to have a higher FO% and estimated prey weight per fish of pelagic prey categories relative to the intertidal zones in Balsfjord and Porsangerfjord. The diet of 0-group cod in the intertidal zones in Balsfjord and Porsangerfjord had similar patterns, but there were some differences in FO% of individual prey categories. Bivalvia larve, isopoda, and ostracoda had significantly higher FO% in the intertidal zone in Balsfjord than the intertidal zone in Porsangerfjord. Small pelagic copepods had a significantly higher FO% in the intertidal zone in Porsangerfjord than in the intertidal zone in Balsfjord. In addition the 0-group cod from Balsfjord had a few prey categories not found in any of the stomachs from the intertidal zone in Porsangerfjord. This may reflect that there is a difference in the diet of 0-group cod in the three habitats. To reveal some of the differences in diet between the habitats some prey groups will be discussed individually.

That crustaceans was dominating in the diet in all habitats, is consistent with previous studies (Grant and Brown, 1998, Michaelsen, 2012, Wiborg, 1948a, Copeman et al., 2008). Copepods were found to be the most important in terms of FO% and also the average number of prey per fish. Harpacticoida showed the highest frequency of occurrence in the intertidal zones, whereas cladocerans closely followed by small pelagic copepods and large calanoida, had the highest

frequency of occurrence in the pelagic zone. Copepods has previously been reported to be numerous in the stomachs of 0-group cod but regarded to be of little significance due to their small size (Wiborg, 1949). However in the present study, small zooplankton (i.e., small pelagic copepods, large calanoida, and cladocera) and harpacticoida had a relatively high estimated prey biomass per fish in all habitats indicating that they are of significant importance. The importance of small zooplankton in the diet of juvenile cod has been acknowledged in various studies (Copeman et al., 2009, Grant and Brown, 1998, Copeman et al., 2008, Fjøsne and Gjøsæter, 1996). The fatty acids of copepods are considered to be important for growth and development of larval fish (Sargent et al., 1999). There has been observed a decline in lipid storage of juvenile cod when *Calanus* sp. is removed from the diet (Grant and Brown, 1999).

The diet data in the present study show that large calanoida (i. e., *Calanus* sp.) had low FO%, estimated prey biomass per fish, and average prey number per fish in the intertidal zones of Balsfjord and Porsangerfjord. The low presence of large calanoida in the diet of the 0-group cod from the intertidal zones in Balsfjord and Porsangerfjord was probably due to initiated diapause in *Calanus* sp. (Conover, 1988). However the 0-group cod from the pelagic in Porsangerfjord had relatively high amounts of large calanoida. This is consistent with Grant and Brown (1999), where it has been suggested that pelagic marine juvenile fish have access to lipid rich overwintering zooplankton throughout the winter (Grant and Brown, 1999).

The prey categories that were found only in the intertidal zones were; insects, isopoda, polychaetae, bivalvia larvae and faecal pellets. The insects were equally important in both fjords with regards to FO%. However, in terms of estimated prey biomass per fish and the average prey number per fish insects were observed to be much more important in the area of Porsangerfjord. As a terrestrial source the insect typically contains the shorter C₁₈ PUFA (Polyunsaturated Fatty Acid) that is of lower nutritional value than the longer PUFAs C₂₀ and C₂₂ (Sargent et al., 1999). In addition cold-water marine fish have a requirement for needs longer PUFAs in order to maintain their membrane fluidity (Cossins et al., 1977). Isopoda was only found in Balsfjord and polychaetae was fairly similar in FO%, estimated prey biomass per fish and average prey number per fish.

Bivalvia had the higher FO%, estimated prey biomass per fish and number of prey per fish in Balsfjord than in Porsangerfjord. In a previous study from Arendal, Norway, bivalvia larvae were not found

in the diet of 0-group cod (Fjøsne and Gjøsæter, 1996) however, in Newman Sound, Newfoundland Canada bivalvia veligers was found at relatively high proportions (Copeman et al., 2008). This may indicate that available prey items are more alike at locations with similar physical environment than locations one in northern and southern areas.

The fact that fish only, was found in the intertidal zone of Balsfjord and in the pelagic zone within Porsangerfjord may purely be a result of chance of catch, due to a previous study (Michaelsen, 2012) finding relatively high FO% of fish in the stomachs of 0-group cod in Porsangerfjord. However this study does not mention any details with regards to the size of the 0-group cod. Therefore, it might be of larger size, thus making it capable of utilizing larger prey than in the present study. To conclude; there is a difference in the diet between the habitats.

Body condition and habitats

The body condition, expressed as weight at length, is seen to vary between the habitats. This can be suggested as being in response to the quality and quantity of available food resources in their respective habitats. The body condition has been shown to reflect the lipid content of the diet of juvenile cod (Grant and Brown, 1999), and a decline in body condition is generally linked to reduction in quantity and/or quality of prey (Pedersen and Jobling, 1989). Grant and Brown (1999) found that when lipid rich preys such as *Calanus finmarchicus* was consumed the liver and muscle energy reserves increased rapidly. However, when the lipid rich prey was unavailable there was an abrupt decline in energy reserves.

The 0-group cod in the intertidal zone in Porsangerfjord had a significantly lower body condition (weight at length) in comparison to the 0-group cod in the intertidal zone in Balsfjord and in the pelagic in Porsangerfjord. In larval cod about 50 % of the lipid storage has been found to be structural phospholipids PL stored in the flesh (Ackman, 1989) in (Copeman et al., 2008). Copeman et al. (2008) found that after settlement the fish increased the utilization of PL, contributing to a decrease of lipids in the flesh. The decline of lipids was suggested to be a consequence of poor food quality. The food resources in the intertidal zone in Porsangerfjord can therefore be interpreted to be of lower quality than those in the intertidal zone in Balsfjord and also in the pelagic in Porsangerfjord.

In contrast to the present study Persson et al. (2012) found that the foraging profitability was the same between bladderwrack *Fucus vesiculosus* L. and eelgrass in peak season. Overall the macroalgal habitat

was the most profitable through seasons due to loss of biomass in eelgrass bed during the autumn and winter (Persson et al., 2012). The juvenile cod responds quickly to changes in quality and quantity of available food resources (Grant and Brown, 1999). An earlier study has shown that the quality of the diet of juvenile cod change with season (Copeman et al., 2009). Grant and Brown (1998) found a shift in the diet of 0-group cod from the higher lipid *Calanus* sp. in the summer to the smaller lipid prey items towards the winter in shallow waters. In addition to available prey, a seasonal change in the polyunsaturated fatty acids (PUFAs) in zooplankton and epibenthic prey has been observed. The proportion of C₁₈ PUFA increased relatively to C₂₀ and C₂₂ PUFAs from late summer to fall (Copeman et al., 2009). As previously mentioned the C₁₈ PUFA is shorter and has lower nutritional value than the longer PUFAs C₂₀ and C₂₂ typically found in marine zooplankton (Sargent et al., 1999, Falk-Petersen et al., 2009). This suggests that the food quality in general will decrease towards winter. Considering that the average temperature in Porsangerfjord was 2.5 °C lower than in Balsfjord, and keeping in mind that the overall foraging profitability was highest in the bladderwrack habitat in the study of Persson et al. (2012), the low body condition in the intertidal zone in Porsangerfjord, compared to the intertidal zone in Balsfjord may reflect that fall has progressed more in Porsangerfjord than in Balsfjord.

Another potential explanation for the difference in body condition between the intertidal zone in Balsfjord and Porsangerfjord may be reflected in the energy content of the prey categories consumed. Although the diet was fairly similar between the intertidal zones in the two fjords there were some differences, such as the high occurrence and biomass of insects in Porsangerfjord. As discussed previously, terrestrial sources of lipids such as insects, has lower energy content compared to food from the marine realm. Therefore filling their stomachs with insects will not be beneficial to the fish, when compared to prey items of marine origin. The prey categories of krill and fish, which can be assumed to have a high-energy content, was in terms of estimated prey biomass per fish was very important prey in the intertidal zone in Balsfjord but did not occur in the diet of the 0-group cod from the intertidal zone in Porsangerfjord at all. In addition isopods, which also are a relatively large prey item, had a significantly higher occurrence in the intertidal zone in Balsfjord than in the intertidal zone in Porsangerfjord. Thus to summarise, prey categories assumed to be rich in lipids had higher FO% and estimated prey biomass per fish in the intertidal zone in Balsfjord than in intertidal zone in Porsangerfjord.

Whereas one of the most important prey categories in terms of estimated prey biomass per fish in the intertidal zone in Porsangerfjord was assumed to have low quality lipids due to its terrestrial origin. Hence the body condition was observed to be lower for the 0-group cod in the intertidal zone in Porsangerfjord, when compared to the intertidal zone in Balsfjord. This is due to the nature of food of the 0-group cod in the intertidal zone in Balsfjord had a higher quality than that of the intertidal zone in Porsangerfjord.

The difference in body condition between the intertidal zone in Porsangerfjord and the pelagic in Porsangerfjord may be explained due to the pelagic 0-group cod having access to energy rich *Calanus* sp. and the additional prey items assumingly having a lower proportion of the less energy rich terrestrial C₁₈ PUFA (Copeman et al., 2009). This provides the 0-group cod in the pelagic with food recourses containing higher quality lipids, than those in the intertidal zone within Porsangerfjord.

The processes determining the body condition of juvenile cod are many and complex. In addition to what is discussed above other factors such as heredity and size and nutritional state of the mother are contributing factors to the growth and body condition of juvenile fish (Fuiman and Werner, 2009, Fevolden et al., 2012).

Summary

There is a correlation between the vegetation coverage and the abundance of 0-group cod. The highest abundance was found between 50 – 70 %, which is consistent with previous studied and imply that there is a nonlinear relationship between vegetation coverage and abundance of 0-group cod. There was found a difference in diet between the three habitats, with the intertidal zones of Balsfjord and Porsangerfjord having a diet significantly higher diversity than the 0-group cod in the pelagic zone of Porsangerfjord. The diet of the intertidal zones of Balsfjord and Porsangerfjord had a fairly similar composition, with a mixture of pelagic and bottom dwelling prey categories, whereas the diet of the cod in the pelagic zone had a dominance of pelagic prey categories. Body condition, expressed as weight at length, was different between the habitats. The 0-group cod from the intertidal zone from Porsangerfjord had significantly lower weight at length than that of the intertidal zone in Balsfjord and the pelagic in Porsangerfjord.

Acknowledgements

I would like to thank my supervisors Torstein Pedersen, Einar M. Nilssen and Nina Mari Jørgensen

for their guidance and advise. Also I would like to thank Emma Kallgren, Martin Andersen, Carl Ballentine and Therese Smelror Løkken for helping out in the lab. The crew on board R/R Johan Ruud for their assistance in sampling juvenile cod, and the manager at the museum in Balsfjord for lending out locations. Thanks to Eike Muller, Mikko Vihtakari, Mona Maria Fuhrmann, Jesper Andreas Kuhn and Martin Andersen for help with the R. Thanks to Gareth Lord for language check.

Software

R version 2.12.1 (2010-12-16) Copyright ©2010 The R Foundation for Statistical Computing ISBN 3-900051-07-0 Platform: x86_64-pc-mingw32/x64 (64-bit).

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Appendix A. Table showing the percent coverage of aquatic vegetation

St.	Habitat	Haul	Rock	<i>Ascophyllum nodosum</i>	<i>Fucus vesiculosus</i>	<i>Fucus serratus</i>	<i>Laminaria saccarina</i>	<i>Chorda phitum</i>	<i>One year algae</i>	<i>Zostera marina</i>	<i>Fucellaria lumbricalis</i>	Total % vegetation
1	IB	1	15.00	0.00	0.00	15.00	5.00	40.00	0.00	5.00	20.00	85
1	IB	2	15.79	0.00	0.00	15.79	36.84	10.53	0.00	5.26	15.79	84
2	IB	1	25.00	0.00	0.00	10.00	15.00	5.00	0.00	45.00	0.00	75
2	IB	2	15.00	0.00	0.00	30.00	30.00	0.00	0.00	25.00	0.00	85
3	IB	1	30.00	15.00	10.00	25.00	0.00	14.00	0.00	1.00	5.00	70
3	IB	2	35.00	15.00	10.00	23.00	0.00	10.00	0.00	2.00	5.00	65
4	IB	1	39.00	0.00	0.00	10.00	15.00	7.00	0.00	25.00	4.00	61
4	IB	2	45.00	0.00	0.00	10.00	0.00	5.00	0.00	20.00	20.00	55
5	IB	1	65.00	0.00	0.00	5.00	0.00	5.00	0.00	25.00	0.00	35
5	IB	2	70.00	0.00	0.00	0.00	0.00	20.00	0.00	10.00	0.00	30
6	IB	1	30.00	0.00	0.00	0.00	0.00	5.00	0.00	65.00	0.00	70
6	IB	2	40.00	0.00	0.00	0.00	0.00	5.00	0.00	55.00	0.00	60
7	IP	1	25.00	0.00	0.00	5.00	20.00	25.00	25.00	0.00	0.00	75
7	IP	2	40.00	0.00	0.00	5.00	20.00	20.00	15.00	0.00	0.00	60
9	IP	1	45.00	5.00	0.00	5.00	0.00	10.00	35.00	0.00	0.00	55
10	IP	1	30.00	0.00	0.00	0.00	0.00	20.00	50.00	0.00	0.00	70
10	IP	2	40.00	0.00	0.00	0.00	0.00	20.00	40.00	0.00	0.00	60
11	IP	1	30.00	0.00	0.00	5.00	10.00	20.00	35.00	0.00	0.00	70
11	IP	2	36.36	0.00	0.00	4.55	9.09	18.18	31.82	0.00	0.00	64
13	IP	1	20.00	5.00	0.00	5.00	0.00	30.00	40.00	0.00	0.00	80
13	IP	2	15.00	10.00	0.00	5.00	0.00	30.00	40.00	0.00	0.00	85
14	IP	1	30.00	0.00	0.00	10.00	0.00	30.00	30.00	0.00	0.00	70
14	IP	2	35.00	0.00	0.00	10.00	0.00	5.00	50.00	0.00	0.00	65
16	IP	1	87.76	1.02	3.06	2.04	0.00	3.06	3.06	0.00	0.00	12
16	IP	2	45.00	20.00	20.00	10.00	0.00	0.00	5.00	0.00	0.00	55

St.	Habitat	Haul	Rock	<i>Ascophyllum nodosum</i>	<i>Fucus vesiculosus</i>	<i>Fucus serratus</i>	<i>Laminaria saccharina</i>	<i>Chorda philum</i>	<i>One year algae</i>	<i>Zostera marina</i>	<i>Fucellaria lumbricalis</i>	Total % vegetation
17	IP	2	30.00	0.00	0.00	0.00	30.00	40.00	0.00	0.00	0.00	70
19	IP	1	50.00	0.00	10.00	10.00	0.00	20.00	10.00	0.00	0.00	50
19	IP	2	55.00	0.00	10.00	5.00	0.00	20.00	10.00	0.00	0.00	45
20	IP	1	79.00	1.00	10.00	10.00	0.00	0.00	0.00	0.00	0.00	21
20	IP	2	93.00	1.00	3.00	3.00	0.00	0.00	0.00	0.00	0.00	7
23	IP	1	60.00	0.00	0.00	0.00	0.00	30.00	10.00	0.00	0.00	40
23	IP	2	20.00	0.00	0.00	0.00	0.00	70.00	10.00	0.00	0.00	80

Appendix B. All stations sampled, displaying the station number, station name, how many cod have been obtained at each station, what the temperature (°C) was, at which date, at what time of the day and at which locations the samples have been obtained. BS: beach seine, PT: pelagic trawl.

Location	St.	St. name	Method	Nr. 0-gr. cod	Temp	Date	Time	Latitude	Longitude
Balsfjord	1	Skjeret	BS	1	13.2	07.08.2012	13:00	69 15`99``	1918`20``
Balsfjord	2	Mellaskjæret	BS	28	11.9	08.08.2012	23:40	6916`58``	1917`62``
Balsfjord	3	Sjåneset	BS	8	12.9	07.08.2012	14:45	6915`40``	1915`13``
Balsfjord	4	Holmenes	BS	166	13.1	09.08.2012	13:00	6915`55``	1915`29``
Balsfjord	5	Loddebukt	BS	69	12.1	08.08.2012	10:20	6914`06``	1922`79``
Balsfjord	6	Sørkjosen	BS	24	12.3	08.08.2012	13:30	6913`87``	1917`33``
Porsangerfjord	7	Kåfjord	BS	4	9.0	14.08.2012	08:55	7052`39``	2544`04``
Porsangerfjord	8	Repvåg	PT	12	10.6	14.08.2012	09:12	7054`90``	2543`84``
Porsangerfjord	9	Repvåg	BS	30	9.3	14.08.2012	15:05	7045`89``	2540`26``
Porsangerfjord	10	Ytre Svartvik	BS	87	9.0	14.08.2012	20:15	7044`65``	2540`24``
Porsangerfjord	11	Smørfjord	BS	185	9.8	15.08.2012	08:30	7031`82``	2505`76``
Porsangerfjord	12	Smørfjord	PT	84	9.8	15.08.2012	10:13	7032`90``	2512`72``
Porsangerfjord	13	Indre Billefjord	BS	44	11.1	15.08.2012	12:30	7019`10``	2505`03``
Porsangerfjord	14	Holmfjord	BS	137	10.2	16.08.2012	08:35	7021`90``	2527`95``
Porsangerfjord	15	Holmfjord	PT	14	11.1	16.08.2012	10:17	7022`76``	2525`23``
Porsangerfjord	16	Trollholmsund	BS	2	10.4	16.08.2012	11:35	7018`15``	2510`63``
Porsangerfjord	17	Reinøya øst	BS	88	9.2	16.08.2012	17:30	7016`07``	2520`30``
Porsangerfjord	18	Reinøya øst	PT	4	12.1	16.08.2012	19:14	7014`22``	2519`09``
Porsangerfjord	19	Handelsbukt	BS	2	9.9	17.08.2012	08:50	7005`37``	2512`68``
Porsangerfjord	20	Hattøya	BS	20	11.2	17.08.2012	11:00	7006`84``	2505`97``
Porsangerfjord	21	Østerbotn	PT	292	10.2	18.08.2012	12:36	7006`95``	2509`44``
Porsangerfjord	22	Østerbotn	PT	15	9.1	18.08.2012	08:33	7006`90``	2509`99``
Porsangerfjord	23	Rakkut	BS	38	9.0	18.08.2012	10:00	7014`77``	2517`79``
Porsangerfjord	24	Østerbotn	PT	992	10.1	18.08.2012	15:29	7007`33``	2511`25``

Appendix C. Spearman's Rank Order correlation coefficients assessing the degree of relationship between the number of cod found at station and haul and the percent coverage of aquatic vegetation. Because the pelagic does not have any vegetation correlation have not been tested for in PP. R-code: cor(vegetation, number of cod, method = "spearman", use = "everything"). IB: intertidal zone Balsfjord, IP: intertidal zone Porsangerfjord.

Habitat	n	% vegetation, #cod
IB	12	-0.6977164
IP	22	0.3817142

Appendix D. Table with prey categories showing weights, counts and frequency of occurrence in the intertidal zone in Balsfjord (n = 25).

Prey categories	#Prey that has been weighed	Total weight (µg)	Mean weight pr. prey (mg)	Total nr prey	Estimated biomass (mg)	Prey weight pr. fish (mg)	#Stomachs prey occur in	FO%
Amphipoda	5	0.76	0.15	10	1.52	0.06	7	28
Bivalvia larvae	623	1.75	0.00	640	1.80	0.07	8	32
Large calanoida	24	0.08	0.00	55	0.18	0.01	6	24
Cladocera	143	0.48	0.00	143	0.48	0.02	10	40
Small pelagic copepods	980	2.16	0.00	587	1.30	0.05	4	16
Decopoda larvae	0	0.00	0.00	0	0.00	0.002	0	0
Crustacea	2	0.02	0.01	4	0.04	0.08	2	8
Faecal pellet	0	0.00	0.00	1	0.00	0.00	1	4
Fish	5	11.29	2.26	5	11.29	0.45	4	16
Gastropoda	3	0.02	0.01	3	0.02	0.0006	2	8
Harpacticoida	417	4.68	0.01	449	5.04	0.20	24	96
Insect	13	1.92	0.15	13	1.92	0.08	6	24
Isopoda	13	2.27	0.17	16	2.79	0.11	8	32
Krill	12	5.16	0.43	12	5.16	0.21	2	8
Mycida	1	0.94	0.94	1	0.94	0.04	1	4
Ostracoda	16	0.17	0.01	24	0.25	0.01	10	40
Polychaetae	2	0.68	0.34	3	1.02	0.04	3	12
Shrimp	1	0.59	0.59	1	0.59	0.02	1	4

Appendix E. Table with prey categories showing weights, counts and frequency of occurrence in the intertidal zone in Porsangerfjord (n=49).

Prey categories	#Prey that has been weighed	Total weight (mg)	Mean weight pr. prey(mg)	Total nr prey	Estimated biomass (mg)	Prey weight pr. fish (mg)	#Stomachs prey occur in	FO%
Amphipoda	24	3.07	0.13	57	7.30	0.15	18	37
Bivalvia larvae	181	0.55	0.00	181	0.55	0.01	6	12
Large calanoida	36	0.05	0.00	149	0.20	0.004	8	16
Cladocera	57	0.23	0.00	57	0.23	0.005	16	33
Small pelagic copepods	1175	5.44	0.00	1222	5.66	0.12	20	41
Decopoda larvae	0	0.00	0.00	0	0.00	0.00	0	0
Crustacea	31	0.11	0.00	31	0.11	0.002	1	2
Faecal pellet	23	0.24	0.01	46	0.48	0.01	4	8
Fish	0	0.00	0.00	0	0.00	0.00	0	0
Gastropoda	7	0.13	0.02	7	0.13	0.003	4	8
Harpacticoida	6070	39.27	0.01	6726	43.51	0.89	47	96
Insect	72	20.43	0.28	73	20.71	0.42	11	22
Isopoda	1	0.21	0.21	1	0.21	0.004	1	2
Krill	0	0.00	0.00	2	0.00	0.00	0	0
Mycida	0	0.00	0.00	0	0.00	0.00	0	0
Ostracoda	15	0.24	0.02	3	0.05	0.001	7	14
Polychaetae	2	0.73	0.37	9	3.31	0.07	6	12
Shrimp	2	6.78	3.39	3	10.17	0.21	3	6

Appendix F. Table with prey categories showing weights, counts and frequency of occurrence in the pelagic in Porsangerfjord (n = 29).

Prey categories	#Prey that has been weighed	Total weight (mg)	Mean weight pr. prey (mg)	Total nr prey	Estimated biomass (mg)	Prey weight pr. fish (mg)	#Stomachs prey occur in	FO%
Amphipoda	3	1.31	0.44	3	1.31	0.05	2	7
Bivalvia larvae	0	0.00	0.00	0	0.00	0.00	0	0
Large calanoida	1294	6.74	0.01	1295	6.74	0.23	12	41
Cladocera	31	6.05	0.20	31	6.05	0.22	16	55
Small pelagic copepods	3556	49.90	0.01	3556	49.90	1.72	12	41
Decopoda larvae	34	12.10	0.36	34	12.10	0.42	2	7
Crustacea	11	8.44	0.77	6	4.60	0.16	3	10
Feacal pellet	0	0.00	0.00	0	0.00	0.00	0	0
Fish	1	75.13	75.13	1	75.13	2.59	1	3
Gastropoda	29	0.18	0.01	29	0.18	0.01	2	7
Harpacticoida	8	0.06	0.01	9	0.07	0.003	4	14
Insect	0	0.00	0.00	0	0.00	0.00	0	0
Isoopoda	0	0.00	0.00	0	0.00	0.00	0	0
Krill	28	0.55	0.02	28	0.55	0.02	3	10
Mycida	1	0.24	0.24	1	0.24	0.01	1	3
Ostracoda	3	0.03	0.01	3	0.03	0.001	3	10
Polychaetae	0	0.00	0.00	2	0.00	0.00	0	0
Shrimp	22	123.82	5.63	28	157.59	5.43	10	34

Appendix G. A Welch Two Sample t-test assuming separate variances was used to test if there was a difference in average number of prey categories in cod juvenile stomachs between IB IP and PP. The degrees of freedom (df) are a function of the difference in the variance. $t.test(BC(habitat_1), BC(habitat_2))$. IB: intertidal zone Balsfjord (n = 26), IP: intertidal zone Porsangerfjord (n = 48), PP: pelagic Porsangerfjord (n = 33).

	t	df	p-value	Confidence interval 95%	
				Lower	Upper
IB-IP	1.23	47.1	0.227	-0.41	1.70
IB-PP	4.70	40.25	0.023	1.33	3.37
IP-PP	4.45	76.67	0.019	-2.47	-0.94

Appendix H. Chi-square test; testing the if occurrence of the different prey groups are the same between the habitats. $\chi^2 = (\text{observed values} - \text{expected values}) / \sqrt{\text{expected values}}$. Df=2, (n rows-1)*(n columns-1). The expected proportion is estimated from the observed proportions. The rows with shading are the prey categories that overall do not have different proportions of the given prey category, between the habitats.

Prey category	χ^2	p-value
Amphipoda	12.58	0.0147
Bivalvia larvae	12.63	0.0018
Large calanoida	10.57	0.0051
Cladocera	13.90	0.0010
Small copepods	13.44	0.0012
Decapoda larvae	8.71	0.0129
Crustacea	6.23	0.0445
Faecal pellet	6.23	0.0444
Fish	12.38	0.0021
Gastropoda	3.81	0.1487
Harpacticoida	56.10	0.0000
Insect	17.07	0.0002
Isopoda	20.87	0.0000
Krill	8.42	0.0148
Mysida	6.09	0.0476
Ostracoda	9.75	0.076
Polychaetae	7.19	0.0274
Shrimp	16.65	0.0002

Appendix I. Chi-square test; pairwise testing of H_0 : equal proportions of prey categories between the habitats. $X^2 = (\text{observed values} - \text{expected values}) / \sqrt{\text{expected values}}$. $Df=1$, $(n \text{ rows}-1) * (n \text{ columns}-1)$. The expected proportions are estimated from the observed proportions. The rows with shading are the prey categories that overall have different proportions of the given prey category, between the habitats. IB: intertidal zone Balsfjord ($n = 25$), IP: intertidal zone Porsangerfjord ($n = 49$), PP: pelagic Porsangerfjord ($n = 29$).

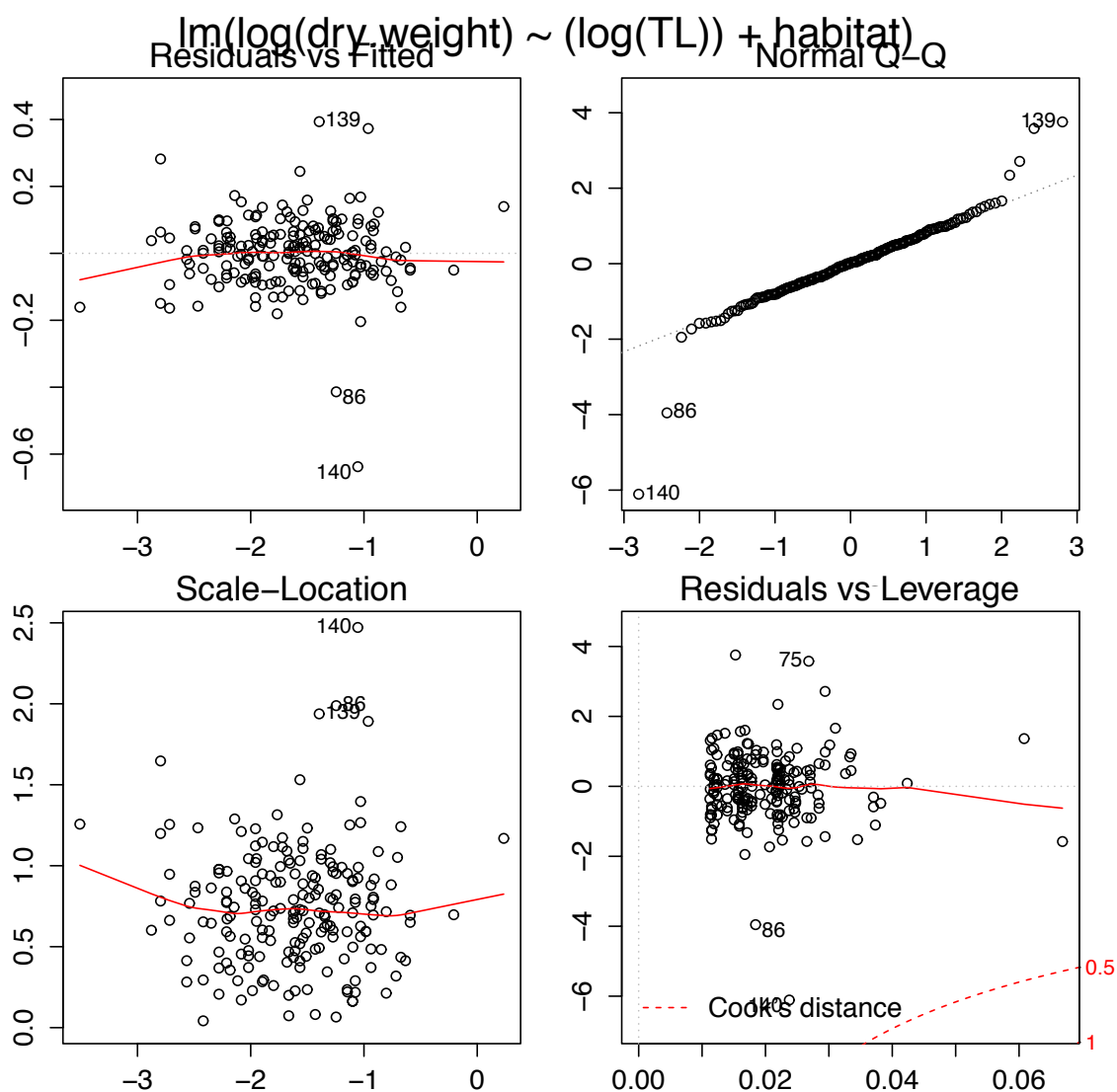
Prey category	IB-IP		IB-PP		IP-PP	
	X^2	p	X^2	p	X^2	p
Amphipoda	0.56	0.4524	4.31	0.0380*	8.51	0.0035*
Bivalvia larvae	4.21	0.0401*	10.89	0.0010**	3.85	0.0498*
Large calanoida	0.64	0.4254	1.82	0.1767	6.00	0.0143*
Cladocera	0.39	0.5312	1.24	0.2659	3.82	0.0507
Small copepods	4.65	0.0310*	4.15	0.0417*	0.00	0.9610
Decapoda larvae	-	-	1.79	0.1809	3.47	0.0626
Crustacea	1.51	0.2189	0.09	0.7669	2.58	0.1081
Feacal pellet	0.46	0.4998	1.18	0.2770	2.50	0.1142
Fish	8.29	0.0040**	2.52	0.1126	1.17	0.1908
Gastropoda	0.00	0.9806	0.02	0.8773	0.04	0.8392
Harpacticoida	0.00	0.9866	36.34	<0.0001***	54.29	<0.0001**
						*
Insect	0.02	0.8808	7.83	0.0051**	7.58	0.0059**
Isopoda	13.91	0.0002***	10.89	0.0010**	0.60	0.4388
Krill	4.03	0.0447*	0.09	0.7669	5.27	0.0217*
Mysida	1.99	0.1587	0.01	0.9148	1.71	0.1908
Ostracoda	6.19	0.0129*	6.46	0.0110*	0.25	0.6149
Polychaetae	0.00	0.9757	3.68	0.0549	3.85	0.0498*
Shrimp	0.15	0.7025	7.69	0.0055**	10.55	0.0012**

Significance codes: * < 0.05, ** 0.01 < p < 0.005, *** 0.001 < p < 0.01

Appendix J. Regression statistics for the three habitats. Model: $\ln(\text{dry weight}) = \alpha + \ln(\text{total length})$. Multiple R^2 gives information about how much of y (dry weight (g)) that can be explained by x (total length (mm)), the closer the R^2 is to one, the better the model fits the data. IB: intertidal zone Balsfjord, IP: intertidal zone Porsangerfjord, PP: pelagic Porsangerfjord.

	n	Estimate (α)	Slope (β)	Residual std. error	Multiple R^2	F-statistic	Df1/df2	P-value
IB	46	-15.00	3.32	0.0747	0.97	1287	1/44	$<2e^{-16}$
IP	89	-14.63	3.21	0.1306	0.95	1673	1/87	$<2e^{-16}$
PP	64	-14.16	3.11	0.0825	0.97	2069	1/62	$<2e^{-16}$

Appendix K. The body condition is the residuals of the linear regressions. The plots show the distribution of the residuals from the log-linear regression model. From the Q-Q plot one can see that the residuals are normally distributed. In the Residual vs Fitted and Scale location plot one can see that there is no patterns in the distribution of the residuals. And in the Residual vs Leverage plot one can see that none of the residuals have to influential outliers. The results from the diagnostics plot will allow us to continue the analysis of the length-weight relationship using parametric methods.



Appendix L. Test statistic from linear model ($\ln(\text{dry weight}) = \text{habitat} + \beta \ln(\text{total length})$), there no difference in slope (β) between the habitats. R-code: `lm(ln(dry weight)~log(total length)*habitat)`. Residual standard error: 0.1050 on 193 degrees of freedom. Multiple R^2 : 0.9667, F-statistic: 1119 on 5 and 193 degrees of freedom, p : $2.2e^{-16}$. IB: intertidal zone Balsfjord (n = 46), IP: intertidal zone Porsangerfjord (n = 89), PP: pelagic Porsangerfjord (n = 64).

	Slope (β)
IB-IP	P = 0.420
IB-PP	P = 0.175
IP-PP	P = 0.370

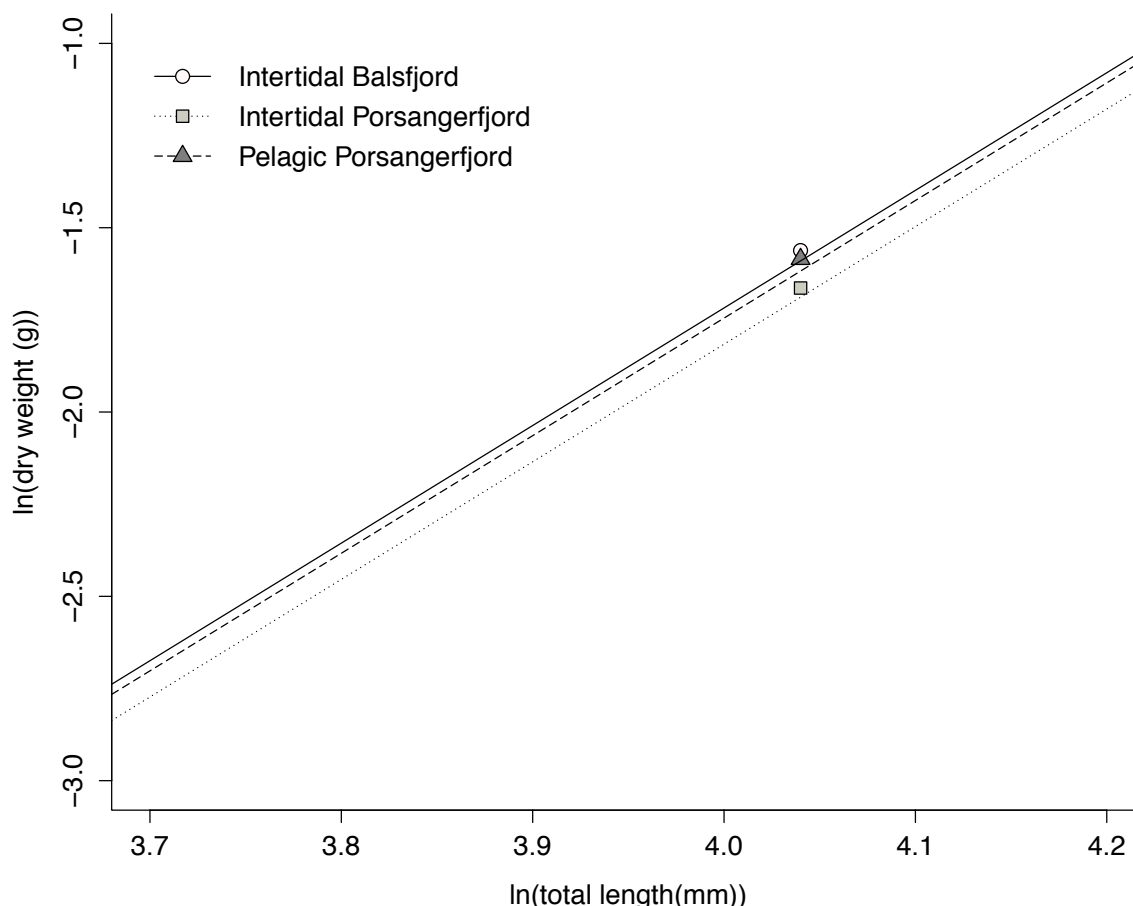
Appendix M. Linear model ($\ln(\text{dry weight}) = \text{habitat} + \beta \ln(\text{total length})$), with common slope (β). R-code: `lm(ln(dry weight)~ln(total length)+habitat)`. P-value: testing the H_0 of no dependence of length on the weight of the 0-group cod. IB=intertidal zone Balsfjord, IP=intertidal zone Porsangerfjord, PP=pelagic Porsangerfjord.

	n	Estimate (α)	Slope (β)	Residual std. error	P-value
IB	46	-14.47764	3.19	0.0747	$<2e^{-16}$
IP	89	-14.57598	3.19	0.1306	$<2e^{-16}$
PP	64	-14.50516	3.19	0.0825	$<2e^{-16}$

Appendix N. Testing the intercept (α) with common slope. R-code: `lm(ln(dry weight)~ln(total length)+habitat)`. Residual standard error: 0.1056 on 195 degrees of freedom. Multiple R^2 : 0.9663, F-statistic: 1865 on 3 and 195 degrees of freedom, $p < 2.2e^{-16}$. IB=intertidal zone Balsfjord (n=46), IP=intertidal zone Porsangerfjord (n=89), PP=pelagic Porsangerfjord (n=64).

	p-value
IB-IP	0.007
IB-PP	0.2
IP-PP	0.0002

Appendix O. Regression lines with estimated dry weight (g) at given total length (mm) for the three habitats. The length is 57 mm [ln(4.04)], and the expected dry weight (g) is 0.2097, 0.1895 and 0.2049 in IB, IP and PP respectively (Appendix G). There is a significant difference in intercept (α), where the regression lines of IB and PP are significantly higher than IP (Appendix D1). IB: intertidal zone Balsfjord (n = 46), IP: intertidal zone Porsangerfjord (n = 89), PP: pelagic Porsangerfjord (n = 64).



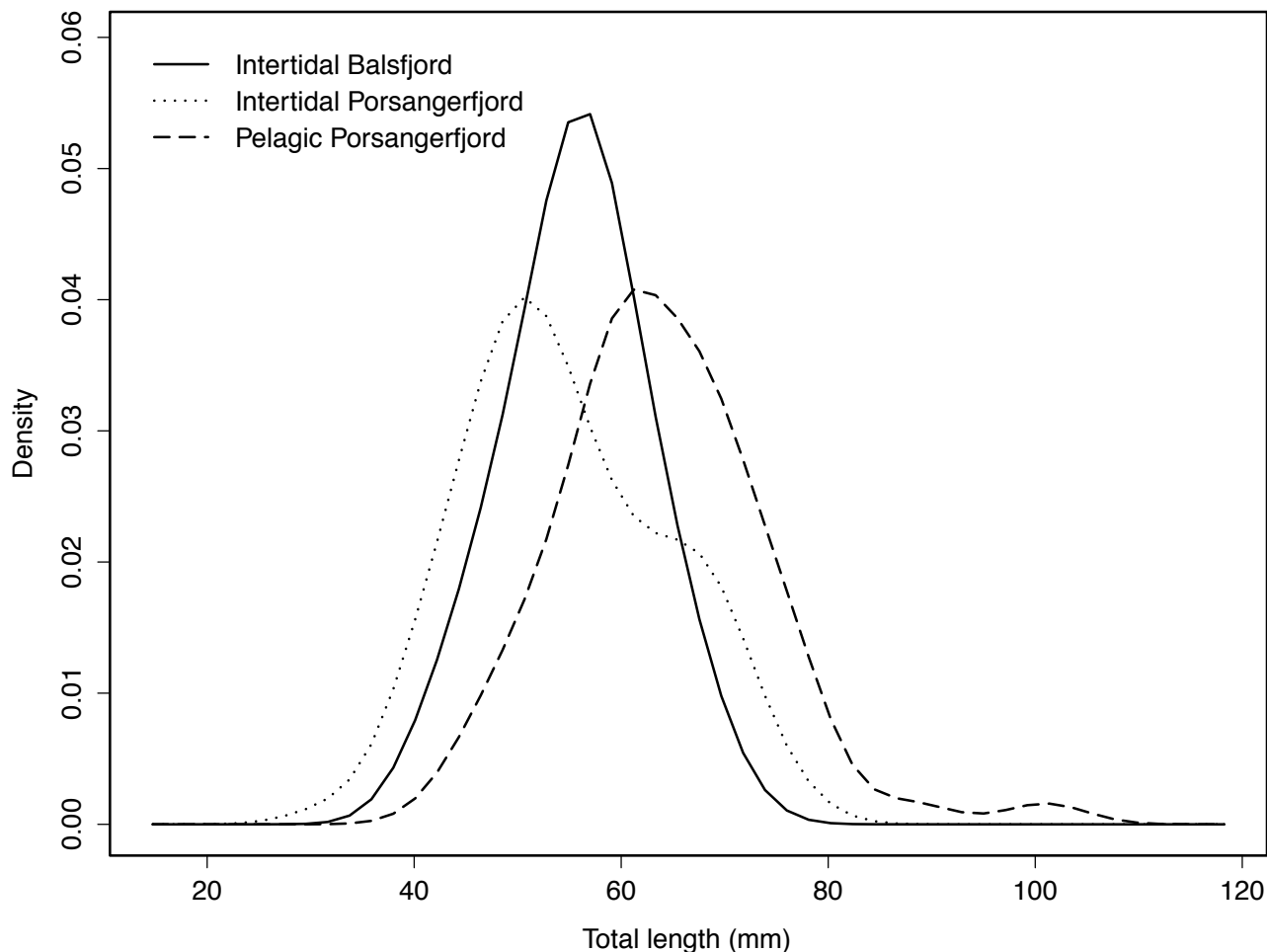
Appendix P. Percent difference in estimated weights (g) at 57 (mm) length, between the habitats. Smaller than= (smaller fish-larger fish)/smaller fish*100. IB=intertidal zone Balsfjord, IP=intertidal zone Porsangerfjord, PP=pelagic Porsangerfjord.

Comparisons	Percent difference
IP smaller than IB	10.66
IP smaller than PP	8.13
PP smaller than IB	2.34

Appendix Q. Estimated ln(weight) at given length (57mm, ln: 4.04), for the three different habitats. Fit is the estimated ln(weight). IB=intertidal zone Balsfjord, IP=intertidal zone Porsangerfjord, PP=pelagic Porsangerfjord.

Habitat	Length (mm)	ln(estimated weight)	Estimated weight (g)	Confidence interval 95%	
				Lower	Upper
IB	57	-1.5619	0.2097	-1.5849	-1.5389
IP	57	-1.6636	0.1895	-1.6925	-1.6346
PP	57	-1.5850	0.2049	-1.600	-1.5601

Appendix R. Comparative Kernel density plot of length distribution between the habitats. The area under the curve is the same in all habitats, showing the relative length distribution within each habitat. The sm package in R was used to create the plot. R-code: `sm.density.compare(total length, habitat)`.



Appendix S. A Welch Two Sample t-test assuming separate variances was used to test if there was a difference in total length (mm) between IB IP and PP. The degrees of freedom (df) are a function of the difference in the variance. R-code: `t.test(total length(habitat1), total length(habitat2))`. IB: intertidal zone Balsfjord (n = 46), IP: intertidal zone Porsangerfjord (n = 89), PP: pelagic Porsangerfjord (n = 64).

	t	df	p-value	Confidence interval 95%	
				Lower	Upper
IB-IP	0.62	123.32	0.538	-1.911	3.65
IB-PP	-5.28	107.28	0.007	-11.40	-5.18
IP-PP	-5.70	133.47	0.002	-12.33	-5.98

Appendix T. Comparative Kernel density plot of weight distribution between the habitats. The area under the curve is the same in all habitats, showing the relative length distribution within each habitat. The sm package in R was used to create the plot; `sm.density.compare(total length, habitat)`.

