Faculty of Biosciences, Fisheries and Economics

Department of Arctic and Marine Biology

Epibenthic Fauna in Balsfjord

Potential food for the invasive red king crab (Paralithodes camtschaticus) with special attention to the deposit-feeding sea star Ctenodiscus crispatus.

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BIO-3950 Master thesis in Biology, May 2017

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Supervisor

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Front page photo of Balsfjord

By Caroline Aas Tranang 2016

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Caroline Aas Tranang

Abstract

After its introduction to the Barents Sea in the 1960's, the red king crab *Paralithodes camtschaticus* has become an invasive species in northern Norwegian fjords and it is continuing to spread southward along the coast. Due to its negative effects on native benthic fauna through predation, establishing baseline studies in undisturbed fjords is important. In this study, the soft-bottom epibenthic macrofauna (> 5 mm) was investigated at four localities in Balsfjord, south of Tromsø, aiming at discussing potential prey for the red king crab. Samples were collected from the inner, outer and middle part of the fjord. The differences in species composition and biomass were linked to environmental conditions, biotic factors and general patchiness of benthic fauna. The similarities to invaded fjords, and observations of the red king crab in Balsfjord suggests that an invasion most likely will occur and the crab might reach high population densities in the next few years.

An important prey item for the king crab is the mud star *Ctenodiscus crispatus*, which is a dominating species in northern Norwegian fjords, including Balsfjord, but whose abundance is strongly reduced in invaded areas. Little is known about its population dynamics, but this study attempts to provide some answers. Size-frequency distributions of mud stars collected during the year revealed no major recruitment events and were consistently dominated by a large mode of adult individuals, probably of many age classes. Low numbers of newly settled juveniles were observed between March and June, which could confirm spawning during mid-winter, suggested by previous studies. Patterns varied between investigated areas which indicates that depth, environmental conditions and biological interactions influence spawning, recruitment, growth and size-structures.

Key words: Epibenthos • Macrofauna • *Ctenodiscus crispatus* • Introduced species • Red king crab (*Paralithodes camtschaticus)* • Population structure • Reproduction • Northern Norway

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1. Introduction

Balsfjord is one of the most investigated fjords in northern Norway and has received the attention of marine scientists for more than a century. One of the earliest descriptions of the benthic fauna was provided by Hans Kjær, who during a 3-year period collected samples from the fjord and described the species compositions of different habitats, from the littoral zone to the deep soft-bottom (Kjær 1905). Due to the high abundance of deep-water shrimps (*Pandalus borealis*, Krøyer 1838) he discussed the opportunities for a commercial fishery of this species. He argued for a profitable fishery, provided increased knowledge of the capture procedure (Kjær 1903). In 1931, commercial harvests began and in the next few years an increasing export to France, England, Belgium and Sweden provided a profitable fishery (Hjort and Ruud 1938). However, due to concerns regarding bycatch of cod, shrimp trawling at depths less than 200 m was banned in 1983 (Hopkins and Nilssen 1990).

In the mid-1970's, a multi-disciplinary research programme, "the Balsfjord project", was established with the purpose of describing the biological production/energy flow in a high-latitude fjord ecosystem (Hopkins et al. 1989). Field and experimental studies were conducted on fish, shell-fish, zooplankton, phytoplankton and hydrography (Eilertsen et al. 1981; Klemetsen 1982; Eilertsen and Taasen 1984; Hopkins et al. 1984; Hopkins 1987). The results of these and more recent studies of biological production in Balsfjord (Wassmann et al. 1996) concludes that due to grazing along with periodically extensive advection of water masses, most of the spring bloom is mineralised in the pelagic food chain or transported out of the fjord. It has been estimated that less than 1 % of the annual carbon production reaches the sea floor and the organic material is mostly in the form of krill pellets which are quickly catabolised by micro-organisms in the sediment (Sargent et al. 1983b; Hopkins et al. 1989; Lutter et al. 1989). Analyses of sediments from the Svartnes basin concurs these results as they revealed a major composition of fatty acids characteristic of microorganisms and little planktonic material (Sargent et al. 1983b).

The most extensive benthic study from Balsfjord is Eivind Oug's (2000) long-term monitoring survey of the Svartnes basin (185 m), where numerous grab samples were collected between 1977 and 1994. He described the infaunal species assemblage as being relatively homogenous and clearly dominated by annelids (mainly polychaetes) in terms of abundance and deposit-feeders in terms of trophic position (Oug 2000). Similar benthic communities have been described for basins of other northern Norwegian fjords (Larsen 1997; Holte 1998). Other benthic studies in Balsfjord includes a description of the vertical species distribution of the rocky hard-bottom in Balsfjord (Haugbergnes) based on photographs taken at different depths (Evans et al. 1980; Sandnes and Gulliksen 1980).

Systematic descriptions of the epibenthic soft-bottom communities in Balsfjord are however missing. The epibenthos has generally received less attention than the infauna, mostly due to sampling difficulties (Rees et al. 1999), but several surveys describing the diversity of epibenthic communities have been conducted in the North Sea (Jennings et al. 1999; Zühlke et al. 2001; Callaway et al. 2002).

The faunal structure of benthic communities reflects the environmental conditions of the habitat. Many benthic species are characterised by longevity or low mobility, which makes them good indicators of impacts from disturbances such as heavy trawling and pollution from e.g. oil activities and sewage discharge (Callaway et al. 2002; Velvin et al. 2013). Regularly monitoring is important to detect changes in the community structure caused by disturbances, including invasive species. A baseline study providing information of community species composition, interactions and processes, accounting for natural spatial and temporal variation, should ideally be established prior to a disturbance if changes are to be related to it. When these are missing (which is often the case), comparing the disturbed site with control or reference locations is an alternative (Underwood and Chapman 2013). Benthic monitoring of soft-bottoms has traditionally focused on the infauna, due to easier sampling procedures (e.g. grabs) and the opportunity to obtain good quantitative data, but the importance of including epibenthic fauna has been discussed by Jørgensen et al. (2011).

Balsfjord is currently threatened by an invasion of the red king crab, *Paralithodes camtschaticus* (Tilesius, 1815). After the first reported finding in 2007, observations have been made on a regular basis. Crabs of both sexes and various sizes have been found in inner and outer parts of the fjord (Kyst og fjord 2016). The red king crab is native to the North Pacific Ocean, but is now well established in the southern Barents Sea. The invasion of this large decapod is the result of an intentional release of a vast number of larvae, juveniles and adult crabs by Russian scientists between 1961 and 1969. The majority of crabs were collected from Peter the Great Bay in the Sea of Japan and released in the Kola fjord in the east Barents Sea with the purpose of establishing a commercial fishery that could improve local economy and living standards (Orlov and Ivanov 1978; Jørgensen and Nilssen 2011).

Invasive species are considered to be one of the greatest threats to global biodiversity together with habitat degradation, population growth, pollution, climate change and over-exploitation of resources (Gray 1997). Introduced species can have severe negative impacts on native populations and communities through interspecific interactions such as predation and competition or they can inflict physical disturbances to the habitat. Ultimately, production and key ecosystem functions may be altered with potential implications on human health and economy (Ruiz et al. 2000; Simberloff et al. 2013).

The ability of an invasive species to become successfully established in a non-native area is often reflected in their life history strategies. The red king crab is characterized by large body size, longevity, high fecundity and mobility. They can tolerate temperatures between -1.7 and 15°C, dependent on their life stage. The larvae are pelagic before settling in shallow kelp beds, while adults reside in the deep soft-bottoms except during breeding season (Rodin 1990; Jørgensen and Nilssen 2011; Sundet 2014). The crab is an active predator and feeds either by tearing apart larger prey items or by scooping up sediments with their lesser chela from which they can filter out organisms. Adult crabs are omnivorous opportunistic feeders on the most abundant fauna (Jørgensen 2005).

Comparative studies of macrobenthic biomass composition in Varangerfjorden before and after the invasion of the red king crab discovered a drastic reduction of previously dominating species. Both species diversity and abundance had significantly decreased, although some small species of bivalves and polychaetes seemed to have become more abundant (Oug et al. 2011). Several stomach content and feeding studies have been conducted on red king crabs from both native and invaded areas (Cunningham 1969; Tarverdieva 1976; Feder & Paul 1980; Jewett and Feder 1982; Sundet et al. 2000; Jørgensen 2005; Fuhrmann et al. 2017). The results of these studies emphasize their omnivorous feeding behaviour as everything from phytoplankton to fish was represented in the stomach content. Dominant prey groups included bivalves, gastropods, barnacles, echinoderms and polychaetes and were found to vary between areas, depths, size groups, seasons and sexes (Jewett and Feder 1982; Sundet et al. 2000).

One of the species being preyed upon by the king crab is the deposit-feeding mud star (*Ctenodiscus crispatus,* Retzius 1805) (Oug et al. 2011). It is a common species in clayey silt soft-bottom communities and it often constitutes a large fraction of the local macrobenthic biomass. The mud star is stenothermic and considered to have an arctic-circumboreal distribution (Figure 1), but observations of the mud star have been made as far south as Panama, though southern populations occur at greater depths than northern populations (Grainger 1966;

Shick et al. 1981b). Despite its widespread distribution and abundance, there are only a handful of studies focused on this species. Although they have provided insights to *C. crispatus*' morphology (Turner 1971; Turner and Dearborn 1972), physiology and reproduction (Shick et al. 1981a; Falk-Petersen 1982a; Sargent et al. 1983a), there is a lack of knowledge regarding population dynamics, including growth rates and age classes.

Figure 1. Global distribution of *Ctenodiscus crispatus.*

According to Scheltema (1994), size class distributions have been useful to assess temporal reproductive patterns in many benthic invertebrates. In bivalves, bony fish, echinoids and ophiurids, information on age and growth can often be obtained by studying growth rings. Growth curves fitted to growth ring measurements in several species of brittle stars gave estimations of population age-structures that corresponded well to those obtained from size-frequencies of measured disc diameters (Gage 1990). In echinoids, growth rings arise when newly formed calcareous plates are added on to existing plates. Skeletal growth in asteroids occur in the same fashion, but growth rings have not been discovered (Crump and Emson 1978; Nauen and Böhm 1979). Thus for asteroids, the designation of distinct size- or age classes based on growth rates has proven to be difficult.

In their study of skeletal growth in *Asterias rubens* (Linnaeus 1758), Nauen and Böhm (1979) discovered three distinct growth stages, from which they inferred that sea stars equal in size, may not be the same age. Thus, at least for this species, they advise against the application of size-frequency analysis as a means to determine age-classes due to the risk of erroneous conclusions. The three growth patterns in *A. rubens* were also discovered by Guillou et al. (2012). They attempted to analyse modes in the size-frequency distribution of different populations, but were only able to appoint two modes, juvenile and adult sea stars.

As a part of their study on genetics and reproduction in *C. crispatus*, Shick et al. (1981a) performed a size-frequency analysis on the Damariscove Island population. The mud stars exhibited a continuous and normal distribution, and the authors were unable to detect distinct size classes in the population, neither for adults nor juveniles. They hypothesized that this was the result of substantial genetic variation in the population and highly variable individual growth rates in mud stars, a trait shared by other asteroids. In his investigation of benthic fauna in Balsfjord, Kjær (1905) measured the length of 50 mud stars, which graphically displayed a bimodal size-frequency distribution. He speculated that the two peaks represented two age-classes.

Genetic studies have not been conducted on the mud star population in Balsfjord, but their reproduction based on histological studies have been investigated by Falk-Petersen (1982a). Low variability in gonad index, asynchronous oocyte development and continuous presence of gametes lead to the suggestion of aseasonal and continuous reproduction in this species. Similar results were demonstrated for mud stars in Maine (Damariscove Island) and Newfoundland (Conception Bay) (Shick et al. 1981a; Jaramilo 2001). If they really do have continuous, asynchronous reproduction, age groups cannot be determined from size-frequency distributions (Gray and Elliot 2009) which has been done for e.g. deep-water shrimps from Svartnes in Balsfjord (Hopkins and Nilssen 1990).

The continuous presence of mature gametes suggests that the supply of quality food is constant (Shick et al. 1981a). Sediment analyses from Balsfjord and Damariscove Island revealed a stable composition and a mean organic content (% of sediment dry weight) of 9.3 and 9.7 respectively, with low interannual variation (Shick et al. 1981b; Sargent et al. 1983b). However, the Balsfjord population showed a reproductive peak mid-winter, while the Conception Bay and Maine populations had intensified reproduction shortly after phytoplankton blooms (Shick et al. 1981b; Falk-Petersen 1982; Jaramilo 2001). Jaramilo (2001), suggested that spawning is influenced by temperature and that increased food quality and quantity from sinking phytodetritus may result in intensified gamete production and spawning.

In this study, samples of epibenthic fauna were collected from several locations, at different depths between the inner and outer part of Balsfjord. The aim is to describe the epibenthic communities in terms of which taxa are present and which are dominating in the soft-bottom areas of the fjord. It is expected that the epibenthic fauna resembles that of other northern Norwegian fjords, with variations according to depth and position in fjord. Species composition, abundance and biomass will be compared between stations and related to environmental parameters including depth, substrate, temperature and food supply. Based on knowledge regarding prey species and effects of king crab invasion in other sub-arctic fjords, potential prey and key species for future monitoring will be discussed. The results can be implemented in a more extensive baseline study for further monitoring of the benthic communities in Balsfjord which should include sediment analyses, infaunal communities and studies of population dynamics and ecology of individual species.

Particular attention will be given to the mud star *Ctenodiscus crispatus*, as this is an important prey species for the red king crab and their life history is rather unknown. They may play a key role as habitat modifiers and information on their population dynamics could be helpful in predicting their recovery from a disturbance. A methodology for the processing of mud stars will be established and statistical methods for the analysis of size data will be explored. The main focus will be determining the best size measurement, assessing the relationship between different length measurements and the weight-length relationship and analysing size-frequency distributions.

2. Materials and methods

2.1 Study area

The northern Norwegian coastline is characterised by numerous fjords stretching several kilometres inland. The fjords are topographically diverse, but their hydrography is influenced by the same regional and local forcings such as wind fields, currents, turbulence and tides. Climatic factors including temperature, precipitation and wind are largely controlled by the North Atlantic Oscillation (NAO) (Mankettikkara 2013). There are two major currents influencing northern waters. The Norwegian Coastal Current (NCC) originates from the Baltic Sea and follows the Norwegian coast to the Barents Sea. The NCC carries water masses that are relatively cold and fresh, due to its brackish origin and input of low-salinity water from the North Sea and freshwater from rivers along the coast. It constantly mixes with warmer and more saline Atlantic Water (AW) from the adjacent Norwegian Atlantic Current (NAC) as it proceeds northwards (Mankettikkara 2013). Due to the influence of Atlantic Water, the sub-arctic high-latitude fjords of northern Norway have relatively high temperatures, and are for the most part ice-free throughout the year (Wassmann et al. 1996).

An important feature that separates northern fjords from those further south is the degree and duration of stratification. During winter, most of the northern fjords have an unstable water column that enables vertical mixing and exchange of water masses with the outer coast, facilitated by the prevailing Bora winds (Eilertsen et al. 1981; Mankettikkara 2013). The precipitation is low compared to further south and freshwater is usually stored as snow and ice on land. The shallow pycnocline arising in late spring is mainly caused by the differences in salinity resulting from snow melt rather than increasing temperatures (Mankettikkara 2013). The absence or presence of sills determines the extent of water mass exchange that can take place between the fjord and the outer coast, and thus particle fluxes and water mass properties (Wassmann et al. 1996). Extensive mixing due to the limited strength and duration of stratification is likely a contributing to factor to why northern fjords in general are well oxygenated while many boreal fjord-basins are prone to suffer from hypoxia (Larsen 1997; Holte et al. 2005).

The present study was carried out in Balsfjord (69°13’N - 69°60’N) (Figure 3) which is located south of Tromsø, northern Norway and has a south-southeast orientation. The fjord is approximately 45 km long and has a maximum depth of 195 m in the Svartnes basin which has a length of about 12 km (Sargent et al. 1983b). Balsfjord is a single-basin fjord, separated from the outer coastal waters by three sounds: Tromsøysundet, Sandnessundet and Rystraumen, with respective sill depths of 8, 9 and 30 m (Eilertsen et al. 1981; Mankettikkara 2013). The narrow sills restrict the exchange of water between Balsfjord and the outer coast, but in early spring there is an inflow of coastal water passing through Kvalsundet in the north and Rystraumen in the west, resulting in a renewal of the deep basin-water that keeps the fjord well oxygenated with a saturation level of 70-120 % (Eilertsen et al. 1981). Salinity is between 32.80 and 34.00 ‰, annual sea temperature varies between 1 and 7°C, while the bottom temperature remains in the range of 1-4°C (Eilertsen et al. 1981). The low temperatures are mainly due to the limited water mass exchange (Oug 2000).

2.2 Hydrography

The University of Tromsø has a permanent station in the Svartnes area where hydrographical variables, i.e. temperature, salinity, density and in vivo fluorescence are collected regularly using a SBE 911plus CTD (Seabird Inc.). Long-term hydrographical trends in Balsfjord are described in great detail in the doctoral dissertation of Rahman Mankettikkara and in the master thesis of Nina Henriksen (Mankettikkara 2013; Henriksen 2015).

Isoplots of temperature and salinity from 2015 and 2016 are presented (Figure 2). The bottom temperature (~170 m) was relatively constant throughout the year. Colder bottom temperatures were recorded in 2015 (3.1 - 4.7 °C) with an average temperature of 3.6 °C, compared to 2016 (3.3 - 4.3°C) with an average temperature of 4.0 °C. The water column was quite homogenous in regards to temperature between January and April, before surface warming during spring and summer. During autumn, there was a sinking of warm water masses, consistent with the decrease of stratification (Figure 2a). However, temperatures were not measured every month during these two years, thus the results presented here may be somewhat inaccurate, although they give an overall view of the temperature regime during the year. The observed bottom temperatures were relatively high compared to earlier years (Mankettikkara 2013; Henriksen 2015), which is further discussed in section 4.1.

Bottom salinities (Figure 2b) were lowest during winter followed by an increase in April/May resulting from the exchange of basin water which usually occurs during spring (Mankettikkara 2013). The surface salinity dropped markedly during summer due to snow-melt and run-off.

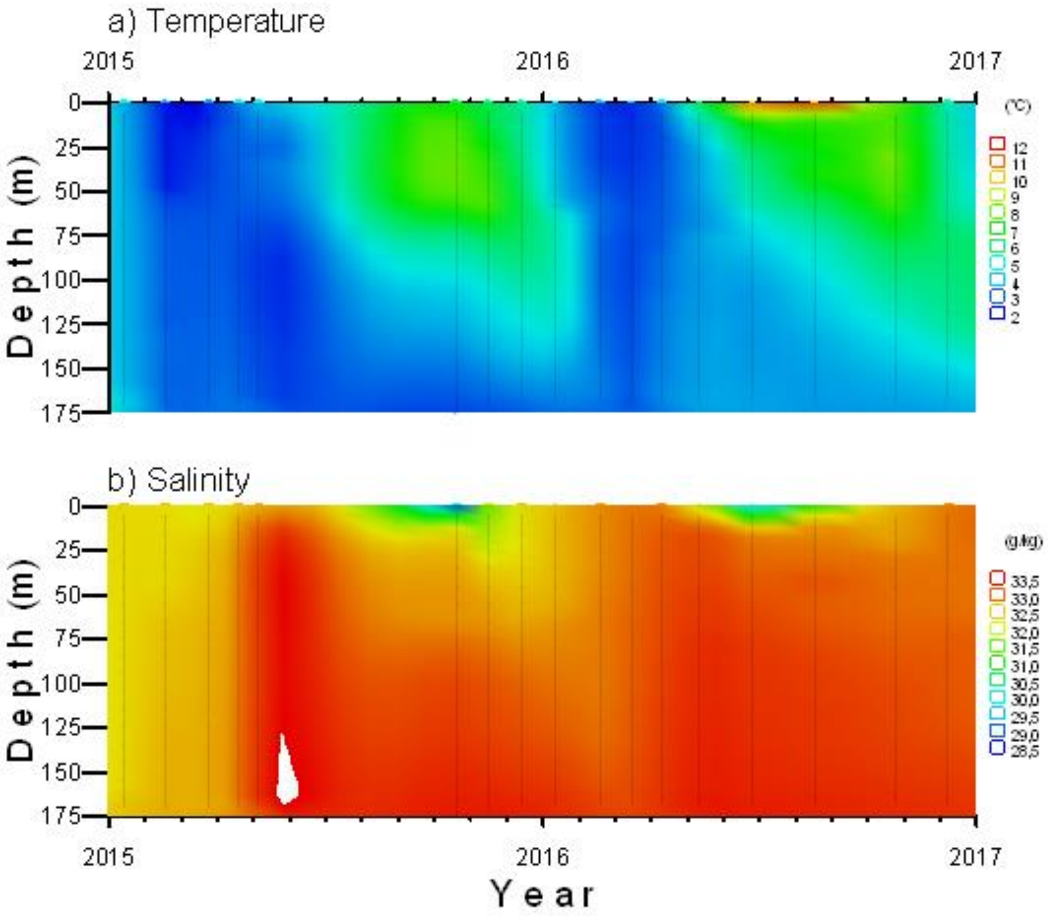

Figure 2. Svartnes, Balsfjord 2015-2016. Isoplots of temperature (a) and salinity (b). Lines represent months with recorded data. No data were available for June-September 2015 and July, September and November 2016. Non-coloured area is due to the combined effect of missing data and the interpolation routine.

2.3 Field work

Sampling took place between March and October 2016 during cruises with R/V Johan Ruud. Epibenthic fauna was collected using a newly acquired 2m beam trawl, which design was based on the trawl described by Jennings et al. (1999). The trawl was fitted with an outer 20 mm mesh and an inner mesh of 4 mm (cod-end). A chain mat was attached to exclude rocks. A SCANMAR© depth/height sensor was attached to the trawl. The sensor measures the depth of the trawl as its distance from the surface or its distance (height) from the bottom. These data gave indications of towing distance, based on when the trawl was reaching and leaving the seafloor. A detailed description of the beam trawl construction supplied with illustrations can be found in Jennings et al. (1999). Since the trawl had never been used, a few trial hauls were conducted in the field (Ramfjord, March) from which a few adjustments were made. Beam trawl efficiency is discussed in section 4.3.

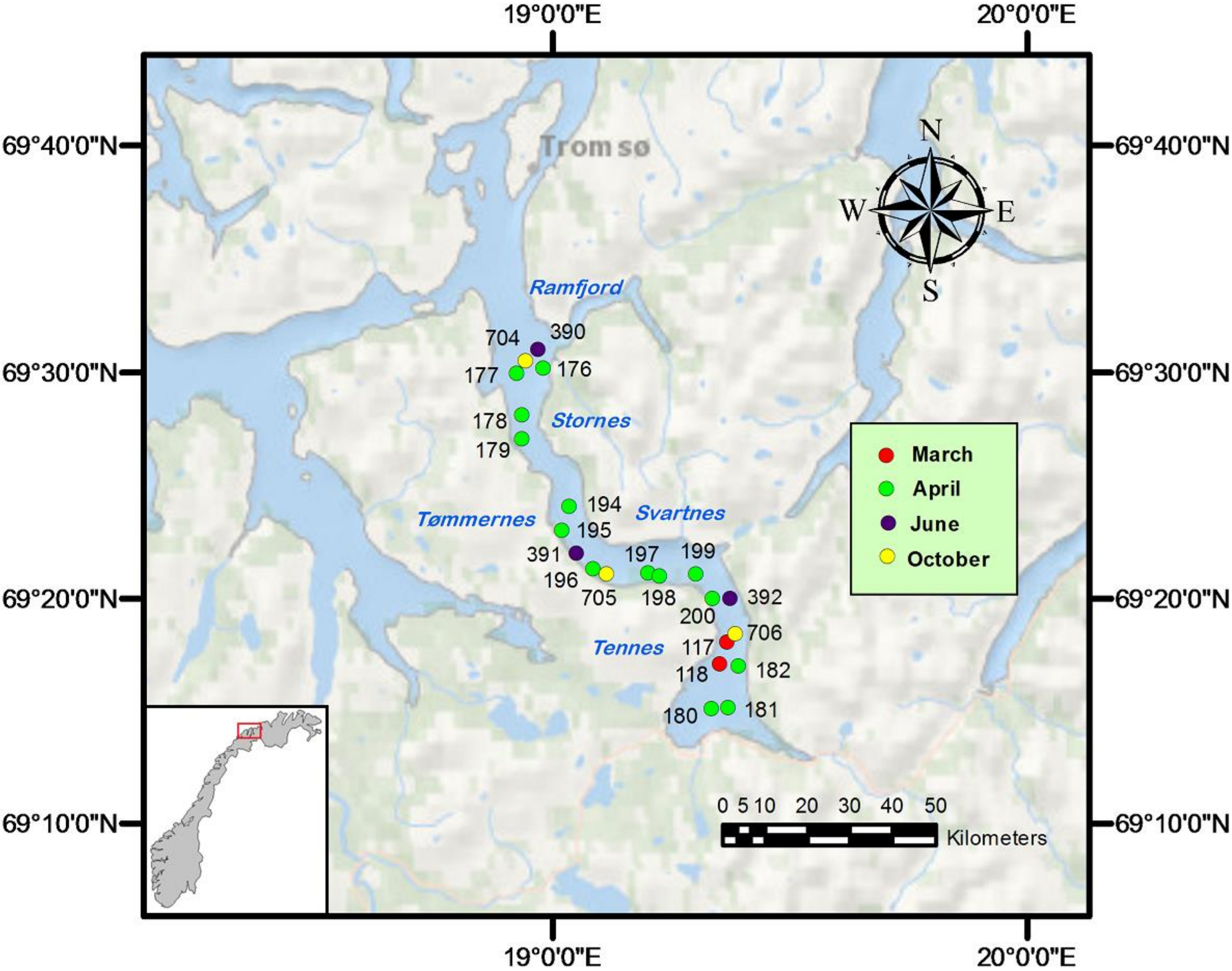

Figure 3. Beam trawl sampling stations in Balsfjord 2016.

Samples were taken at depths of 84 to 187 m in several parts of the fjord (Figure 3, Appendix Table 1). At each station, the trawl was hauled for approximately five minutes, with a speed of 0.5 knots. Hence, the area covered by each haul was calculated to be 150 m^2. One trawl haul represents one sample and 22 samples were collected in total. At all stations, the full fraction (1 mm and 5 mm) of the sample was preserved, except for St. 181 where only 50 % was kept due to an excessively large sample. Samples were carefully washed and sieved through 5 and 1 mm round steel mesh using an integrated sieve table similar to the one illustrated in Rumohr (1999). Mud stars were taken out from the 5 mm fraction of the sample and frozen in plastic bags. Other large species were occasionally sorted out and weighed (wet weight) on board. Remaining fauna was transferred to buckets which were either frozen or added 4% buffered formalin for preservation. The 5 mm and 1 mm sieve fractions were kept separately.

During the sampling period, crab cages were regularly put out in the fjord in order to monitor the occurrence of the red king crab.

2.4 Data treatment

2.4.1 Data transformations

Data transformations are useful to better meet the assumptions (i.e. normality and homogeneity of variance) of statistical tests as they stabilize variances and reduce skewness of distributions (Bakus 2007). For weight and morphometric data (L1, L2 and L3 length), logarithmic transformations are recommended (Whitlock and Schluter 2015). The natural logarithmic scale (ln) is often used, and this scale transformation was applied for length-and weight measurements of mud stars. Length measurement relationships was analysed on both untransformed and ln-transformed data to see the effects of data transformation. Length data does not necessarily need to be transformed because the spread of values is low. Weight data on the other hand, often have a larger spread of values, with several orders of magnitude and increasing variability with weight. Ln-transformation provides a scale in which the smaller values are more spread. When analysing the allometric relationship between weight and length, both variables should be log-transformed to linearize the relationship (Quinn and Keough 2002).

2.4.2 Linear regression

Linear regression is used to assess the relationship between two numerical variables. The aim is to see if an independent variable (X) can predict the outcome of a dependent variable (Y) and how well the independent variable explains the variability in the dependent variable (Whitlock and Schluter 2015). The general equation for the relationship between X and Y is:

$$Y = a + bX + \epsilon$$

where a and b are the intercept and the coefficient estimate (slope) of the regression. A single linear regression assumes linearity, normality and homogeneity of variance of residuals (Logan 2010). The null hypothesis of a linear regression states that there is no linear relationship between X and Y, i.e. the slope is *not* different from zero:

$$H_0\colon b = 0$$

In this study, linear regression was used to analyse the relationship between length measurements, the weight-length relationship and the wet weight-dry weight relationship of *Ctenodiscus crispatus*.

Regarding length measurements, the first round of measurements was chosen. The relationship between dry weight and length was analysed on ln-transformed data. The standard allometric equation for predicting weight (W) at length (L) is (De Robertis and Williams 2008):

$$W = a\, L^{\,b}$$

By transforming the weight and length measurements to the natural logarithmic scale the equation is linearized to the form of the linear regression model:

$$\ln W = \ln a + b \ln L$$

2.4.3 Segmented regression

Segmented regression is an approach to analyse models where the relationship between the explanatory variable and the response variable is piecewise linear, i.e. consists of two or more straight lines joined at an unknown value (breakpoint) (Muggeo 2008). The segmented package developed for R provides the means to estimate the breakpoint, and plot the results via iterative procedures. Length measurement relationships and the weight-length relationship of *Ctenodiscus crispatus* were analysed with segmented regression.

2.4.4 K-means clustering

K-means clustering is an algorithm that uses the squared Euclidean distance as its measure of dissimilarity (Shahbaba 2012). The aim is to appoint the observations in the data to clusters where the measure of dissimilarity is low within and high between clusters. K-means clustering was applied to analyse the relationship between length measurements (L1, L2 and L3, section 2.5.2.1) and the weight- length relationship of *C. crispatus*. *A priori* selection of number of clusters (K) for this procedure was based on patterns observed in the models from the linear regression.

2.4.5 Size-frequency analysis: mixed distributions

Type of modality and peak of modes in size-frequency distributions from length - and weight measurements of *Ctenodiscus crispatus* were determined by visual inspection of histograms. Growth via modal progression was evaluated. Mixed distribution analysis was performed on some of the size-frequency distributions.

Mixed distributions

Du (2002) defines the mixture distribution as "*a compounding of statistical distributions, which arises when sampling from inhomogeneous populations (or mixed populations) with a different probability density function in each component*". A size-frequency distribution with distinct modes is an example of a mixed distribution. Normal mixtures were fitted to the size-frequency distributions from length-and dry weight measurements of mud stars exhibiting relatively clear bimodality or polymodality. The dry weights of mud stars were measured in grams, but converted to milligrams and ln-transformed prior to the mixed distribution analysis because negative mean values are not accepted. The fitting procedure requires the input of starting values of the mixing parameters of the normal distributions:

π = proportions
μ = means
σ = standard deviations

Starting values for the analysis were based on component parameter values suggested from the size-frequency distributions in histograms. From the starting values, the procedure fits normal mixtures based on estimates obtained via the standard maximum likelihood estimation method (Du 2002).

2.5 Laboratory work

2.5.1 Macrobenthos 5 mm fraction

Samples preserved in formalin were rinsed in running water under a fume hood for 24 hours prior to processing. The samples were washed over sieves with a smaller mesh size than the sample fraction size, to avoid loss of fauna. Frozen samples were thawed overnight. All samples were further preserved in 70 % ethanol.

Preliminary sorting was done by examining 1-2 table spoons at a time. Large animals such as fish and sea stars were sorted out first and remaining animals were grouped according to phyla or lower taxonomic groups. A magnification lamp and stereomicroscope were used to aid further sorting and identification. Individuals of an identified taxon were placed in containers with 70 % ethanol and labelled with station number, taxon name, date of identification and initials. Polychaetes were mainly identified to family or genus level, as species identification is an exceptionally time-demanding task and some were found in exceedingly large numbers. Specimens of Porifera, Bryozoa and macroalgae were not considered in this study.

Samples from Tennes, Ramfjord and Svartnes were prioritised for processing, i.e. identification, counting and biomass calculation. Due to time constraints, only 5 mm fractions of four samples from stations 118, 176, 194 and 196 were processed (Figure 3, Appendix Table 1)

Identification literature

The main published literature used for identification is presented in Table 1. Reference literature from surveys in the Barents Sea and Porsangerfjorden in northern Norway was also used as well as special compendiums for polychaete identification and the Marine Species Identification Portal (URL) based on the work of Hayward and Ryland (1990) (with newer additions).

Table 1. A selection of identification literature

Literature
Enckell (1980)
Golikov (1995)
Hayward and Ryland (1990)
Moen and Svendsen (2004)
Vassilenko and Petryashov (2009)

Counting and weighing

For each identified taxa, animals were counted and blotted dry for a few seconds before wet weight was measured. Only heads were counted. Weights were measured to nearest 0.1 g or 0.001 g. Large fish and sea stars were weighed individually. Individual polychaetes belonging to the taxa *Pectinaria hyperborea*, Sabellidae and Ampharetidae were removed from their tubes prior to weighing. Molluscs were weighed with their shell. Actiniarians and *Balanus* sp. attached to substrates and gastropods acting as substrates were not weighed. Lost arms of ophiuroids were weighed and denoted as *Ophiura* indet.

2.5.2 *Ctenodiscus crispatus*

One of the main challenges was to establish appropriate laboratory routines for the processing of mud stars (*Ctenodiscus crispatus*). Finding a suitable size measurement with good reproducibility was of particular importance, since the aims of this study included analysis of size-frequency distributions and assessment of the weight-length relationship. Due to few studies, there is no standard size measurement for this species and consequently there have been no evaluations of which is the best. Length is commonly used as a measure of size and for size-frequency analysis of *C. crispatus*, Kjær (1905) measured the disc radius, while Shick et al. (1981a) measured the distance between the mouth and the tip of the longest arm as well as the distance between the mouth and the madreporite interradius (disc radius) (Figure 4).

For ophiuroids, size is almost exclusively measured as the disc diameter (Schoener 1968; Tyler and Gage 1980; Fujita and Ohta 1990; Packer et al. 1994), while for asteroids it is commonly measured as the distance between the tip of the longest arm and the opposite end of the disc (Callaway et al. 2003; Robinson et al. 2010).

For the development of methodology for size measurements of *Ctenodiscus crispatus*, individuals from Svartnes (St.196, April) were selected. The total sample contained 627 individuals, from which 125 were randomly chosen for exploration of length measurements and subsequent analyses. Another 334 individuals were used for assessing the weight-length relationship. Only dry weight was measured for the remaining 168 individuals in this sample.

2.5.2.1 Length measurements: morphology

A good size measurement needs to be repeatable, i.e. low variation between repeated measurements. It should not be biased by who is doing the measurement (i.e. comparability to other studies) and reduce the effect of e.g. shape differences. To evaluate which is the best length measurement for mud stars, i.e. which is more reproducible, three different measurements were selected (Figure 4):

- L1 = The central disc diameter.
- L2 = The distance between the interradius and opposite arm tip.
- L3 = The distance between opposite arm tips.

L1, L2 and L3- lengths were each measured three times on all individuals (= 9 measurements). 124 individuals were measured in round 3. Length was measured to the nearest 0.01 mm using a digital caliper. The size-frequency distributions of these measurements are illustrated in Appendix Figure 1.

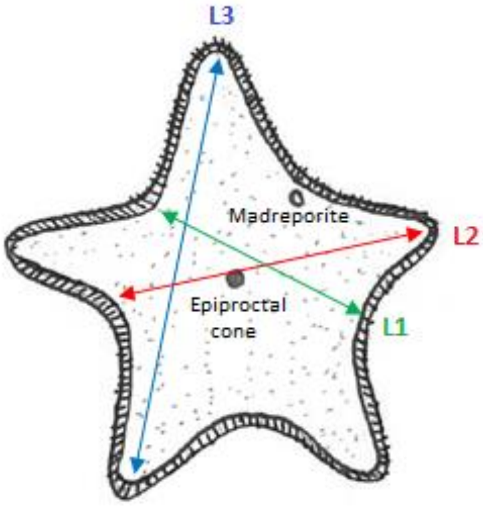

Figure 4. *Ctenodiscus crispatus*. The three length measurements chosen for reproducibility assessment. Aboral view.

To evaluate the reproducibility of the three length measurements, the *coefficient of variation* (*CV*) (Table 2) was calculated to find the variability in each measurement (L1, L2 and L3) in each round. The coefficient of variation is defined as "(…) *the standard deviation as a percentage of the mean*" (Whitlock & Schluter 2015):

$$CV = \frac{SD}{\bar{Y}}\ x\ 100\%$$

The reproducibility was further assessed with the Kolmogorov-Smirnov (KS) two-sample test, which determines whether two samples come from the same distribution. It is a non-parametric test, i.e. it does not assume a normal distribution. The KS test produces cumulative fraction plots based on the empirical distribution function of the two samples and calculates the maximum distance between the distributions (*D*) (Quinn and Keough 2002):

$$D = E_1(i) - E_2(i)$$

Where E_1 and E_2 are the empirical distributions of sample (round) 1 and 2. The null hypothesis states that the data come from the same continuous distribution. The three replicates of each length measurement was tested and plotted against each other. Significance level was set at $\alpha = 0.05$. Hypotheses for the Kolmogorov-Smirnov two-sample test are:

H_0: Length measurement replicates come from the same distribution.

H_A: Length measurement replicates do not come from the same distribution.

Results

The *coefficient of variation* was fairly similar for all three length measurements (Table 2), but the lowest variability was found in the L1 (disc diameter) measurements, with an average *CV* of 32.3 % for the three rounds. The L2 - and L3 lengths had average values of 34.6 and 36.2 % respectively. The variability between rounds were however lowest for L3 and highest for L1.

Table 2. *Ctenodiscus crispatus*. Coefficient of variation of different length measurements (L1, L2 and L3: see Figure 4) and rounds.

Measurement (L)_round (r)	**L1_r1**	**L1_r2**	**L1_r3**	**L2_r1**	**L2_r2**	**L2_r3**	**L3_r1**	**L3_r2**	**L3_r3**
Coefficient of variation (%)	31.3	33.0	32.5	34.1	34.7	35.1	36.0	36.3	36.3

The Kolmogorov-Smirnov test revealed a non-significant difference in distributions between rounds of repeated length measurements (Table 3). The cumulative distribution plots are shown in Appendix Figure 2. The null hypothesis of equal distributions was accepted. The *D*-values, i.e. the maximum distance between distributions were lowest for L1. The coefficients of variation and the results of the KS test contributed to the conclusion that the central disc diameter (L1) serves as the best length measurement in mud stars. See section 4.5.1 for further discussion.

Table 3. Ctenodiscus crispatus. Kolmogorov-Smirnov two-sample test. Maximum distance between distributions (D) and p-values are presented. L1, L2 and L3 are length measurements. r1, r2 and r3 are rounds.

Measurement (L)_round (r)	***D***	***p***
L1_r1 - L1_r2	0.040	> 0.999
L1_r1 - L1_r3	0.055	0.991
L1_r2 - L1_r3	0.059	0.980
L2_r1 - L2_r2	0.040	> 0.999
L2_r1 - L2_r3	0.056	0.988
L2_r2 - L2_r3	0.062	0.967
L3_r1 - L3_r2	0.048	0.999
L3_r1 - L3_r3	0.062	0.967
L3_r2 - L3_r3	0.054	0.993

2.5.2.2 Weight measurements and weight-length relationship

For all weight measurements, the mud stars were cleaned thoroughly in advance of weighing to remove sediment and organic residue. Individual mud stars were placed in numerated weighing ships, each weighed in advance, to ensure the weights were as accurate as possible. Mud stars were dried at 60°C for approximately 48 hrs prior to weighing. Weighing ship weight was subtracted from measured weight to give the actual dry weight of the mud star. Dry weight was measured to the nearest 0.0001 g for mud stars in most samples. Large individuals from samples collected in June were measured to the nearest 0.1 g dry and wet weight.

Based on the conclusion that the central disc diameter (L1) is the best length measurement, this was used when analysing the weight-length relationship. After length measurements, each individual was transferred to the weighing ship whose number corresponded to the individual's number in the length measurement data sheet.

For the remaining mud star samples, weight was chosen as the size-measurement. Even though the disc diameter (L1) was found to be a good measure of size, factors such as asymmetry likely contributes to more variability than what is expected from weight measurements. Weight measurements are generally less time-consuming, though in some cases the cleaning effort can be considerable. See section 4.5.1 for further discussion. Individual dry weights were measured on mud stars from twelve stations (Appendix Table 1) sampled in March, April, June and October.

2.5.2.3 Wet weight - dry weight relationship

The wet weight-dry weight relationship of *Ctenodiscus crispatus* was established by measuring both wet and dry weight of mud stars collected in June (Stns. 390, 391, 392) (Appendix Table 1). The three samples contained 98, 800 and 1618 (= 2516) individuals respectively. The relationship between wet weight and dry weight was analysed by single linear regression (see section 2.4.2) on ln-transformed data. The three samples were first analysed separately and their slopes were compared by performing an ANCOVA homogeneity of slopes test (analysis of covariance). ANCOVA models are ANOVA models that incorporates continuous variables (covariates) in order to reduce the amount of unexplained variability and increase the power of any treatment effects. The ANCOVA model assumes that the relationship between the response variable and the covariate is the same for each treatment level (categorical variable). The homogeneity of slopes test examines whether there is an interaction between the categorical and the continuous predictor (Logan 2010). In this case, station was the treatment (with three levels) and dry weight (ln) the predictor (covariate). The null hypothesis is that the slopes are equal (i.e. no treatment effect):

$$H_0: b_1 = b_2 = b_3$$

Linear regression of pooled data provided the equation used to estimate the wet weight of individuals were only dry weight was measured:

$$\ln\ WW = \ln a + b \ln\ DW$$

An alternative approach to obtain a conversion factor from dry weight to wet weight is to calculate the ratio between wet weight and dry weight (WW: DW). In this case, the average ratio was found for each of the three samples and a final conversion factor was the average of these three. Individual dry weights were multiplied by the conversion factor to obtain an estimate of the wet weight.

Results

As expected, there was a strong relationship between the wet weight (WW) and dry weight (DW) of mud stars (Figure 5), statistically confirmed by high F-values and correlation coefficients (R^2) of 0.91 for Ramfjord (St. 390) and 0.99 for Svartnes (St. 391) and Tennes (St. 392). All three models were highly significant ($p < 0.001$) and had a good fit (Table 4).

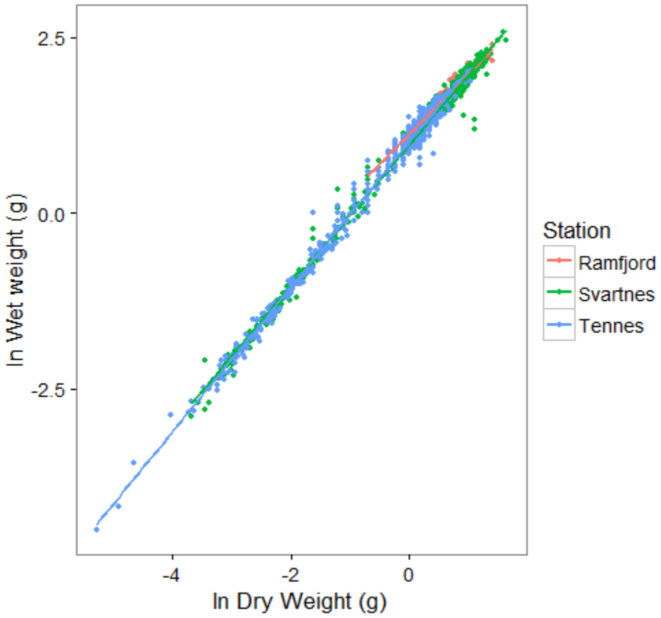

Figure 5. *Ctenodiscus crispatus*. Linear regression of wet weight-dry weight relationship with separately fitted regression lines for the three stations.

Table 4. *Ctenodiscus crispatus* from Balsfjord in June. Regression coefficients (a, b), r^2, F-statistic and p-values of linear regressions of ln wet weight (g) against ln dry weight (g). n = number of mud stars.

Station nr.	**Station name**	**n**	**ln a**	**b ± SE**	**r^2**	**F**	***p***
390	Ramfjord	98	-1.140	1.070 ± 0.030	0.91	1018.0	<< 0.001***
391	Svartnes	800	-0.964	0.991 ± 0.003	0.99	8.9×10^4	<< 0.001***
392	Tennes	1618	-0.970	0.958 ± 0.003	0.99	1.1×10^5	<< 0.001***
Pooled data		2516	0.996	1.010 ± 0.002	0.99	2.1×10^5	<< 0.001***

*** Highly significant results

However, it was evident from the model that the Ramfjord sample had a slightly different slope This sample was deviant in that it contained much fewer and exclusively larger individuals compared to the samples from Svartnes and Tennes (Table 4, Figure 5). If the sample had contained individuals from the whole size spectra, the regression line might have been more parallel to the other two.

The ANCOVA homogeneity of slopes test gave a highly significant result ($p < 0.001$) (Table 5), i.e. stating that the regression lines are *not* parallel. However, this is likely a consequence of the combined effects of a very large sample size (n = 2516), and the absence of a wide range of small mud stars in the Ramfjord sample (St. 390).

Table 5. *Ctenodiscus crispatus*. Results from the ANCOVA homogeneity of slopes test with ln dry weight as covariate (predictor) and station as treatment factor. df = Degrees of freedom.

Source	**Type I Sum of squares**	**df**	**Mean square**	**F**	***p***
ln DW	2171.99	1	2171.99	214875.4	<< 0.001***
Station	0.63	2	0.32	31.4	<< 0.001***
ln DW * Station (slope)	0.63	2	0.32	31.4	<< 0.001***
Error	25.37	2510	0.01		

*** Highly significant results

Despite these results, the three samples were pooled for the practical concerns of establishing a wet weight-dry weight relationship. The linear regression of the pooled data provided a highly significant ($p < 0.001$) model with a good fit (Figure 6, Table 4), where 99 % of the variability in wet weight was explained by dry weight. The equation for wet weight-dry weight conversion is thus:

$$ln\,WW = 0.9955 + 1.010\,ln\,DW$$

Four decimals were used for the intercept constant when converting dry weight measurements to wet weight in order to obtain more accurate estimates. The results of the conversions based on the equation and the wet weight-dry weight ratio were similar (Table 6).

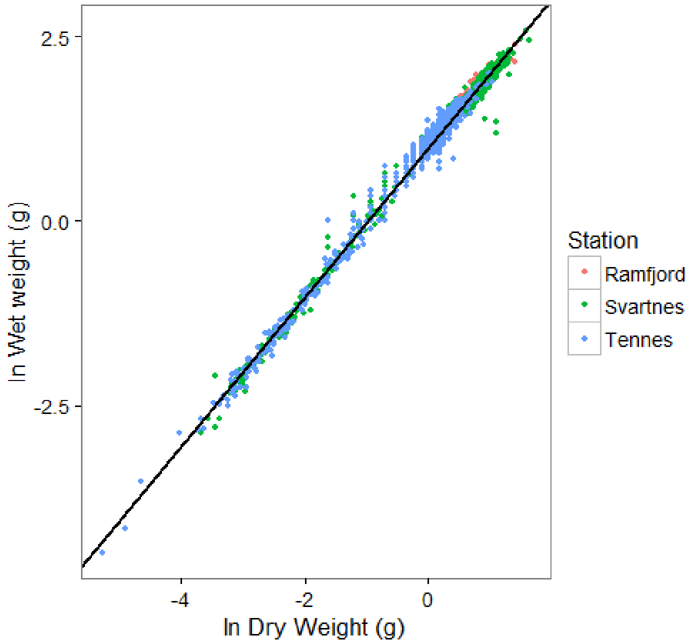

Figure 6. *Ctenodiscus crispatus*. Wet weight-dry weight relationship from pooled data with fitted regression line.

Table 6. *Ctenodiscus crispatus*. Results from estimating wet weight from dry weight using the linear equation for the weight-relationship and the wet weight - dry weight ratio.

Station nr.	**Station name**	**n**	**Total WW (g)**	
			WW:DW	*Y = a + bX*
118	Tennes	185	477.3	475.4
176	Ramfjord	422	2121.4	2125.7
182	Tennes	146	517.9	517.2
196	Svartnes	627	2003.7	2001.0
197	Svartnes	1066	2509.5	2498.5
200	Tennes	115	447.7	448.1
704	Ramfjord	314	1591.4	1594.1
705	Svartnes	706	1948.7	1943.8
706	Tennes	166	1054.9	1061.3

2.6 Software

All statistical analyses were performed in R (2015). Isoplots were made in SYSTAT 13.1. Calculations were performed in Microsoft Excel (2016) and maps were created in ArcGis(ArcMap) 10.4.1 (ESRI Inc. USA).

3. Results

3.1 Macrobenthos 5 mm fraction

A complete taxa list with abundances per trawl haul (150 m^2) is presented in Appendix Table 2. A total of 91 taxa were identified from the processed 5 mm fraction of samples collected in March and April at Tennes (St. 118), Ramfjord (St. 176), Tømmernes (St. 194) and Svartnes (St. 196) in Balsfjord (Figure 3). St. 176 had the highest number of both individuals and taxa, followed by Stns. 118, 194 and 196. Total biomass (wet weight, g 150 m^2) was highest at St. 176 and lowest at St. 118. (Figure 7a-c).

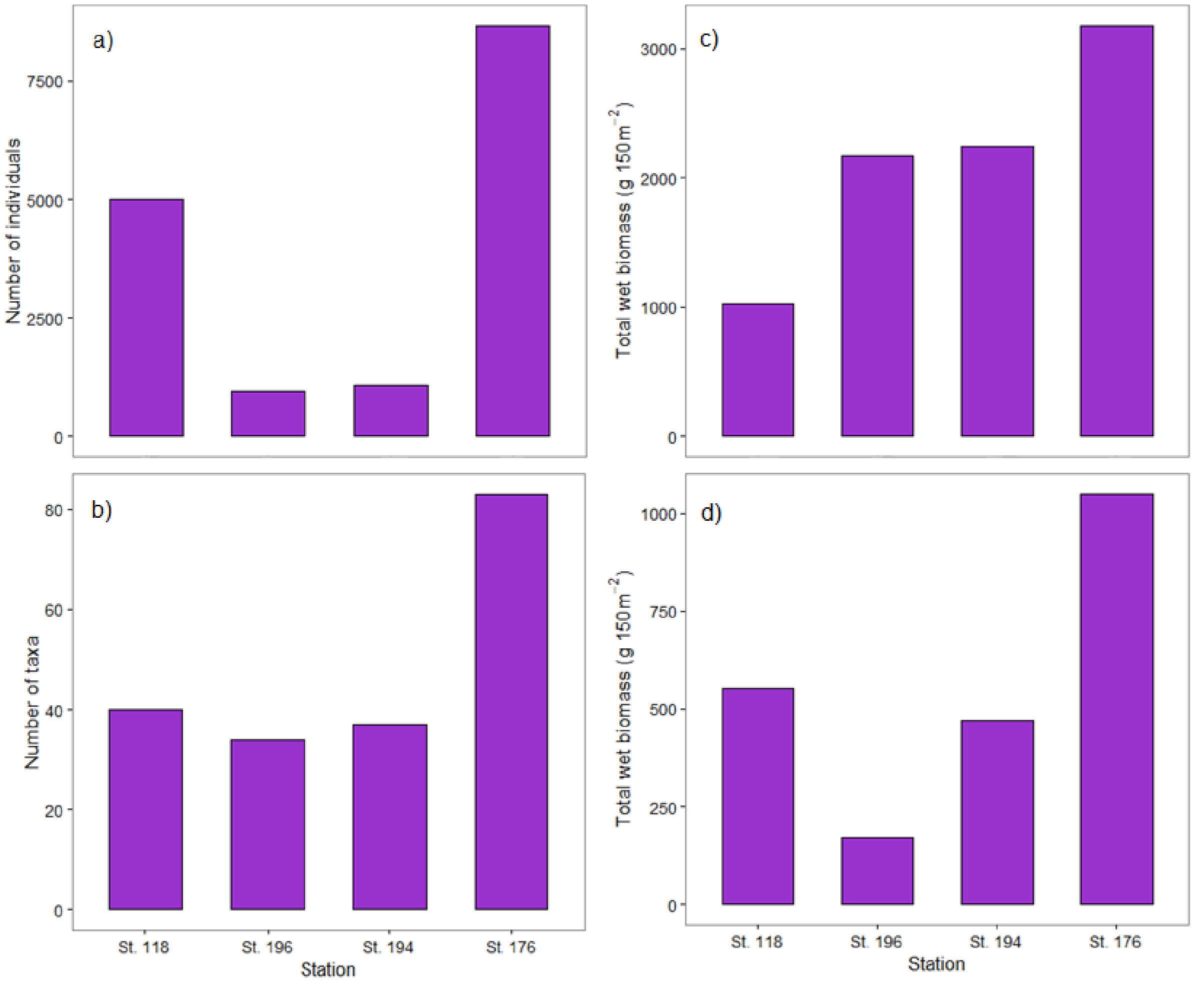

Figure 7. Macrobenthos 5 mm fraction from March* and April 2016. Bars arranged from the inner to the outer part of Balsfjord. a) Total number of individuals, b) Total number of taxa, c) Wet biomass per sampling station (g 150 m^{-2}), d) Wet biomass per sampling station when *Ctenodiscus crispatus* is excluded.

*St. 118 sampled in March

Stns. 194 and 196 were relatively similar in regards to number of individuals and taxa, while St. 118 had a high number of individuals relative to number of taxa. St. 194 and 196 had high biomass relative to number of individuals, due to high numbers of *Ctenodiscus crispatus* which contributed to 79 and 92 % of the total biomass, respectively. At Tennes and Ramfjord (St. 118 and 176), *C. crispatus* constituted 45.9 and 66.8 % of the total biomass (Figure 7c, Appendix Table 1). Excluding *C. crispatus* from the total biomass, gave profoundly different results which clearly demonstrates its dominance in terms of weight (Figure 7d).

Grouping the fauna according to phylum (Figure 8), unveiled a strong dominance of annelids at St. 176 (Ramfjord) in terms of abundance, and they made up 79 % of the total number of individuals in the sample (Figure 8a). Arthropods, echinoderms and molluscs accounted for 19 %. St. 118 (Tennes) was numerically dominated by molluscs, which constituted more than half of the individuals, closely followed by annelids. Together they accounted for 94 % of individuals. Both St. 194 (Tømmernes) and St. 196 (Svartnes) were dominated by echinoderms in terms of abundance, followed by annelids and arthropods (Figure 8a). As illustrated in Figure 7c-d, *Ctenodiscus crispatus* was dominating in terms of biomass at all stations and the dominance of echinoderms (i.e. *C. crispatus*) in terms of biomass is clearly seen in Figure 8b. Annelids had only minor contributions to biomass.

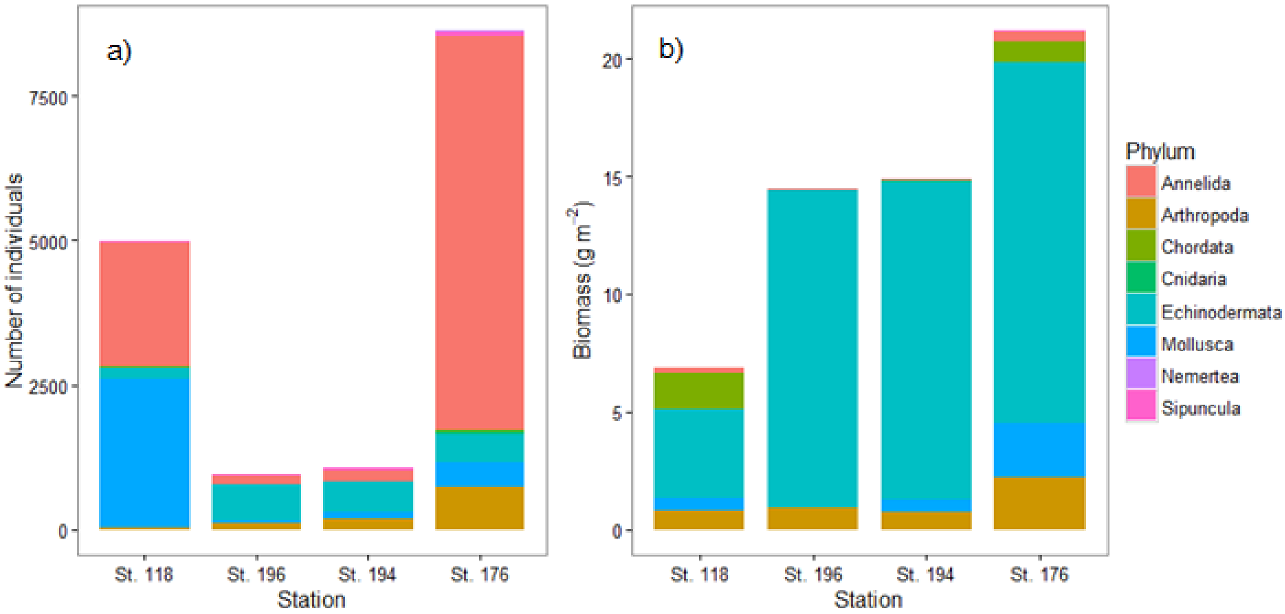

Figure 8. Macrobenthos 5 mm fraction of samples taken in Balsfjord in March (St. 118) and April (Stns. 196, 194 and 176). Bars arranged from the inner to the outer part of the fjord. Number of individuals (a) and biomass (b) per phylum.

At all sampling stations, the numerically most abundant taxon contributed largely to the total abundance (Figure 9). At Tennes (St. 118), *Yoldiella* sp. constituted 48 % of the total number of individuals, while maldanid polychaetes contributed to 49 % of the total abundance in Ramfjord (St. 176). *C. crispatus* made up 48.8 and 65.7 % of the total abundance at Tømmernes (St. 194) and Svartnes (St. 196). When combining the samples, polychaetes represented six out of the ten most dominating taxa in Balsfjord (Figure 9).

A list of the ten most numerically abundant taxa in each of the processed samples (Stns. 118, 194, 196 and 176) is presented in Appendix Table 3. Among the ten top taxa at each station, polychaetes represented five in Ramfjord and seven at Tennes. At Svartnes and Tømmernes, polychaetes represented three out of the ten dominating taxa.

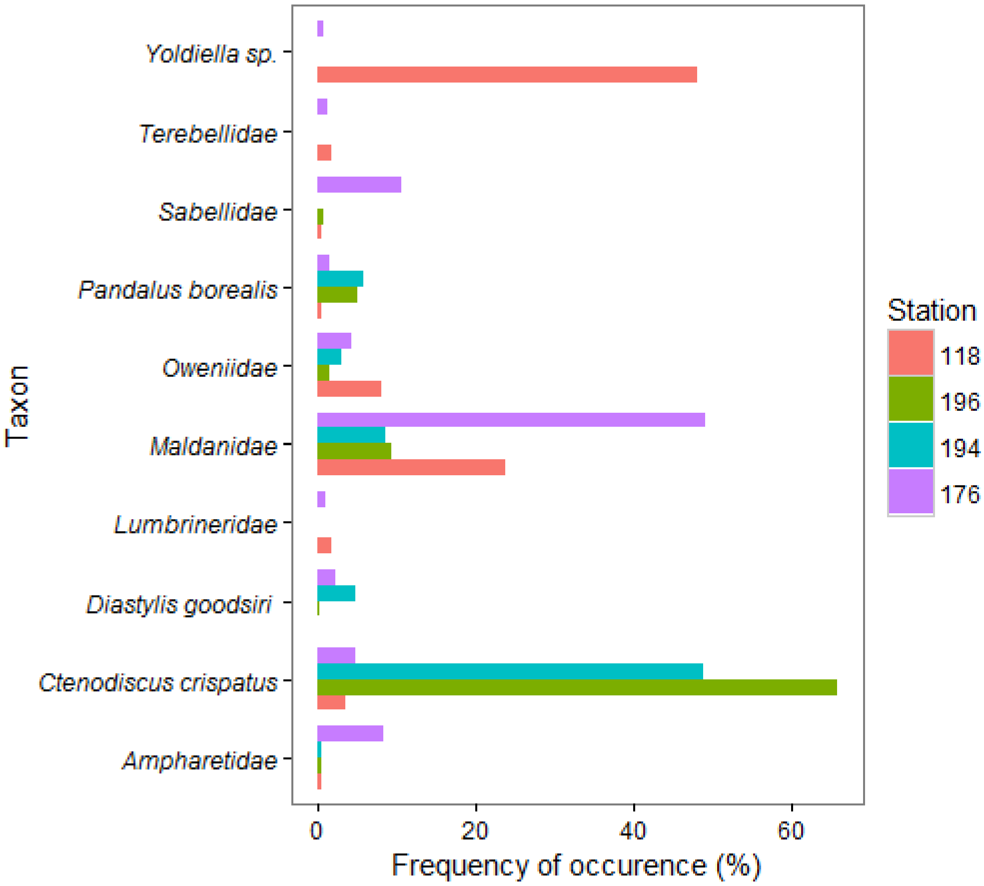

Figure 9. Macrobenthos 5 mm fraction. The ten numerically most abundant taxa from beam trawl samples collected in Balsfjord in March and April 2016. Frequency of occurrence (%) at each station.

3.2 *Ctenodiscus crispatus*

3.2.1 Biomass distribution of *Ctenodiscus crispatus* in Balsfjord

The wet biomass (g m^{-2}) distribution of mud stars in Balsfjord is presented in Figure 10. There were no obvious patterns, but the lowest biomass was usually found in the inner part of the fjord. A relatively high biomass of *C. crispatus* was found at Svartnes in all sampled months, while Ramfjord exhibited the highest variability in mud star biomass. At Svartnes and Tennes the highest mud star biomass was registered in June (St. 391, 392), while Ramfjord had the lowest biomass in June (St. 390).

Mud star abundances from the sampled stations are given in Appendix Table 1. Relating biomass to abundance suggests that mud stars collected at Svartnes were on average smaller than those from Tennes and Ramfjord.

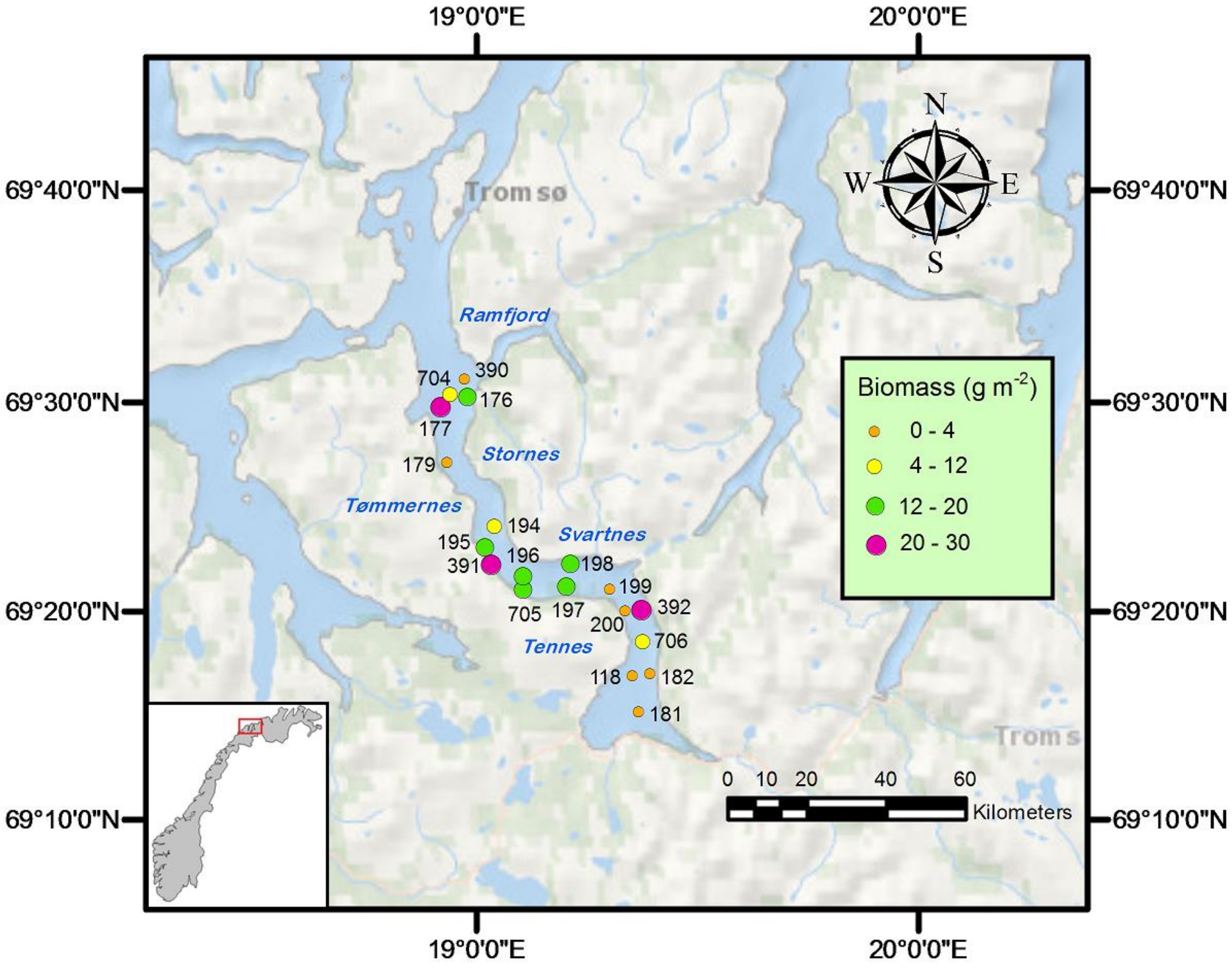

Figure 10. *Ctenodiscus crispatus.* Wet biomass (g m^{-2}) distribution in Balsfjord 2016.

3.2.2 Relationship between length measurements: morphology

The single linear regression of the L2 ~ L1 and L3 ~ L1 relationships (Figure 11) produced at first glance a good fit of the data, with a clear linear relationship between the two length measurements (Table 8). All models were highly significant ($p < 0.001$), but both visually and statistically the ln-transformed data gave a better fit with higher correlation coefficients (r^2) and F-values (Table 8). Inspecting residual plots (Appendix Figure 3 and 4) and comparing the models using the Akaike information criterion (AIC) further confirmed the better fit of the ln-transformed data (Table 8).

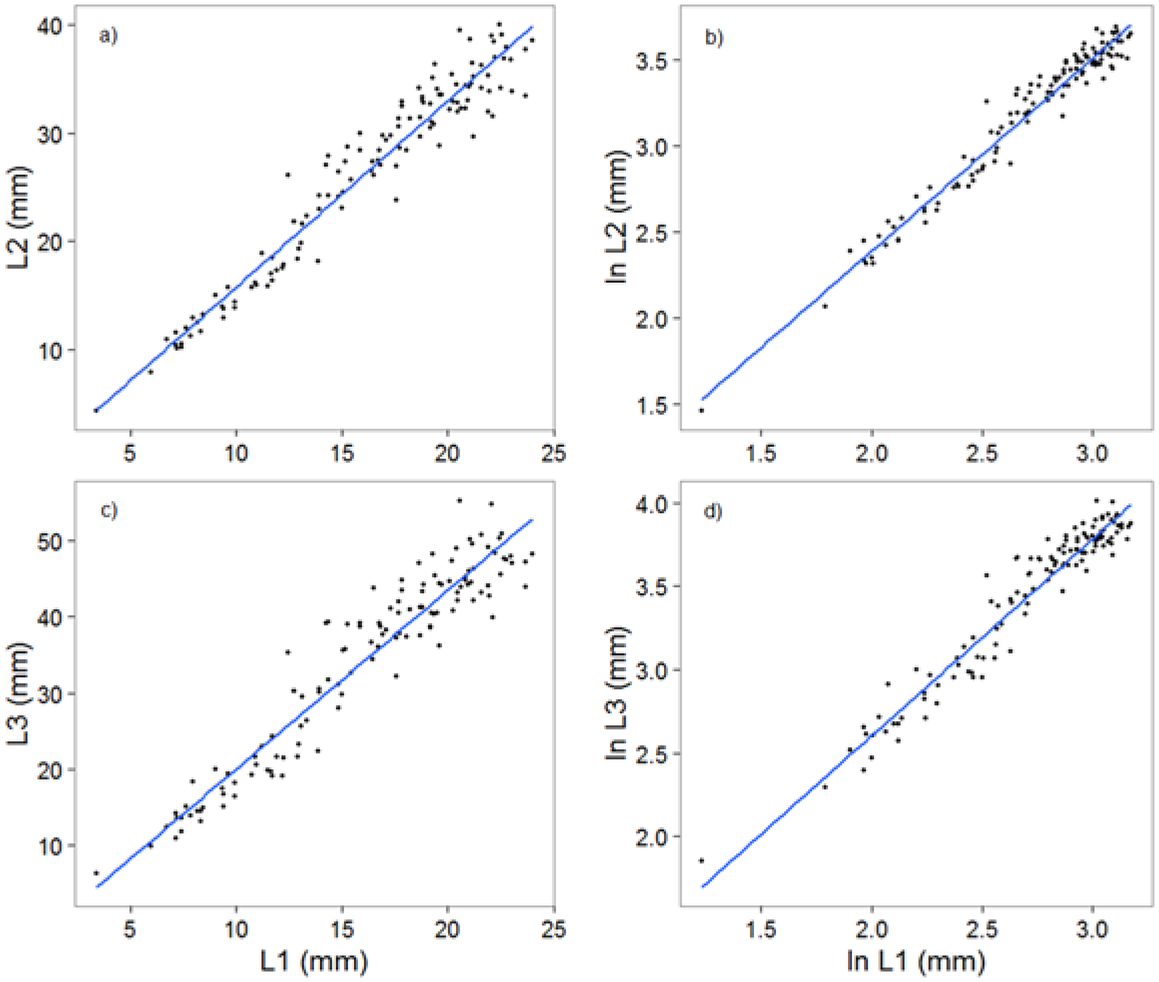

Figure 11. *Ctenodiscus crispatus* from Svartnes, April 2016 (St. 196, n = 125). Linear regressions of relationship between length measurements. a - b) Relationship between L2 and L1 on untransformed and ln-transformed data. c - d) Relationship between L3 and L1 on untransformed and ln-transformed data.

Table 8. *Ctenodiscus crispatus* from Svartnes, April 2016 (St. 196, n = 125). Regression coefficients (a, b), r^2, F-statistic, AIC and p-values of the linear regressions relating the L2 and L3 length measurements to the L1 length measurement.

Linear regression							
Linear model (y ~ x)	**n**	**a**	**b ± SE**	**r^2**	**F**	***p***	**AIC**
L2 ~ L1	125	-1.505	1.726 ± 0.040	0.94	1887	<<0.001***	559.766
L3 ~ L1	125	-3.492	2.350 ± 0.066	0.91	1257	<<0.001***	687.704
ln (L2 ~ L1)	125	0.157*	1.117 ± 0.020	0.96	3059	<<0.001***	-258.232
ln (L3 ~ L1)	125	0.251*	1.177 ± 0.027	0.94	1868	<<0.001***	-183.594

*ln-values; *** Highly significant results

However, from a closer inspection of the linear models and their residual plots (Figure 11, Appendix Figure 3 and 4), the relationship seemed to consist of two separate relationships, evident by the spread of values in the top right corner. The relationships were initally re-analysed by fitting two regression lines, joined at an estimated breakpoint (Segmented package, R). The segmented regression fitted two contigous lines with breakpoints at L1 18.8 (± 1.8) and 18.4 (+2.4/-2.2) mm in the L2 ~ L1 and L3 ~ L1 relationships of ln-transformed length measurements (Appendix Table 4, Appendix Figure 5).

Further examination of the two groups was done via K-means clustering, which provided the number of individuals and the centers (means) in each cluster (Table 9 and 10). Separate regression lines were fitted to each cluster and the results illustrated in Figure 12 revelaed non-parallel lines between clusters, confirmed by the slope coefficients provided by the separate regressions (Table 10). The ANCOVA homogeneity of slopes test confirmed significant differences between cluster slopes (Table 11). Residual plots improved when length relationships were analysed for separate clusters, altough one small mud star appeared to be an outlier in Cluster 1 in the ln L2 ~ ln L1 relationship (Appendix Figure 3 and 4). Removing it did not improve the regression, but provided a more stable residual plot.

As with the single linear regression, there was a better fit for ln-transformed data. The same number of individuals was observed in each of the two clusters of ln-transformed data for both the L2 ~ L1 and L3 ~ L1 relationships and they had the same mean of ln L1 in the clusters, i.e. 9.3 mm and 18.6 mm in cluster 1 and 2 respectively (Table 9).

Compared to segmented regression, the K-means clustering method seemed to provide a more accurate picture of the relationships as it displayed the overlapping areas between clusters, rather then defining a fixed inflexion point.

Table 9. *Ctenodiscus crispatus* from Svartnes, April 2016 (St. 196, n = 125). Mean values of clusters identified from K-means clustering.

	L2 ~ L1				**L3 ~ L1**			
	L1	**L2**	**ln L1**	**ln L2**	**L1**	**L3**	**ln L1**	**ln L3**
Cluster 1	10.09	15.15	2.229	2.611	10.28	19.26	2.229	2.818
Cluster 2	19.15	31.94	2.922	3.436	19.26	42.55	2.923	3.714

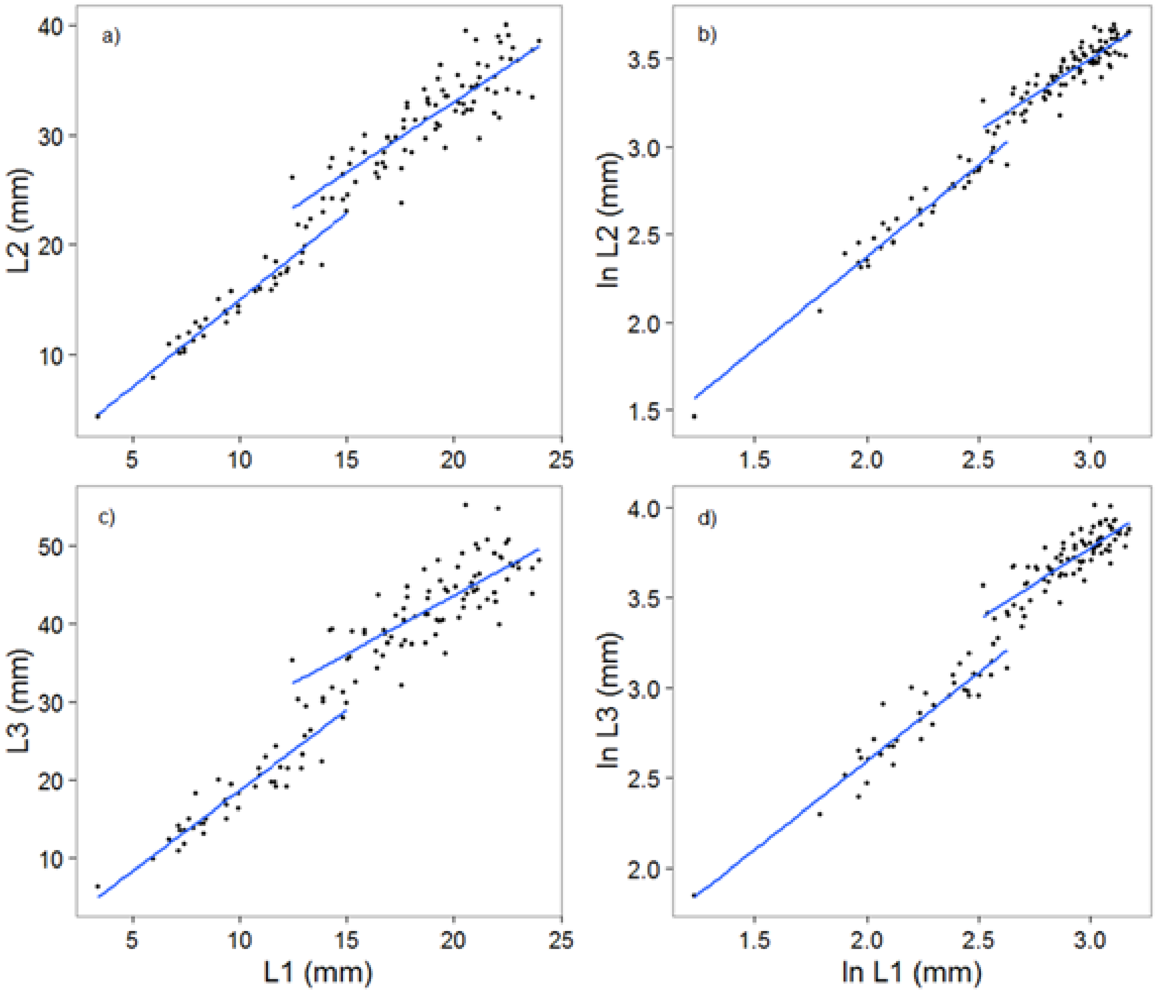

Figure 12. *Ctenodiscus crispatus* from Svartnes, April 2016 (St. 196, n = 125). Linear regressions with separately fitted lines for clusters identified by K-means clustering. a - b) Relationship between L2 and L1 on untransformed and ln-transformed data. c - d) Relationship between L3 and L1 on untransformed and ln-transformed data.

Table 10. *Ctenodiscus crispatus* from Svartnes, April 2016 (St. 196, n = 125). Results from K-means clustering. Regression coefficients (a, b), r^2, F-statistic, AIC and p-values of the linear regressions relating the L2 and L3 length measurements to the L1 length measurement. n = number of individuals in each cluster.

K-means clustering							
Linear model (y ~ x)	**n**	**a**	**b ± SE**	**r^2**	**F**	***p***	**AIC**
L2 ~ L1							
Cluster 1	42	-0.926	1.589 ± 0.070	0.93	522.4	<<0.001***	134.869
Cluster 2	83	7.307	1.287 ± 0.090	0.71	202.4	<<0.001***	372.054
L3 ~ L1							
Cluster 1	44	-2.014	2.068 ± 0.130	0.86	254.5	<<0.001***	433.046
Cluster 2	81	13.738	1.496 ± 0.145	0.57	106.4	<<0.001***	201.218
ln (L2 ~ L1)							
Cluster 1	37	0.289*	1.042 ± 0.041	0.95	638.5	<<0.001***	-211.193
Cluster 2	88	1.035*	0.821 ± 0.047	0.78	308.6	<<0.001***	-89.312
ln (L3 ~ L1)							
Cluster 1	37	0.640*	0.977 ± 0.059	0.88	276.5	<<0.001***	-63.092
Cluster 2	88	1.386*	0.796 ± 0.058	0.69	191.9	<<0.001***	-174.783

*ln-values; *** Highly significant results

Table 11. *Ctenodiscus crispatus* from Svartnes, April 2016 (St. 196, n = 125). Results from the ANCOVA homogeneity of slopes test. df = degrees of freedom.

Linear model (y ~ x)	**Source**	**Type I Sum of squares**	**df**	**Mean square**	**F**	***p***
ln L2 ~ L1	L1	21.979	1	21.979	4421.8	<< 0.001***
	Cluster	0.221	1	0.221	44.4	<< 0.001***
	L1 * Cluster	0.062	1	0.062	12.4	<<0.001***
	Error	0.602	121	0.005		
ln L3 ~ L1	L1	24.395	1	24.395	2966.1	<< 0.001***
	Cluster	0.569	1	0.569	69.2	<< 0.001***
	L1 * Cluster	0.041	1	0.041	5.0	0.027
	Error	0.995	121	0.008		

*** Highly significant results

The following allometric equations were obtained for the relationships between the two ln-transformed length measurements from fitting separate regression lines through clusters identified by K-means clustering:

$$\ln L2 \sim \ln L1 \rightarrow \text{Cluster 1: } \ln L2 = 0.289 + 1.042 \ln L1$$

$$\ln L2 \sim \ln L1 \rightarrow \text{Cluster 2: } \ln L2 = 1.035 + 0.821 \ln L1$$

$$\ln L3 \sim \ln L1 \rightarrow \text{Cluster 1: } \ln L3 = 0.640 + 0.977 \ln L1$$

$$\ln L3 \sim \ln L1 \rightarrow \text{Cluster 2: } \ln L3 = 1.386 + 0.796 \ln L1$$

Overlapping areas between clusters were determined by estimating the maximum lengths (ln L1, ln L2 and ln L3) of cluster 1 and the minimum of cluster 2 based on the end and beginning of respective regression lines. Approximate values of ln L1 were estimated through eyeballing until the best fit was found (Appendix Figure 6). The allometric equations were applied to calculate the equivalent value of the response variables ln L2 and ln L3.

The maximum disc diameter (L1, mm) in cluster 1, and the minimum in cluster 2 was observed to be approximately 13.9 and 12.5 mm respectively in both the L2 ~ L1 and the L3 ~ L1 relationship. The maximum L2 - and L3 lengths in cluster 1 were 20.7 and 24.8 mm, while the minimum lengths in cluster 2 were 22.2 and 29.7 mm respectively (Table 12).

Thus the overlapping area between clusters of length measurement relationships is suggested to be between approximately 12 and 14 mm disc diameter, 21 and 22 mm L2-length and 25 and 30 mm L3-length (Figure 4, Appendix Figure 6). In the size-frequency distributions these size ranges appear to be in the transition zone between two modes (Appendix Figure 1).

Table 12. *Ctenodiscus crispatus* from Svartnes, April 2016 (St. 196, n = 125). Overlapping range between clusters identified from K-means clustering. Maximum and minimum values determined by the eyeball method and allometric equations from separately fitted regression lines.

	ln L2 ~ ln L1 (mm)		ln L3 ~ ln L1 (mm)	
	ln L1	**ln L2**	**ln L1**	**ln L3**
Max. Cluster 1	2.63	3.10*	2.63	3.39**
Min. Cluster 2	2.52	3.03*	2.52	3.21**

*ln L2 = ln a + b ln L1
**ln L3 = ln a + b ln L1

3.2.3 Size-frequency distribution at Svartnes in April.

From my test sample from Svartnes in April (St. 196, n = 627), size-frequency distributions of *Ctenodiscus crispatus* from length (disc diameter L1, mm) and dry weight (g) measurements are presented (Figure 13). Size-distributions from both length - and dry weight measurements of 334 individuals indicated two modes in the population, i.e. a bimodal distribution. Combining all length (n = 459) and dry weight (n = 627) measurements from the test sample (St. 196), resulted in size-distributions that were virtually identical to those derived from the size-measurements of 334 individuals. Modal peaks were at 8 and 20 mm in length-distributions and at 0.2 and 1.8 g in dry weight-distributions (Figure 13). Results from fitting normal mixtures to the size-frequency distributions are presented in section 3.2.6.

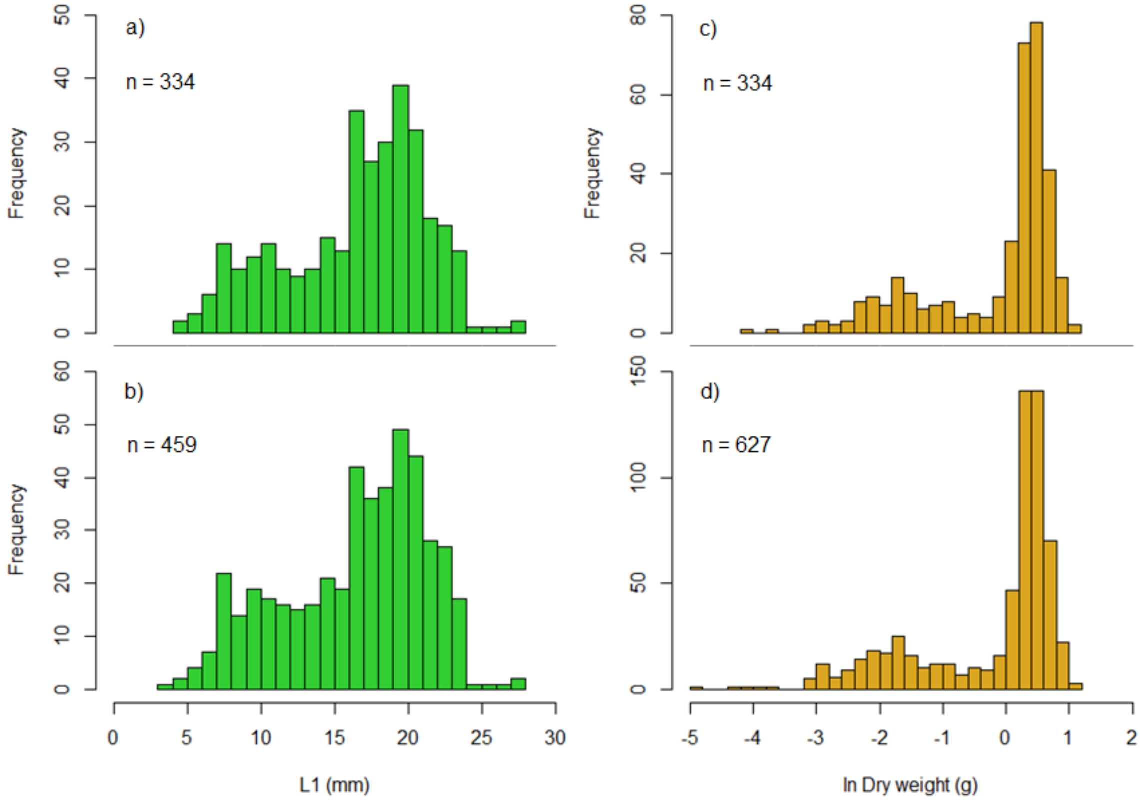

Figure 13. *Ctenodiscus crispatus*. Size-frequency distributions from Svartnes, April (St. 196, n = 627). a - b) Disc diameter, L1 (mm) of 334 and 459 individuals, c - d) ln-transformed dry weight (g) of 334 and 627 individuals.

3.2.4 Weight-length relationship

Linear regression did not produce a visual acceptable fit of the data (Figure 14a), despite being highly significant ($p < 0.001$) with a correlation coefficient of 0.88 and high F-value (Table 13). Similarly to the length measurement relationships, the weight-length relationship appeared to change at a certain point, which is evident from the cluster in the top right corner and clearly seen in the residual plot (Appendix Figure 7).

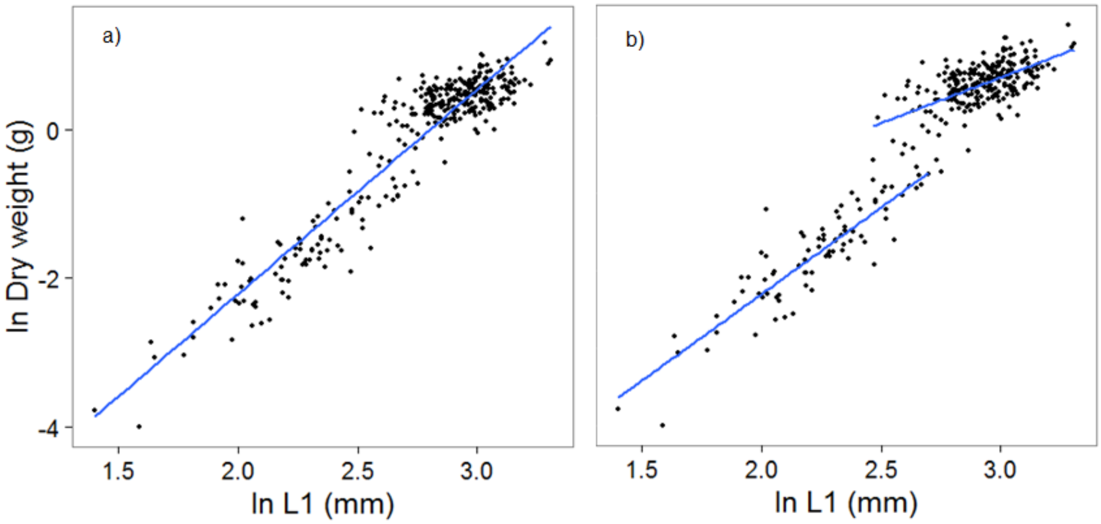

Figure 14. *Ctenodiscus crispatus*. Svartnes April (St. 196, n = 334. a) Linear regression of the relationship between ln-transformed weight (DW, g) and length (L1, mm); b) Linear regression with separately fitted lines for clusters identified by K-means clustering.

Table 13. *Ctenodiscus crispatus* from Svartnes, April 2016 (St. 196, n = 334). Regression coefficients (a, b), r^2, F-statistic, AIC (Akaike's information criteria) and p-values of the linear regressions relating ln dry weight (g) to ln length (disc diameter L1, mm).

Linear regression						
n	**ln a**	**b ± SE**	**r^2**	**F**	***p***	**AIC**
334	-7.725	2.755 ± 0.055	0.88	2544	<<0.001***	254.762

*** Highly significant results

The relationship was initally re-analysed via segmented regression by fitting two regression lines, joined at a breakpoint estimated to be at 17 (± 1) mm (Appendix Table 5). The model visually confirmed non-linearity. The results from the segmented regression with breakpoint estimation are presented in Appendix Figure 8 and Appendix Table 5. As previosuly suggested, segmented regression was not the best solution for assesing allometric relationships in mud stars.

Hence, the relationship was further investigated by K-means clustering which identified two clusters in the weight-length relationship with 83 and 251 individuals in cluster 1 and 2 respectively (Table 14). The regression lines fitted to each cluster were markedly non-parallel, confirmed by the slope values of the regressions (Figure 14b and Table 14). The ANCOVA homogeinety of slopes test confirmed a significant difference ($p < 0.001$) between the slopes (Table 15). The mean disc diameter (L1) was 9.3 and 18.6 mm in cluster 1 and 2, mean dry weights were 0.17 and 1.50 g (Table 16). The residual plot was markedly improved when the two clusters were analyzed separately (Appendix Figure 9). The results confirmed the suspicion that the weight-length relationship in mud stars is discontinous.

Table 14. *Ctenodiscus crispatus* from Svartnes, April 2016 (St. 196, n = 334). Regression coefficients (a, b), r^2, F-statistic, AIC (Akaike's information criteria) and p-values of the linear regressions of the weight-length relationship in clusters identified from K-means clustering.

Linear regression of clusters identified from K-means clustering							
	n	**ln a**	**b ± SE**	**r^2**	**F**	***p***	**AIC**
Cluster 1	83	-6.777	2.237 ± 0.123	0.80	333.0	<<0.001***	-14.327
Cluster 2	251	-3.044	1.178 ± 0.097	0.37	146.3	<<0.001***	36.404

*** Highly significant results

Table 15. *Ctenodiscus crispatus* from Svartnes, April 2016 (St. 196, n = 334). Results from the ANCOVA homogeneity of slopes test. df = degrees of freedom.

Source	**Type I Sum of squares**	**df**	**Mean square**	**F**	**p**
L1	315.534	1	315.534	5063.9	<< 0.001***
Cluster	17.404	1	17.404	279.3	<< 0.001***
L1 * Cluster (slope)	3.218	1	3.218	51.6	<< 0.001***
Error	20.562	330	0.062		

*** Highly significant results

Table 16. *Ctenodiscus crispatus* from Svartnes, April 2016 (St. 196, n = 334). Mean values in clusters identified by K-means clustering.

	Ln L1 (mm)	**ln DW (g)**
Cluster 1	2.231	-1.772
Cluster 2	2.925	0.405

Based on separate regression of the two clusters, the following allometric equations were obtained:

$$\text{Cluster 1:} \ln DW = -6.777 + 2.237\,(\ln\ L1)$$

$$\text{Cluster 2:} \ln DW = -3.044 + 1.178\,(\ln\ L1)$$

Overlapping areas between clusters was determined by identifying the maximum size of cluster 1 and the minimum of cluster 2 based on the end and beginning of respective regression lines. Approximate values of ln length (disc diameter L1, mm) were estimated through eyeballing until the best fit was found (Appendix Figure 10). The equivalent dry weights were calculated via the allometric equations.

The maximum disc diameter in cluster 1, was visually found to be at approximately 14.9 mm, while the regression line of cluster 2 had a minimum at approximately 11.8 mm. The corresponding dry weights were at 0.48 and 0.87 g (Table 17). Thus the overlapping area between clusters in the weight-length relationship is suggested to be between approximately 12 and 15 mm (disc diameter), corresponding dry weights between 0.5 and 0.9 g. In the bimodal size-frequency distributions these size ranges appear to be in the transition zones between the two modes (Figure 13).

Table 17. *Ctenodiscus crispatus* from Svartnes, April 2016 (St. 196, n = 334). Overlapping range between clusters identified from K-means clustering. Values determined by the eyeball method and allometric equations from separately fitted regression lines.

	ln L1	**ln DW**
Max. Cluster 1	2.70	-0.73*
Min. Cluster 2	2.47	-0.14*

*ln DW = ln a + b ln L1

3.2.5 Size-frequency distributions in Balsfjord

Ln-transformed dry weight (g) measurements of mud stars collected in April provided the size-frequency distributions illustrated in Figure 15. There was a prevalence of bimodality in the distributions in all samples except for St. 176, due to a low number of small individuals. Mud star samples from Svartnes (Stns. 196, 197) had the highest sample sizes and relatively high numbers of small individuals which made up clearly identifiable modes in the bimodal size-distributions. The right-hand frequencies in April were converged into one dominant mode containing the largest individuals with peaks concentrated at dry weights between 1.2 and 2.2 g. Smaller individuals were spread out over a wider range and there were no visual indications of recruitment events in samples collected in April. The peaks in the presumably adult modes were at 1.6, 1.2 and 1.5 g dry weight at Stns. 196, 197 and 182, while a higher peak of 2.2 g dry weight was found at St. 176 and St. 200 in Ramfjord and Tennes. The mode of small mud stars in the bimodal distributions had the clearest peaks at Stns. 196, 197 and 200, at a size of 0.2 and 0.1 g in the latter two.

Similar patterns were found in the size-frequency distributions of mud stars collected in March, June and October (Figure 16). Ramfjord consistently had a low occurrence of small mud stars resulting in left-skewed unimodal distributions. The mode of large individuals ranged from approximately 0.7-5 g dry weight, with peaks at 2.2 g in April and June, and at 1.8 g in October. At Svartnes, the bimodal distributions found in the April samples (Stns. 196, 197) was apparent at St. 705 sampled in October, but not so evident in the June sample (St. 391). The mode of large mud stars at Svartnes in April (St. 196 and 197), peaked at approximately 1.7 and 1.2 g (DW), while at 2.7 g in June (St. 391) and 1.5 g in October (St. 705). The range of the right-hand mode was difficult to determine in June, but was between approximately 0.7 and 3.3 g in April and October. The mode of small individuals from Stns. 196 and 197 in April had peaks at 0.2 and 0.1 g, but due to difficulties of visually assigning a mode to the smaller size classes in June, modal progression cannot be discussed. In October, the smaller mud stars seemed to form a mode with a peak at approximately 0.2 g.

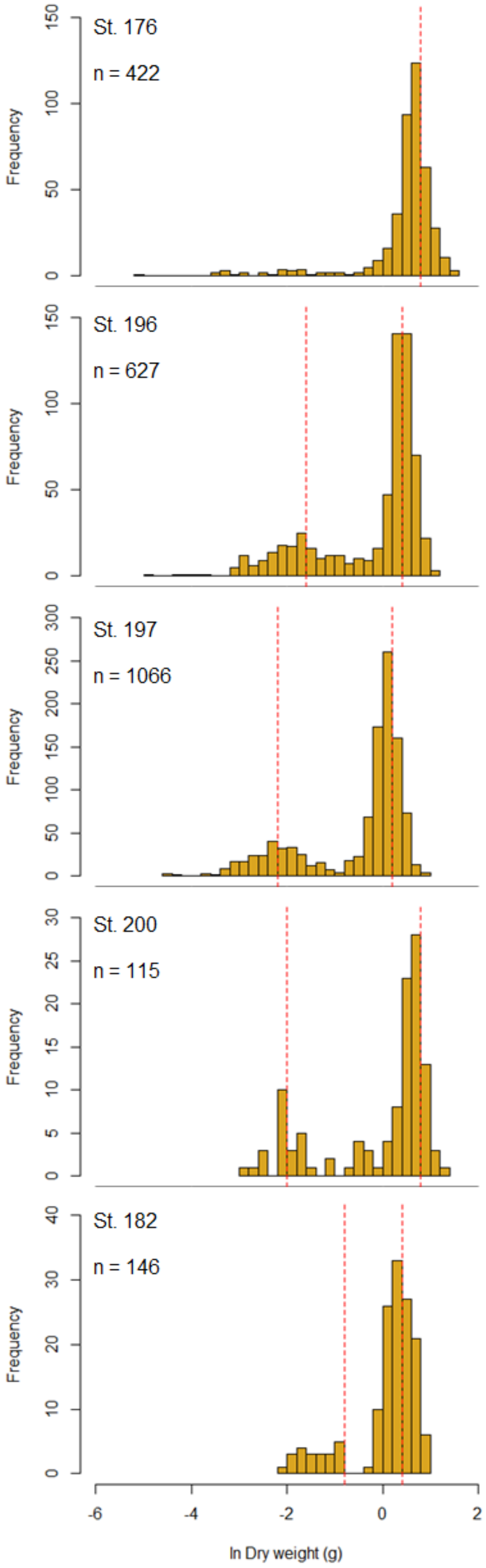

Figure 15. *Ctenodiscus crispatus*. Size-frequency distributions of mud stars collected in Balsfjord in April. From the inner (bottom) to the outer part of the fjord. Dotted lines at modal peaks.

At Tennes, bimodal distributions were observed in March, April and October. The depths of the sampled stations at Tennes were more variable than in Ramfjord and Svartnes, which possibly influenced the size-frequency distributions. Samples from St. 118 (March) and St. 182 (April) were sampled at approximately 104 m, while the samples from Stns. 200 (April), 392 (June) and 706 (October) were collected at approximately 124, 123 and 116 m (Appendix Table 1). Thus, St. 200 was chosen to represent Tennes in April when comparing with samples from June and October. Modal progression was detected when comparing St. 118 with St. 182 (Appendix Figure 11). The peak in the left-hand mode of small mud stars increased from 0.2 to 0.5 g dry weight.

At Tennes in April (St. 200) and October (St. 706), the peaks of the left-hand modes where at dry weights of approximately 0.1 and 0.7 g. The peak of the large right-hand modes was at 2.2 and 3.3 g, while at 1.2 g in June (St. 392). Modal progression is suggested of the small mode in April to the large mode in June, i.e. a shift in peak from 0.1 to 1.2 g. At Tennes in June (St. 392), although there was a good representation of a wide range of small individuals, they did not form a clear mode in the size-frequency distribution, probably because the number of large mud stars was very high. However, when looking at the size-frequency distributions of the smaller, presumably juvenile individuals, excluding the mode of adults, a bi - or polymodal distribution was evident and was further inspected with mixture analysis. The size-frequency distribution of the 208 presumably juveniles (< 0.6 g) is presented in Appendix Figure 12.

Further investigation of size-frequency distributions and mode identification by fitting normal mixtures was done for the frequency distributions from stations 182, 200, 196, 197, 391, 705 and 706, as well as for the distribution of small individuals from St. 392. Additionally, size-frequency distributions of the 334 mud stars measured (Disc diameter L1 and dry weight) for the analysis of the weight-length relationship were analysed with mixed distributions.

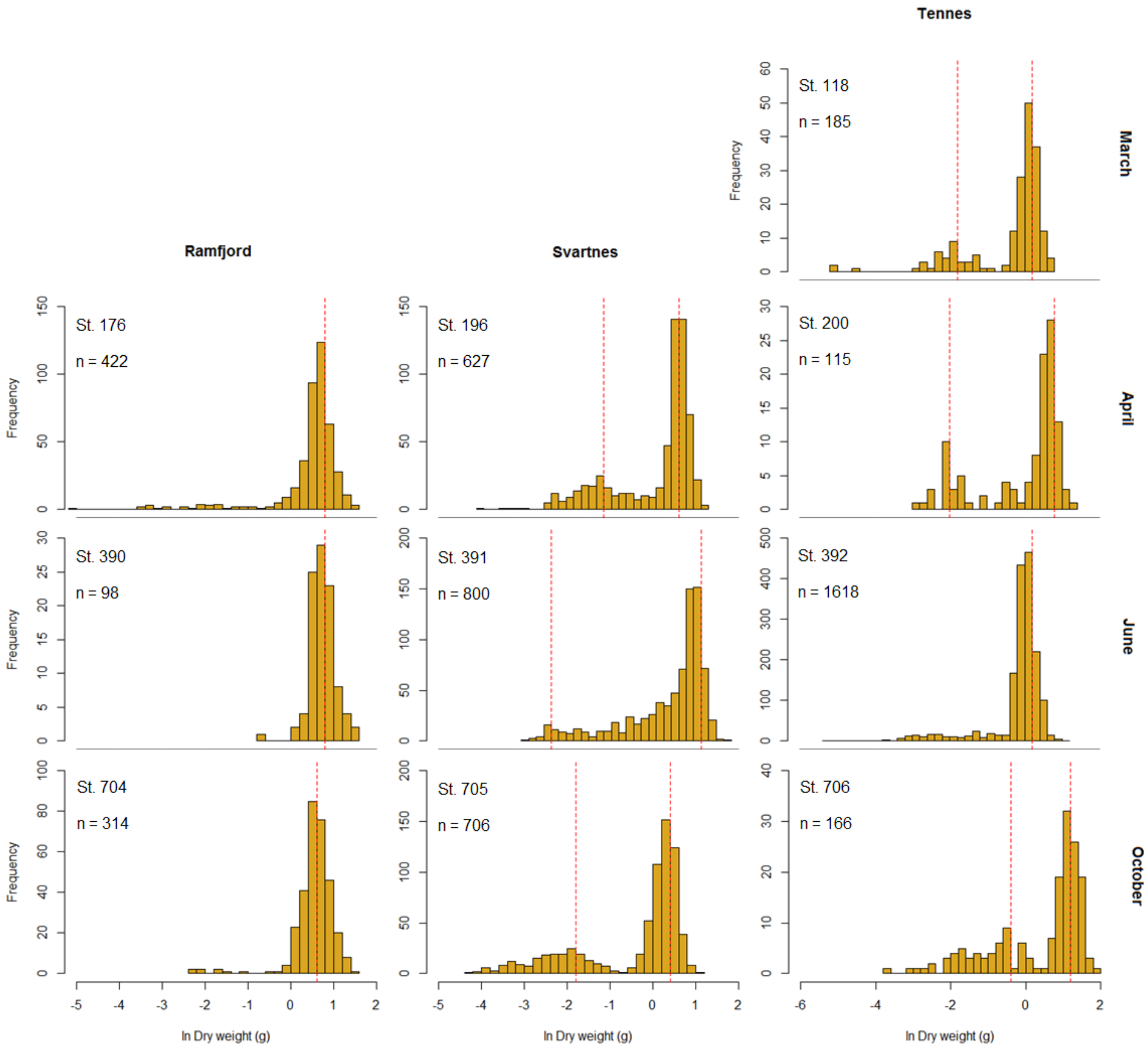

Figure 16. *Ctenodiscus crispatus* in Balsfjord 2016. Size-frequency distributions of mud stars collected in Ramfjord, Svartnes and Tennes in March*, April, June and October. Dotted lines represents modal peaks.

*Samples in March only collected at Tennes.

3.2.6 Mixed distributions

Svartnes April (St. 196)

The results from fitting normal mixtures to the size-frequency distributions of *Ctenodiscus crispatus* from the weight-length relationship (St. 196, n = 334) are presented in Figure 17. The best fits were obtained for size class intervals of 1 mm and 0.5 mg (ln). Two modes were identified in the size-distribution of length measurements (L1, mm). The left mode contained 23 % and the right mode 77 % of the individuals. The analogous proportions from dry weight measurements were 30 and 70 % (Table 18). To investigate the effects of sample size, normal mixtures were fitted to the size-distribution of length measurements of 459 mud stars from St. 196 (Figure 18). The results were similar to those with 334 individuals, in that the mean value in the modes increased only from 9.31 to 9.66 and from 18.73 to 18.84 (Table 18). Fitting normal mixtures to the size-frequency distribution of dry weight measurements of 334 mud stars, provided estimates of means and proportions similar to those of 627 individuals (Table 18 and 19) The estimated mean of the right-hand mode was 1.56 g in both cases, while the mean of the left-hand mode decreased from 0.22 to 0.19 g in the distribution of 627 mud stars. The chi-square statistics and p-values confirmed a good fit for all distributions (Table 18 and 19).

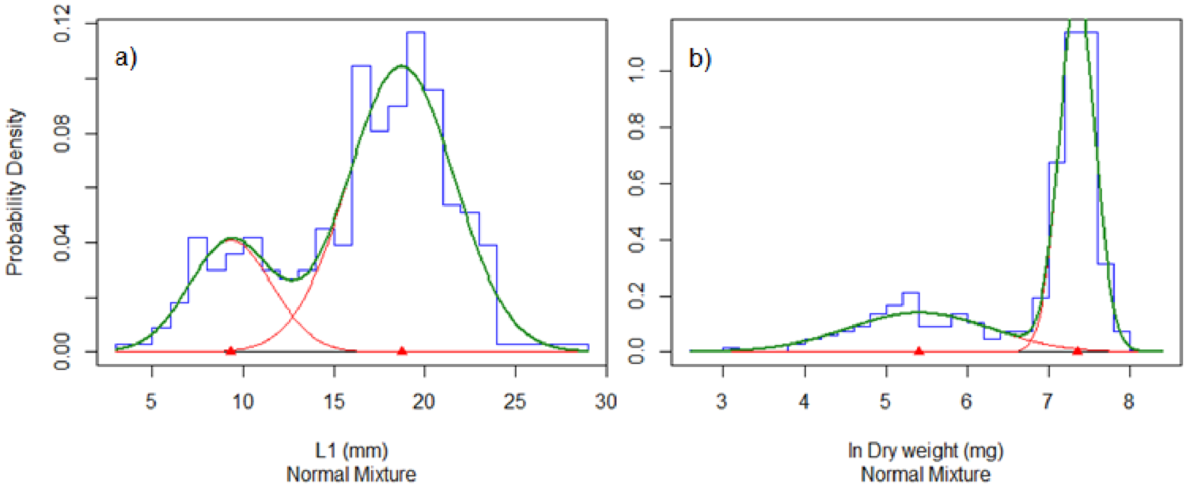

Figure 17. *Ctenodiscus crispatus*. Svartnes April (St. 196, n = 334). Percent frequencies showing frequencies expected from fitted Gaussian mixtures with arrows indicating component means. a) Length measurements (L1, mm), b) ln-transformed dry weight measurements (mg).

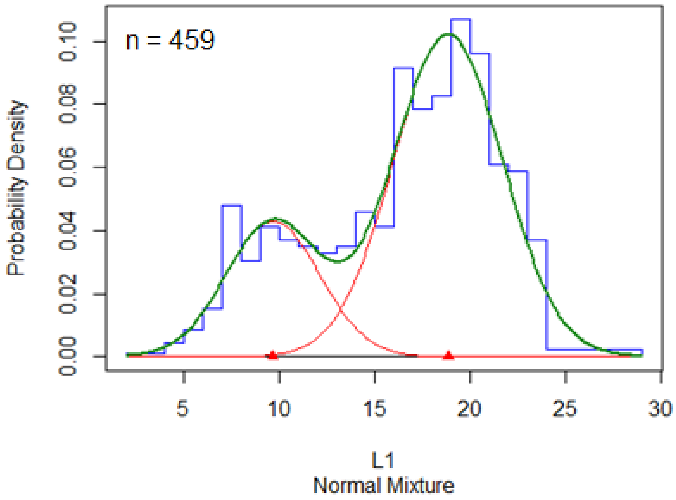

Figure 18. *Ctenodiscus crispatus*. Length measurements from Svartnes April (St. 196, n = 459). Percent frequencies showing frequencies expected from fitted Gaussian mixtures with arrows indicating component means.

It is noteworthy that the mean values of the identified modes in the bimodal distributions were very similar to the center (mean) values in the clusters identified in the weight-length relationship via K-means clustering (Table 16). Regarding the disc diameter (L1), the mean value of cluster 1 was 9.31 mm, equal to the mean value of mode 1 in the fitted distribution. The second cluster had a mean value of 18.63, while the corresponding mode had a mean value of 18.73 (Table 16 and 18). There was slightly more variation in the mean values of clusters and modes for the dry weight measurements. Mean values were 0.17 and 1.50 g (DW) in cluster 1 and 2 respectively, while corresponding means in identified modes were 0.22 and 1.56 g (Table 16 and 18).

Table 18. *Ctenodiscus crispatus*. Svartnes April (St. 196). Estimated parameters of Gaussian mixtures fitted to ln-transformed dry weight measurements (mg) and their and p-values. SD = standard deviations, χ^2 = Chi square statistic, df = degrees of freedom.

		Proportions		Means		SD		χ^2	df	*p*
	n	π_1	π_2	μ_1	μ_2	σ_1	σ_2			
L1 (mm)	334	0.23	0.77	9.31*	18.73*	2.27	2.93	20.8	18	0.287
"	459	0.26	0.74	9.66*	18.84*	2.46	2.87	28.3	19	0.078
ln DW (mg)	334	0.30	0.70	5.407**	7.355**	0.87	0.22	17.3	21	0.693

*Values in mm; ** Values in ln mg

Size-frequency distributions from dry weight measurements

The results from fitting normal mixtures to size-frequency distributions from dry weight measurements of mud stars from Balsfjord are illustrated in Figure 19. Results from St. 182 are in Appendix Figure 13. Mud star samples from Ramfjord were not included because their histograms clearly showed left-skewed unimodal distributions. Size-class intervals of 5 mg (ln) gave the best fit for all samples. The right-hand frequencies in the distributions made up a prominent group containing the major proportion, i.e. between 61 and 85 % of the individuals (Table 19). Two modes were identified in size-frequency distributions from Stns. 182, 196, 197 and St. 706 (Appendix Figure 13, Figure 19, Table 19).

In samples collected at Tennes in April (St. 200) and Svartnes in June and October (St. 391, 705), three modes were identified in the size-frequency distributions (Figure 19, Table 19), which suggests an underlying polymodality. Initial attempts to fit two modes gave a poor fit. The chi-square statistics and p-values suggests good fit for all distributions (Table 19).

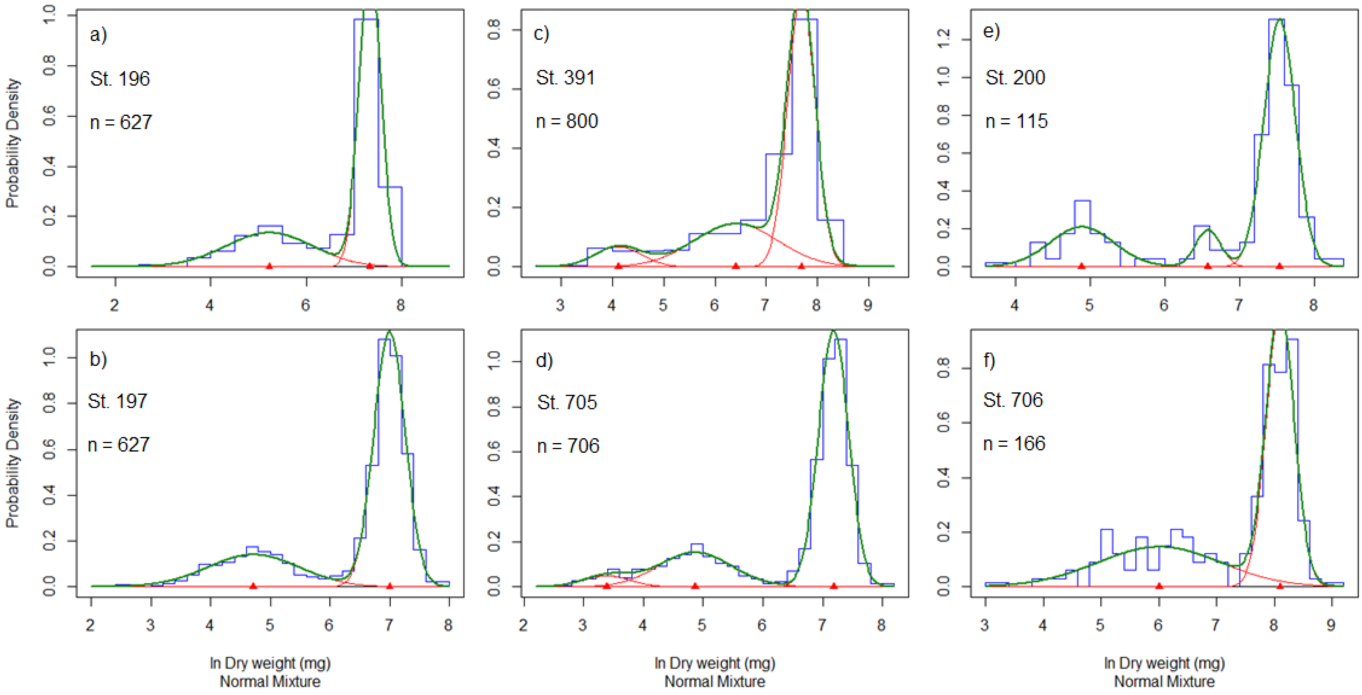

Figure 19. *Ctenodiscus crispatus* collected in Balsfjord 2016. Percent frequencies showing frequencies expected from fitted Gaussian mixtures with arrows indicating component means. a - d) Samples from Svartnes; e - f) Samples from Tennes.

From the identified means of modes from Svartnes, it can be suggested that there was a modal progression in time (Table 19). For comparison, St. 196 rather than St. 197 was chosen as a representative for Svartnes in April, because the depth at which it was collected is closer to depths of samples collected in June and October (Appendix Table 1). The first mode in April (St. 196) with a mean of 0.19 g could be linked to the second mode in June (St. 391) with a mean of 0.61 g. The first out of three modes identified at St. 391 (June) had a mean value of 0.06 g dry weight, which could correspond to the second mode (out of three) of small individuals found in October (St. 705) with a mean of 0.13 g, i.e. a growth of 117 %. Likewise, the second mode from St. 391 could be the mode of larger individuals in the October sample (St. 705), which thus indicates a change in mean size from 0.61 to 1.32 g, i.e. an increase in growth of 116 % in the course of four months.

Due to the high number of large individuals in the sample from Tennes in June (St. 392), it was not possible to do a mixture analysis, since potential modes among the smaller individuals would be masked by the high sample size and the dominance of larger mud stars. Fitting normal mixtures to the 208 individuals making up the left tail (Appendix Figure 12) and comprising 13 % of the total number of individuals in the sample, identified three modes in the size-frequency distribution with mean dry weights at 0.009, 0.08 and 0.34 g (Figure 20, Table 19), indicating four modes in the total sample size-frequency distribution. Even though the smallest mode contained few individuals, fitting 3 modes gave a much better fit than two modes.

Table 19. *Ctenodiscus crispatus*. Estimated parameters of Gaussian mixtures fitted to ln-transformed dry weight measurements (mg) and their and p-values. SD = standard deviations, χ^2 = Chi square statistic, df = degrees of freedom.

Station name	Station nr.	Month	n	Proportions			Means (ln mg)			SD			χ^2	df	*p*
				π_1	π_2	π_3	μ_1	μ_2	μ_3	σ_1	σ_2	σ_3			
Tennes	182	April	146	0.15	0.85		5.555	7.273		0.354	0.291		0.3	1	0.610
Tennes	200	April	115	0.23	0.08	0.69	4.891	6.582	7.541	0.430	0.167	0.211	14.1	13	0.364
Svartnes	196	April	627	0.31	0.69		5.229	7.335		0.911	0.225		10.9	7	0.144
Svartnes	197	April	1066	0.27	0.73		4.716	6.995		0.768	0.262		22.7	22	0.417
Svartnes	391	June	800	0.08	0.30	0.62	4.111	6.406	7.683	0.454	0.825	0.266	8.2	3	0.043
Tennes	392	June	208*	0.02	0.52	0.47	2.166	4.336	5.816	0.300	0.522	0.347	1.54	1	0.215
Svartnes	705	October	706	0.05	0.23	0.72	3.386	4.862	7.184	0.390	0.615	0.251	13.1	19	0.834
Tennes	706	October	166	0.39	0.61		6.008	8.096		1.068	0.242		25.4	23	0.332

*208 juveniles from the total sample (n = 1618)

As discussed earlier, the modal peaks in the samples from Tennes seemed to show a temporal progression. The first mode of presumably juveniles in April (St. 200) could be the third mode of small individuals identified in June with a change in mean from 0.13 to 0.34 g dry weight, i.e. a 162 % increase in growth. The second mode of small mud stars from St. 200, with a mean of 0.72 g could be integrated in the mode of large individuals from June, observed in the histogram with a peak at 1.2 g (Figure 16). In the size-frequency distribution of the assumingly juvenile mud stars from June (St. 392), the second mode with a mean of 0.08 g could correspond to the first mode in October (0.41 g), indicating an increase in growth of 413 %. The third juvenile mode from June with a mean of 0.34 g could have been joining the adult mode in October with a mean of 3.28 g.

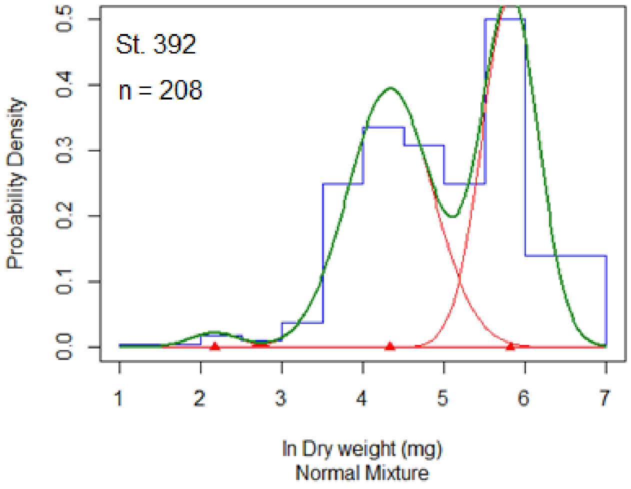

Figure 20. *Ctenodiscus crispatus* from Tennes, June (St. 392, n = 208). Individuals <0.6 g dry weight. Percent frequencies showing frequencies expected from fitted Gaussian mixtures with arrows indicating component means.

4. Discussion

4.1 Hydrography

The bottom temperatures recorded at Svartnes (~170 m) in Balsfjord in 2015 and 2016 (Figure 2) were slightly higher than those observed in earlier years. The average temperature the last 40 years has been approximately 3.1 °C (Henriksen 2015). In 2015 and 2016, the average temperature was 3.6 and 4.0 °C, and temperatures did not drop beneath 3 °C. The results could be biased by the fact that temperatures were not measured every month in 2015 and 2016, although the winter months with the usually lowest temperatures were included.

The seemingly higher temperatures may have many explanations. Balsfjord have historically been subjected to warmer and colder periods. Considering the last 40 years, the 1980's was characterised by several cold periods followed by a warm period between 1990 and 1993. During the last 20 years, the temperatures have been relatively stable above the 40-year average, apart from some fluctuations in the late 1990's (Henriksen 2015). Interannual variability in temperatures in inner Balsfjord have been correlated to the NAO index (Mankettikkara 2013).

Furthermore, temperatures of northern Norwegian fjords are closely connected to air temperatures (Eilertsen and Skarðhamar 2006). The 1930's in Norway were characterised by high air temperatures, reflected in the relatively high sea temperatures recorded in Balsfjord, and a trend of increasing annual mean air temperatures has been observed in Tromsø the last 10 years (Mankettikkara 2013; Lundstad and Tveito 2016).

Ramfjord, located in the outer part of the fjord has slightly higher bottom temperatures (~100 m) than the Svartnes basin (~170 m) and Tennes in the inner part of the fjord (~100 m) (Mankettikkara 2013).

4.2 Benthic sampling

Regarding the sampling of benthic fauna, it is of unequivocal importance that aims and purposes are clearly defined so that an appropriate study design can be constructed before sampling and provide valid and valuable results. A good design will increase the precision of estimates, maximise the power of statistical tests and reduce the probabilities of errors (Underwood and Chapman 2013). The ultimate goal of most studies is to obtain results that are convincing so that management decisions can be made, and gaining support for further studies.

When designing benthic monitoring programmes or impact assessment studies, it is especially important that the design considers the natural variation in species assemblages that exists in space and time. Ideally, a pre-disturbance baseline study of the communities should be constructed, with sufficient sampling in time and space. When natural variation is accounted for, changes in communities can more confidently be linked to the disturbance.

Benthic fauna is known to have an extremely patchy distribution on both spatial and temporal hierarchical scales due to external and internal processes. These include anthropogenic disturbances such as large-scale trawling and natural disturbances acting on several spatial scales including wave action and currents (Underwood and Chapman 2013). Small-scale disturbances in the habitat are also caused by the fauna itself through bioturbation (Gray and Elliot 2009). Furthermore, biological interactions within assemblages can greatly alter the habitat and its species composition. Competition for limited resources (i.e. food and space) and predation are especially important. Recruitment is another major factor affecting benthic assemblages. Most benthic species have pelagic larvae and their settlement process is affected by processes acting in the water column as well as physiological cues and conditions in the settlement site (Gray and Elliot 2009).

A great deal of the variation among samples in the present study could likely be contributed to natural spatial and temporal variation and patchiness caused by a variety of the mentioned abiotic and biotic processes.

4.3 Beam trawl efficiency

When describing epibenthic communities, the catching efficiency of the sampling gear should be taken into consideration. The catching efficiency has been defined as the biomass or number of individuals of species caught, expressed as a proportion of the total population in the sampled area (Kaiser et al. 1994; Reiss et al. 2006). Trawls are commonly designed to sweep over the sea floor, with limited penetration into the sediment, which consequently affects which organisms are being captured (Eleftheriou and Moore 2013). Sampling by trawling is considered to be semi-quantitative and thus, the fauna collected does not represent the actual community, but it provides a view of its composition (Greenstreet et al. 2007).

Beam trawl efficiency has been investigated by Reiss et al. (2006). They found that the catch rates of species were affected by several factors including size, motility, position on or within the sediment and sediment type which determines the penetration depth of the trawl, i.e. deeper penetration in muddy compared to sandy grounds. In conclusion, the catch efficiency was low for the overall epibenthic fauna, particularly for burrowing and highly mobile species.

Trawl design and sampling procedure greatly affects the outcome of a sampling. The mesh size of the cod-end (inner mesh) should be considered when choosing trawling speed and distance. Rumohr (2009) recommends a maximum mesh size of 1 x 1 cm, for which the trawl can be towed at a speed of 2 knots. With an inner mesh of 2 x 2 mm, the speed and duration should not exceed 1 knot and 5 minutes, i.e. larger nets can be towed longer distances at higher speeds. In this study the cod-end mesh size was 4 mm (2 x 2) and the trawl was towed at 0.5 knots for 5 minutes, which was appropriate according to the given recommendations.

Another important aspect to consider is the mesh size of sieves, as it determines which animals are being retained. As with gear selection, choice of mesh size should reflect the purpose of the study, but the time and resources available for sample processing must be taken into consideration as decreasing mesh size leads to increased time consumption of processing (Callaway et al. 2002). Grab and trawl samples are commonly sieved with 1 and 5 mm mesh size, respectively. In this study, both 1 and 5 mm fractions from round hole sieves were preserved. According to Rumohr (2009), there has been an increase in the use of sieves with round holes as opposed to square holes as the former is thought to preserve the condition of the animals better.

Repeated beam trawl sampling aiming at comparing spatial or temporal patterns in a site is an intricate task due to the difficulties of obtaining consistent sampling procedures. Sampling in exact positions can be challenging due to inaccuracies related to the gear positioning (Reiss et al. 2006). Additionally, the exact duration of the towing can vary (Eleftheriou and Moore 2013), unless specific equipment is attached to the trawl like the probe (SCANMAR ©) used by Reiss et al. (2006) and in this study. Finally, the generally low catch efficiency, patchy distribution of benthic fauna and the behaviour of species including migration can result in significant variability between samples and over - or underestimation of abundance and biomass. (Reiss et al. 2006).

An approach to ensure repeated sampling of an area using trawls is by attaching 3 nets as done by Reiss et al. (2006). This method will sample a larger fraction of the present fauna because the first net will disturb the sediment and expose infaunal and burrowing species. Furthermore, attaching chain mats to trawls has become a common practice and studies have shown that it leads to reduced variation between replicates and increased biomass compared to trawls without a chain mat (Kaiser et al. 1994).

The advantage of beam trawl sampling as opposed to grab sampling, besides collecting epifauna, is the increased possibility of obtaining rare and mobile species, since a much greater area is covered. In this study, the aim was to give a general description of the soft-bottom epibenthic communities in Balsfjord which reduces the importance of replicates. Replicate sampling for each station would have been necessary if the purpose was to perform e.g. multivariate community analyses and compare quantitative data including diversity, evenness and similarity (Underwood and Chapman 2013).

4.4 Sample processing

Sample processing and identification of epibenthic macrofauna proved to be an extraordinarily laborious and time-consuming task. Sorting animals from sediments, one spoon at a time required great focus. Becoming familiarized with identifiable traits of a multitude of taxa representing 8 different phyla, took time for an untrained eye and most of the identification had to be done with the help of a stereomicroscope. Very small or fragmented organisms were frequently encountered. All gastropod shells and tubes of *Pectinaria* sp. were examined to see if they were inhabited by their original owner or the sipunculid *Phascolion strombus*, in which case they were carefully extracted. Finally, more than 25 000 individuals, including *Ctenodiscus crispatus* were processed in this study.

4.5 Epibenthic fauna in Balsfjord: Macrobenthos 5 mm fraction

The epibenthic species assemblage was typical of that of northern Norwegian fjords (Holte et al. 2004; Oug and Fuhrmann 2013). *Ctenodiscus crispatus* and the polychaetes Maldanidae and Oweniidae were among the ten most abundant taxa at all stations. Ramfjord (St. 176), located in the outer part of the fjord at approximately 118 m depth had the highest number of individuals and taxa, dominated by maldanid polychaetes, in agreement with Henriksen (2015), who compared beam trawl - and grab samples from Ramfjord (Andersdal), Tennes and Svartnes. Tennes (St. 118), located in the inner part of the fjord at approximately 104 m depth had the second highest number of individuals and taxa, strongly dominated by the bivalve *Yoldiella* sp. The polychaetes Maldanidae and Oweniidae were the second and third dominating taxa, in agreement with grab samples from Tennes (Henriksen 2015).

The deep basin at Svartnes (179 m) had the lowest number of individuals and taxa and the lowest biomass, concurring the results from grab samples (Henriksen 2015). *Ctenodiscus crispatus* was the dominant taxon both in terms of abundance and biomass, and had the highest abundance among the processed samples, which indicates that the habitat is favourable for the mud star. The sample from St. 194 (Tømmernes) was also taken in a deep part of the fjord (170 m) and the faunal composition was relatively similar to that of St. 196, with a clear dominance of *Ctenodiscus crispatus* in terms of abundance and biomass. Maldanidae was the second dominating taxon at both stations.

Collecting infauna through grab sampling has been the traditional method for investigating benthic communities, as is the case for most benthic studies from northern Norway. These samples are typically dominated by polychaetes, both in numbers and biomass, although molluscs (bivalves) and *C. crispatus* often contributes considerably in terms of biomass (Oug 2000; Oug and Fuhrmann 2013; Henriksen 2015).

In my samples, polychaetes were numerically dominating only at station 176 (Ramfjord), but were among the dominant taxa at all stations. Polychaetes contributed little to the total biomass, due to high individual weights of large fish, crustaceans, molluscs and echinoderms who are typically not collected by grabs. The fairly high abundance of infaunal polychaetes in the samples suggests that the trawl was digging relatively deep in the sediment.

Depth and sediment characteristics are among the major abiotic factors affecting the variability in species composition, density and biomass of benthic fauna (Gray and Elliot 2009). Indeed, Oug (1998) found depth to be an important factor explaining variation in species patterns of infaunal macrofauna between several sites in the Tromsø area, but argued that depth-related differences are caused by depth-dependent environmental parameters including temperature, sediment type (particle size) and food quality. However, he suggested that most of the variation was likely due to general patchiness, natural variation and biological factors including recruitment, bioturbation and competition.

In a fjord system like Balsfjord, the hydrodynamic regime is an important determinant of the benthic community structure, as it influences the food supply to the benthos, which is generally low in this fjord (Oug 2000). The processed samples in this study were collected from different depths and locations in Balsfjord, which likely contributed to the differences observed between samples.

Studies characterizing sediments in the Svartnes basin revealed a major composition (~ 95 %) of the fine fraction sediments based on the Wentworth scale, with a preponderance of clay and silt (Sargent et al. 1983b; Oug 2000). Sediment characteristics from the sampled stations in Ramfjord and Tennes are to my knowledge not available in the literature, but from personal observations they seemed to have a slightly higher fraction of coarser material. Without sediment analyses from all stations, relating faunal differences to sediment type will be a subject of speculation.

The reason why Svartnes (St. 196) had the lowest number of individuals and taxa, but the highest number of *Ctenodiscus crispatus* is presumably linked to the prevailing environmental conditions in the basin, including lower food input and possibly poorer oxygen conditions. An experimental study by Shick et al. (1976) demonstrated that *C. crispatus* has a high tolerance to hypoxia, and the highest survival among echinoderms in hypoxic conditions (at the time of their study). The authors suggest that their infaunal lifestyle has made them well-adapted to variable and low oxygen conditions. The mud stars' epiproctal cone, which can be extended to great lengths relative to body size, enables them to be connected to the oxygenated water column while being buried in the sediment (Shick et al. 1981b).

The fauna in Ramfjord (St. 176) and Tennes (St. 118) was observed to consist of larger and more colourful individuals than conspecific individuals from St. 194 (Tømmernes) and 196 (Svartnes), which might be linked to depth in terms of food availability. This was particularly evident in the taxa *Ctenodiscus crispatus,* Maldanidae and other large polychaetes. Differences in coloration of conspecific individuals have been linked to depth and hence the amount of primary production that reaches the sea floor in the Antarctic sea star *Odontaster validus* (McClintock 1988). In the present study, an alternative, but less likely explanation for these coloration differences is the preservation method. Samples from Ramfjord and Tennes were preserved in formalin, while those from Svartnes and Tømmernes were frozen.

The larger individual sizes observed in Ramfjord (St. 176) and Tennes (St. 118) could likewise be related to depth, i.e. food supply, but also biological interactions. Growing to larger sizes could be a competitive advantage, especially in Ramfjord where many species coexist and interspecific competition probably acts stronger than in the other areas. Ramfjord had nearly twice the number of taxa found at Tennes.

Limited food supply and low predation pressure have been linked to decreased body size (Olabarria and Thurston 2003). Hence small-sized and less pigmented individuals at Svartnes

(St. 196) and Tømmernes (St. 194) could be the result of limited advection of surface production and less interspecific competition and predation. The infauna at Svartnes is known to be dominated by small sediment-ingesting forms (Oug 2000).

In conclusion, differences in food availability and quality as a function of depth are plausible explanations for the differences observed between samples. Even if temperatures are slightly higher in Ramfjord, it is probably not a determining factor. The role of differences in sediment characteristics remain uncertain. Patchiness and natural variation due to biotic and abiotic processes probably contributed greatly to the variation between areas. Additionally, due to the semi-quantitative nature of beam trawl samples, Callaway et al. (2002) argued that information on abundances may be of limited value.

If the 1 mm fractions had been processed, the results might have been different, but because the dominating taxon constituted about half of the total number of individuals in the samples, I would expect the overall patterns to remain the same and *Ctenodiscus crispatus* would still be dominating in terms of biomass.

4.6 *Ctenodiscus crispatus*

4.6.1 Best size measurement

In this study, the central disc diameter (L1) was statistically found to be the best length measurement of *Ctenodiscus crispatus* based on the calculations of the *coefficient of variation* and the results of the Kolmogorov-Smirnov two-sample test. In terms of feasibility, this measurement was in my experience more practical and less time-consuming than the L2 - and L3 length measurements. Reproducibility was the criteria for what defines a good size-measurement and the reason why the disc diameter proved more reproducible was at least partially because the arms were excluded from the measurement. From the vast number of mud stars processed in this study, pronounced asymmetry and strongly curved arms were frequently observed, particularly in larger individuals. The latter is in agreement with observations made by Turner and Dearborn (1972) who argued that the standard size measurement in asteroids (from the center of the disc to the tip of a ray) was not applicable to *Ctenodiscus crispatus* due to rigidity and curliness of rays, but also because this measurement is commonly made on the aboral side, whose center is the epiproctal cone. Its position is highly variable due to the flexibility of the aboral integument, i.e. extension determined by stomach content.

In similarity to ophiuroids, the margins of the central disc appeared to display lower plasticity, which makes the disc diameter a reliable measurement when numerous individuals of various sizes are to be measured and when comparing studies. There are however factors which can bias the disc measurements of mud stars, including the amount of mud present in the stomach and desiccation which can cause swelling or shrinking of the disc (Gage 1990). For future length measurements, asymmetry of the disc can be accounted for by measuring all five interradial diameters, and use the mean value as done by Tyler and Gage (1981). Increased processing time should be taken into consideration.

However, weight (dry) was chosen as the standard size measurement of mud stars in this study, despite establishing that the disc diameter is a good measurement. A major concern regarding sample processing is often time consumption (especially in benthic studies). Measuring weight is in many ways more efficient and it may provide a more accurate measurement, because it is not affected by the shape (i.e. asymmetry) of the individuals. The drawback with weight measurements is the requirement of more thorough cleaning than length measurements, which might be time-demanding.

In conclusion, sample sizes and availability of resources (e.g. time) should be considered when choosing a size-measurement.

4.6.2 Biomass distribution in Balsfjord

Biomass and abundance of *Ctenodiscus crispatus* were most variable in Ramfjord, which could be explained by general patchiness and a heterogeneous environment. At Svartnes, both biomass and abundance were relatively stable throughout the year, probably due to homogenous environmental conditions. Tennes had constantly low biomasses, except for the sample from June. Spatial distribution of mud stars is further discussed in Section 4.6.5.

4.6.3 Morphology and maturation

Based on 125 mud stars collected at Svartnes in April (St. 196), segmented and linear regression relating the L2- and L3 length measurements to the central disc diameter (L1) revealed a discontinuous growth with non-parallel lines (different slopes) between the two groups identified by K-means clustering. The second clusters of both relationships contained more than half (65-66 %) of the individuals in the sample (Table 10), corresponding to the mode of probably adult mud stars identified in the size-frequency distributions of the three length measurements (Appendix Figure 1).

The same pattern was discovered in the weight-length relationship of 334 individuals where cluster 2 contained 75 % of the individuals (Table 14). When combining the results of the length measurement relationships and the weight-length relationship of mud stars from Svartnes, April (St. 196), I found overlapping areas between disc diameters (L1) of 12 and 15 mm and equivalent dry weights of 0.5 and 0.9 g. These size ranges were usually representing the transition zone between two consecutive modes in the bimodal size-frequency distributions (Figure 13, 16, Appendix Figure 1).

The apparent change in growth (slope) could suggest morphological changes when the mud stars reach a certain a size, possibly linked to maturation. A definite age or size of maturation has not been determined for *Ctenodiscus crispatus*. Skeletal morphology of the mud star has been described in great detail, but apart from morphological changes during metamorphosis, changes related to maturation are not accounted for. Most of the ontogentic morphological changes occur in the rays, including continuous addition of paired ossicles and a change in orientation of the terminal plate at the tip of the ray (Turner and Dearborn 1972).

In brachyuran crabs, morphological changes related to maturity is well known and presents itself through sudden rapid growth of secondary sexual characteristics such as the chelae (Hartnoll 1974; Gerhart and Bert 2008). The phenomenon is often graphically displayed by relating the growth of these characteristics to the growth in body size (e.g. carapace length), via linear regression, which results in similar patterns to those found in allometric relationships of *C. crispatus* in this study, though in mud stars, the change is a decrease rather than an increase in the slope because the response variable is body length and not a secondary sexual characteristic. Regarding crabs, the overlapping area between separate regression lines is perceived as the size range where puberty moult occurs. As with my results, this overlapping area is not shown when fitting one discontinuous line with an inflexion point (breakpoint), but requires separately fitted lines for the pre-mature and post-mature groups of crabs.

Hence, the size range of overlap between clusters could be where *Ctenodiscus crispatus* become mature and somatic growth rate decreases.

Based on their study of mud stars in Maine, Shick et al. (1981a) considered individuals > 0.4 g (DW) to be adults. Their size range was 0.4 - 3.4 g dry weight, with a mean of approximately 1.7 g. When combining the size-frequency distributions from dry weight measurements in this study, the range of the right-hand mode was between approximately 0.7 and 7.4 g, with a mean value of 1.7 g dry weight, calculated from the means of identified right-hand modes in the mixed distributions (Table 19). This suggests that clusters and left-hand modes of small mud stars in this study were groups of juveniles, who begin maturing around a disc diameter of 12 mm (0.5 g DW). The combined mean value of juvenile modes from the mixture analyses was 0.1 g dry weight.

Falk-Petersen (1982a) dissected mud stars < 15 mm, measured from the center of the disc to the ray tip (R) which revealed no evidence of gonadal growth. L2 length (Figure 4) is the closest equivalent length measurement in this study, from which it can be suggested that a 15 mm R length would have a maximum L2 length of 20 mm. These mud stars would thus belong to cluster 1 in my study, i.e. among juveniles.

The consistency of the right-hand clusters and modes in containing more than half of the individuals suggests many adult age classes with low mortality and slow growth (Fujita and Ohta 1990; Packer et al. 1994). Hence, rapid growth to adulthood where mortality and growth rates decrease could be the dynamics in mud stars.

4.6.4 Reproduction and size-frequency distributions

The classic paradigm of increasing seasonality in reproduction with increasing latitude is based on the consensus that environmental parameters (temperature and salinity) and larval food supply are the proximate and ultimate causal factors affecting reproduction and recruitment in marine benthic invertebrates (Orton 1920; Thorson 1950; Bauer 1992). In tropical waters, where temperature and food supply is relatively constant, continuous reproduction is considered to be the common strategy. In temperate and boreal areas, where the primary (and secondary) production exhibits strong seasonality and temperatures are fluctuating, gametogenesis and spawning are accordingly expected to be seasonal. Species inhabiting polar and deep-sea areas were previously considered to show no seasonality in their reproduction due to stable environmental conditions, analogous to those of tropical habitats, but today it is widely accepted that seasonality or periodicity in reproductive events does indeed occur in these areas, as well as among tropic benthic invertebrates (Tyler et al. 1983; Bauer 1992).

Bauer (1992) argued that reproductive patterns cannot be predicted solely from latitude, because the selective pressures of biotic and abiotic factors varies between habitats and taxa. Different species occupying the same habitat and thus experiencing the same environmental conditions are constrained by their physiology, ecology and phylogenetic history resulting in different modes of reproduction. Additionally, conspecific populations from different latitudes or habitats, influenced by different environmental conditions and biological interactions may show differences in spawning and recruitment patterns.

According to Vance (1973), direct or lecithotrophic larval development should be expected in polar and deep-sea areas, as opposed to planktotrophic due to the combined effects of limited food availability for larvae and low temperatures. The latter is thought to decrease survival of planktotrophic larvae because low temperatures increase the duration of the larval development stage, and when food is only available in short periods, the prolonged larval stage put them at higher risk of starvation and predation (Thorson 1950).

Tyler et al. (1983) studied reproductive patterns of deep-sea echinoderms. They found that all three reproductive strategies, characterised by fecundity, oocyte size and mode of larval development were present among species inhabiting this seemingly stable environment. The dominant reproductive strategy among asteroids was the production of a few large (~ 900 μm) oocytes, and direct larval development. There were no indications of seasonality in reproduction among the studied species. Oppositely, species who produced a large number of small oocytes (~ 100 μm) and had planktotrophic larvae showed periodicity in reproduction, where the predicted larval and settlement stages were synchronised to the period with the maximum surface production and vertical flux of organic matter (Tyler et al. 1983; Bauer 1992). This appears to be a common strategy among ophiuroids including the species *Ophiura sarsii*, *O. albida*, and *O. ljungmani* (Falk-Petersen 1982b; Tyler et al. 1983).

Lecithotrophic larval development and the production of medium-sized eggs (~ 400 μm) was a less frequent strategy amongst the studied species. The ophiuroid *Ophiomusium lymani*, did not provide evidence of a seasonal gametogenetic cycle, but recruitment appeared to appear in pulses during summer (Tyler et al. 1983). Further investigations of this species suggested that the annual peak in recruitment was related to seasonal variations in survival of settling larvae in response to the annual flux of organic matter reaching the bottom (Gage and Tyler 1982).

When investigating reproduction in asteroids, assessing the relationship between the pyloric caecum index and the gonad index is common, as it can reveal how the food availability is in their habitat. The pyloric caecum is an important storage organ in sea stars, and during gametogenesis, stored nutrients are transported to the developing gonads in periods of low food abundance. Thus an inverse relationship between these indices is prevailing where food availability is seasonal (Farmanfaraian et al. 1958; Lawrence and Lane 1982).

Ctenodiscus crispatus is shown to have a strong positive correlation between pyloric caecum index and gonad index for both sexes, indicating that their environment offers a stable food source throughout the year (Shick et al. 1981a), supported by the continuous presence of mature gametes. A similar pattern was found for the asteroid *Patiria miniata* which is an omnivorous scavenger and who similarly to the mud star had well-developed gonads throughout the year and could spawn at any time (Farmanfarian et al. 1958).

However, the few studies of reproduction in *Ctenodiscus crispatus*, have been somewhat contradictory, in that the size of oocytes and fecundity varied between three populations sampled from Maine (Damariscove Island), Newfoundland (Conception Bay) and Balsfjord. The maximum recorded oocyte sizes were 400 and 650 µm in Maine and Balsfjord, while the mean size was 450 µm in Conception Bay. The lowest fecundity (10^2 - 10^3) was observed in the Balsfjord population (Shick et al. 1981a; Falk-Petersen 1982b; Jaramilo 2001). These findings exemplify Bauer's (1992) theory of conspecific variations in reproductive strategies due to inhabitation of different geographic areas. Egg size is generally thought to increase with latitude and fecundity is expected to be highest where food is more abundant (Vance 1983). Indeed, Balsfjord is located at a higher latitude (ca. 20 degrees) than the other sites, and is considered sub-arctic rather than boreal. All three authors suggested that *Ctenodiscus crispatus* have lecithotrophic larval development with feeding beginning after metamorphosis (Shick et al. 1981a; Falk-Petersen 1982b). Hence, food availability for settling larvae is probably an important causal factor for the reproductive patterns in mud stars.

The mud star populations in Damariscove Island and Conception Bay are likely subjected to more predictable and seasonally high food abundances, due to rapid sinking of phytodetritus shortly after spring and autumn blooms, periods in which spawning were more intense (Shick et al. 1981a; Jaramilo 2001). These depositional events could supply higher-quality food for post-larval mud stars and might explain why fecundity was higher in these populations. In Balsfjord, there is usually no autumn bloom, and very little of the spring surface production reaches the sea floor (Wassmann et al. 1996). Hence, both juvenile and adult mud stars must rely solely on the homogenous nutrient composition in the sediments, maintained by resuspension of organic matter and microbial activity (Sargent et al. 1983b). Suggested mid-winter peak in breeding among the Balsfjord population (Falk-Petersen 1982a) might be due to lower predation and competition for the settling larvae.

Biological interactions affecting reproductive patterns in conspecific populations has been demonstrated by studies of *Ophiura sarsii*, a species with planktotrophic larvae, high fecundity and small oocytes having continuous, but seasonally variable spawning (Falk-Petersen 1982b; Packer et al. 1994). Fujita and Ohta (1990) suggested that recruitment and growth in *Ophiura sarsii* were closely linked to competition, based on their studies of size-frequency distributions in samples collected at different depths, with marked differences in densities, size-structures and presence of competing species.

In the shallowest part (250 m) there was an overall polymodality in size-frequency distributions with a dominating right-hand mode of large individuals. Relatively high abundances of small individuals were found in the spring samples from which they suggested a continuous reproduction, but with seasonal peaks in recruitment (March-May) at this depth. The shallow habitat was almost exclusively occupied by high densities of small *O. sarsii*, hence inter-specific competition was assumed to be low, while intra-specific competition resulted in small-sized individuals due to suppression of growth in high-density populations (Fujita and Ohta 1990). In the deeper areas (450-550 m), size-frequency distributions were characterised by a higher proportion of larger individuals. No recruitment events were observed. The authors suggested that at these depths, mortality was high due to interspecific competition with other co-existing dominating ophiuroid species, which was evident from low densities and larger individual sizes of *Ophiura sarsii*, the latter assumed to be a competitive advantage.

From the size-frequency distributions of mud stars collected in Balsfjord in March, April, June and October I found no indications of major recruitment events. Distributions were mostly bimodal, and all mud star samples had one right-hand dominant mode which probably is a stacked mode of adults of many age-classes. These modes consistently contained more than half of the individuals in the samples, which could confirm that mud stars do not exhibit seasonal reproduction. By comparison, Schoener (1968) and Lightfoot (1979) provided evidence of seasonal reproduction in *Ophiura ljungmani* by showing that the smallest size classes constituted 90 - 100 % of the population in size-frequency distributions from samples collected during summer when food from the spring bloom reaches settlement sites.

Bimodal distributions where adults made up the dominant mode were also found in size-frequency distributions of *Ophiomusium lymani* studied by Gage and Tyler (1982). They speculated that there was an underlying polymodality in the distribution which was only detected by the largest sample sizes. This did not seem to be the case for size-frequency distributions of *Ctenodiscus crispatus* in this study. The largest sample size containing over 1600 individuals (St. 392) did not display neither a clear bimodal nor polymodal distribution, before juveniles and adults were separated. The second highest sample size was from St. 197 collected at Svartnes in April and it was clearly bimodal.

The shape of a size-frequency distribution results from variability in age - or size specific growth and survival, together with seasonal and interannual variation in recruitment (Ebert 1981; Ebert et al. 1993). Most methods for estimating growth and mortality rates from size-structures are based on separation of age-classes, which depend on modes resulting from annual recruitment pulses (Macdonald and Pitcher 1979; Smith et al. 1998). Size-distributions often fail to display clear age-classes, although in some cases, they occur in the lower size range, while larger individuals form a single mode at the right side of the distribution from which age-classes cannot be separated (Ebert 1973; Smith et al. 1998).

Such models, for simplicity reasons, often assume that the population has a stable age-structure, constant or continuous recruitment and constant age-independent growth and mortality rates, assumptions which cannot result in the bimodal distributions frequently observed among species (Barry and Tegner 1990; Ebert et al. 1993). Hence, bimodality has been explained in terms of age-specific variation in growth and /or mortality rates, where the mode of large individuals in bimodal distributions is a result of reduced growth and mortality among adults (Wilson 1983; Barry and Tegner 1990).

Another explanation is seasonal recruitment pulses. Based on simulated size-frequency distributions, Ebert et al. (1993) linked bimodality to pulsed recruitment if there was a temporal progression in the smallest mode. When there was no shift in the smallest mode, the explanation was continuous recruitment and decreasing mortality with size, in agreement with the views of Wilson (1983) and Barry and Tegner (1990).

Polymodality was detected in four size-frequency distributions of mud stars from Balsfjord, including the juveniles from Tennes (St. 392). Mixture analysis identified two modes among the small individuals, in the size-frequency distributions from Svartnes in June (St. 391) and October (St. 705), with mean dry weights of 0.06 and 0.03 g in the first modes and 0.6 and 0.13 g in the second modes, indicating a growth in the smallest cohort from June to October. Based on my suggestion of a maturing stage between 0.5 and 0.9 g (dry weight), these two modes were composed of juvenile mud stars, although the second mode in June was partially overlapping with the adult mode. Three modes were identified among the small individuals at Tennes in June (St. 392) with mean dry weights of 0.009, 0.08 and 0.34 g, i.e. well within the suggested juvenile range.

The unimodal size-frequency distribution of juvenile mud stars from Maine (Shick et al. 1981a), had a mean value of 6 mg dry weight in August and probably represented a group of newly settled mud stars, based on the main spawning period in late spring. In March, the mean value had increased to 15 mg, indicating growth in this cohort (Shick et al. 1981a). If the main breeding in Balsfjord occurs during mid-winter, I would expect to find newly settled mud stars in early spring. Thus, it can be suggested that the mode from Tennes in June with a mean size of 0.009 g (9 mg), represented recently recruited *C. crispatus*.

However, because the smallest mud stars (1 mg) were found in both August and March, Shick et al. (1981a), suggested more frequent recruitment. At Tennes in March (St. 118), a few mud stars < 5 mg were observed in the 5 mm fraction of macrofauna samples and were probably newly settled. Mud stars down to 5 mg were present among samples from March, April and June in Balsfjord, but in low numbers and absent in October at all stations. However, at Svartnes (St.705) and Tennes (St. 706), the smallest individuals were 10 and 30 mg in October.

The results could suggest more than one recruitment event at Tennes and Svartnes. According to Ebert et al. (1993), a positive slope from the small left-hand to the large right-hand mode in size-frequency distributions is indicative of two or more recruitment episodes per year.

The previous studies of *Ctenodiscus crispatus* in Balsfjord were based on samples collected in Ramfjord at 80-120 m between 1978 and 1980. They may not be representative for the whole fjord, because of differences in depth, food availability and biological interactions.

4.6.5 Spatial variation

At Svartnes, mud stars were found in high densities throughout the year, while usually in lower densities at Tennes and in Ramfjord, with a few exceptions. The 5 mm fractions of epibenthic fauna in this study and studies of infauna at Svartnes, demonstrated that the number of taxa is low compared to Tennes and Ramfjord (Henriksen 2015). By drawing comparisons to the studies of *Ophiura sarsii* (Fujita and Ohta 1990), it can be suggested that mud stars at Svartnes, experience low interspecific competition and are able to maintain high densities of seemingly smaller individuals whose growth is suppressed by intraspecific competition (McClintock et al. 1988). In Ramfjord, larger individuals, lower densities and few juveniles suggest higher interspecific competition and juvenile mortality.

The presence of juvenile individuals (6 mg) in Ramfjord in April (St. 176) could be indicative of a mid-winter spawning, but it is unlikely that the smallest individual (0.5 g) collected in June

(St. 390) was recruited in spring. In October (St. 704), the smallest mud star was 0.1 g, which could have been recruited in spring, although implying a very rapid growth. If the smallest individuals from Tennes (St. 706) and Svartnes (St. 705) in October (30 and 10 mg) were recruited in March, growth is considerably slower or a second recruitment event occurred. The juveniles from Maine grew 9 mg (1500 %) in seven months. Assuming that newly settled mud stars in March have a dry weight of 1 mg, the growth of the 10 and 30 mg juveniles would be 900 and 2900 % in 7 months at Svartnes and Tennes. Thus, them being spawned in mid-winter seems more likely than a second recruitment event.

Based on the results from Ramfjord, postlarvae spawned in mid-winter, settling in March, would not grow rapid enough to be mature within seven months, if they reach 0.1 g dry weight in October, neither would the those from Tennes and Svartnes. Furthermore, there appears to be size - or age dependent growth rates among juveniles, where newly settled individuals grow faster than older juveniles based on the estimated growth from modal progressions of larger juveniles. Additionally, growth rates seem to vary between stations with particularly rapid growth in Ramfjord.

Highly variable individual growth rates due to substantial genetic variation within populations have been suggested for *Ctenodiscus crispatus* (Shick et al. 1981a), while different growth rates throughout the year could be linked to changes in environmental factors e.g. temperature and nutrient composition (Falk-Petersen 1982a).

The results obtained from size-frequency distributions of *Ctenodiscus crispatus* are potentially biased by the fact that the 1 mm and most of the 5 mm fractions were not processed and they might have included smaller individuals. Extreme patchiness could likewise have affected the sampling.

Conclusion

Kjær's (1905) suggestion that bimodal size-frequency distributions of *Ctenodiscus crispatus* is representing two age-classes is unlikely and the results of this study suggest rather two separate groups of juvenile and adult mud stars.

A mid-winter spawning is suggested to have occurred in all three areas, due to the presence of probably newly settled individuals in April. In Ramfjord, low fecundity, high juvenile mortality and/or rapid growth to escape predation could explain why juvenile modes were never detected.

Although, the absence of the smaller size-classes in June and October could be due to strong patchiness causing them to not be sampled.

At Svartnes, lower predation pressure, homogenous environmental conditions including low food supply and high mud star densities could explain the observed patterns. The smallest individuals in October from both Svartnes and Tennes were probably recruited in early spring because growth rates were similar to those in Maine, although a seemingly faster growth of postlarvae mud stars at Tennes.

Mortensen (1927) suggested that *C. crispatus* reaches full size in three years. The results of this study are not sufficient to neither confirm nor disprove it, but they indicate that growing to the size of maturation possibly takes minimum a year, with variations between individuals and areas due to highly variable growth rates. Reaching adulthood in three years is possible, but future studies should focus on obtaining independent growth rates and estimates of age. Variability in environmental conditions and biological interactions and genetic variation could result in differences in reproductive output, timing of spawning, juvenile mortality and growth rates.

Previous studies revealing a positive correlation between pyloric caecum and gonad index, and the presence of mature oocytes throughout the year together with sediment analysis from Svartnes indicate a stable food source. Low fecundity and continuous reproduction with minor spawning peaks in mid-winter, explain the patterns observed in size-frequency distributions.

4.6.6 Future studies

To improve our understanding of the population dynamics in *Ctenodiscus crispatus*, further studies should focus on regularly (e.g. monthly) sampling over a longer period of time.

Additional histological studies of mud stars from Balsfjord should aim at collecting samples from both Svartnes, Tennes and Ramfjord to uncover whether there are significant differences between these areas related to densities, size structures and reproduction linked to depth, environmental conditions and biological interactions in the communities. Experimental studies could be helpful in determining growth rates and age of maturation, while genetic analyses could provide the means to explain individual differences. It can be worth investigating whether growth rings exist in *Ctenodiscus crispatus* in combination with these studies.

4.7 Potential food for the red king crab in Balsfjord

During their investigations in Varangerfjorden, Oug et al. (2011) discovered a decrease in the populations of the most common soft-bottom species by 70-90 %. These included echinoderms, burrowing polychaetes and large mussels. *Ctenodiscus crispatus* was completely absent from their samples. The authors suggested that functional traits such as small size, high mobility, living in tough tubes and deep burrowing were characteristic of species that increased in abundance after the king crab invasion in Varangerfjorden, possibly because these traits enable them to escape predation. Thus, free-living, shallow burrowers and larger species of low mobility may be more available as prey for the crab (Oug et al. 2011).

Stomach content analyses of red king crabs from the more recently invaded Porsangerfjorden, identified sediment-dwelling bivalves and polychaetes to be the most important prey, although 69 taxa were identified including echinoderms, amphipods, cumaceans, sipunculids, gastropods, forameniferans and bryozoans (Fuhrmann et al. 2017). Differences between stomach contents were related to crab size and location (depth). *Yoldiella* sp. and the tube-building polychaetes Maldanidae, Oweniidae and *Pectinaria* sp. were important prey for crabs of all sizes. *Ctenodiscus crispatus* was mainly eaten by large crabs (Fuhrmann et al. 2017). However, in Varangerfjorden, Maldanidae and Oweniidae seemed to have increased in abundance after the king crab invasion (Oug et al. 2011). Maldanidae has a very fleshy body, but is concealed in a tough tube. Their high occurrence in stomachs of both small and large crabs suggests that they are capable of penetrating the tube.

Several of the taxa identified in Balsfjord occurred in the stomachs of king crabs from Porsangerfjorden (Fuhrmann et al. 2017). Ramfjord, Tennes and Svartnes are potential habitats for adult and large juvenile crabs in Balsfjord, and the dominating mud star would likely be an important prey item as king crabs are suggested to select the prey with highest biomass (E. Nilssen pers. comm.). Furthermore, Maldanidae, Oweniidae, ophiuroids, sipunculids, and molluscs including the natacid gastropod *Euspira pallida* and the bivalves *Yoldiella* sp. and *Astarte* sp. were occasionally abundant in Balsfjord and frequently observed in king crab stomach contents (Fuhrmann et al. 2017). According to my results, Ramfjord has the widest selection of potential prey including cumaceans, amphipods and several taxa of bivalves and polychaetes.

The tubicolous polychaetes Sabellidae and Ampharetidae were quite abundant in Ramfjord (St. 176), but were not found in the stomach content of king crabs (Fuhrmann et al. 2017). Their tubes are perhaps too strong for the crab to tear up and are thus not selected. The relatively abundant Terebellidae and Trichobranchidae were also absent from stomach contents. All these polychaetes have in common a large tentacular crown which could provide a defence mechanism against predation, while their bodies reside in tubes or sediments. An experimental study of defensive traits in polychaetes revealed that exposed body parts usually are less palatable then overt parts. Most of the terebellid and sabellid species had unpalatable tentacles due to chemical deterrents (Kicklighter and Hay 2006).

Furthermore, pycnogonids, *Musculus niger*, *Thyasira* sp., scaphopods and the large mobile polychaete Nepthyidae were not important prey (Fuhrmann et al. 2017). These taxa, except for *Thyasira* sp., had relatively high contributions to the biomass in my samples, but may not be a food source for king crabs in Balsfjord.

Based on observations from Varangerfjorden, it is reasonable to assume that a similar situation will occur in Balsfjord after an invasion, with a reduction in the populations of several dominating species. Monitoring should focus on *Ctenodiscus crispatus*, due to its established dominance in the fjord and the knowledge that it is strongly affected by the king crab. Even though Maldanidae is an important prey, they may not be heavily affected, but able to maintain high densities. Potential bivalve prey, including *Yoldiella* sp. could be worth monitoring as well.

4.8 Invasion potential of the red king crab in Balsfjord

The successful invasion of the red king crab in sub-arctic fjords of northern Norway is probably linked to their occupation of different habitats, variety of feeding mechanisms and a highly omnivorous diet in addition to tolerance and adaptivity to varying environmental conditions. Lack of parasites and low fishing pressure during establishment are also suggested to enable their success (Falk-Petersen et al. 2011).

Studies of predation mortality in king crab populations from the native Bering Sea, suggests that predation is of negligible importance regarding population control. No species appeared to target the king crab as a prey item. However, they are vulnerable during the larval and post-settlement stages, where they may be a food source for some species of fish and sea stars. After reaching maturity, their large body size makes them unsuitable as prey for most predators, except for humans (Falk-Petersen et al. 2011; Stevens and Jewett 2014).

Competition and predation are the main mechanisms through which the red king crab alters the native ecosystem (Falk-Petersen et al. 2011). Due to their opportunistic feeding and dense populations, they have the ability to outcompete other species for both food resources and space. In Balsfjord, native competitors at risk may include the northern stone crab, *Lithodes maja*, predatory fish, starfish and gastropods whose prey items are amongst those of the red king crab. These competitors, including *Buccinum undatum*, *Asterias rubens* and *Pontophilus norvegicus* were suggested to have overlapping niches with the red king crab in Porsangerfjorden (Fuhrmann et al. 2017).

In soft-bottom habitats, maintaining proper environmental conditions (e.g. oxygen levels) is crucial. Despite the limited water exchange in Balsfjord, oxygen conditions are sufficient and many benthic species probably contribute positively to the water quality through bioturbation. The potential decline of such key species can have negative effects on species who are not directly threatened by the king crab through predation or competition. In Varangerfjorden, the depth of biogenic activity in the sediments seemed to be reduced in areas where the abundance of benthic organisms had decreased, with possible implications for e.g. oxygen supply, remineralization of organic matter and nutrient cycling (Mermillod-Blondin 2011; Oug et al. 2011). *C. crispatus*, in addition to many polychaetes and bivalves may play a key role in maintaining the sediment characteristics through their burrowing behaviour (Shick et al. 1981b). However, reduced bioturbation may be counteracted by the crab's activities (Oug et al. 2011).

The results of the present study indicate that conditions are suitable for the king crab in Balsfjord. The faunal composition was similar to that of other northern Norwegian fjords, including the invaded Varanger - and Porsangerfjorden. Its preferred food is abundant and all four investigated stations are potential habitats (feeding grounds) for adult and large juvenile king crabs (> 100 m).

Samples were collected at a time were king crabs would be migrating to shallow water for moulting and mating (10 - 30 m). The Iceland scallop *Chlamys islandica* is a common species in the shallow hard-bottom areas of Balsfjord, including Berg (pers. obs.; Juliussen 2007). Scallop beds are known to be suitable settlement sites for young crabs as they provide shelter from predation (Falk-Petersen et al. 2011). Potential prey for young crabs in these areas include littoral gastropods and the sea urchin *Strongylocentrotus droebachiensis*. *C. islandica* and *S. droebachiensis* could be important prey for adult crabs during spring (Fuhrmann et al. 2017).

4.9 Future monitoring

Reduced biomass, diversity and sediment conditions have been detected in invaded areas, but long-term effects on ecosystem functioning and recovery are hard to predict (Falk-Petersen et al. 2011; Oug et al. 2011), and will require further studies on both species - and ecosystem level.

A few crabs have been found in Balsfjord, but have as of today not reached high densities. This study provides a good baseline of which are the main epibenthic taxa present in different parts of the fjord, and which are potential food for the red king crab. Due to long-term monitoring there is already good data on the infauna at Svartnes. Further monitoring should focus on infauna and epifauna collected by grabs and trawls in several areas of the fjord, so that all taxonomic and functional components of the benthos are included (Jørgensen et al. 2011) and supplemented with sediment analyses and measurements of environmental parameters.

In Porsangerfjorden, a commercial fishery of the red king crab was established six years after the initial catches, illustrating that high population densities can be reached in a few years. Establishment occurred later in the inner part of the fjord possibly due to sub-zero temperatures (Fuhrmann et al. 2017). Balsfjord does not have sub-zero temperatures, thus the whole fjord could potentially be invaded more or less simultaneously.

Regularly sampling, before the king crab reaches high abundances is advised in order to establish what is the natural variation in species assemblages, thus providing the means to separate this from effects of the potential invasion.

5. Conclusion

The epibenthic fauna in Balsfjord resembled that of other northern Norwegian fjords and was numerically dominated by the mud star *Ctenodiscus crispatus* and polychaetes including Maldanidae. Differences between stations were related to depth and position in the fjord, which determines the food supply and hence the species composition, abundance and biomass of species. Biological interactions and natural spatial and temporal variation due to biotic and abiotic factors probably contributed to the observed differences. An imminent invasion of the red king crab in Balsfjord is likely and the results of this study suggests that food availability and environmental conditions are optimal for a successful invasion. Based on the effects observed in Varanger - and Porsangerfjorden, continued monitoring of the benthos (epi - and infauna) in Balsfjord is advised to obtain a better understanding of the processes causing natural spatial and temporal variations in the communities so that post-invasion effects can be detected and measured.

This study supports the suggestion of a continuous reproduction, with a mid-winter peak in spawning of the mud star *Ctenodiscus crispatus.* Size at maturation was proposed to be between 12 and 15 mm (0.5 and 0.9 g dry weight). Further investigations should include genetic, histological and experimental studies focusing on estimating growth rates and age-structures and assess whether there are local differences in population dynamics. Regularly sampling from different parts of Balsfjord over a long period of time is advised.

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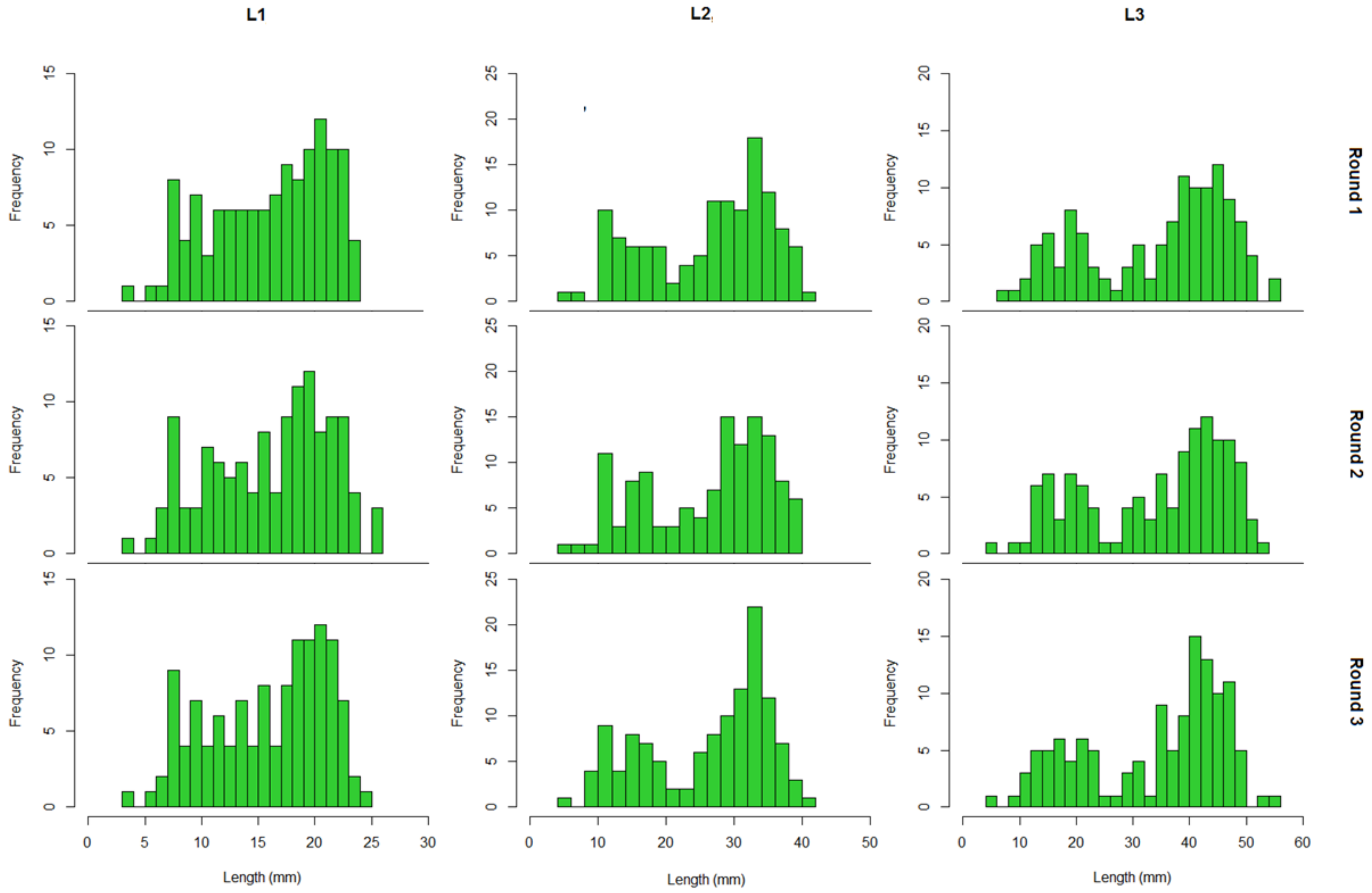
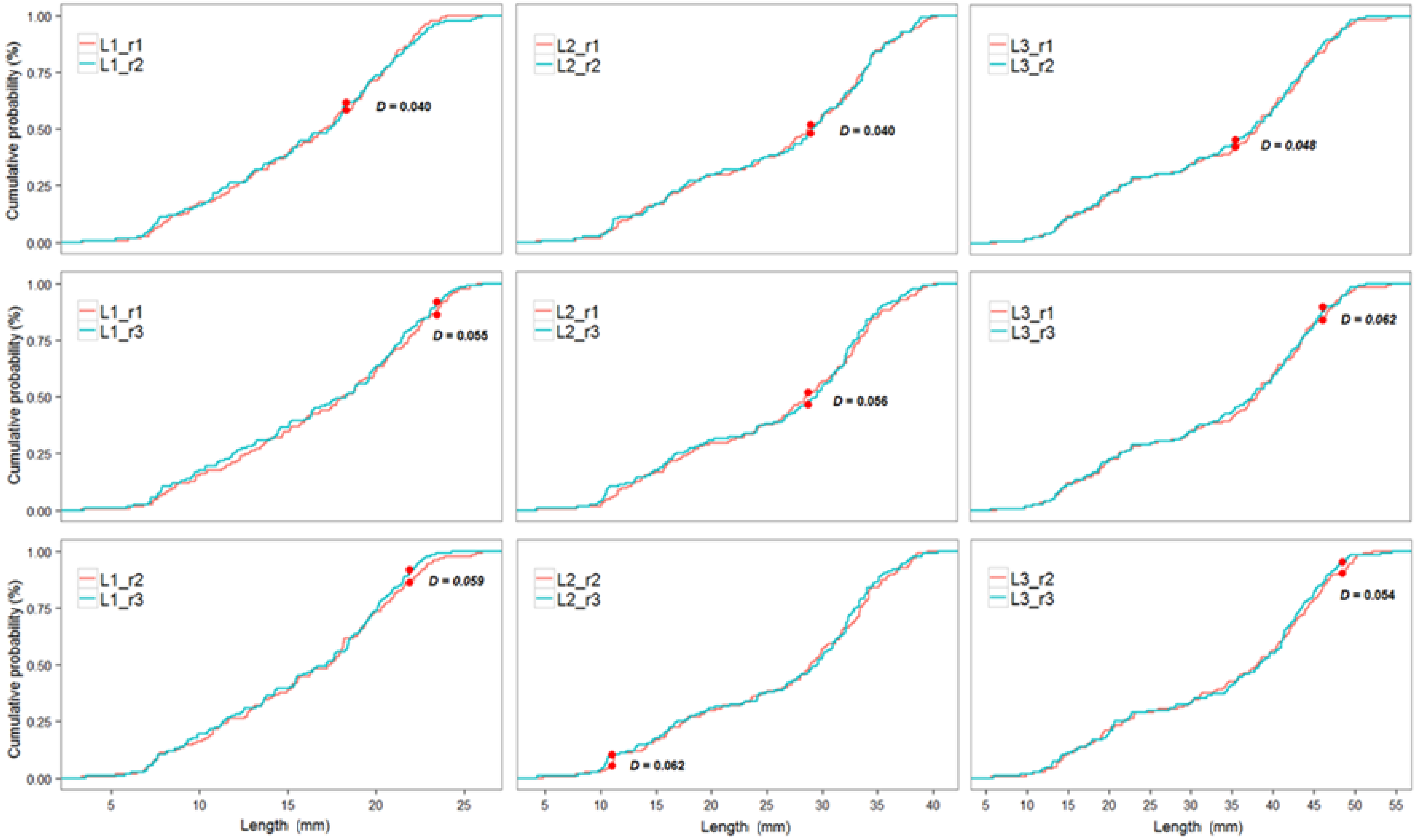
7. Appendix of figures



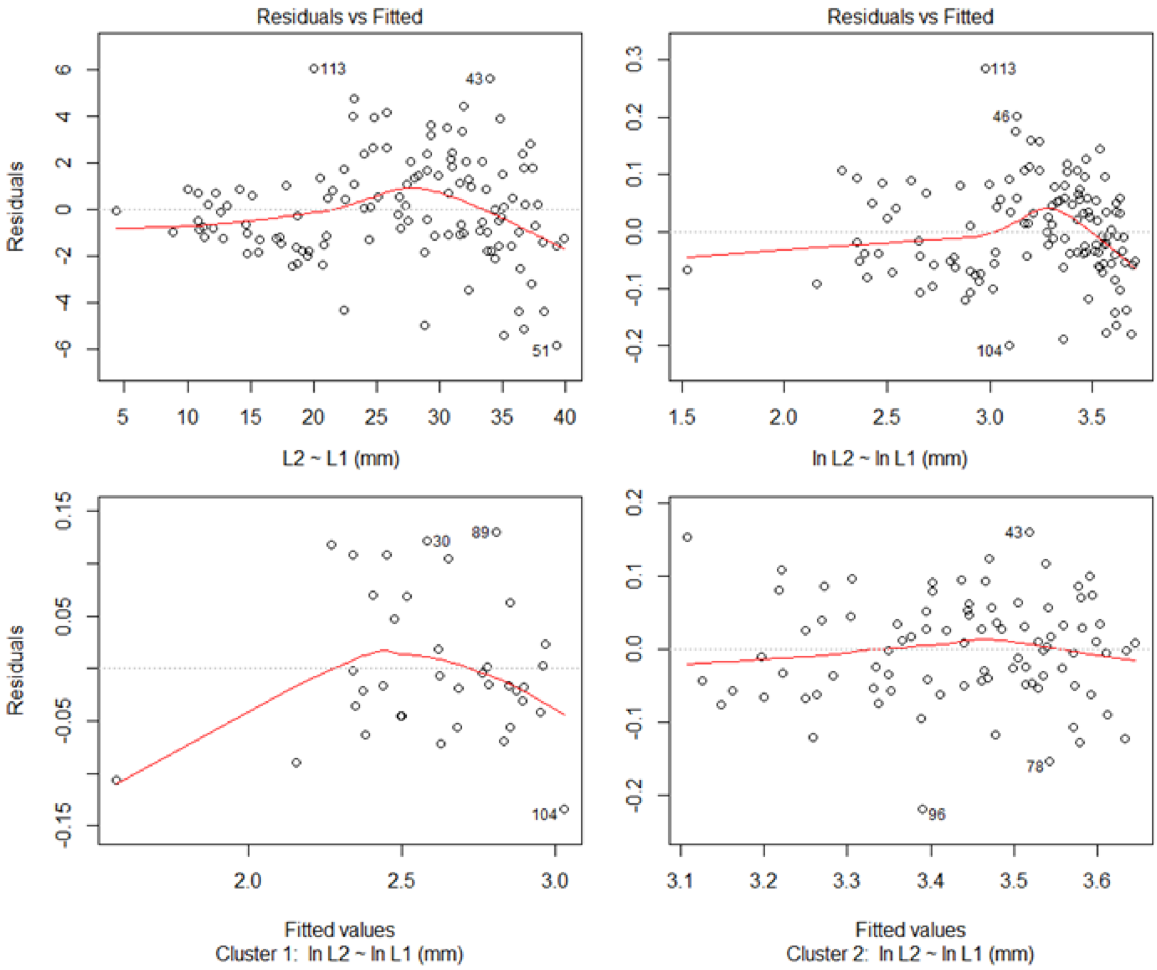
Appendix Figure 1. *Ctenodiscus crispatus* from Svartnes, April (St. 196, n = 125*). Size-frequency distributions from the three length measurements (L1, L2 and L3) from each consecutive round.

*Round 3: 124 individuals measured

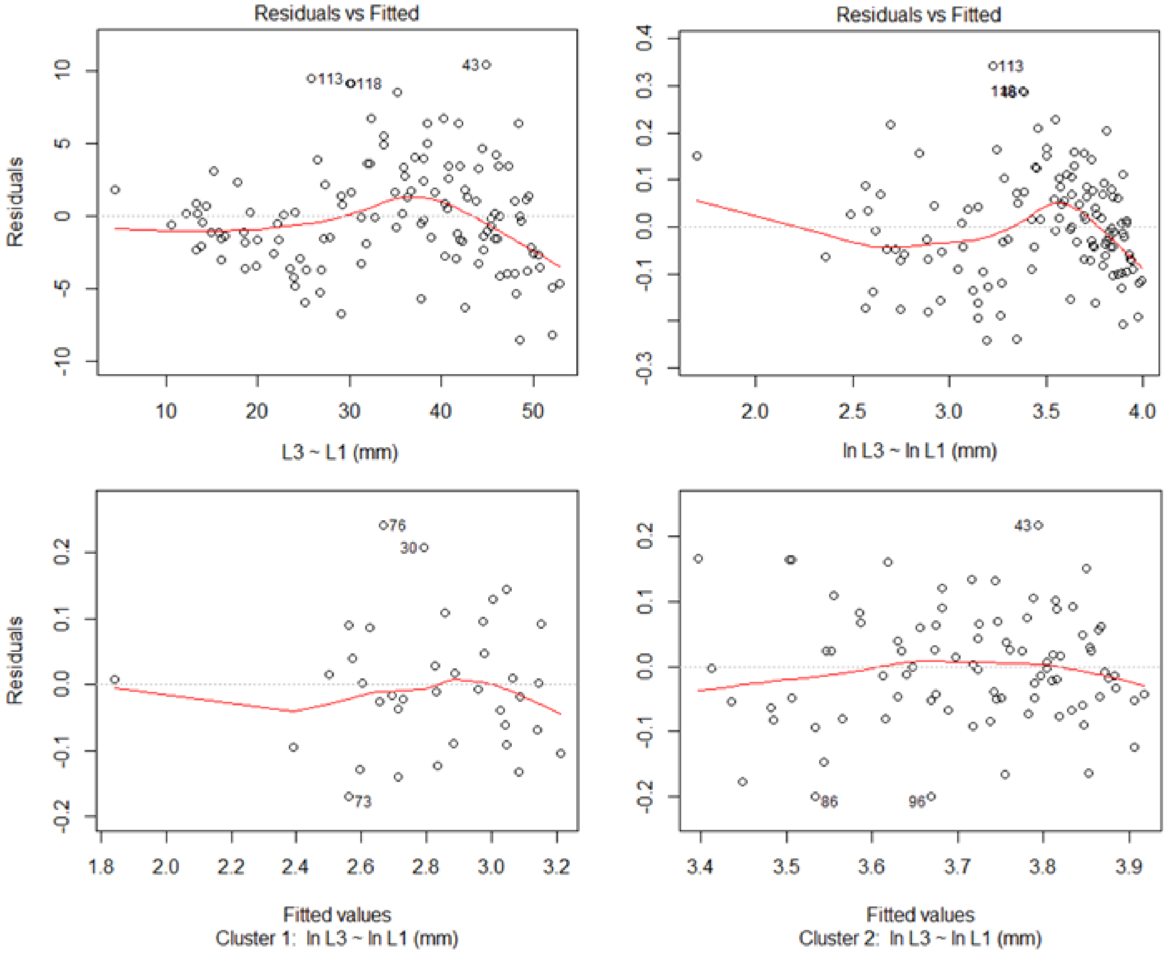


Appendix Figure 2. *Ctenodiscus crispatus* from Svartnes, April (St. 196, n = 125*). Cumulative distributions of length measurements from the Kolmogorov-Smirnov two-sample test. *D* = maximum distance between distributions of repeated measurements (rounds). L = length measurement (L1, L2, L3), r = round.

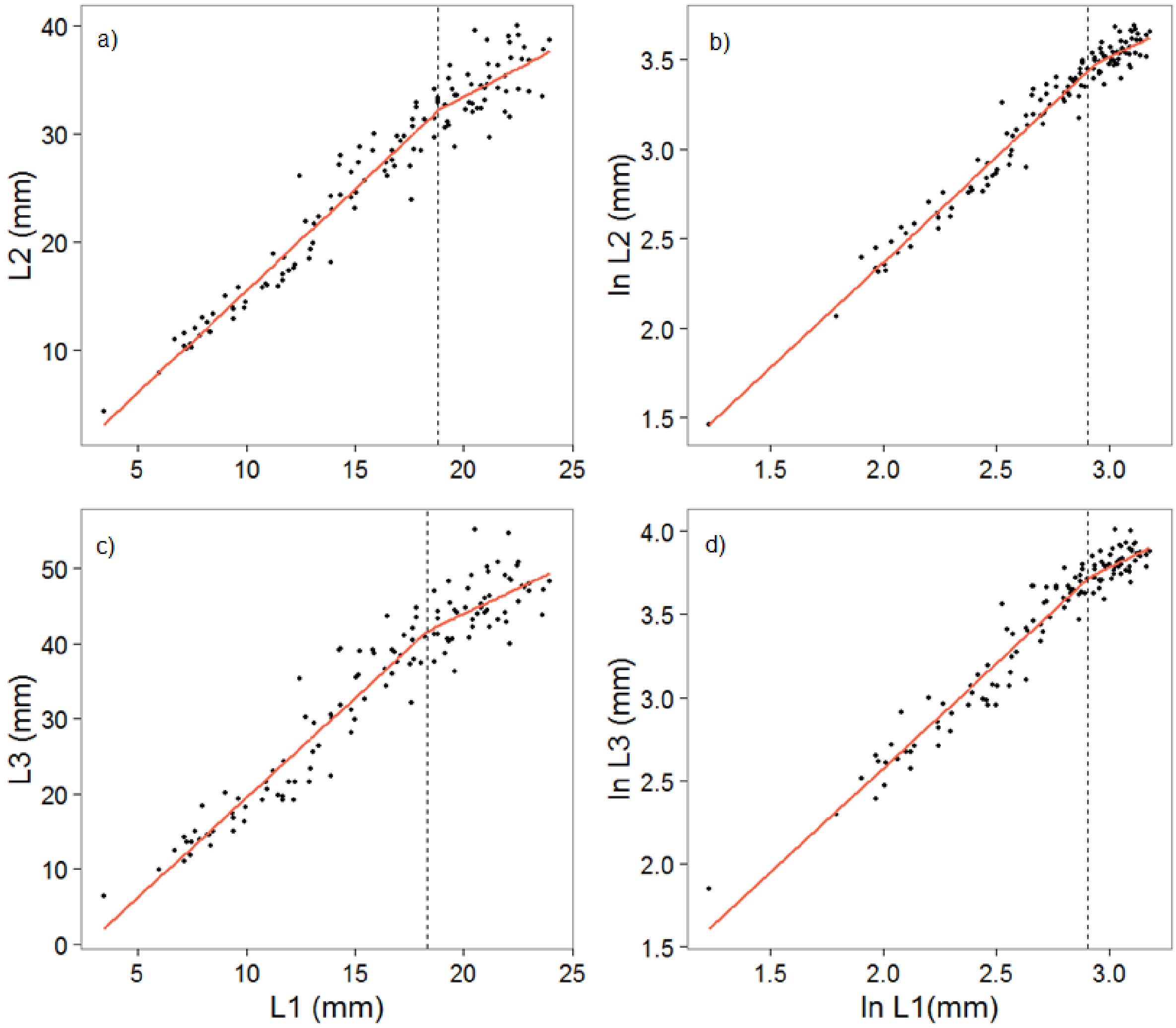
*124 individuals measured in round 3.



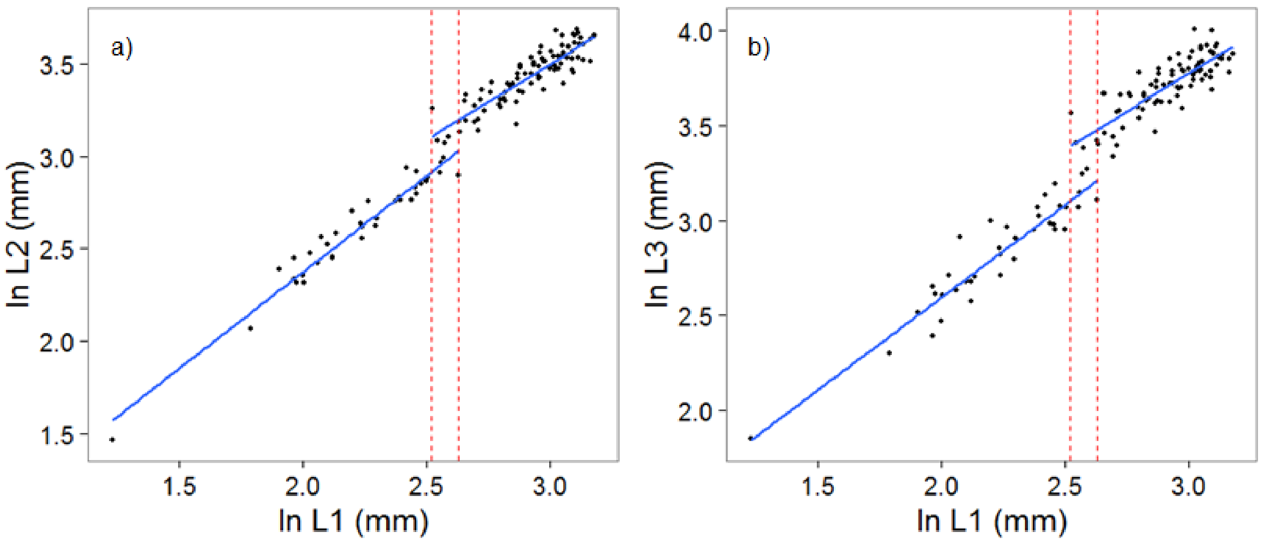
Appendix Figure 3. Fitted vs. residuals plots of the L2 ~ L1 relationship of untransformed and ln-transformed length measurements and for clusters identified by K-means clustering.



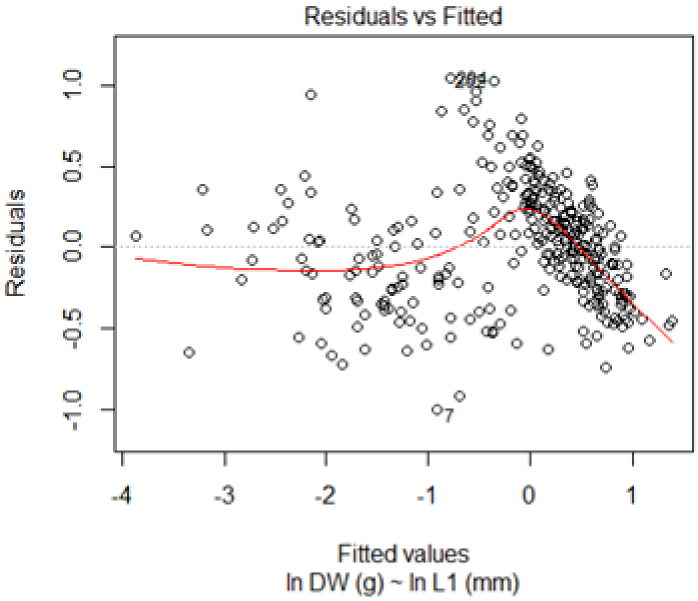
Appendix Figure 4. Fitted vs. residuals plots of the L3 ~ L1 relationship of untransformed and ln-transformed length measurements and for clusters identified by K-means clustering.



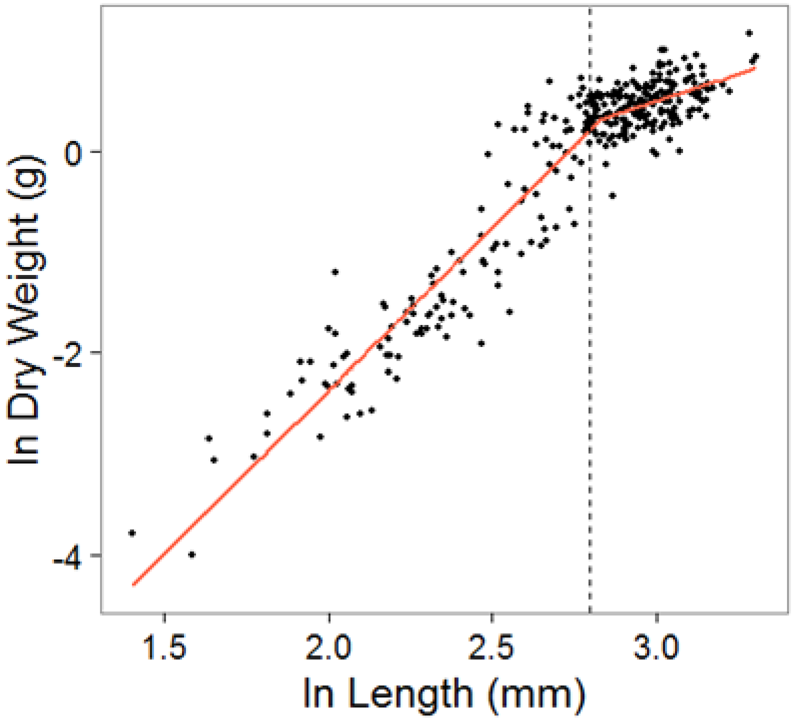
Appendix Figure 5. *Ctenodiscus crispatus* from Svartnes, April (St. 196, n = 125). Segmented regression of relationship between length measurements and estimated breakpoints indicated by dotted lines. a-b) L2 ~ L1 relationship for untransformed and ln-transformed (ln) data. c-d) L3 ~ L1 relationship for untransformed and ln-transformed data.



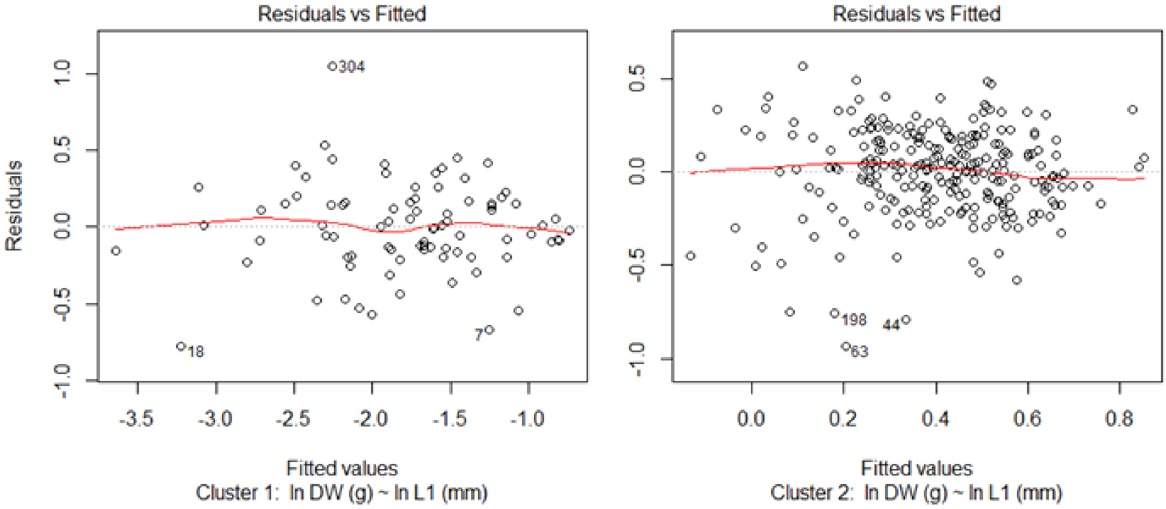
Appendix Figure 6. *Ctenodiscus crispatus* from Svartnes, April (St. 196, n = 125). Overlapping areas between clusters identified from K-means clustering. Maximum size of cluster 1 and minimum size of cluster 2 indicated by dotted lines fitted through eyeballing. a) ln L2 (mm) ~ ln L1 (mm), b) ln L3 (mm) ~ ln L1 (mm)



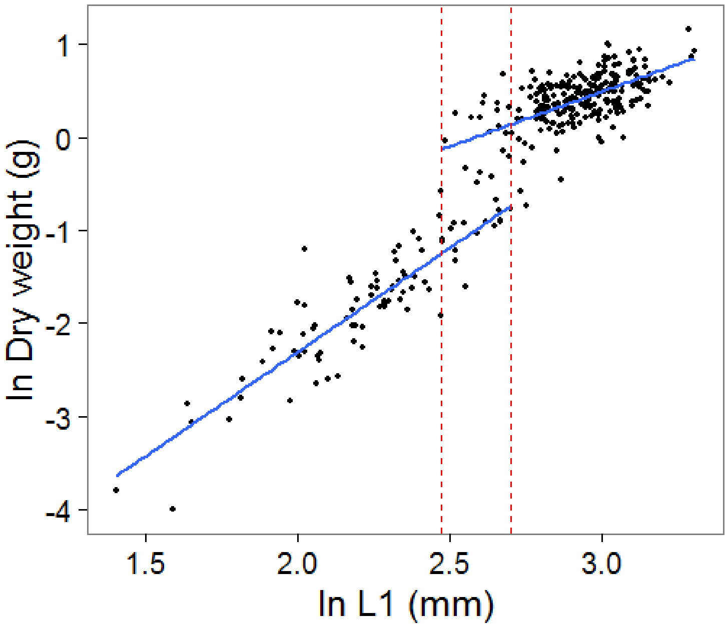
Appendix Figure 7. *Ctenodiscus crispatus* from Svartnes, April (St. 196, n = 334). Fitted vs. residuals plot from linear regression relating ln dry weight (g) to ln length (L1, mm).



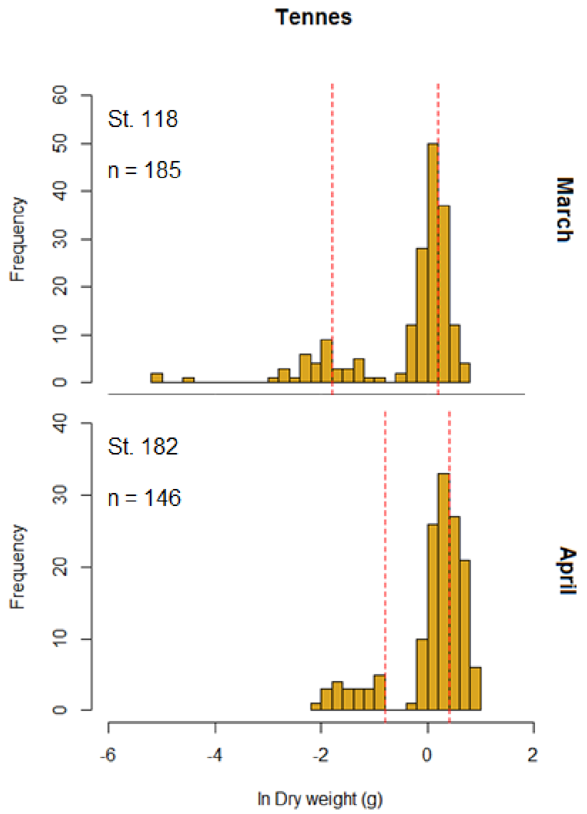
Appendix Figure 8. *Ctenodiscus crispatus*. Segmented regression of relationship between weight (dry weight, g) and length (L1, mm) for ln-transformed data. Estimated breakpoint is indicated by dotted line.



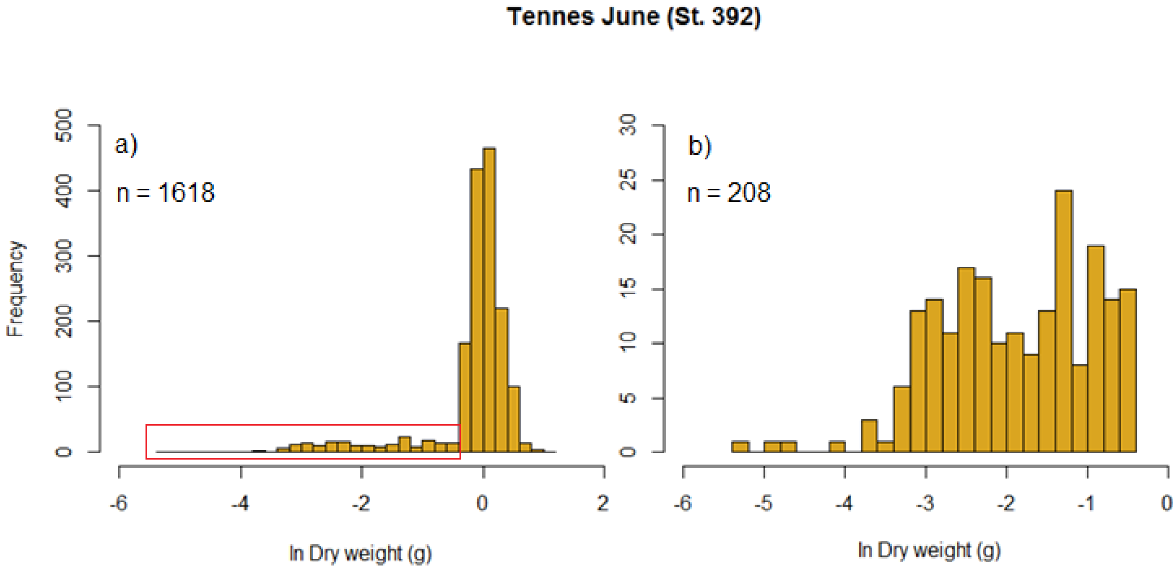
Appendix Figure 9. *Ctenodiscus crispatus* from Svartnes, April (n = 334). Residuals vs. fitted plots from separate linear regression of clusters identified from K-means clustering. Cluster 1: n = 83, cluster 2: n = 251.



Appendix Figure 10. *Ctenodiscus crispatus* from Svartnes, April (St. 196, n = 334). ln DW (g) ~ ln L1 (mm). Overlapping areas between clusters identified from K-means clustering. Maximum size of cluster 1 and minimum size of cluster 2 indicated by dotted lines fitted through eyeballing.



Appendix Figure 11. *Ctenodiscus crispatus* from 104 m depth at Tennes. Size-frequency distributions of mud stars collected in March and April. Dotted lines represents modal peaks.



Appendix Figure 12. *Ctenodiscus crispatus* from Tennes, June (St. 392). a) Size-frequency distribution of the total sample (n = 1618); b) Size-frequency distribution of individuals < 0.6 g dry weight (n = 208).

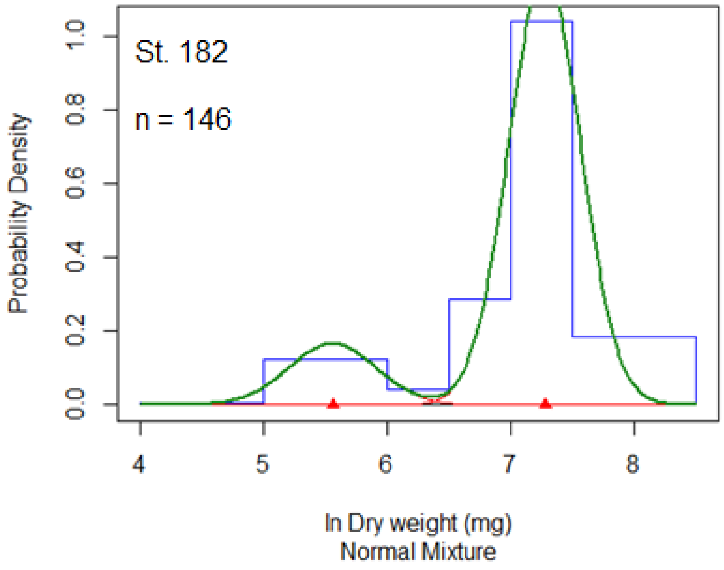


Figure 13. *Ctenodiscus crispatus*. Dry weight measurements from Tennes, April (St. 182, n = 146). Percent frequencies showing frequencies expected from fitted Gaussian mixtures with arrows indicating component means.

8. Appendix of Tables

Appendix Table 1. Beam trawl samples (150 m^2) from Balsfjord 2016. Station information; *Ctenodiscus crispatus*: total number of individuals, dry weights and wet weights; Macrobenthos 5 mm fraction: total number of individuals and biomass ($g.m^{-2}$)

Station information

Month	**Station nr.**	**Station name**	**Latitude**	**Longitude**	**Depth (m)**
March	117	Tennes	69°18.5N	19°22.9E	115
March	118	Tennes	69°17.1N	19°22.4E	104
April	176	Ramfjord	69°30.9N	18°58.0E	118
April	177	Ramfjord	69°30.2N	18°56.0E	99
April	178	Stornes	69°28.9N	18°56.4E	112
April	179	Stornes	69°27.5N	18°56.1E	125
April	180	Tennes	69°15.5N	19°20.3E	87
April	181	Tennes	69°15.8N	19°22.8E	84
April	182	Tennes	69°17.0N	19°22.3E	104
April	194	Tømmernes	69°24.5N	19°02.5E	170
April	195	Tømmernes	69°23.1N	19°01.8E	176
April	196	Svartnes	69°21.6N	19°04.8E	179
April	197	Svartnes	69°21.7N	19°12.4E	162
April	198	Svartnes	69°21.3N	19°13.9E	162
April	199	Svartnes	69°21.4N	19°18.0E	131
April	200	Tennes	69°20.0N	19°20.7E	124
June	390	Ramfjord	69°31.2N	18°58.8E	119
June	391	Svartnes	69°22.8N	19°02.8E	187
June	392	Tennes	69°20.0N	19°21.7E	123
October	704	Ramfjord	69°30.9N	18°57.8E	116
October	705	Svartnes	69°21.4N	19°05.6E	177
October	706	Tennes	69°18.7N	19°22.7E	116

Appendix Table 1 continued.

Station information		*Ctenodiscus crispatus*			Macrobenthos 5 mm fraction	
Station nr.	**Station name**	**n**	**Total DW (g)**	**Total WW (g)**	**n**	**Biomass (WW g.m^{-2})**
117	Tennes					
118	Tennes	185	175.5	475.4*	4993	6.9
176	Ramfjord	422	759.6	2125.7*	8663	21.2
177	Ramfjord	771		3374.3		
178	Stornes					
179	Stornes	20		66.7		
180	Tennes					
181	Tennes	133		590.5		
182	Tennes	146	190.4	517.2*		
194	Tømmernes	524		1767.0	1074	14.9
195	Tømmernes	597		2495.5		
196	Svartnes	627	736.6	2001.0*	955	14.5
197	Svartnes	1066	922.6	2498.5*		
198	Svartnes	816		2263.9		
199	Svartnes	259		553.1		
200	Tennes	115	164.6	448.1*		
390	Ramfjord	98	215.1	588.6		
391	Svartnes	800	1317.1	3457.2		
392	Tennes	1618	1617.7	4455.6		
704	Ramfjord	314	585.1	1594.1*		
705	Svartnes	706	716.4	1943.8*		
706	Tennes	166	387.7	1061.3*		

*Wet weight calculated from the equation ln WW = ln *a* + *b* ln DW (section 2.5.2.3)

Appendix Table 2. Macrobenthos 5 mm fraction. Complete taxa list.

Taxon	**No. Individuals per sampling station (150 m^2)**			
	Tennes St. 118	**Svartnes St. 196**	**Tømmernes St. 194**	**Ramfjord St. 176**
ARTHROPODA				
CHELICERATA				
Pycnogonida				
Nymphon spp.				125
CRUSTACEA				
Decapoda				
Pandalus borealis (Krøyer)	33	50	64	126
Pontophilus sp.		19	13	83
Hyas sp.	1			2
Pagurus pubescens (Krøyer)		1	4	13
Euphausiacea				
Meganyctiphanes norvegica (M. Sars)		30		
Euphausiacea indet.			6	
Cumacea				
Diastylis goodsiri (Bell)	1	4	54	208
Diastylis sp.			2	44
Bodotriidae indet.	1	1		1
Amphipoda				
Stegocephalus inflatus (Krøyer)				7
Lepidepecreum sp.			2	16
Anonyx sp.				2
Amphipoda indet.	6		7	20
Caprellidae indet.				25
Epimeria sp.				2
Metopa sp.				19
Isopoda				
Gnathidae indet.	4			10
Isopoda indet.		15	29	24
Sessilia				
Balanus sp.				1
ECHINODERMATA				
Asteroidea				
Ctenodiscus crispatus (Retzius)	185	627	524	422
Henricia sp.				3
Urasterias lincki (Müller & Troschel)	1		3	
Ophiuroidea				
Ophiura sarsii (Lütken)		4	18	56
Amphiura sp.	1			7
Echinoidea				
Strongylocentrotus droebachiensis (O.F. Müller)				5

Appendix Table 2 (continued).

Taxon	**No. Individuals per sampling station (150 m^2)**			
	Tennes St. 118	**Svartnes St. 196**	**Tømmernes St. 194**	**Ramfjord St. 176**
ANNELIDA				
Polychaeta				
Maldanidae	1186	91	95	4255
Oweniidae	409	14	33	394
Sabellidae	28	8		923
Ampharetidae	32	5	8	727
Nephtyidae	129	17	6	30
Terebellidae	92			125
Trichobranchidae	60	1	2	102
Spionidae	12			13
Serpulidae		1	1	
Phyllodocidae	4			23
Polynoidae	8			4
Pectinaria hyperborea (Malmgren)	21	2	34	51
Aphroditidae				1
Lumbrineridae	93			93
Cirratulidae	60			43
Flabelligeridae sp.	2			1
Brada sp.				1
Nothria conchylega (Sars)				2
Eunicidae sp.				1
Syllidae				2
Opheliidae	1			1
Capitellidae	5			5
Nereididae	2		5	2
Glyceridae		1		1
Scoloplos sp.				17
CNIDARIA				
Actiniaria				
Edwardsiidae spp. (Andres)	12			61
Hormathia digitata (O.F. Müller)			2	8
CHORDATA				
Osteichthyes				
Hippoglossoides platessoides (Fabricius)	6			3
Lumpenus lampretaeformis (Walbaum)				3
Anisarchus medius (Reinhardt)				1
Leptoclinus maculatus (Fries)				1
Leptagonus decagonus (Schmidt)		1		
Tunicata				
Ascidiacea sp.				6

Appendix Table 2 (continued).

Taxon	**No. Individuals per sampling station (150 m^2)**			
	Tennes **St. 118**	**Svartnes** **St. 196**	**Tømmernes** **St. 194**	**Ramfjord** **St. 176**
MOLLUSCA				
Bivalvia				
Yoldiella sp.	2401	1	1	82
Musculus niger (J.E. Gray)	7	2	15	24
Nuculana pernula (O. F. Müller)	14	2	1	33
Thyasira sp.	13	2	1	8
Hiatella arctica (Linnaeus)	1			
Astarte sp.			36	102
Astarte elliptica (Brown)				2
Crenella decussata (Montagu)				4
Dacrydium vitreum (Møller)		1	4	22
Ennucula tenuis (Montagu)	1	1		12
Yoldiella lucida (Lovén)				11
Delectopecten vitreus (Gmelin)			1	1
Bathyarca pectenculoides (Scacchi)				1
Mytilus edulis (Linnaeus)		1		1
Chlamys islandica (O. F. Müller)		1		17
Pseudamussium peslutrae (Linnaeus)			1	2
Gastropoda				
Euspira pallida (Broderip & Sowerby)	69	1	14	22
Admete sp.	2	8	14	
Retusa truncatula (Bruguière)		3	3	3
Retusa obtusa (Montagu)				7
Neptunea antiqua (Linnaeus)		1	2	
Neptunea despecta (Linnaeus)				1
Buccinum undatum (Linnaeus)			10	2
Buccinum sp.				6
Oenopota sp.		6	3	
Patellogastropoda indet.				6
Limneria undata (T. Brown)				1
Cryptonatica affinis (Gmelin)				1
Scaphopoda				
Antalis entalis (Linnaeus)	53	19	14	55
Aplacophora				
Aplacophora indet.	2			27
NEMERTEA				
Nemertea indet.	19			20
SIPUNCULA				
Phascolion strombus (Montagu)	16	14	42	69

Appendix Table 3. Macrobenthos 5 mm fraction. The ten most numerically abundant taxa (bold numbers) in processed samples from Balsfjord 2016 (per 150 m^2).

Taxon	Station name and number			
	Tennes	**Svartnes**	**Tømmernes**	**Ramfjord**
	118	**196**	**194**	**176**
Polychaeta				
Maldanidae	**1186**	**91**	**95**	**4255**
Oweniidae	**409**	**14**	**33**	**394**
Nepthyidae	**129**	**17**	6	30
Lumbrineridae	**93**	0	0	93
Terebellidae	**92**	0	0	**125**
Sabellidae	28	8	0	**923**
Ampharetidae	32	5	8	**727**
Cirratulidae	**60**	0	0	43
Trichobranchidae	**60**	1	2	102
Pectinaria hyperborea	21	2	**34**	51
Crustacea				
Pandalus borealis	33	**50**	**64**	**126**
Pontophilus sp.	0	**19**	13	83
Diastylis goodsiri	1	4	**54**	**208**
Isopoda indet.	0	**15**	**29**	24
Chelicerata				
Nymphon spp.	0	0	0	**125**
Echinodermata				
Ctenodiscus crispatus	**185**	**627**	**524**	**422**
Ophiura sarsii	0	4	**18**	56
Mollusca				
Yoldiella sp.	**2401**	1	1	82
Euspira pallida	**69**	1	14	22
Astarte sp.	0	0	**36**	**102**
Antalis entalis	53	**19**	14	55
Admete sp.	2	**8**	14	0
Sipuncula				
Phascolion strombus	16	**14**	**42**	69
Top ten % of total	**93.8**	**91.5**	**86.5**	**85.5**

Appendix Table 4. *Ctenodiscus crispatus* from Svartnes, April (St. 196, n = 125). Segmented regression of length measurements with breakpoints.

Linear model (y ~ x)	**n**	**a**	**b ± SE**	**b: CI (95%)**	**r^2**	***p***	**AIC**	**Breakpoint [CI (95%)] mm**
L2 ~ L1	125				0.95	<<0.001***	546.392	18.8 (17.03 – 20.64)
Lower segment		-3.445	1.891 ± 0.061	1.770 - 2.012				
Upper segment		12.140	1.063 ± 0.227	0.614 - 1.512				
L3 ~ L1	125				0.92	<<0.001***	674.086	18.3 (16.45 – 20.20)
Lower segment		-7.076	2.659 ± 0.111	2.440 -2.878				
Upper segment		16.690	1.362 ± 0.331	0.707 - 2.017				
ln (L2 ~ L1)	125				0.97	<<0.001***	-271.49	2.933* (2.841 – 3.026)
Lower segment		0.008*	1.180 ± 0.027	1.127 - 1.234				
Upper segment		1.667*	0.615 ± 0.171	0.276 - 0.955				
ln (L3 ~ L1)	125				0.94	<<0.001***	-192.33	2.910* (2.787 – 3.033)
Lower segment		0.063*	1.258 ± 0.038	1.182 - 1.333				
Upper segment		1.820*	0.654 ± 0.217	0.225 - 1.083				

*ln-values; ***Highly significant results

Appendix Table 5. *Ctenodiscus crispatus* from Svartnes, April (St. 196, n = 334). Segmented regression of ln dry weight (g) on ln L1 (disc diameter, mm) with estimated breakpoint.

	n	**ln a**	**b ± SE**	**b: CI (95%)**	**r^2**	***p***	**AIC**	**Breakpoint [CI (95%)] ln mm**
	334				0.91	<<0.001***	172.672	2.830 (2.776 - 2.884)
Lower segment		-8.834	3.229 ± 0.078	3.076 - 3.383				
Upper segment		-2.758	1.082 ± 0.233	0.623 - 1.541				

***Highly significant results