UNIVERSITETET I TROMSØ UIT

FACULTY OF BIOSCIENCES, FISHERIES AND ECONOMICS
DEPARTMENT OF ARCTIC AND MARINE BIOLOGY

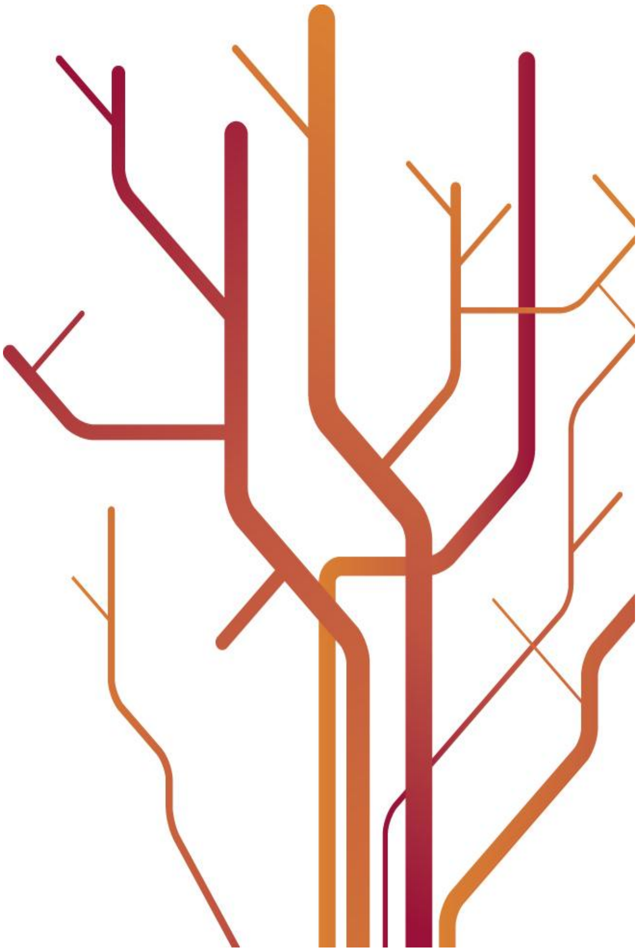
Population dynamics, diet and trophic positioning of three small demersal fish species within Porsangerfjord, Norway

Emma Katarina Källgren

Master's thesis in Marine Ecology

BIO-3950 (60p)

November 2012



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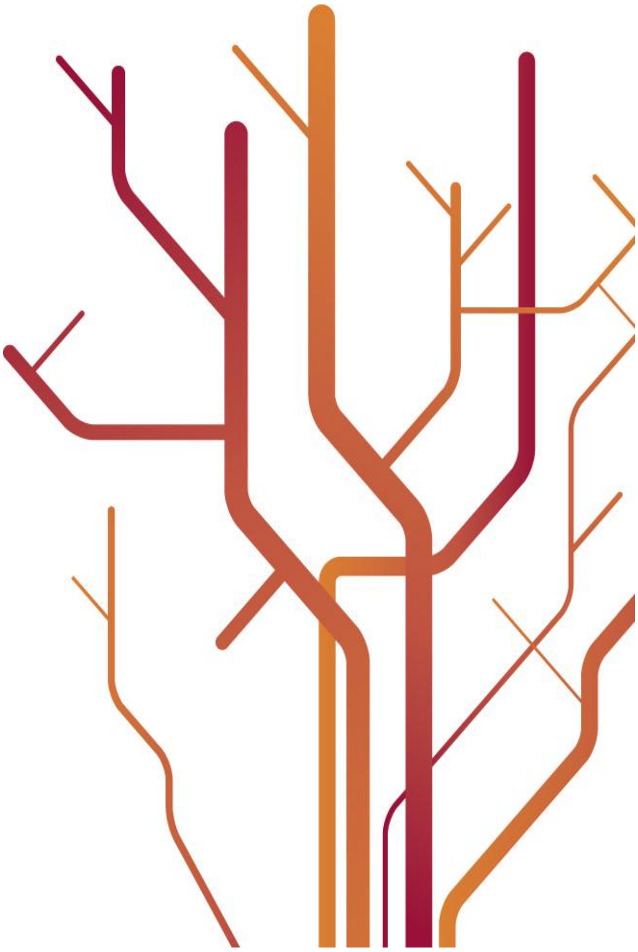

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Tromsø, November 2012

Emma Källgren

SUMMARY

In today’s society, one often stumbles over the quote “you are what you eat”. Diet is closely related to fish size and physical conditions, so in order to understand the food web one must first understand the population dynamics of the fish. Three demersal species in the northern hemisphere are; *Artediellus atlanticus*, *Myoxocephalus scorpius* and *Leptagonus decagonus*. The study was undertaken in 2009-2011, within the inner basin of Porsangerfjord (70°N 25°E) through the project ‘Ecological Processes and Impacts Governing the Resilience and Alternations in the Porsangerfjord and Hardangerfjord’. The study objectives were to provide basic information about these species population dynamics and feeding ecology. The length distribution varied between both sex and species, whereas the age structure was the same. The growth were different for *L. decagonus* but not for *A. atlanticus* and *M. scorpius*. The dominant prey found in *A. atlanticus* was Polychaeta, whereas *M. scorpius* fed on fish, and *L. decagonus* had fed on Copepoda. Correlations were found within the species diets, but not between any of these species. The stable isotope analysis showed that *L. decagonus* had a pelagic related diet whereas the *A. atlanticus* had a benthic related diet and *M. scorpius* demonstrated a mixed benthic-pelagic diet signature. The study found that the three species had different diets but similar trophic positions. Thus, indicating that they had individual food chains within the food web of inner Porsangerfjord.

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INTRODUCTION

Background

In today's society, one often stumbles over the quote "you are what you eat". This is well known within the scientific community, as many methods for investigating trophic interactions utilises different diet analyses. Predator-prey relationships shape the community, and knowledge about these interactions can broaden the understanding of the systems (Siversten et al., 2006). By establishing who eats who and the trophic positioning of the species the interactions within that food web become evident (Parrish, 1975; Wootton, 1998). Understanding the dynamics operating between trophic relationships is fundamental for increased scientific knowledge and management (Ahlbeck et al., 2012). Diet is closely related to fish size and their physical conditions, so in order to understand the connections within the system one must first understand the development and growth patterns of the fish species in question.

A good way to start analysing a species is to evaluate the weight-length relationship, which provides useful information about the fish's development. Secondly, by estimating the age structure of the fish from otolith readings and combining this with the weight-length relationship information, the first clues about the species population dynamics will become apparent (Bartoo & Parker, 1983). Thirdly, excess energy acquired by the fish from its diet is incorporated into new tissue and have one of these three fates; structural tissue (e.g. liver), visceral fat or gametes (Wootton, 1998). The liver is used by many teleosts as the primary storage of excess energy in the form of lipids. Therefore, the liver indicates the energy reserves available to the fish and makes it possible to directly evaluate the nutritional history through the Hepatosomatic Index (HSI) (Lambert & Dutil, 1997). Finally, reproduction is costly for the individual and the age at first maturity have generally been found to be a function of size rather than age (Parrish, 1975). By analysing the species onset of reproduction through sexual maturity, estimations such as the Gonadosomatic Index (GSI) can further broaden the knowledge about the population dynamics (Wootton, 1998).

Stomach analysis is a common approach to study diet through prey choice since the method provides direct information about the interactions between both predators and prey (Siversten et al., 2006). However, this method is limited as it only provides a ‘snapshot’ of the prey ingested by the species within the recent timeframe prior to capture (Wootton, 1998). Stable isotope analysis on the other hand investigates the isotopic signatures of stable carbon (^{13}C) and nitrogen (^{15}N) from the digested prey over time for traces that are stored within the predator’s tissues (Peterson & Fry, 1987). Fish are relatively long-lived consumers with tissue turnover rate ranging from months to years (Post, 2002; Fukumori et al., 2008). The turnover rate in long-lived consumers is commonly slower and less variable within its isotopic composition compared to short-lived consumers (Tiezen et al., 1983). Although, the signature enrichment is species-specific in stable isotopic data, it also depends on the local and environmental conditions (Nilsen et al., 2008; Xu et al., 2011). The ratio of the stable isotopes, carbon and nitrogen, can differ between pelagic and benthic habitats, where primary consumers feeding within the pelagic habits have been found to be more depleted in heavy isotope signatures compared to consumers feeding from the benthic environment (Post, 2002). Thus a combination of stomach content analysis and the stable isotope approach will yield information both on the short term and long term feeding habits of the species.

Although our understanding of the oceanic and coastal environments continues to advance, the research has been heavily skewed towards commercially important species and single species predatory-prey relationships (Klemetsen, 1982). In modern research all species that play an important role within an ecosystem are emphasised and the objectives have shifted from species based research towards ecosystem based research and management (Byrkjedal & Høines, 2007; Ramsvatn & Pedersen, 2012).

The species

Within both arctic and boreal waters all around the northern hemisphere three small demersal fish species (*Artediellus atlanticus, Myoxocephalus scorpius* and *Leptagonus decagonus*) with no commercial value are commonly encountered (Andriyashev, 1964; Mecklenburg et al., 2002) (Figure 1). All three species belongs to the taxonomical order; Scorpaeniformes which consists of 25 families and 266 genera (Wootton, 1998). Searching within the published literature for information on these species provided relatively little material, yet most of which could be attained came from the Russian author Andriyashev during the 1950s.

Artediellus atlanticus Jordan & Evermann, 1898

In Norway the Atlantic hookear sculpin goes by the common name 'krokulke' and belongs to the family Cottidae. *Artediellus atlanticus* has a depth range between 35-410 m, but is frequently encountered at depth around 150-350 m (Andriyashev, 1964). It is regarded as an arctic species and grows to a maximum length of about 15 cm (von Dorrien, 1993). This species prefer finer sediments such as mud where it predominately feeds on different polychaets and at times, small molluscs and crustaceans (Andriyashev, 1964; Pethon, 2005).

Myoxocephalus scorpius (*Linnaeus, 1758)*

Short horn sculpin or 'vanlig ulke' as the species is referred to in Norway, is the second species that belongs to the family Cottidae. *Myoxocephalus scorpius* is a widespread species in shallow arctic and boreal waters in the northern hemisphere (Mecklenburg et al., 2002). The species is commonly encountered at depths shallower than 25 m, but have been found on rare occasions at depths down to 250 m (Andriyashev, 1964). However, in Alaskan waters the species has been captured at a depth of 550 m (Mecklenburg et al. 2002). It grows to a maximum length of 60 cm, but is normally no longer than 30 cm on the eastern side of the Atlantic. *Myoxocephalus scorpius* prefers coarser sediment, such as sand mixed with mud and stony bottoms which are suitable for these opportunistic ambush predators (Andriyashev, 1964). The diet consists mostly of juvenile fish and large crustaceans, and to a much lesser extent polychaets and amphipods (Andriyashev, 1964; Pethon, 2005).

Leptagonus decagonus (*Bloch & Schneider, 1801*)

In Norwegian the species is called 'tiskjegg', but is known as the Atlantic poacher in English. It belongs to the family Agonidae and differs from the Cottidae as this species is completely covered with bony plates (Mecklenburg et al., 2002). The fish prefers deeper waters (150-1475 m) (Pethon, 2005) with individuals being rarely found at depths shallower then 100 m in the Atlantic Ocean (Andriyashev, 1964). However, in the Chuckchi and Bering seas individuals of this species have been found in depths as shallow as 24 m (Mecklenburg et al. 2002). *Leptagonus decagonus* inhabits muddy sediments mixed with sand and stones. This predator grows to a maximum length of 21 cm and retains a diet thought to consist of mainly small crustaceans, such as copepods, but also on rare occasions benthic crustaceans and polychaets (Andriyashev, 1964; Pethon, 2005).

Due to the range of common names acquired by species around the world, the scientific names will be used herein to address the species and thus, abbreviated as follow: *A. atlanticus, M. scorpius* and *L. decagonus.*

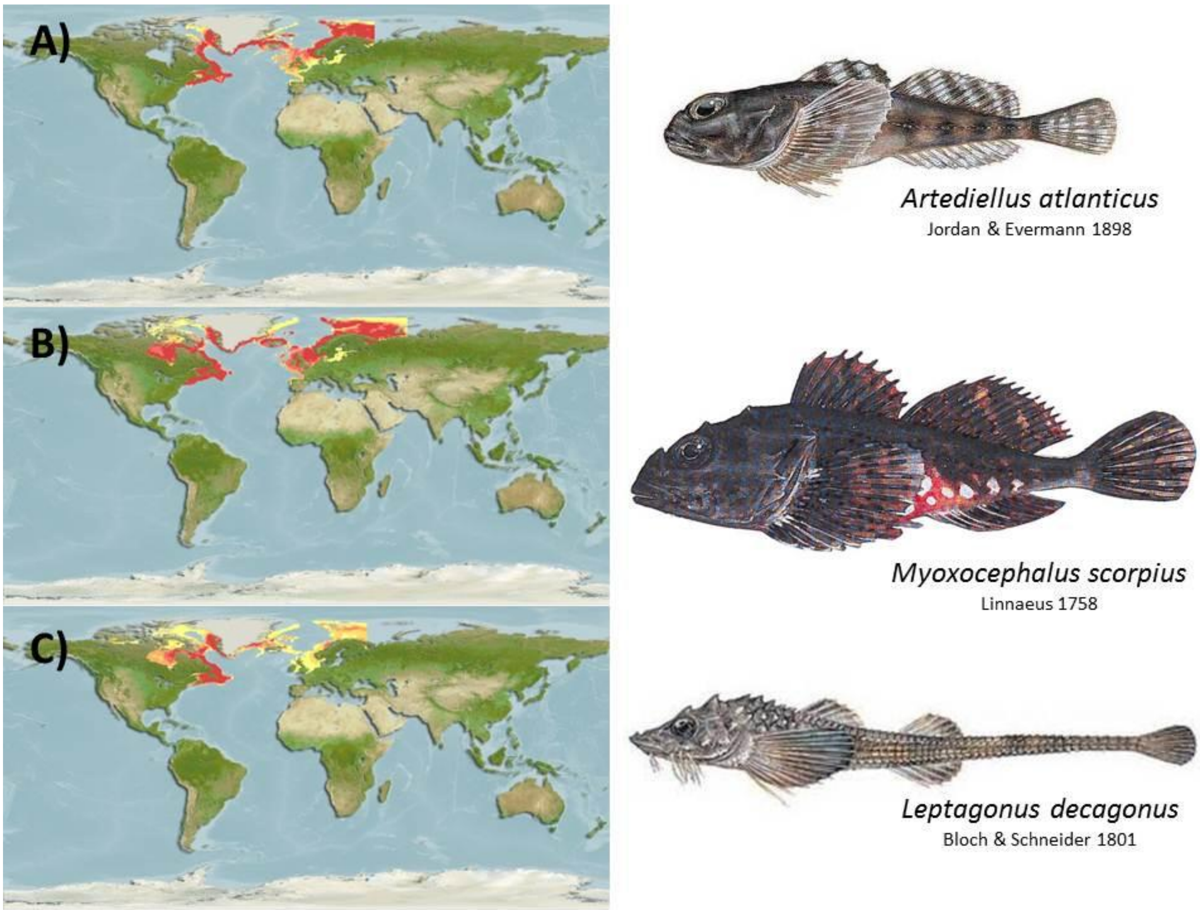

Figure 1: The species known distribution and concentrations within the North Atlantic Ocean where the colours indicates the community congregations. Red indicates highest concentrations of fish and it declines as the colour changes towards yellow. The maps represent the individual species known distribution, where A) *Artediellus atlanticus*, B) *Myoxocephalus scorpius* and C) *Leptagonus decagonus*. (Maps downloaded from www.fisbase.org, last update 3 July 2012, Drawings of all species were duplicated from Pethon, 2005).

Predictions, Approach and Hypotheses

Back in 2008 the project 'Ecological Processes and Impacts Governing the Resilience and Alternations in the Porsangerfjord and Hardangerfjord' (EPIGRAPH) was initiated and one of the aims was to develop an ecosystem model for the entire Porsangerfjord complex. Porsangerfjord is a high latitude fjord located in northern Norway and the inner part, Østerbotn, is the only arctic fjord system found in mainland Norway today (Soot-Ryen, 1951). The inner part of Porsangerfjord used to sustain a local fishery industry for Atlantic cod (*Gadus morhua*), but the stock has been declining since the 1970's (Ennis, 1970; Myksvoll et al., 2012). Furthermore, in the 1970's large quantities of the green sea urchin

(*Strongylocentrotus droebachiensis*) entered the fjord, which today have a persisting grazing pressure on the kelp forest (mainly *Laminaria hyperborea*) (Norderhaug & Christie, 2009). In addition, the introduction of the red king crab (*Paralithodes camtschaticus*) from the western Kamchatka Peninsula to the Barents Sea during the 1960s has today resulted in the dispersal of red king crab along the Norwegian coast, including Porsangerfjord (Pedersen et al., 2006).

Artediellus atlanticus, Myoxocephalus scorpius and *Leptagonus decagonus* are all found coexisting within the inner parts of Porsangerfjord. Very little is known about these species, their interactions as cohabitants, diet and trophic positioning within the ecosystem of inner Porsangerfjord. Nonetheless, recently it has been revealed that the local population of harbor seals (*Phoca vitulina*) within inner Porsangerfjord essentially fed upon fish within the family Cottidae (commonly referred to as cottids). The evidence show that over 50% of the otoliths found in seal's scat were from cottids, e.g *Myoxocephalus scorpius* (Virginie Ramasco Institute of Marine Research, Tromsø, pers. comm.).

The fish used for this study exhibited a typical biology for cold water species inhabiting arctic environments and the study objectives were to provide basic information about these species population dynamics and feeding ecology.

Hypotheses

H1: The size and age structure is different for the entire sample population.

H2: Growth pattern and conditional state of the individual differ between the sexes and fish species.

H3: The diet is different for the entire sample population and changes with increased body size.

H(4): All species have a different trophic positioning within the food web of inner Porsangerfjord.

H(5): Diet predictions from stomach content- and stable isotope analyses are different for all species.

Material and Method

Study area

Porsangerfjord between 70°N-71°N and 25°E-26°E is the largest fjord found in Northern Norway, located in the county of Finnmark adjacent to the Barents Sea (Figure 2). Porsangerfjord covers an area of 1800 km^2 and it is classified as a semi-enclosed fjord system with its shallow 60 m deep sill located at the point where the fjord is divided into an outer and an inner basin (Svendsen, 1991; Eilertsen & Frantzen, 2007). The outer basin has a maximum depth of 285 m and is regarded as an extension of the coastal zone due to the continuous or at least frequent exchange of deep water with the Norwegian Coastal Current (NCC) (Wassmann et al., 1996; Eilertsen & Skarðhamar, 2006). At the other end of the fjord, the inner basin of Porsangerfjord is considered to be an isolated arctic environment (Soot-Ryen, 1951) with subzero temperatures below the thermocline in Østerbotn (Svendsen, 1991; Christiansen & Fevolden, 2000) (Figure 3).

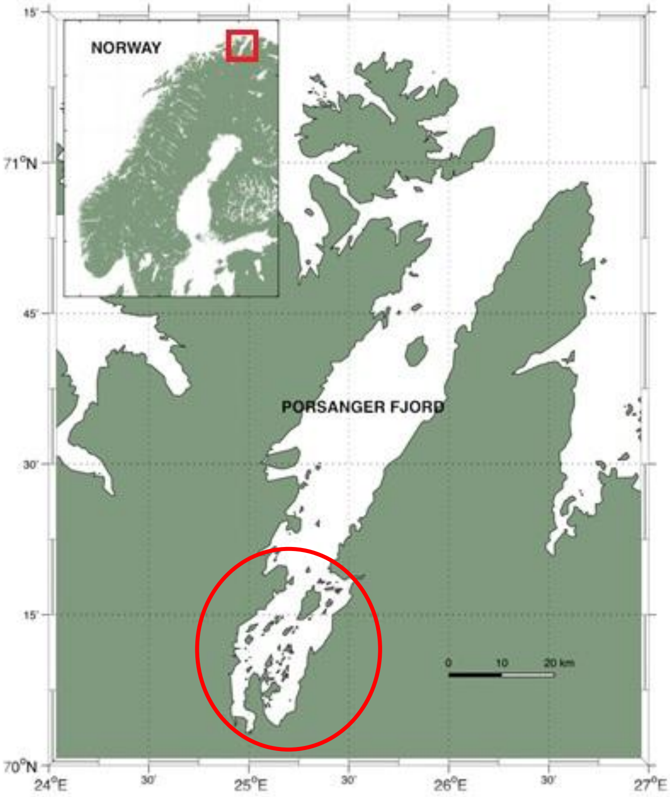

Figure 2: Geographical location and positioning of Porsangerfjord. The red circle demonstrates the undertaken study area.

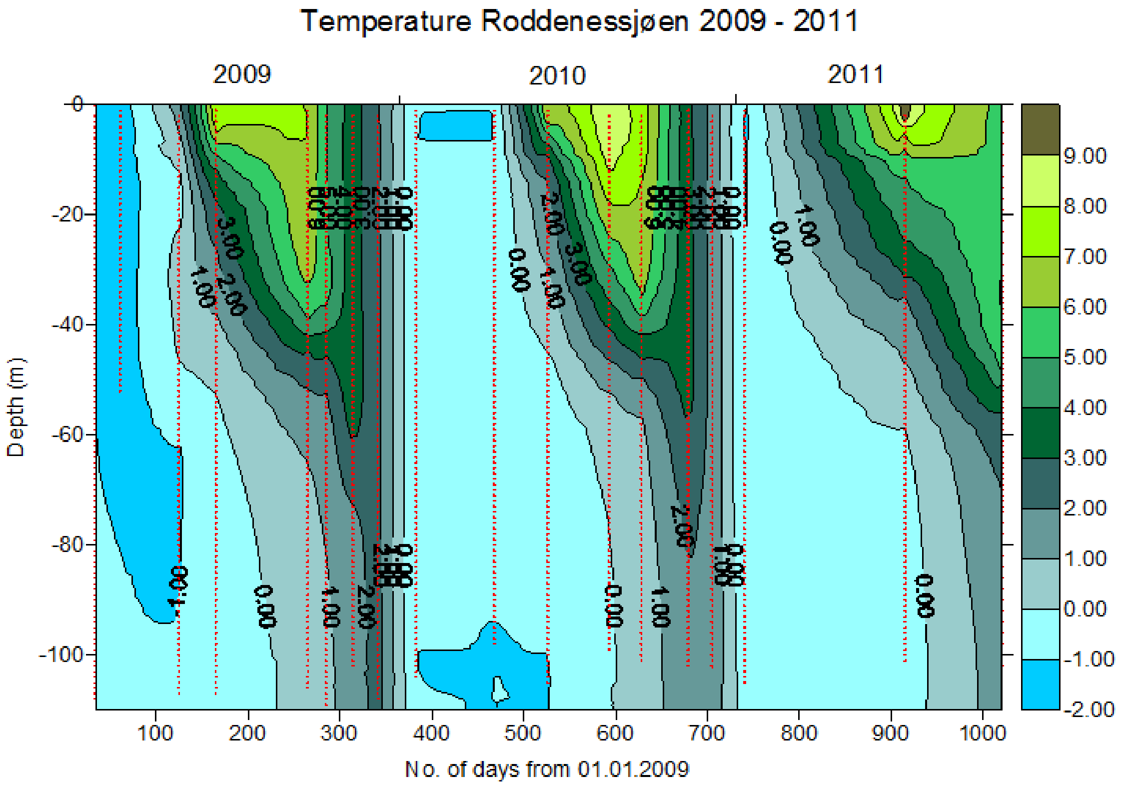

Figure 3: Isoplot of temperature (°C) changes over the sampling years (2009-2011) recorded from Roddnessjøen, located in Østerbotn within the inner basin of Porsangerfjord. The dotted red lines indicate the number of times data were gathered in the field and their corresponding sampling depth. The figure was produced by Ulf Normann, UiT with the Golden software, SURFER. Temperature data were provided by the project "Havmiljødata fra nordnorske fjorder".

The study was undertaken within the inner basin of Porsangerfjord (70°N 25°E) which is characterised by many islands and two fjord arms (Hegseth et al., 1995). The two fjordarms, Vesterbotn on the south-west side and Østerbotn on the south-east side, differ from one another not only in depth but also in sediment types. Vesterbotn is shallow (<27 m) with sand and mud as the main sediment type. Østerbotn reaches a total depth of 115 m where the sediment is predominately sand, gravel and rocks (Christiansen & Fevolden, 2000; Sunnset, 2008). The three sources of runoff water are from the rivers; Lakselv, Stabburselv and Børselv, and all runs into the inner part of Porsangerfjord (Svendsen, 1991; Wassmann et al., 1996) (Figure 4). Moreover, the major part of the inner basins surface waters freeze over in winter and is therefore characterised as an arctic fjord (Hegseth et al., 1995). It holds a rich arctic fauna, including arctic species of bivalves (E.g *Serripes groenlandicus* and *Cliocardium ciliatum*) (Soot-Ryen, 1951), a decapod species (*Sclerocrangon boreas*) and the demersal fish species *Boreogadus saida* and *Lycodes rossi* (Christiansen & Fevolden, 2000).

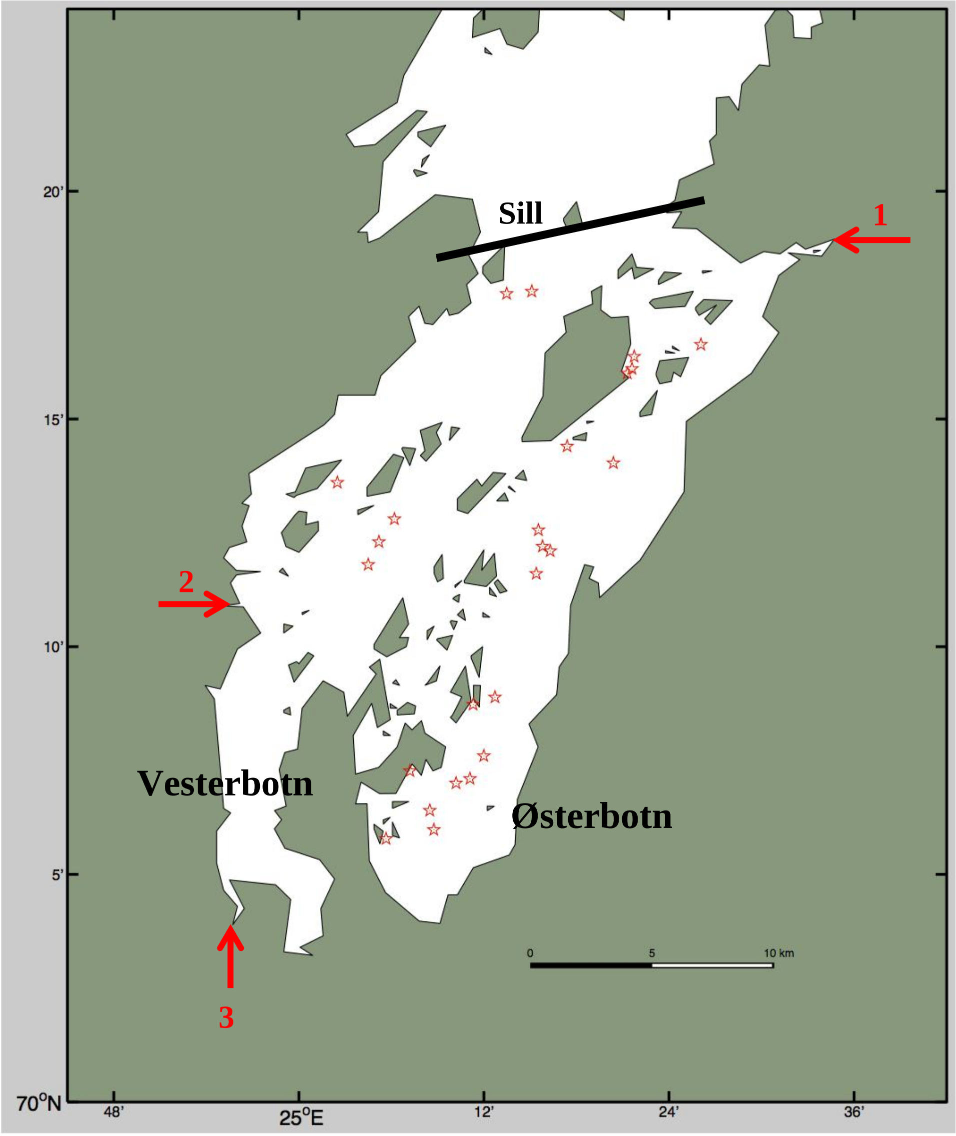

Figure 4: Sampling positions within inner Porsangerfjord as denoted by the red stars. The rivers with substantial amounts of freshwater runoff are indicated with red arrows, where 1) Børselv, 2) Stabburselva and 3) Lakselva.

Sampling procedures

Sampling the area for the three species: *A .atlanticus*, *M. scorpius* and *L. decagonus*, was conducted onboard the R/V Johan Ruud throughout seasons in 2009, 2010 and 2011 (Figure 4). Due to avoidance of the species from the sampling equipment, four different types of gear had to be used (Table 1).

Table 1

Gear efficiency of the different sampling procedures used to collect the specimens (n=171) throughout the sampling period, 2009-2011. The species are abbreviated as follows: *A. atlanticus* (A.a), *M. scorpius* (M.s) and *L. decagonus* (L.d).

Year (month(s))	Equipment	Number of stations	Depth range (m)	Species	Fish count
2009 (Aug.)	Beach seine	1	5	M.s	2
2010 (Aug.)	Beach seine	2	5	M.s	6
2009 (June)	Beam trawl	6	34-118	A.a M.s L.d	46 2 7
2011 (May)	Beam trawl	2	29-115	A.a	44
2009 (Feb., Aug.)	Bottom trawl	5	53-115	A.a M.s L.d	20 9 9
2010 (Feb., Aug.)	Bottom trawl	5	49-113	A.a M.s L.d	1 8 7
2010 (June)	Traps	4	19-31	M.s	4
2011 (June)	Traps	1	25	M.s	6

A **2 m beam trawl** fitted with an outer mesh of 20 mm and an inner 4 mm mesh lining the cod-end was used in June, 2009 and May, 2011. The beam trawl was further equipped with a chain mat to exclude large stones from the net (Jennings et al. 1999). Active trawling time was 3 min with an average speed of 1 knot (1.85 km h^{-1}).

The **bottom trawl** was a Campelen 1300 shrimp trawl equipped with rockhopper ground gear, with the cod-end having a 20 mm mesh size. All hauls were carried out in February and August, 2009 and 2010. Active sampling varied between 5 min and 22 min at the average speed of 2 knots (3.7 km h^{-1}).

Baited traps were only used in June each year. Each trap was baited with fish (e.g. cod) then stationed at a predetermined depth for 24 h before collection and processing.

Beach seine was the only sampling procedure that was not conducted onboard the R/V Johan Ruud and the sampling occurred in August, 2010. The net was used to sample the shallow coastal water close to shore (maximum depth 5 m). Each sample covered an area of approximately 500 m^2. The net was divided into three sections in accordance to its mesh size: 1). Outer 10 m had 16 mm stretched mesh, 2). Central 10 m, mesh size of 9 mm, 3). Cod-end, with initial 2 m of 9 mm stretched mesh and the final 2.6 m with 5.2 mm stretched mesh (van der Kooij, 2001).

The entire catch for each sampling procedure were sorted into lowest possible taxonomical level and frozen at a temperature of -20^o C.

Laboratory procedures

Species identification

Fish were defrosted in the laboratory within weeks and up to years after sampling. Taxonomical identification was performed down to species level, along with the characteristics observed from the identification using Andriyashev (1964) and Pethon (2005).

Body measurements

Fish length was measured as total length to the nearest 5 mm and the weight was recorded as both the total weight before dissection and as gutted weight after removing the entire abdominal contents (Table 2). Both total weight and gutted weight were recorded in g with one decimal point (Sartorius BP8100, d=0.1g). The sex was recorded for each individual and afterwards both the gonads and the liver were weighed to the nearest mg (Sartorius ED2145, d=0.1mg) (Mikalsen, 1995; Mikkola, 1996) (Appendix 1).

Table 2

Overview of the sample population and the number of individuals recorded for each measurement. Here, the numbers in each column represents how many individuals were recorded and available for further analysis. Numbers in bold indicates the differences in individual numbers from the total fish number since some measurements could not be established for all individuals. Note that the age of the fish was estimated twice and therefore shown as two columns: Otolith reading 1 and Otolith reading 2.

Species	Total number	Sex	Total length (cm)	Total weight (g)	Gutted weight (g)	Liver weight (g)	Gonad weight (g)	Stomach weight (g)	Empty stomachs	Stomachs used for analysis	Stable isotope samples analysed	Otolith reading 1	Otolith reading 2
A. atlanticus	111	111	111	111	***110***	111	***110***	111	***27***	***84***	***18***	***110***	111
M. scorpius	37	37	37	37	***36***	37	***33***	37	***6***	***31***	***8***	37	37
L. decagonus	23	23	23	23	23	23	***20***	23	***1***	***22***	***9***	23	***21***

Age determination

Age was assessed through otolith readings. Both otoliths were removed with tweezers after cutting the fish's head open. Both sagittae otoliths were stored and dried until the age was to be determined. Aging the fish was conducted by rehydration of the otoliths in water for a few minutes prior to the counting of the annuli. The counting was undertaken with reflecting light on a dark background through the use of a stereoscope (Wild Heerbrugg Plan 1x). Annuli were counted from the center to the edge and each annulus was defined as where the opaque zone (period associated with fast growth) meets the translucent zone (period with slow or no noticeable growth). Under reflecting light the opaque zone appears white and the translucent zone appears dark (C.A.R.E, 2006). However, one might observe one or more sporadic translucent zones within the opaque zone and these are known as checks. Checks forms irregularly as a result of the present circumstances rather than an annual reflection of passing time (C.A.R.E, 2006). The presence of checks can easily be misinterpreted as one or several annuli, thus proposing to the observer that the fish was older than it truly was at time of capture. Therefore, both otoliths were surface read twice on two separate occasions in order to accurately determine the age of the fish. The fast growth period was expected to begin around April and last until winter arrived in late October. As a result, the age was read as completed 'years of growth'. This refers to the age being recorded and presented as: year+, which translates to a fish with three complete annuli, was recorded as three years old but was caught during its fourth year of life (Figure 5).

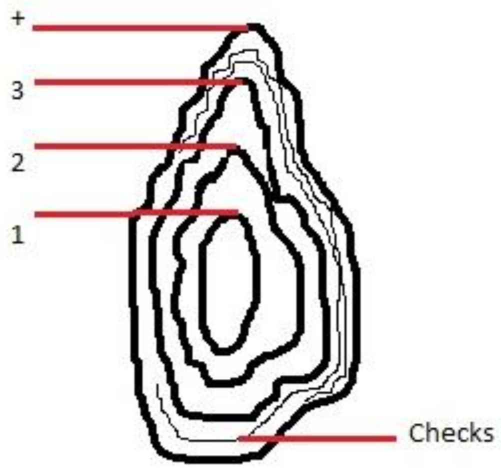

Figure 5: Schematic drawing of an otolith which illustrates how the aging of the fish was carried out for this study. This example shows an *A. atlanticus* otolith which was in its fourth year at capture. For the purpose of this study it was aged as 3+. The white area represents the opaque zone and the thick black lines represent the translucent zones. The thin black lines illustrate two checks within the otolith which are not to be misinterpreted as translucent zones during age determination.

Stomach retrieval and content identification

The stomach samples were attained by the removal of the whole stomach between the esophagus and the intestines. Fish waiting to be analysed were kept on ice to slow down the decomposition of the stomach contents. Each stomach was weighed initially as "intact" just after retrieval and once more after the removal of all gut contents as "empty tissue" to the nearest milligram (Sartorius ED2145, d=0.1mg). All gut contents were analysed under a stereoscope (Wild Heerbrugg Plan 1x) and smaller prey item were also on occasion identified using a higher resolution microscope (Leitz Laborlux 11, 100/1.25 OEL). Each prey item was counted and identified down to the lowest taxonomical level possible (Hayward & Ryland, 1990; Moen & Svensen, 2003; Rupert et al., 2004). However, the identification of the encountered fish depended on the level of decomposition and two procedures were utilised: direct species identification (Pethon, 2005) of samples which had experienced little deterioration or by otolith identification (Svetocheva et al., 2007) where the specimen's morphological features were unrecognizable from digestion.

Afterwards, the contents were once again grouped into higher 'functional groups' in order to carry out statistical diet analyses of the stomach contents. Eleven prey categories were selected to describe the diet components: Unidentified (digested soup of unrecognizable material), Amphipoda, Isopoda, Copepoda, Decapoda, Euphausiacea, unidentified Crustacea, Mollusca, Polychaeta, Pisces or Other (everything that did not fit into one of the other categories). The category Unidentified was excluded from all further diet analyses as the degree of digestion was too severe for accurate evaluation. Therefore, ten prey categories have been used for all investigations regarding the species diet compositions.

Stable isotope analysis

Stable isotope analysis facilitates the comparison of species across ecosystems (Nilsen et al., 2008) which, in the present study, will shed light onto the fish trophic interactions within the unknown food web of inner Porsangerfjord. During the dissection of the fish, an approximate 2 cm^3 muscle sample from the left dorsal side was collected for stable isotope analyses and re-frozen until further analyses could proceed. The stable isotope preparation included two main procedures. Firstly, after defrosting the sample it was stripped of all skin fragments, bones and material which were not 'pure' muscle tissue. Each sample was rinsed with distilled water, after which it was put into a drying oven for 48 h at 62^oC. Secondly, the dried samples were further prepared by grinding them into a fine powder using a pestle and mortar. Between each sample, both the pestle and mortar were washed with soap water, rinsed with alcohol (70%)

and blown dry with pressured air. The powder was then put into micro tubes, frozen and analysed at the ‘Stable Isotopes in Nature Laboratory’ (SINLAB) Rivers Institute, Canada. The samples were analysed for stable isotopic carbon and nitrogen, where the ratio in parts per thousand (‰) of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ were exclaimed by $\delta^{13}C$ and $\delta^{15}N$ denotation, respectively.

The $\delta^{13}C$ signature provides information about the original source of the isotope, where isotopically light carbon ($\delta^{13}C$ -20‰ to -35‰) is derived from the pelagic zone and isotopically heavy carbon ($\delta^{13}C$ -7‰ to 0‰) is related to the littoral zone (Post, 2002). Because of the modest increase in $\delta^{13}C$ (0.8‰) along the food change, $\delta^{15}N$ is frequently used for trophic level calculations due to its higher fractionation rate (3.4‰) up the food chain (Peterson & Fry, 1987). Trophic levels are estimated in order to evaluate the hierarchical positioning and function of each species. Therefore, it is not surprising that the application of trophic level estimations from stable isotopes is highly influenced by the baseline value, since it is meant to reflect the structure of the food web (Xu et al. 2011).

The baseline for the trophic level estimation in this study was the bivalve *Chlamys islandica*, with a trophic level=2. Both the fish samples and the baseline samples were analysed using a Carlo Erba NC2500-Plus Element Analyser (SINLAB). The $\delta^{13}C$ and $\delta^{15}N$ values were further corrected by SINLAB according to the IAEA (International Atomic Energy Agency) scale, which calibrate carbon against Vienna Peedee Belemnite carbonate (VPDB) and nitrogen against atmospheric nitrogen (AIR) in accordance with the following equation (Equation 1):

$$\delta X = \left[\left(R_{sample}/R_{standard}\right) - 1\right] \times 1000 \qquad \textbf{(Equation 1)}$$

where δX is the isotope ratio for either carbon or nitrogen and is expressed as parts per thousand (‰), R is the corresponding ratio of $^{13}C/^{12}C$ or $^{15}N/^{14}N$ for the study samples and standards.

Data analyses

Data set

The study is based upon a total number of 171 fish, encompassing the three species; *A. atlanticus* (n=111), *M. scorpius* (n=37) and *L. decagonus* (n=23) (Table 2).

Fish growth analyses

Log-likelihood ratio (G^2)

In order to analyse if the two age estimations differed between the readings a goodness of fit test was applied. The log-likelihood ratio (G^2) (Equation. 2) were chosen over a Chi-Squared test (X^2) due to the fact that both models often yield the same results but the former model (G^2) presents a more powerful test case (Zar, 1999).

$$G^2 = -2ln(\Lambda) \qquad \textbf{(Equation 2)}$$

where Λ is the likelihood ratio of the reduced model to the full model (Quinn & Keough, 2002).

von Bertalanffy growth function

Absolute growth in fish has commonly been described by S-shaped models, such as the von Bertalanffy growth function which incorporates the fish's different growth patterns over its entire lifetime (Fuiman & Werner, 2002). The von Bertalanffy growth function is expressed as:

$$L_t = L_\infty\left(1 - e^{-K(t-t_0)}\right) \qquad \textbf{(Equation 3)}$$

where L_t is the length at time t, L_∞ is the theoretical maximum length, K is the growth coefficient and t_0 is the hypothetical age when L equals zero.

Simple Linear Regression

A statistical model which describes the changing relationship between an independent- (predictor) and a dependent (response) factor is the simple linear regression model (Zar, 1999). The regression analysis investigated the weight-length relationship for all species and was conducted for both males and females. This model has the ability to define how the relationship between species gutted weight (dependent factor, Y) will increase with total length (independent factor, X) from the linear equation:

$$ln\ gutted\ weight = \ln a + b * \ln total\ lenght \qquad \textbf{(Equation 4)}$$

where ‘a’ is the intercept of the described relationship and the regression coefficient ‘b’ represents the slope of the expressed line. The b value is commonly used to describe the type of growth that the animals is experiencing, where a value of b=3 is equivalent to isometric growth, and a higher or lower value (commonly ranging from 2-4) indicates a positive or negative allometric growth relationship (Zar, 1999).

Analysis of variance (ANOVA) and Analysis of Covariace (ANCOVA)

ANOVA is a statistical technique, which analyses the variation in a continuous response variable for several treatments, or groups at the same time and tests whether the sexes; female and male, were equal to one another within the species.

The resemblance in slope (b) was further analysed with an ANCOVA, where sex and species were grouping variables and length was the covariate. A covariate adds unwanted variability to the dependant variable (in this case gutted weight) and is therefore regarded as a quantitative independent variable which the analysis corrects for by either adjusting or removing variability in the dependent variable (Quinn & Keough, 2002).

All statistical analysis were carried out using the statistical programs SYSTAT 13 (2009)

Hepatosomatic Index (HSI)

The HSI is expressed as the liver weight in relation to gutted weight of the fish (Kingdom & Allison, 2011) (Equation 5).

$$HSI = \frac{Liver\ weight\ (g)*100}{Gutted\ weight\ (g)} \qquad \textbf{(Equation 5)}$$

Gonadosomatic Index (GSI)

The GSI describes the gonad weight as a percentage of the gutted weight of the fish and can be related to both fish length and age (Pollock, 1984) (Equation 6).

$$GSI = \frac{Gonad\ weight\ (g)*100}{Gutted\ weight\ (g)} \qquad \textbf{(Equation 6)}$$

Both indices were computed using Microsoft Excel (2010).

Diet analyses

The diet of the species were analysed from a range of statistical approaches in order to quantify the composition and importance of the prey.

Frequency of occurrence index (FO)

The diet of each species and the length groups within the species were all analysed by the FO which expresses the proportion by number of the prey category within the stomachs (Alhbeck et al. 2012) (Equation 7).

$$FO_i = \left(\frac{N_{Fish,i}}{N_{Fish}}\right) * 100 \qquad \textbf{(Equation 7)}$$

where the FO_i equals the estimated percentage of prey i in the diet, $N_{Fish,\ i}$ is the number of individuals containing prey *i* within their stomachs and N_{Fish} is the number of fish examined (excluding the categories: empty and unidentified).

The index was computed by the use of Microsoft Excel (2010).

Spearman’s rank correlation coefficient (r_s)

To analyse if the diet were similar both within the species length-groups and among the three species the r_s was used. The coefficient is a non-parametric correlation analysis that determines the relationship between monotonic variables and lacks unit (Zar, 1999). The coefficient ranges between -1 and +1.

Bootstrap

The bootstrap technique was used in order to estimate the 95% confidence intervals around the estimated Spearman’s rank correlation coefficient. This resampling procedure of the data (1000 replications) allows the confidence interval (CI) to be estimated directly through the percentile method (Krebs, 1998; Quinn & Keough, 2002).

Both the correlation and Bootstrap analysis were carried out using the statistical programs SYSTAT 13 (2009)

Trophic positioning

Trophic level estimations for each species were determined by calculations from the dietary enrichment in isotopic nitrogen ($\delta^{15}N$) up the food chain (Peterson & Fry, 1987) (Equation 8).

$$TL_{consumer} = \left(\frac{\delta^{15}N_{consumer} - \delta^{15}N_{base}}{\Delta\delta^{15}N}\right) + TL_{base} \qquad \textbf{(Equation 8)}$$

where $\delta^{15}N_{consumer}$ is the $\delta^{15}N$ of the fish species and $\Delta\delta^{15}N$ is the increasing fractionation of $\delta^{15}N$ (3.4‰) between each trophic level. The baseline; *Chlamys islandica*, with trophic level 2 (TL_{base}), where estimated from the mean value of three individual $\delta^{15}N$ signatures. Therefore, $\delta^{15}N_{base}$ equals 7.92‰ in the present study.

The trophic level calculations were carried out with the use of Microsoft Excel (2010).

RESULTS

Size, age and sex distribution

The length distribution varied between both sex and species, whereas the age range was equal. The total number of specimens (n=171) were divided into *A. atlanticus* (n=111), *M. scorpius* (n= 37) and *L. decagonus* (n=23) where the sex ratio were skewed towards females. Fish length differed in overall mean for all three species but overlapped in range. The smallest species *A. atlanticus* had a mean length of 9.2cm (3.5-12 cm), followed by *L. decagonus* mean length 11.7cm (5-18 cm) and finally *M. scorpius* mean length 18.0cm (3.5-27 cm). *Leptagonus decagonus* recorded a bimodal distribution unlike the other two species which had a normal distribution. The longer specimens of *L. decagonus* were almost exclusively females and the shorter specimens consisted predominately of males. This sex distribution was not observed for the other two species either (Figure 6A).

The age resulted in the approximated age range of 1-7 years for *A. atlanticus*, 0-7 years for *M. scorpius* and 1-7 years for *L. decagonus* (Figure 6B,). The recorded age; reading 1 (R1) and reading 2 (R2) and the age estimations for *A. atlanticus* was statistically different (G^2= 16.0, df= 6, p=0.014), whereas *M. scorpius* and *L. decagonus* did not demonstrate a difference between the two readings (G^2= 8.1, df= 5, p=0.149 and G^2= 6.9, df= 4, p=0.143 respectively). Although, because of the low sample size for *M. scorpius* and *L. decagonus* these results should be interpreted with utmost caution.

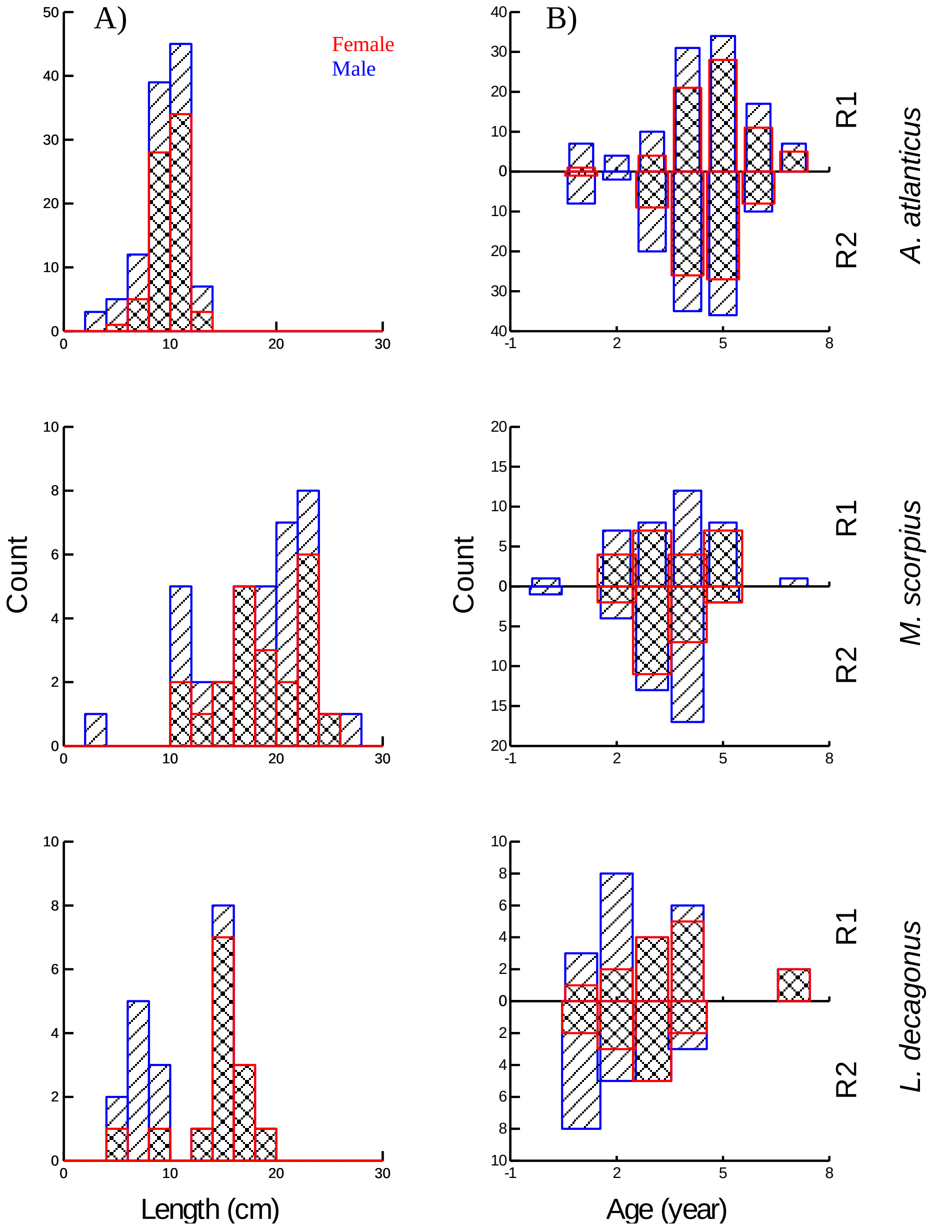

Figure 6: Fish distributions of the three species, where A) Length frequency distribution of female (red) and male (blue), and B) Age distribution (reading 1 (R1) and reading 2 (R2)) for female (red) and male (blue).

Species growth, conditions and reproduction

The slope for each sex within the species (Figure 7A, Appendix 2) were then analysed by an ANCOVA, which stated that there were no differences between the sexes weight-length relationships (*A. atlanticus* $F_{1, 106}$=0.41, p=0.64; *M. scorpius* $F_{1, 32}$=0.35, p=0.56; *L. decagonus* $F_{1, 19}$=0.44, p=0.51). Next the height between the sexes weight-length relationship were analysed by an ANOVA, which also stated that there was no difference between the sexes growth patterns (*A. atlanticus* $F_{1, 106}$=0.41, p=0.12; *M. scorpius* $F_{1, 32}$=0.35, p=0.70; *L. decagonus* $F_{1, 19}$=0.44, p=0.72). Hence, both sexes were integrated into species level and individual species weight-length relationships were established (Appendix 2).

The slopes suggest a difference among the species, where both *A. atlanticus* and *M. scorpius* documented values above 3.0 (b=3.16 and b=3.18, respectively), whereas *L. decagonus* retains a value lower but not different from 3.0, 95% CI (b=2.89) (Figure 7B). The suggested intercept differences between the species were confirmed by an ANCOVA ($F_{2, 163}$=7.9, p=0.0001), which demonstrated that *L. decagonus* differed from both *A. atlanticus* and *M. scorpius* due to its lower increase in weight at the same length. Furthermore, there were no overlap, 95% CI, between the regression line of *L. decagonus* and the other two species weight-length relationship (Figure 8). In addition, the slope for *A. atlanticus* and *M. scorpius* were explored and the ANCOVA analysis did not find any difference within these two species slope ($F_{1, 142}$=0.03, p=0.86). However, removing slope as a factor, the ANCOVA did show weight differences between *A. atlanticus* and *M. scorpius* ($F_{1, 143}$=23.8, p=0.001) (Figure 8).

An ANOVA was performed to test if length and weight varied for the estimated ages for only *A. atlanticus* individuals (3-6 years) (Figure 9, Appendix 3). No size differences were indicated ($F_{1,185}$=1.0, p=0.32) between the two readings (R1 and R2). This analysis was only carried out for *A. atlanticus* since it was the only species considered to have a sufficient sample size for statistical validation. Moreover, the von Bertalanffy growth equation further emphasised that there were no difference between *A. atlanticus* age readings, including all years (95 % CI) (Table 3).

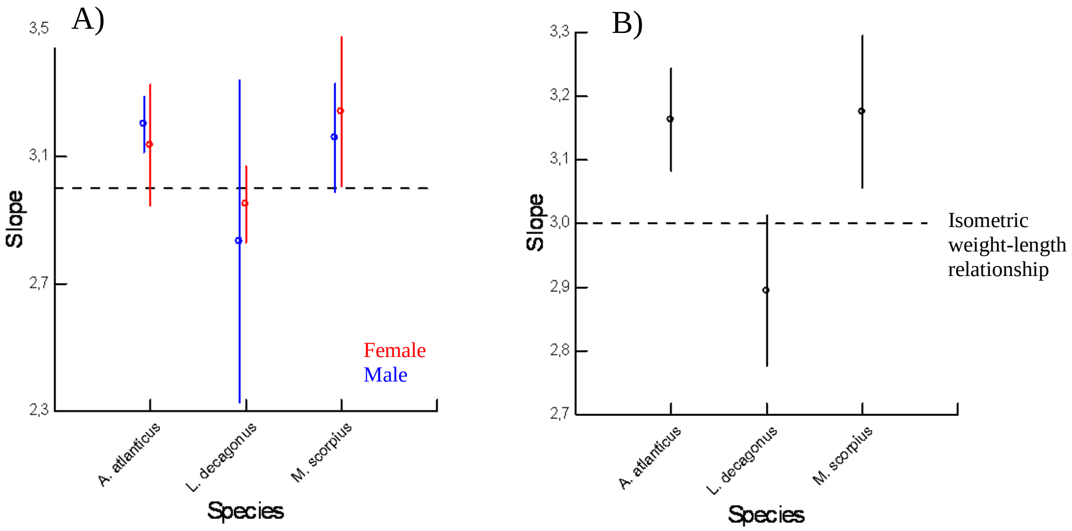

Figure 7: The species growth patterns indicated by their slope (b). A) The two sexes; female and male, individual growth patterns with a 95% CI around the slope. B) The species different growth pattern with 95% CI around the slope. The dotted line (b=3.0) represents the isometric weight-length relationship.

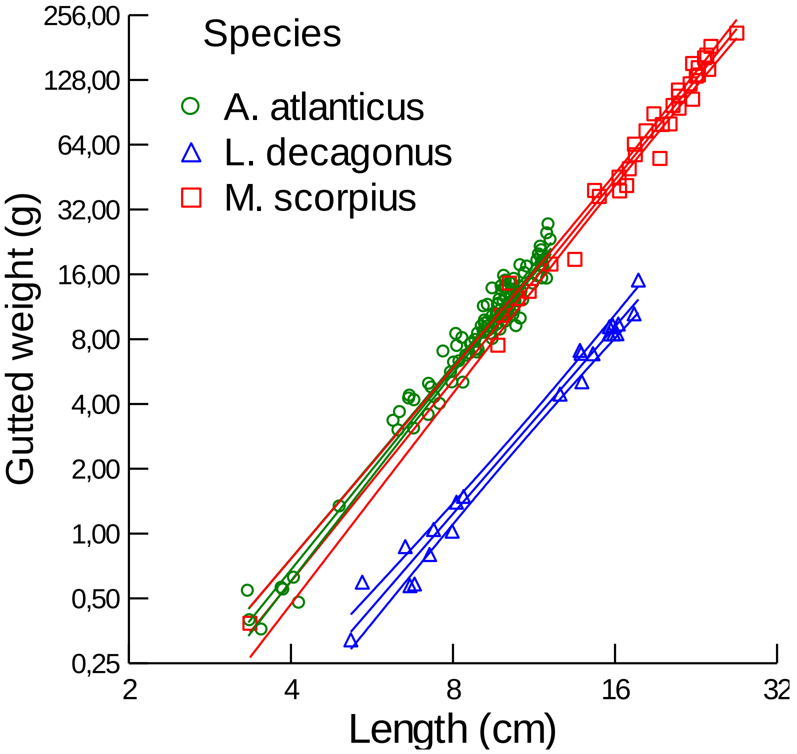

Figure 8: Weight-Length relationship of the three species with 95% CI around the regression line.

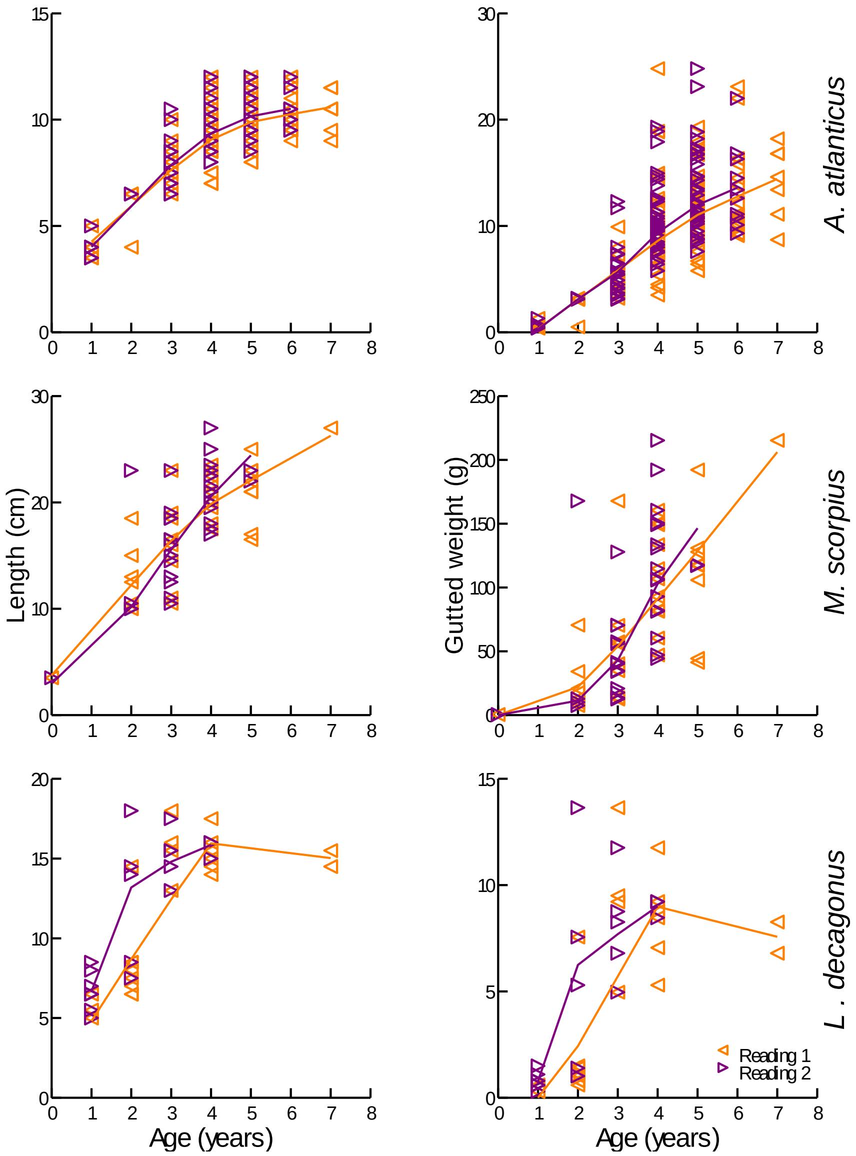

Figure 9: Size dimension with increased age. A) Length at age data for all species (Lowess, tension 0.9). B) Weight at age for the species (Lowess, tension 0.9).

Table 3

von Bertalanffy growth equation estimations for reading 1 and reading 2 of all *A. atlanticus* specimens. Given values for the equation estimation: L_{inf}=13 cm, k= 0.2 and t_0=-0.5.

	Reading 1	Reading 2
L∞ (95% CI)	11.11 (10.17 to 12.04)	11.79 (10.56 to 13.01)
k	0.46 (0.29 to 0.63)	0.42 (0.27 to 0.56)
t_0	0.11 (-0.31 to 0.52)	0.06 (-0.32 to 0.44)

All species, here separated into males and females, demonstrated different patterns from the Hepatosomatic Index (HSI) with increasing fish length (Figure 10). *Artediellus atlanticus* showed no overlapping intersection from the HSI estimation and none of the sexes demonstrated a significant correlation with length (female r_s= -0.03, p >0.5; male r_s= -0.22, p >0.1). *Myoxocephalus scorpius* demonstrated a fairly parallel increase in both sexes HSI with fish length, where the index were significantly correlated with increasing fish length (female r_s= 0.605, p=0.005; male r_s= 0.595, p=0.05). *Leptagonus decagonus* two sexes had overlapped in HSI with increasing size, but did not demonstrated a significant correlation with length (female r_s= 0.238, p >0.2; male r_s= -0.085, p >0.5).

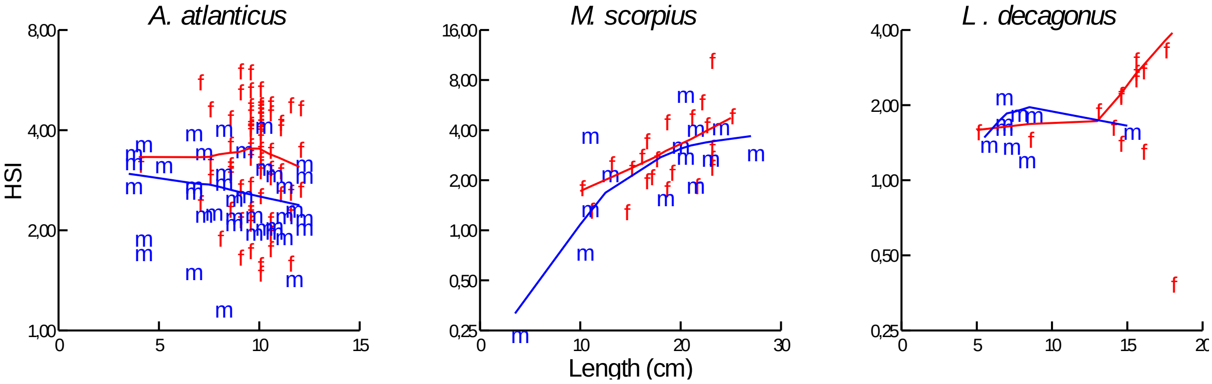

Figure 10: Hepatosomatic Index (HSI) in relation to fish length (cm) for the three species with a lowess line (tension 0.9).

The GSI index was higher for females than males *A. atlanticus*, and the index was correlated with increasing length for both females (r_s= 0.26, p= 0.05) and males (r_s= 0.77, p= 0.001). Female GSI stagnated around 6% for fish that had reached a total length of 10 cm or more, whereas male GSI did never exceed 1% regardless of length (Figure 11). *Myoxocephalus scorpius* displayed a parallel and similar increase pattern in both sexes GSI, but where not correlated with length (female r_s= 586, p=0.005; male r_s= 0.837, p=0.001). Female *L. decagonus* recorded a rather exponential GSI with increasing fish length, but this was not correlated (r_s=0.837, p=0.001). Male *L. decagonus* on the other hand, had only three observations available for the GSI and were therefore not interpreted further.

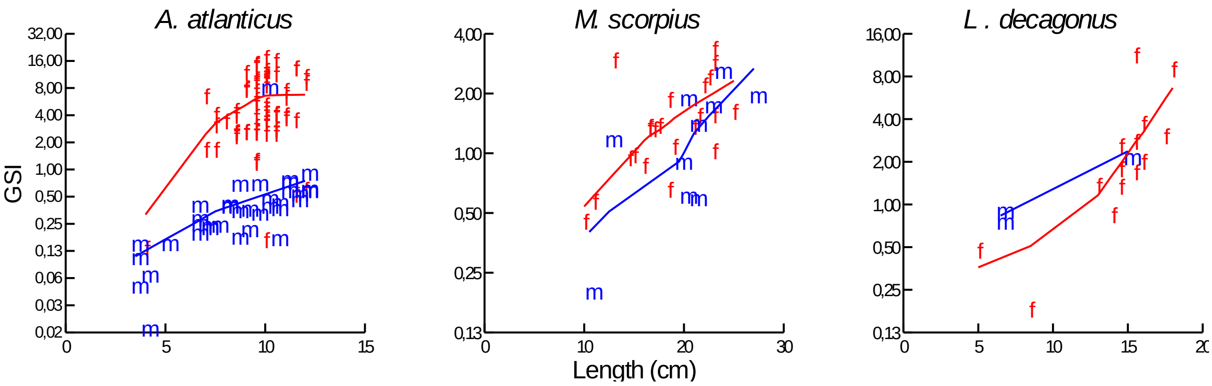

Figure 11: Gonadosomatic Index (GSI) with increasing fish length (cm) for each species with a lowess line (tension 0.9).

Stomach analysis

The three most encountered prey items in all the stomachs analysed were as followed, in descending order: Polychaeta, Copepoda and Pisces (Figure 12). The dominant prey found in *A. atlanticus* was Polychaeta, *M. scorpius* was the only species that had fed on fish, and *L. decagonus* had only fed upon Copepoda out of the three most encountered prey categories. Differences between the species diet can also be observed when their entire stomach contents were compared to one another. All species show some overlap in the prey categories; however the significance of each prey to the diet presents differences among the species (Figure 12). When all prey classes were presented with their overall contribution to the diet of each species, it became apparent that *A. atlanticus* retained a diet consisting of nine out of ten prey categories, but Polychaeta (76.2%) had the highest frequency of occurrence (FO). *M. scorpius* had fed on eight of the ten categories, with Pisces (50.0%) and Decapoda (43.3%) having the largest contributions to the diet. *L. decagonus* on the other hand demonstrated a diet incorporating many different crustacean preys, with the predominant prey categories being Copepoda (54.6%) and Amphipoda (27.3%) (Appendix 4). Furthermore, since *L. decagonus* had fed upon four prey categories within the taxonomical sub-phylum Crustacea, it retained a large percentage of unidentifiable material combined from the prey categories; Amphipoda, Copepoda, Decapoda and Euphausiacea.

Taking a closer look at the individuals within a species, where functional groups by fish length were used to distinguish dietary differences, demonstrated some expected and

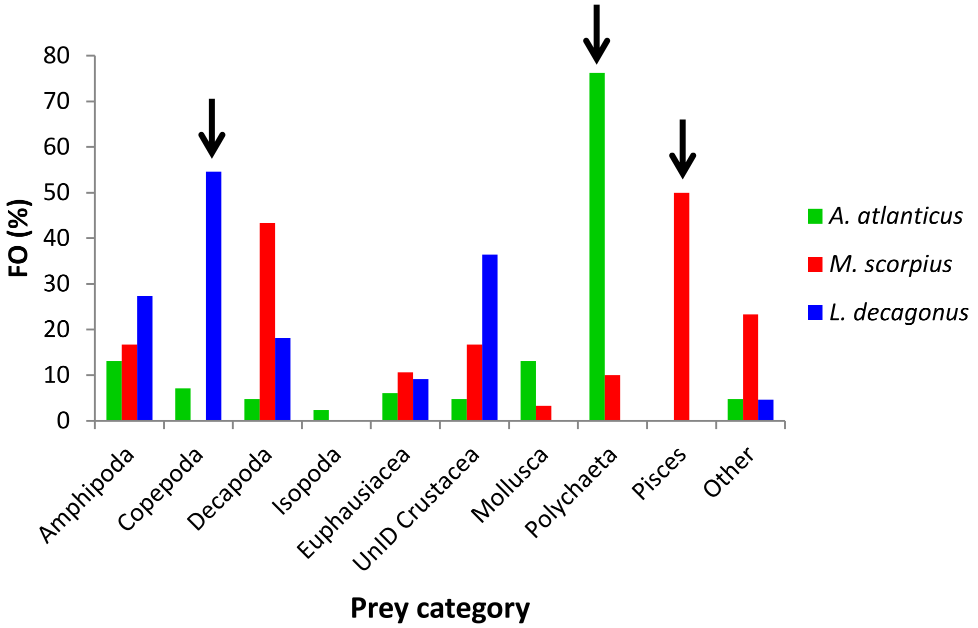

Figure 12: Histogram of the three species ingested prey categories as documented by the FO (%), where the arrows indicate the three most encountered prey categories observed within the fish stomachs for all species.

unexpected patterns (Table 4). *Artediellus atlanticus* was divided into three functional groups (A1: 3.5-7.5cm, A2: 8-9.5cm and A3: 10-12cm) where all length groups demonstrated that the prey Polychaeta was the prey category with the highest FO (Table 4). Also, small Mollusca (Bivalvia) continued to be a representative part of the *A. atlanticus* diet independent of fish length. Small *A. atlanticus* (A1) fed upon filter- and detritus-feeding polychaets families such as Oweniidae and Maldanidae, whereas the larger individuals (A2 and A3) shifted towards more predatory feeding polychaets families such as Nepthyidae and Ophellidae. Moreover, the smaller individuals (A1) had ingested a greater proportion of some additional small prey categories such as Amphipoda and Copepoda, in comparison to the larger individuals. The two larger length-groups (A2 and A3) diets were correlated (r_s=0.84, p=0.005), but the smallest individuals (A1) did not demonstrate any correlation in diet to the other two length groups (A1:A2 r_s=0.34, p>0.2 and A1:A3 r_s=0.38, p>0.2) (Appendix 5).

Both *M. scorpius* and *L. decagonus* were divided into two functional length groups due to their small sample size. *Myoxocephalus scorpius* was separated into individuals smaller and larger then 20cm (M1: <20cm and M2: >20cm). All individuals recorded a rather similar diet regardless of fish length (Table 4) and were also significantly correlated with one another (r_s=0.83, p=0.005) (Appendix 5). On the other hand, *L. decagonus* documented a difference within their FO between the length groups diet (L1: 5-8.5cm and L2: 14-18cm) (Table 4). The smaller individuals fed mainly on few prey categories and predominantly on Copepoda, whereas the larger individuals incorporated more varied crustacean prey into their diets, with the dominant prey being (in descending order): Decapoda, Amphipoda, Copepoda and Euphausiacea. The observed dietary differences in FO for *L. decagonus* were not correlated (r_s=0.62, p >0.05). However, the bootstrap 95% CI did demonstrate a significant correlation between the length groups dietary FO (Appendix 5).

No other correlations between species diets within any length group were observed (p >0.20).

Table 4

The FO (%) for each prey category according to the species individual length groups (n=137).

	Species						
	A. atlanticus			***M. scorpius***		***L. decagonus***	
	3.5 to7.5 cm (n=18)	8 to 9.5 cm (n=29)	10 to 12 cm (n=37)	<20 cm (n=17)	>20 cm (n=14)	5 to 8.5 cm (n=10)	14 to 18 cm (n=12)
Prey category							
Amphipoda	33.3	6.9	8.11	18.8	14.3	30.0	25.0
Copepoda	27.8	0.0	2.7	0.0	0.0	90.0	25.0
Decapoda	0.0	6.9	5.4	50.0	35.7	0.0	33.3
Isopoda	5.6	0.0	2.7	0.0	0.0	0.0	0.0
Euphausiacea	0.0	3.5	10.8	12.5	7.1	0.0	16.7
UnID Crustacea	0.0	6.9	5.4	25.0	7.1	20.0	50.0
Mollusca	16.7	13.8	10.8	0.0	7.1	0.0	0.0
Polychaeta	55.6	86.2	78.4	12.5	7.1	0.0	0.0
Pisces	0.0	0.0	0.0	68.8	28.6	0.0	0.0
Other	5.6	3.5	8.1	18.8	28.6	0.0	8.3

Colour index: Frequency of occurrence (%)

0	>0 to <20	>20 to <50	>50 to 100

Stable Isotope Analysis

The stable isotope analysis demonstrated several patterns for the three species in both the carbon (δ^{13}C) and nitrogen (δ^{15}N) signature (Figure 13). The first observation was that *L. decagonus* was distinguished from both *A. atlanticus* and *M. scorpius* isotopic signatures (δ^{13}C and δ^{15}N). Secondly, *L. decagonus* recorded both the lightest δ^{13}C (-19.95) and the smallest δ^{13}C signature range (δ^{13}C= -18.74 til -19.95), whereas *M. scorpius* recorded the largest δ^{13}C range (δ^{13}C= -17.04 til -18.67), followed by *A. atlanticus* (δ^{13}C= -17.28 til -18.64). Finally, the highest δ^{15}N signature was recorded by *L. decagonus* (δ^{15}N= 16.62) and the lowest δ^{15}N signature by *A. atlanticus* (δ^{15}N= 12.53), whereas *M. scorpius* δ^{15}N signatures were concentrated in the middle (δ^{15}N= 13.38-15.76) (Figure 13).

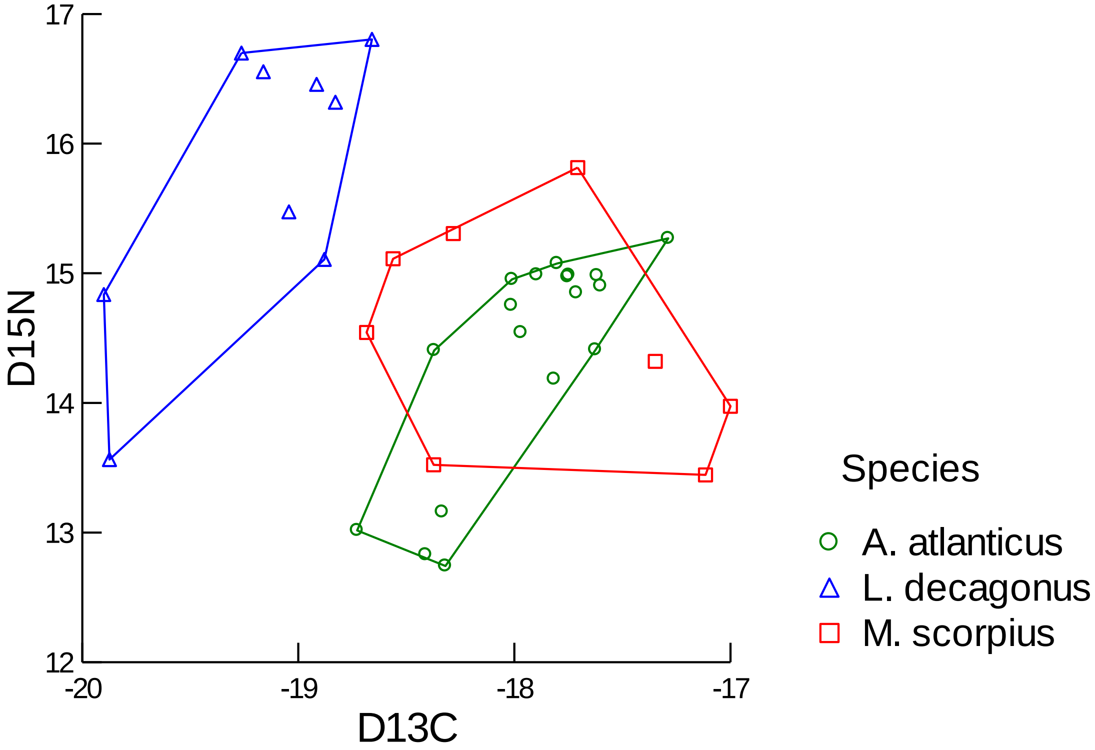

Figure 13: Individual stable isotopic δ13C and δ15N signatures from muscle tissue of the three species from inner Porsangerfjord.

When $\delta^{13}C$ was viewed in relation to fish total length, the trend was that all species altered their nutritional source of $\delta^{13}C$ with increasing length (Figure 14). However, only *A. atlanticus* showed a significant correlation in $\delta^{13}C$ with increasing length (r_s= 0.59, p=0.05). Both *A. atlanticus* and *L. decagonus* (r_s= 0.40, p>0.2) went from a diet with isotopically lighter $\delta^{13}C$ and towards a diet consisting of isotopically heavier $\delta^{13}C$ with growth. *M. scorpius* on the other hand demonstrated the opposite pattern within its dietary intake of isotopic $\delta^{13}C$, as the fish went from isotopically heavy $\delta^{13}C$ towards a lighter $\delta^{13}C$ source with increasing length (r_s= -0.69, p>0.05). Another noteworthy observation was that two *L. decagonus* samples exhibited a lighter $\delta^{13}C$ signature in contrast to other samples with the same total length.

Trophic level (TL) estimations in relation to the fish total length provided further insight into the species diet and positioning within the food web of inner Porsangerfjord. All species had relatively high TL values (TL 3.4-4.6) where *L. decagonus* displayed the highest individual estimate (TL 4.6) (Figure 15). TL of *A. atlanticus* and *L. decagonus* were statistically correlated with fish length (r_s=0.60, p= 0.01 and r_s=0.85, p= 0.005, respectively). Four of the shortest fish samples within *A. atlanticus* demonstrated a TL ranging between 3.4-3.5 and the remaining fourteen fish samples were clustered at a trophic positioning of TL 3.9-4.2. The shortest fish sample from *L. decagonus* (5cm long) demonstrated a TL value of 3.7, which then increased to TL of 4.1-4.2 (6.5-8.5cm long individuals). The highest TL estimations were recorded by the largest *L. decagonus* specimens (13-18cm) at the trophic positioning of 4.5-4.6. *Myoxocephalus scorpius* displayed a narrow TL range (TL 3.6-4.3) and considerable spread within its TL values with fish length, and were thus not significantly correlated (r_s=0.36, p >0.2).

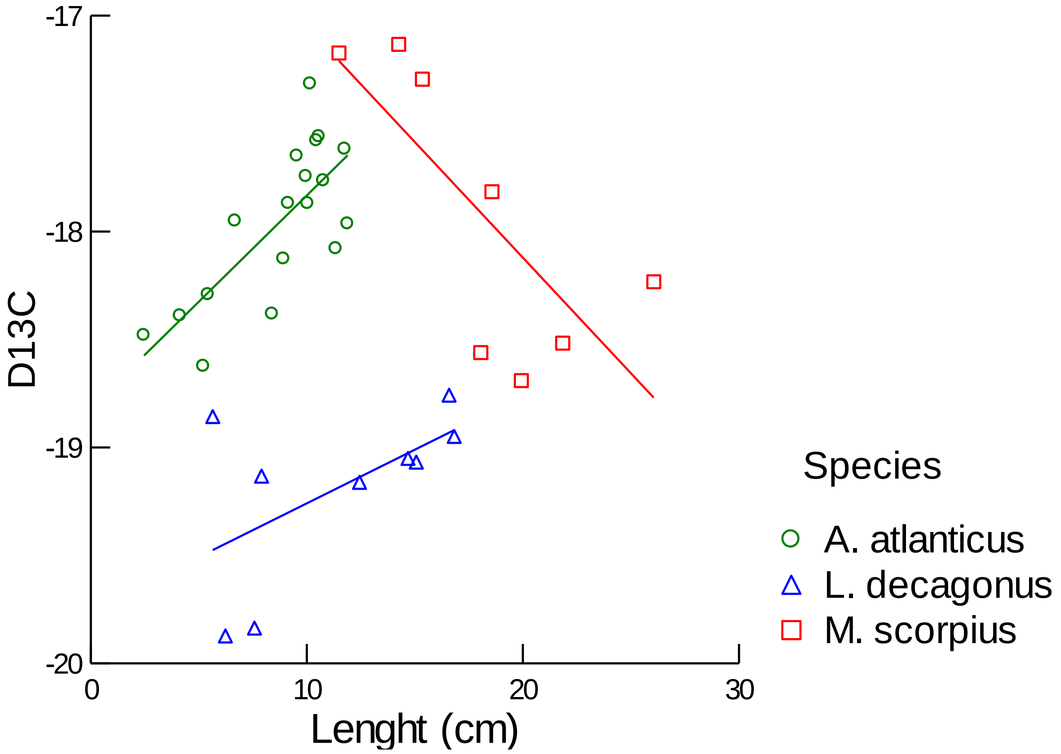

Figure 14: Changing δ13C signature with increasing total length within the three species muscle tissue.

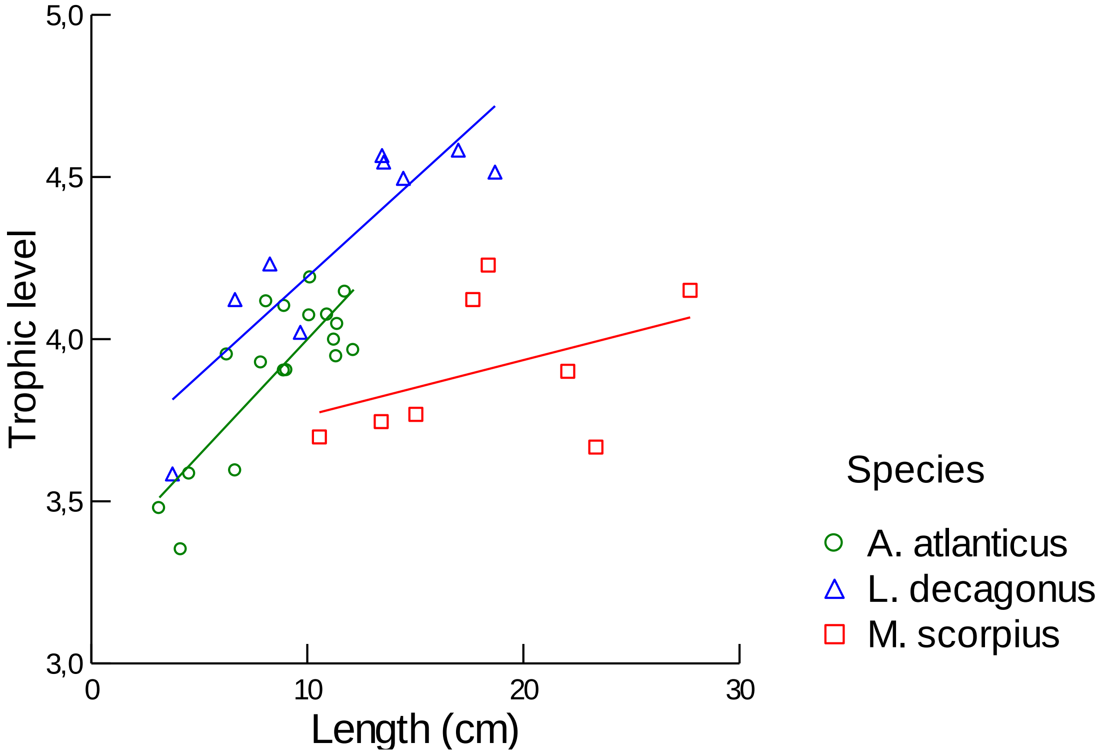

Figure 15: Trophic level (TL) estimation in relation to increasing fish length (cm) for the three species where *Chlamys islandica* (TL=2) was chosen as the baseline.

DISCUSSION

Data set

The data set for the current study was taken from a total of 171 fish divided over three species, with the number of individuals being heavily skewed towards one species; *A. atlanticus*, which accounted for over 50% of the entire sample population. Due to the number of individuals available, it was decided that all samples were to be pooled across sampling months and years in order to acquire a substantial sample population for analysis. Much scientific research today relies upon statistical tools to prove the effects of the study (Wang & Riffel, in press). However, analyses based upon small data sets have a lower statistical power and the chance of conducting a type II error increases (Zuur et al., 2009). Furthermore, pooling of data to sustain a sufficient data set might also result in loss of information on naturally occurring trends, which could be of biological significance (Cardinale, 2000). Hence, it has been suggested that sample sizes should have a minimal number range of 20-30 individuals in order to properly utilise statistical analyses (Wang & Riffel, in press). The restrictions reduce the credibility of the statistical analyses ability to explain the trends for the three species captured within Porsanger and the study proceeded with caution. Conclusions had to be on occasion based upon biological reasoning rather than statistical merits.

Many representations of the data were chosen to be presented in their raw form with smoothing parameters such as: linear trend lines or lowess functions in order to illustrate any patterns or trends present.

Population dynamics

The size structures for both sexes varied among the sampled species within Porsangerfjord, with the species mean length being lower than previously recorded (Andriyashev, 1964). For example, *M. scorpius* captured within Porsangerfjord had a maximum length of 27 cm, but have been recorded to grow to a maximal length of 38 cm around Europe on the eastern side of the Atlantic Ocean (Temple & Johnston, 1998; Cardinale, 2000; Luksenburg & Pedersen, 2002). However, lengths records from Newfoundland have reported a maximum length of 50 cm for *M. scorpius* (Ennis, 1970). The variance in size between geographical regions and fish communities will affect the species role and trophic relationships within that particular food web. For example, differences in community size structure of species allows the individuals to utilise different microhabitats for feeding (Bolnick et al., 2010) and this leads to avoidance of both intraspecific and interspecific competition (Cardinale, 2000). Furthermore, reproductive behavior and allocation of excess energy might also influence the sex's size structure within a species (Wootton, 1998).

The spawning time for *M. scorpius* around Tromsø occurs between January to March (Luksenburg & Pedersen, 2002; Luksenburg et al., 2004) but in already in the Barents Sea it begins as early as December. *Leptagonus decagonus* spawns in the Barents Sea between May-July (Wienerroither et al., 2011). However, *A. atlanticus* does not spawn until later in the year, usually late June (von Dorrien, 1993) to late September (Wienerroither et al., 2011). The difference in spawning time and thus, in the true beginning of the growth season is variable for the species and will have consequences for the HSI and GSI indices calculations. Bearing the true differences of spawning time in mind, the study still assumed that the theoretical growth season started in April and lasted until winter arrived in October.

The otoliths were surface read with reflecting light whilst submerged in water. However, the method of dry storage was not optimal since the otoliths had a tendency to crack as they dried. Hence, the difficulty in determining the accurate age declined with each reading due to time of dry storage.

Age is highly related to the fish ability to survive and grow larger, and the von Bertalanffy growth equation provided the parameters for *A. atlanticus in situ* length-age table within inner

Porsangerfjord. The von Bertalanffy growth equations can probably establish an accurate length-age table for sample sizes of 20-30 individuals (Bartoo & Parker, 1983). However, the study chose not to apply the model for *M. scorpius* or *L. decagonus* because of the small data sets and because it could generate unclear biological conclusions about them.

The estimated age for *A. atlanticus* in Porsangerfjord resemble that of previously captured specimens within the central Barents Sea (von Dorrien, 1993), although the length of the specimens from inner Porsangerfjord were recorded to be longer than individuals from the Barents Sea. The lengths for 8 year old *A. atlanticus* in Porsangerfjord ranged from 9-11.5 cm, whereas the 8 year old individuals in the Barents Sea were estimated to be 9.5 cm (Wienerroither et al., 2011).

The oldest *M. scorpius* (27 cm) in Porsangerfjord was a 7 year old male, unlike a similarly sized female (27.7 cm) in Frobisher Bay, Canada whom was recorded to be 19 years old (Dick et al., 2009). Nevertheless, studies in closer regions show that the length and age structure for *M. scorpius* in Porsangerfjord were comparable to the samples captured around Tromsø, Norway (Luksenburg & Pedersen, 2002).

In Porsangerfjord, the highest recorded age for *L. decagonus* was 7 years. A study from the Barents Sea suggests that 7 year old individuals have a length of 16-17 cm (Wienerroither et al. 2011). This is not the case in Porsanger where specimens of *L. decagonus* reached the same length within 3 years of life.

The current study demonstrated that the studied species had different mean sizes but similar overall age distributions, all the species recording a maximum age of 7 year old. This shows that all of the species under investigation had the ability to survive and grow close to its maximum size within Porsangerfjord. This information is of great significance when investigating the population dynamics of a system because it communicates that the species, although small in comparison to e.g. cod, were characterised by relatively long-lived individuals.

The study documented a significant difference in growth and body allometry between *L. decagonus* and the other two species; *A. atlanticus*, *M. scorpius* which were similar. The growth pattern shows that *L. decagonus* (b<3.0) retains a body allometry that provides the species with a slender body length, unlike the two cottids (b>3.0) which generate a bulky body. This is not surprising since *A. atlanticus* and *M. scorpius* belongs to another taxonomical family. Nevertheless, the two cottids differed in both maximum length and total body weight indicating that taxonomical classification is not enough to distinguish between the two species population dynamics.

Growth pattern, energy storage and age at maturity are highly plastic features within fish, and this is the reason why population dynamics are so important to understand when describing species interactions within a system (Wootton, 1998). Body allometry and growth patterns are highly important when analyzing a species because both will not only alter the species diet through ontogenetic shifts, but also its susceptibility to predators (Fuiman & Werner, 2002). The known predators present within Porsangerfjord is a local population of harbor seals (*Phoca vitulina*) which have only been shown to feed upon *M. scorpius* (Virginie Ramasco Institute of Marine Research, Tromsø, pers. comm.).

The study did note that both male and female *A. atlanticus* had an overall significant correlation in GSI with fish length, unlike the HSI which did not correlate with length. Species conditional state from energy reserves (HSI) and gonad proportion (GSI) could not provide any absolute descriptions for the studied species due to pooling of sampling seasons and years (Lambert & Dutil, 1997). However, female *A. atlanticus* have been found to mature between 3-4 years of age at a length of 6.5 cm (Wienerroither et al., 2011). This suggests that over 90% of the female *A. atlanticus* from inner Porsangerfjord were sexually mature and in the process of reproducing which concurs with personal observations from the laboratory procedures.

The GSI for *M. scorpius* within this study were less than 4 which indicates that all mature females (>14cm) were not in the process of spawning (Luksenburg et al., 2004). As previously discussed, the spawning season for *M. scorpius* is from December to March and since the vast majority of samples were caught during the summer months it is expected that females would be in a recovery state allocating their energy resources elsewhere. The HSI did further emphasise that the species were not reproducing since it recorded a significant correlation in energy storage with length for both sexes.

According to Wienerroither et al. (2011) all but two female *L. decagonus* captured within Porsangerfjord were sexually mature (fish length >11 cm) and since the GSI varied from 1 to 16 it was determined that the females were in the process of spawning or had already laid their eggs before capture. This is in accordance with the spawning season documented for the species within the Barents Sea (Wienerroither et al., 2011).

Both body allometry and growth patterns demonstrate that the species from the study differed from one another. The conditional state and maturity was also different for the species. Only *A. atlanticus* and *L. decagonus* maturity could be evaluated since the data were mostly collected during the summer months when these two species spawn, unlike *M. scorpius* whom has a spawning season in winter. Sexual maturity provides clues into the species life history and investment strategies of the excess energy derived from feeding (Kingdom & Allison, 2011). For example, the fish may choose to invest in growth to avoid predation, but the cost of the choice for somatic growth is: low or delayed first reproduction, which in return prevents the fish from distributing its gene pool through offspring. This information is of biological significance for understanding the population dynamics exhibited by the species, which also provides an inkling into the health condition of the individual, since growth and reproduction ultimately are based upon a successful feeding history.

Diet and trophic positioning

The stomach content analysis demonstrated that the three species had several overlapping prey categories within their diets. *Artediellus atlanticus* preferred polychaets, whereas *M. scorpius* fed mainly on fish and *L. decagonus* ate predominantly copepods. The findings from the study concur with Andriyashev’s (1964) previously published results on the species diets. Furthermore, the Spearman’s rank correlation demonstrated no significant correlation between the species diet and are thus, regarded as species specific. The preferences for a distinct prey category contribute to reducing the feeding overlap amongst the species (Sivertsen et al., 2006).

It is noteworthy to point out that the identification of the prey category ‘unidentifiable Crustacea’, would have the ability to further alter the prey frequency of occurrence (FO) values, thereby changing their overall FO within the species diets. Nevertheless, with the species strong preference for its main prey category, it is unlikely that the identification of the ‘unidentifiable crustacean’ category would alter the diet predictions radically and therefore not discussed further.

Dividing the species into length groups further emphasised the differences in diet between the species, as the Spearman’s rank correlation only demonstrated significant correlations within the species length groups but not across them. Here it is important to restate that the smallest *A. atlanticus* (3.5-7.5 cm) was not correlated to the preys FO along with larger individuals within the species, and this could be the result of a diet shift with increasing fish length. The present study did note a change in composition of the prey category Polycheata between smaller and larger individuals. Smaller *A. atlanticus* fed upon different polycheat families compared to larger individuals. This observed shift in targeted prey within the prey category could explain the observed diverging dietary patterns within *A. atlanticus* that lead to the functional separation of smaller and larger individuals within the ecosystem of inner Porsangerfjord.

The present study found that the *M. scorpius* captured within inner Porsangerfjord started feeding on fish from a length of 11 cm and that there were a statistical correlation in diet between small (<20 cm) and large (>20cm) individuals. However, it has previously been reported that *M. scorpius* undergoes an ontogenetic shift (fish length >21 cm) where the main type of prey changed from the crustacean *Mysis mixta* towards a herring- based (*Clupea harengus*) diet within the Baltic Sea (Cardinale, 2000). This was not the case in Porsangerfjord since *M. scorpius* documented a uniform diet regardless of fish length. This observation could be explained by an example from the three spined stickleback (*Gasterosteus aculeatus*), whom exerts prey segregation as a consequence of the individual’s persistent choice of prey and their specialisation within a microhabitat (Bolnick et al., 2010).

Diet (FO) for the two length groups *L. decagonus* were not statistically correlated when the Spearman’s rank coefficient was analysed against a critical value (α= 0.05). However, bootstrapping showed that the analysis with 95% confidence intervals (CI) did not overlap with zero. Therefore, the study chose to consider the diet of the two size groups of *L. decagonus* to be correlated with length. This reasoning was justified since the CI includes 95% of all cases that are normal values (Drummond & Vowler, 2011).

It was observed that the shorter *L. decagonus* individuals fed on smaller crustacean preys types compared to larger individuals. This is not surprising since prey size usually increases with increasing fish size (Cardinale, 2000). Another avenue to explain the changes in prey size is through morphological restraint such as gape (the size of the mouth), which will only become bigger with increasing body size (Wootton, 1998).

Observed stomach contents from the sample population suggest that the species have individual food chains within the food web of inner Porsangerfjord. The diet analysis demonstrated that the smaller individuals of *A. atlanticus* exerted a different predatory-prey relationship until the individual has grown sufficiently to make the functional change and adopt the predatory-prey interactions observed by larger individuals. Length appeared to be the criteria for *A. atlanticus* diverging diets, whereas the size of the mouth was the suggested reason for the dietary changes observed within *L decagonus*. Conversely, *M. scorpius* was the only species whom documented a uniform diet regardless of fish length within Porsangerfjord.

The study found that *A. atlanticus* and *M. scorpius* displays a more benthic source of $\delta^{13}C$ in their tissues compared to *L. decagonus* whom exhibit a $\delta^{13}C$ signature which was associated with carbon derived from the pelagic zone. These findings exclaim that all three species might be cohabitants, but that *L. decagonus* was dependent on and influenced by the changes in pelagic $\delta^{13}C$ flow. By consuming dietary carbon from another source, *L. decagonus* were successfully reducing the likelihood of interspecific competition with the other two species for prey.

Published literature does not always provide trophic level (TL) calculations from their stable isotope analyses and this makes it very difficult to compare species from different food webs and regions. When TL estimations are provided from a study, the baseline organism frequently used is zooplankton such as copepods. However, the ever-changing environment influences the δ^{15}N signature in these primary consumers. It is therefore favourable to utilise primary consumers with a longer life span, such as bivalves (Xu et al., 2011). Furthermore, use of benthic consumers provides a benthic baseline for food chains based upon particulate organic matter (POM) (Fukumori et al., 2008). For example, oysters such as: *Crassostrea gigas*, have a tissue turnover rate between 120-180 days and the blue mussel (*Mytilus edulis*) requires 333 days for its tissue turnover (Fukumori et al., 2008). These documented turnover rates in bivalves makes them comparable to the isotopic signatures in fish tissue and was the reason behind why this study chose to use *Chlamys islandica* for all trophic level calculations.

Two of the species; *A. atlanticus* and *L. decagonus* TL were significantly correlated with fish length, whereas *M. scorpius* demonstrated a great spread within its TL values with length. Nevertheless, the TL values from the study were similar for all species (TL 3.6-4.6) captured within inner Porsangerfjord. These findings correspond to previous studies TL estimations (2.9 to 4.7) from different species within the families Agonidae and Cottidae (Lesage et al., 2001; Gorbatenko et al., 2008; Nadon & Himmelman, 2010; Iken et al., 2010; Feder et al., 2011; Renaud et al., 2011) (Appendix 6). However, the lengths of the species from Porsanger (4-27cm) were shorter than the species used for previous research (19-55 cm). Nonetheless, the length differences appeared to be of lesser importance since the study documented comparable TL values with previous studies from around the world.

Isotopic δ^{13}C showed benthic origination within both *A. atlanticus* and *M. scorpius* muscle tissues, but of pelagic origin within *L. decagonus*. Despite differences in the dietary δ^{13}C origination within the system, all species did record similar trophic level estimations. Thus, suggesting that the species within inner Porsangerfjord have the same general function and trophic positioning within the food web.

The stomach content analysis resulted in correlation within species diets but not among them, and was opposed by the TL estimation which recorded overlapping values for all species within Porsangerfjord. It has been argued that when two species have the same trophic positioning within a system, they are competitors for the same prey at the next lower TL (Parrish, 1975). However, the origin of isotopic carbon from the fish tissues in the present study was derived from both the pelagic and benthic community. Here the stable isotope method could not provide further information about the complexity of trophic interactions without being used in conjuncture with other methods evaluating the diet directly, such as the stomach analysis (Post, 2002).

Artediellus atlanticus had fed on polychaets with benthic origin. Here, both the stomach content and stable isotope analysis demonstrated the same shift in species diet with length. Hence, the use of stable isotope analysis is preferable over stomach content analysis when the same trends will be observed individually for both analyses (DeNiro & Epstein, 1978). The reason for the author's argument was that visual observations of stomach contents are very time consuming and prone to considerable errors due to the differences in preys digestibility and evacuation rate from the stomach. However, if not for the combined diet analyses the *M. scorpius* diet predictions would not have been observed. *Myoxocephalus scorpius* did not record a statistical difference from the direct diet analysis with fish length. Nonetheless, the species did show from its isotope signatures that the dietary $\delta^{13}C$ was integrated from both the benthic and pelagic environments. Thus, although either method was adequate to show dietary shift in *A. atlanticus*, only one of them would not have been sufficient to explain the diet of *M. scorpius* in Porsangerfjord. It is important to remember that the origin of isotopic carbon can be told with the analysis, but the signatures cannot describe the prey consumed or their relative contributions to the observed diet (DeNiro & Epstein, 1978).

Leptagonus decagonus fed upon copepods, which according to its isotopic signature were of pelagic origin. However, the fish is known as a demersal species (Andriyashev, 1964). This raises the question of how the species can successfully feed in the pelagic environment from its benthic habitat. Another issue that needs to be addressed is why *L. decagonus* sustain such a high enrichment within its $\delta^{13}C$ signature and TL values if the main prey is copepods located at a very low TL. The observed enrichment could be the result of *L. decagonus* indirect dependence upon a detritus food web including both bacteria and meiofauna (McConnaughey & McRoy, 1979). A feasible explanation of how *L. decagonus* access copepods within its benthic habitat could be from sinking. For example, a dead copepod leaves the pelagic zone through sinking, and during its decent it becomes infested with bacteria. When it gets eaten by the fish it still sustains its origin of pelagic carbon, but will also enrich the consumer tissues through the presence of one or several bacterial intermediates, all of which are capable of enriching the $\delta^{13}C$ signature with 1.5‰. Thus, the food chain might be shorter due to stronger fractionations of the bacteria (McConnaughey & McRoy, 1979).

The diet analyses on the fish captured within inner Porsanger showed that the species had different diets, but the same overall trophic positioning. However, without the combined information produced by the stomach content and stable isotope analyses the results would not have been able to generate so many informative conclusions.

Conclusion

The current study revealed similar age distributions, but different mean lengths for the three species; *A. atlanticus*, *M. scorpius* and *L. decagonus*. The somatic growth was unique to the species and the indices, HSI and GSI, showed different patterns for the species. However, due to the pooling of the data set, these results should be interpreted with caution. The diet was found to be species-specific and similar regardless of length for all species, with the exception of the smallest specimens from *A. atlanticus*. Despite the observed differences in diet between the species, they all exhibited similar trophic level estimations. These results support the need for combined direct-diet analysis with stable isotope data to accurately reflect the trophic interactions within the food web. The demersal species within this study, although not commercially important, were proved to sustain ecological significance within the food web of inner Porsangerfjord. Further studies should focus on establishing more seasonally detailed population dynamics for all species. The pressing matter is to improve sampling techniques as well as gathering representative material throughout the year.

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APPENDIX 1

Table:

Thesis laboratory sheet used during identification and dissection of the fish species captured for the study.

Fish no. Date	Fish	Fish	Fish	Fish	Fish
Station no.					
Serie no.					
Sampling date					
Specie					
Length (cm)					
Total weight (g)					
Gutted weight (g)					
Sex					
Maturity estimate (scale 1-4)					
Stomach contense (scale 1-5)					
Stomach- intact (g)					
Stomach- empty (g)					
Stomach contense					

Explanation of stomach contense scale:
1= Empty
2= 25% contense or less
3= 50% contense or less
4= 75% contense or less
5= Full (100%) or stretched

Maturity scale: 1= Immature, 2= Mature, not reproducing, 3= Mature, actively reproducing 4= Senescent

APPENDIX 2

Table:

Weight-Length relationship values for the three species and their significance.

Species	**Sex**	**n**	**ln a**	**b**	**SE_b**	**r^2**	**F**	**p**
M. scorpius	f	22	-5.234	3.241	0.71	0.976	828.6	**<0.001**
	m	14	-4.980	3.159	0.88	0.993	1630.7	**<0.001**
	f+m	36	-5.036	3.175	0.54	0.989	2932.2	**<0.001**
A. atlanticus	f	70	-4.801	3.136	0.38	0.941	1080.3	**<0.001**
	m	40	-4.907	3.202	0.51	0.993	5506.3	**<0.001**
	f+m	110	-4.849	3.163	0.30	0.982	5933.7	**<0.001**
L. decagonus	f	14	-5.946	2.950	0.82	0.996	2809.9	**<0.001**
	m	9	-5.664	2.833	1.00	0.962	175.6	**<0.001**
	f+m	23	-5.796	2.894	0.62	0.992	2566.3	**<0.001**

APPENDIX 3

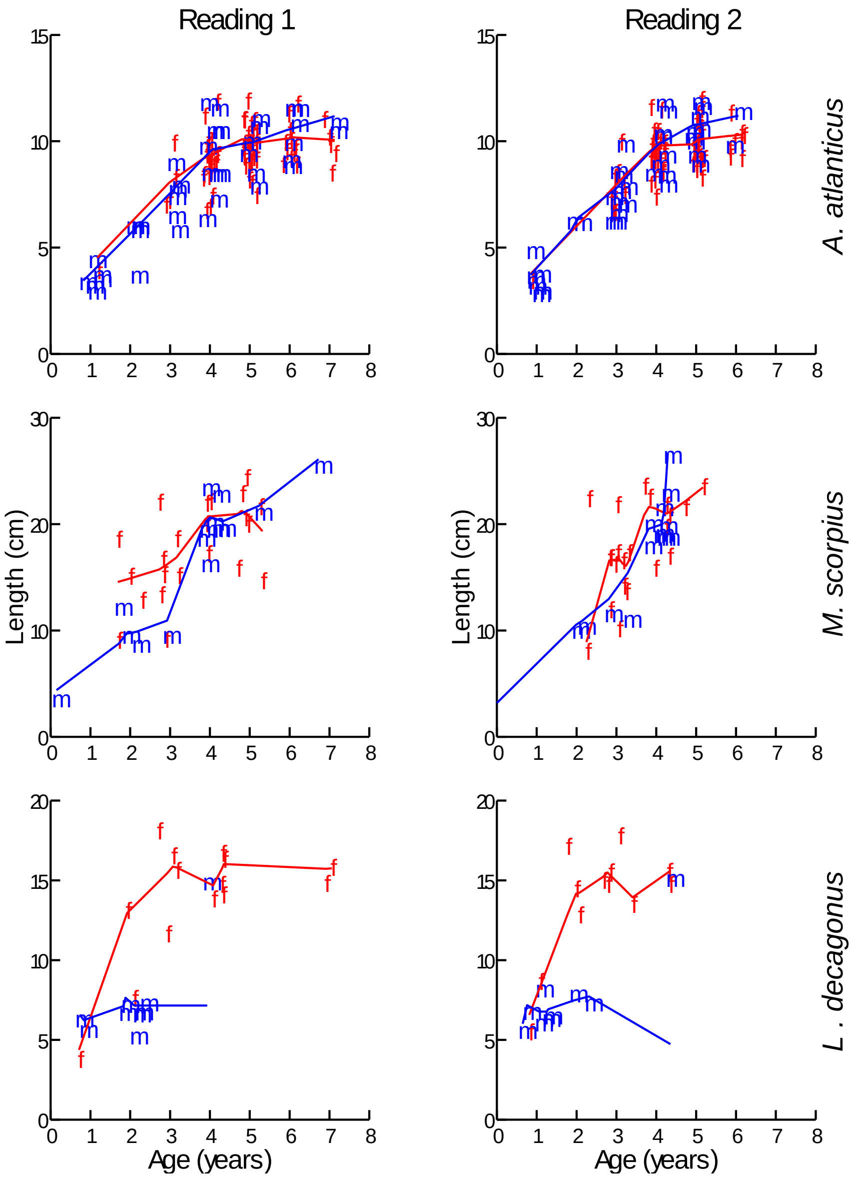

Figure: Length at age estimations, comparing the two readings where the species are represented by their respective sex; female (red) and male (blue).

APPENDIX 4

Table:

FO (%) for all prey categories digested amongst the three species

	Species		
	A. atlanticus (n=85)	*M. scorpius* (n=36)	*L. decagonus* (n=22)
Prey category			
Amphipoda	13.1	16.7	27.3
Copepoda	7.1	0.0	54.6
Decapoda	4.8	43.3	18.2
Isopoda	2.4	0.0	0.0
Euphausiacea	6.0	10.6	9.1
UnID Crustacea	4.8	16.7	36.4
Mollusca	13.1	3.3	0.0
Polychaeta	76.2	10.0	0.0
Pisces	0.0	50.0	0.0
Other	4.8	23.3	4.6

Colour index: Frequency of occurrence (%)

0	>0 to <20	>20 to <50	>50 to 100

APPENDIX 5

Table:

Correlation matrix for the species individual length groups where the Spearman's rank coefficient is statistically correlated at r_2=0.648 (α=0.05) with the percentile method, 95% confidence interval (CI). The correlated length groups were; *A. atlanticus* A2.A3 r_2=0.835 (low: 0.39, high: 0.98), *M. scorpius* M1=M2 r_2=0.830 (low: 0.45, high: 0.99) and *L. decagonus* L1=L2 r_2=0.617 (low: 0.12, high: 0.89).

	A1	A2	A3	M1	M2	L1	L2
A1	1.000						
A2	0.342	1.000					
A3	0.383	0.835	1.000				
M1	-0.556	0.032	-0.242	1.000			
M2	-0.355	0.194	-0.013	0.830	1.000		
L1	0.316	-0.115	-0.190	-0.091	-0.317	1.000	
L2	-0.292	0.065	-0.067	0.358	0.173	0.617	1.000

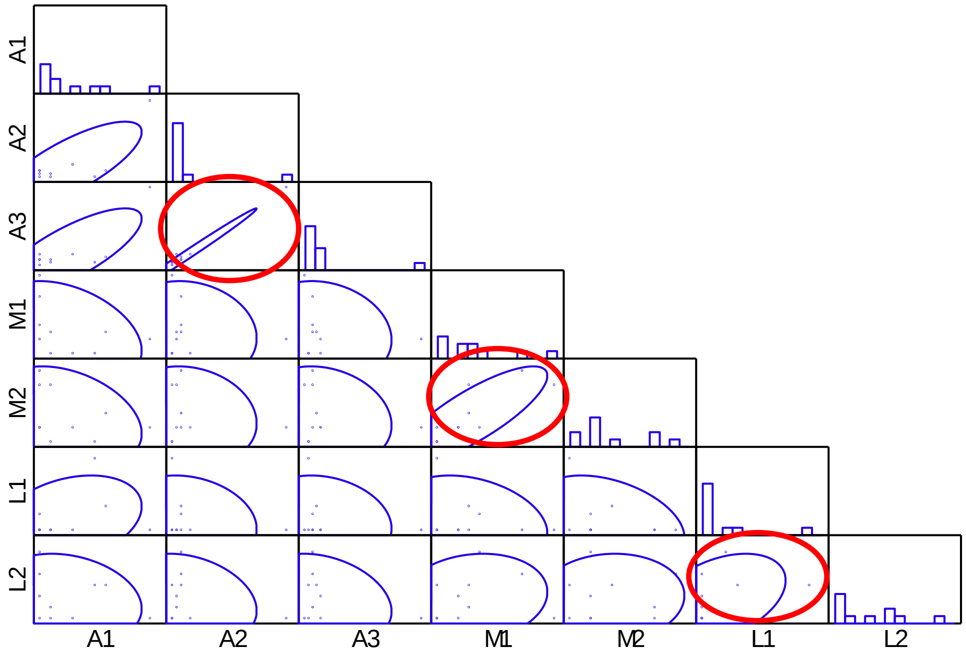

Figure: Scatter plot matrix of the Spearman's rank coefficient, where the red circles show the three correlated diet observed within the length-groups of the species.

APPENDIX 6

Table:

Comparison of stable isotopic signatures and trophic level calculations from several ecosystems around the world with the present study.

Geographical location (Reference, year)	**Specie (Family)**	**δ13C (± SD)**	**δ15N (± SD)**	**Trophic level**	***n***	**Length (cm)**
Porsangerfjord, Norway (Present study)	*Artediellus atlanticus* (Cottidae)	-17.28 to -18.64	12.53 to 15.23	3.4 to 4.2	18	3.5-12
	Leptagonus decagonus (Agonidae)	-18.74 to -19.95	13.55 to 16.62	3.7 to 4.6	9	5-18
	Myoxocephalus scorpius (Cottidae)	-17.04 to -18.67	13.58 to 15.76	3.6 to 4.3	8	10.5-27
Gulf of St. Lawrence (Lesage et al., 2001)	Cottidae	-16.7 ±0.9	14.4 ± 0.4	3.9	2	19.6-20.5
	Cottidae	-17.4	15.8	4.3	1	28
	Cottidae	-18.8 ± 0.5	15.2 ± 0.1	4.1	3	21-26.5
	Cottidae	-18.2 ± 0.9	16.1 ± 0.2	4.4	4	28-30.1
	Cottidae	-18.5 ± 0.3	17.0	4.7	2	32-32.7
Western Bering Sea (Gorbatenko et al., 2008)	*Myoxocephalus polyacanthocephalus (Cottidae)*	-15.58 ±0.3	16.69 ± 0.6	4.4	3	37-55
	Gymnacanthus galeatus (Cottidae)	-16.2 ± 0.7	15.12 ± 0..9	3.9	3	28-36
	Hemilepidotus gilbert (Cottidae)	-15.74 ± 0.2	15.63 ±0.6	4.0	3	25-34
	Hemilepidotus jordani (Cottidae)	-15.79 ± 0.2	15.32 ± 0.2	3.9	3	31-44
	Triglops forficatus (Cottidae)	-17.55 ± 0.1	12.08 ± 0.3	3.0	2	20-27
Southern Chukchi Sea (Iken et al., 2010)	*Artediellus scaber* (Cottidae)	-18.88 ± 0.04	16.24 ± 0.69	3.8	3	--
	Artediellus scaber (Cottidae)	-17.94 ± 0.26	15.80 ± 0.37	4.0	3	--
	Myoxocephalus polyacanthocephalus (Cottidae)	-18.13	15.52	3.6	1	--
	Myoxocephalus scorpius (Cottidae)	-19.06 ±0.33	16.54 ± 0.42	3.9	9	--
	Myoxocephalus scorpius (Cottidae)	-18.72 ± 0.25	12.04 ± 0.36	2.9	3	--
	Triglops pingelii (Cottidae)	-18.97 ± 0.50	16.29 ± 0.65	3.8	5	--
	Triglops pingelii (Cottidae)	-18.94 ± 0.18	14.15 ± 1.23	3.5	2	--
Northern Gulf of St. Lawrence (Nadon & Himmelman, 2010)	*Myoxocephalus scorpius* (Cottidae)	-16.8 ± 0.5	13.7 ± 0.3	3.5	6	--
Southeastern Chukchi Sea (Feder et al., 2011)	Unidentified sculpin	-19.61	14.07	--	1	--
	Unidentified sculpin	-18.71	16.6	--	1	--
Konsfjorden, Svalbard (Renaud et al., 2011)	*Myoxocephalus scorpius* (Cottidae)	-17.5 ± 0.5	13.7 ± 0.5	4.0	6	--
	Gymnocanthus tricuspis (Cottidae)	-17.6 ± 0.6	13.8 ± 0.7	4.0	6	--
	Leptagonus decagonus (Agonidae)	-18.3	15.0	4.3	1	--
	Myoxocephalus scorpius (Cottidae)	-17.8 ± 0.8	14.2 ± 0.7	4.1	7	--
	Gymnocanthus tricuspis (Cottidae)	-18.2 ± 0.7	14.3 ± 0.9	4.1s	6	--