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Feeding ecology and interactions of invasive vendace and DR whitefish in the Pasvik watercourse

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Contents

Acknowledgements 2

1 Abstract 5

2 Introduction 6

3 Materials and Method 10

  3.1 Study area 10

    3.1.1 Study lakes 11

  3.2 Field sampling 13

    3.2.1 Catch per unit effort (CPUE) 14

    3.2.2 Temperature data 15

  3.3 Laboratory work in Tromsø 16

  3.4 Data analyses 19

    3.4.1 Diet composition 19

    3.4.2 Niche width 19

    3.4.3 Diet similarity 20

4 Results 21

  4.1 Zooplankton density 21

  4.2 Zooplankton community composition 23

  4.3 Prey abundance 24

    4.3.1 Vendace 24

    4.3.2 DR whitefish 25

  4.4 Diet similarity between species and among localities 27

    4.4.1 Dietary niche overlap between vendace and DR whitefish 27

    4.4.2 Comparison among localities 29

  4.5 Zooplankton body size 31

5 Discussion 33

6 References 39

7 Appendix 47

1 Abstract

Introductions and invasions of species outside their natural range can have devastating effects on the native species and be a major driver of biodiversity change. When the zooplanktivorous vendace invaded the Pasvik watercourse in the 1990s, it quickly took over the ecological role of the native DR whitefish. In the upper part of the watercourse, DR whitefish was displaced from the pelagic habitat and food resources, whereas in the lower part, the invasion developed at a slower rate and the two fish species have been able to coexist. Heavy predation from vendace led to the disappearance of the biggest cladoceran species in the watercourse and the remaining species have shifted towards smaller body sizes. The present study explores how the zooplankton community differ in density and composition and how the diet utilization and resource partitioning of pelagic vendace and DR whitefish vary among three contrasting lake sites; Ruskebukta and Tjærebukta in the upper and Skrukkebukta in the lower part of the watercourse, over four different study years. Further, the study explores whether inter-annual temperature variations can explain the variations in body size of *Bosmina* spp. and *Daphnia* sp. Samples were collected in September in the four study years in the pelagic zone of the three localities. Stomach content from all vendace and DR whitefish individuals were analyzed and zooplankton species were identified and measured in both the stomach and the environment samples.

A key finding was that the zooplankton communities and the fish diets in Tjærebukta and Skrukkebukta were similar to each other in all study years, as opposed to Ruskebukta, where *Bosmina* spp. was almost depleted from the locality and DR whitefish was chiefly displaced from the pelagic zone and its resources. The body sizes of *Bosmina* spp. and *Daphnia* sp. could not be correlated to inter-annual temperature variations. The study revealed strong zooplankton predation and interspecific competition following the vendace invasion, but the impacts largely varied between sites. In the upper localities, strong interspecific competition for a down-grazed zooplankton resource has forced the DR whitefish in Ruskebukta to change its realized niche to benthic invertebrates and surface insects, whereas in Tjærebukta, DR whitefish has stayed in its original niche but its population densities have been strongly reduced. In Skrukkebukta, a lower density of vendace has led to a lower predation pressure on *Bosmina* spp. and lower interspecific competition, enabling coexistence of the two pelagic fish competitors. In conclusion, the vendace invasion has had major impacts on the pelagic compartment of the ecosystems in the Pasvik watercourse, where both the DR whitefish and the prey community has been negatively affected.

2 Introduction

Introductions and invasions of species outside their natural range have become common and widespread in freshwater systems throughout the world. These non-native species can have devastating effects on the native species and be a major driver of biodiversity change. Common effects are alterations of the native species behavior and demography, which can occur at multiple ecological levels (Simon and Townsend, 2003). At the individual level, the native species may undergo changes in habitat use and foraging patterns. At the population level, the native species may be changed in abundance and distribution. At the community level, direct and indirect interactions between species can be altered by an invasive species. Ultimately, at an ecosystem level, an invasive species may change the way nutrients and energy move through the ecosystem (Simon and Townsend, 2003). Many of these effects are imposed by new predation and competition interactions with the newly arrived invaders (Simon and Townsend, 2003; Lambrinos, 2004; Yokomizo et al., 2017).

Predation can cause ecological changes in both predator and prey, especially when a predator invades ecosystems were it does not naturally occur (Begon et al., 2006; Vitule et al., 2009). Often, the native prey will be more vulnerable to an invasive predator because they have never encountered the species before and thus never developed an effective anti-predator defense (Bateman et al., 2014; Battini et al., 2021). The prey species population can be strongly reduced or even disappear, and the remaining prey species often go through changes in growth, reproduction and behavior to avoid its new predator (Simon and Townsend, 2003; Begon et al., 2006; Strayer, 2010). Also interspecific competition can cause large ecological changes in an inferior competitor species (Giller, 1984; Wootton, 1990; Holway et al., 2002; Begon et al., 2006). A successful invading species will often have a competitive advantage for resource exploitation compared to native species that utilize the same resources (Reitz and Trumble, 2002; Duyck et al., 2004), referred to as asymmetrical competition (Weiner, 1982). The effects from competition on a native, inferior species can be of similar magnitude as the effects on prey from predation, where declines, or even extinction, in the native species can occur (Gause, 1934; Begon et al., 1996). Alternatively, the inferior competitor can be displaced from its preferred habitat and/or food resources and go through a niche shift to survive (Gause, 1934; Begon et al., 1996).

The present study addresses possible effects of predation and competition in respect to the invasion of vendace (*Coregonus albula* L.) into the Pasvik watercourse in northern Norway around 1990 from Lake Inari, Finland (Amundsen et al., 1999, 2019). Vendace is a highly specialized zooplanktivorous fish, and its invasion has led to the decrease in the native, densely rakered (DR) whitefish (*Coregonus lavaretus*) morph, which is also a zooplanktivorous fish (Bøhn et al., 2008; Sandlund et al., 2013). Whitefish used to dominate all the habitats of the lakes and reservoirs in the Pasvik watercourse prior to the vendace invasion (Amundsen et al., 1999). In the pelagic habitat, DR whitefish constituted on average >95% of the total catches (Amundsen et al., 1999). Vendace have shown great inter-annual population variations (Marjomäki et al., 2004; Salonen et al., 2007), including also after its arrival on the Pasvik watercourse (Sandlund et al., 2013; Amundsen et al., 2019). Even so, vendace quickly took over the ecological role of the DR whitefish as the dominant species in the pelagic habitat, whose population density had decreased by more than 90% by 2004 (Amundsen et al., 1999; Bøhn et al., 2008). In the localities Ruskebukta and Tjærebukta in the upper part of the watercourse, DR whitefish was eventually nearly displaced from the pelagic habitat (Amundsen et al., 1999, 2019; Bøhn and Amundsen, 1998, 2001; Bøhn et al., 2004, 2008), whereas in the lower locality Skrukkebukta, the vendace invasion had a slower development with only a gradual increase of density over time and no clear dominance of vendace has been observed (Amundsen et al., 1999, 2019).

The vendace invasion has not only had strong impacts on the DR whitefish population in the Pasvik watercourse, but also the zooplankton community has gone through major changes in both density and composition after the invasion (Bøhn and Amundsen, 1998; Amundsen et al., 1999, 2009), apparently representing the main reason for the relegation of DR whitefish from the pelagic habitat (Bøhn and Amundsen, 2001; Amundsen et al., 2019). Zooplankton communities can be heavily affected by predation from zooplanktivorous fish (Gliwicz, 1994) and both the size structure and species composition can change towards a dominance of smaller zooplankton species and smaller body sizes (O'Brien, 1987; Dodson, 1988; Gliwicz and Pijanowska, 1989; Havens et al., 2015; Leroux and Loreau, 2015). Zooplanktivorous fish typically prefer cladoceran species (Hall, 1982) as they are often more visible, less mobile and move around with jerky movements, making them an easier prey to capture than copepods (Arts, 1999; Gliwicz, 1981; O'Brien, 1987; Skoglund et al., 2013). The invasion of vendace into the Pasvik watercourse gave a unique possibility to document the effects of a new predator on the native zooplankton community while it was happening (Amundsen et al., 2009). As the predation pressure increased, the diversity and density of the zooplankton community declined (Amundsen et al., 1999, 2009; Bøhn and Amundsen, 2001) and the dominating species shifted towards smaller cladoceran species (Amundsen et al., 2009). In the upper part of the watercourse, the numerical density of zooplankton were reduced to only 6-8% of the levels that was present at the beginning of the invasion in 1991 (Bøhn and Amundsen, 1998; Amundsen et al., 2009). This heavy reduction in zooplankton density even gave a shortage in food availability for the predator itself, and vendace experienced reduced somatic growth and altered life-history variables (Bøhn et al., 2004; Bøhn et al., 2008).

Ecosystems are complex structures (Rudolf and Rasmussen, 2013; Romagnan et al., 2016) and it is possible that other mechanisms than predation also may have impacted the zooplankton community in Pasvik, in particular environmental mechanisms like temperature changes (Rudolf and Rasmussen, 2013; Romagnan et al., 2016). Both water and air temperatures has increased in the Pasvik area over the past decades (Gjelland et al., 2012; Ylikörkkö et al., 2015), and the temperature-size rule states that warmer temperatures give faster growth, shorter generation time and smaller body size in organisms (Atkinson, 1994; Angilletta and Dunham, 2003; Gillooly et al., 2001; Havens et al., 2015). Zooplankton are generally believed to decrease in body size as the temperatures increase (Gillooly and Dodson, 2000; Gillooly et al., 2001; Havens et al., 2015). It is unknown how inter-annual temperatures may affect the zooplankton community in the Pasvik watercourse as this has not previously been studied.

The aim of the present study is to explore how the zooplankton community differ in density and composition and how the diet utilization and resource partitioning of pelagic vendace and DR whitefish vary among three contrasting lake sites with different impact of the invaded vendace in the pelagic fish communities, including Ruskebukta and Tjærebukta in the upper part and Skrukkebukta in the lower part, and how this varies over four different study years. Previous studies have showed that vendace dominated the upper localities from the beginning of the invasion, whereas in Skrukkebukta, the development have been slower and a clear vendace domination has not been documented (Amundsen et al., 1999, 2019). Since the vendace population can show great inter-annually variations in density (Salonen et al., 2007; Amundsen et al., 2019), it is important to explore results from different years. Further, I examine whether inter-annual water temperature variations can be the cause of observed inter-annual variations in *Bosmina* spp. and *Daphnia* sp. body size by comparing two relatively warm and two relatively cold years and in the study and by using correlation analyses between the body sizes and annual mean water temperatures from 1991 to 2019.

My hypotheses are:

1. The zooplankton community in Skrukkebukta will be dominated by cladocerans throughout the study, whereas due to the larger predation impact from the vendace invasion in Ruskebukta and Tjærebukta, the cladocerans there will have much smaller densities and a lower contribution to the zooplankton composition.
2. Throughout the study, cladoceran zooplankton will dominate the diets of both vendace and DR whitefish in Skrukkebukta, whereas in Ruskebukta and Tjærebukta, DR whitefish will to a larger extent feed on benthic invertebrates due to the competitive effects of a down-grazing of the zooplankton community by vendace.
3. Inter-annual temperature variations will have an impact on body sizes of *Bosmina* spp. and *Daphnia* sp., which will be smaller in warmer than in colder years.

3 Materials and Method

3.1 Study area

The Pasvik watercourse belongs to three countries. Originating in Lake Inari (1102 km^2) in Finland, it runs into Russia before defining the borderline between Norway and Russia for ~120 km. The Norwegian-Russian part of the watercourse has a total area of 142 km^2, a catchment area of 18 344 km^2 and a mean annual water flow of ~175 $m^3 s^{-1}$ (Bøhn and Amundsen, 1998; Vannportalen, 2015). As a result of the hydropower industry, most rapids and waterfalls have disappeared and today the watercourse consists of seven water impoundments (hydropower reservoirs) linked by slow-flowing river sections (Bøhn and Amundsen, 1998; Bøhn et al., 2008). The water fluctuations are small, normally <80 cm. The summer temperatures are relatively high and the ice-free season in the lakes and reservoirs lasts from late May/beginning of June to the end of October/early November (Vannportalen, 2015). Vegetation is dominated by birch (*Betula* sp.) and pine (*Pinus sylvestris*) with significant areas of *Sphagnum* bogs (Bøhn et al., 2008). Maximum and minimum monthly temperatures range from -13.5°C (January) to +14.0°C (July) with an annual mean temperature of -0.3°C. There is little precipitation in the area, the annual mean is 358 mm (Bøhn et al., 2008).

The Pasvik watercourse is the most species rich watercourse in respect to fish in Northern Norway, and altogether 15 species have been recorded (Vannportalen, 2015). The most abundant native species are polymorphic whitefish (*Coregonus lavaretus* (L.)), perch (*Perca fluviatilis* L.), pike (*Esox Lucius* L.), burbot (*Lota lota* L.), brown trout (*Salmo trutta* L.) (Bøhn et al., 2008), and in the latest decades also vendace (*Coregonus albula*) after its invasion following the introduction into Lake Inari in the 50s and 60s (Amundsen et al., 1999).

Whitefish in the Pasvik Watercourse belong to the Siberian clade that have a distribution from the Arctic Sea to Southwest Norway (Østbye et al., 2005). They are most likely the result of sympatric speciation within the system, partly due to lack of trophic competitors (Østbye et al., 2006). The whitefish in the Pasvik watercourse exists in three commonly occurring sympatric morphs, densely rakered, large sparsely rakered and small sparsely rakered whitefish (hereafter denoted as DR whitefish, LSR whitefish and SSR whitefish) (Amundsen et al., 1999, 2019; Kahilainen and Østbye, 2006; Siwertsson et al., 2010). The LSR whitefish occupies the littoral habitat and its preferred prey consists of benthic macroinvertebrates (Amundsen et al., 2004; Amundsen et al., 2019). The SSR whitefish occupies the profundal habitat and feeds mainly on benthic macroinvertebrates buried in soft sediments (Kahilainen and Østbye, 2006; Siwertsson et al., 2010). LSR and SSR whitefish are not believed to be directly affected by the vendace invasion. DR whitefish occupies the pelagic zone of the watercourse, the same ecological niche as the closely related vendace also prefers (Amundsen et al., 2004; Amundsen et al., 2019).

Vendace is an Eastern species, meaning that its natural habitat are limited to freshwater systems that are presently, or have been, entering the Baltic Sea (Amundsen et al., 1999). The species was translocated and introduced in Lake Inari in Northern Finland in the 1950s and 1960s for commercial fishery (Mutenia and Salonen, 1992; Salonen and Mutenia, 2004). The population grew quickly and had become large by the end of the 1980s (Mutenia and Salonen, 1992). The Pasvik watercourse has its outlet in Lake Inari, thus the vendace eventually spread there through downstream migration from the lake. The first unconfirmed records of vendace in the Pasvik watercourse was in 1989 and the first confirmed records are from 1990 (Amundsen et al., 1999).

3.1.1 Study lakes

Three localities have been investigated for this study (figure 1). Two of them are situated in close vicinity to each other in the upstream part the watercourse (Ruskebukta and Tjærebukta in the Vaggetem region). The third, Skrukkebukta, is situated approx. 50 km downstream from Ruskebukta and Tjærebukta. The three water basins are located adjacent to the main path of the Pasvik Watercourse and have insignificant water flow (Bøhn and Amundsen, 1998).

Lake Ruskebukta (69°12.604'N, 29°14.773'E; 52 m.a.s.l.) in the upstream part has a total area of 5.3 km^2 (Amundsen et al., 1999). The mean depth is 3.6 m and the maximum depth is 15 m. The lake is dimictic, oligotrophic and humic. The Secchi depth ranges from 1.5-2.5 m (Amundsen et al., 2009).

Lake Tjærebukta (69°12.750'N, 29°10.756'E; 52 m.a.s.l.), the other of the two upstream localities, is located adjacent to lake Ruskebukta (approx. 2.5 km apart). The total area is 5.1 km^2. The lake is deeper than Ruskebukta; the mean depth is 6 m and the maximum depth is 26 m. The lake is dimictic, oligotrophic and humic and the Secchi depth ranges from 2 to 6

m. First time vendace was recorded in Ruskebukta and Tjærebukta was in 1991 (Amundsen et al., 1999; Bøhn et al., 2008; Liso et al., 2013).

Lake Skrukkebukta (69°33.296'N, 30°7.302'E; 21 m.a.s.l), the downstream locality, has a total area of 6.6 km^2. Most of the lake is deeper than 3 m, with a mean depth of 14 m and a maximum depth of 38 m (Amundsen et al., 1999). Lake Skrukkebukta is dimictic and oligotrophic (Bhat et al., 2014) and Secchi depth ranges from 2-6 m (Bøhn et al., 2008). The vendace invasion did not reach Lake Skrukkebukta until 1993 and in general, this lake has seen a slower development of the vendace population density than the upstream lakes (Amundsen et al., 1999, 2009).

Figure 1: Map over the Pasvik Watercourse. Arrows show the study localities of Ruskebukta, Tjærebukta, Skrukkebukta as well as Skogfoss where NVE's automatic water temperature logger is located.

3.2 Field sampling

Field sampling has been conducted on annual basis in the Pasvik watercourse since 1991 (Amundsen et al., 2009, 2019). The present study includes data from 2018 and 2019, when I took part in the field sampling and did the laboratory analysis. In addition, I have used data already collected in 2008 and 2009 to get a larger range of comparisons of fish densities and temperatures. The two years were selected based on the temperature data; with the data from 2018 and 2019, choosing 2008 and 2009 gave me two relatively warm years (2008 and 2019) and two colder years (2009 and 2018; figure 2 and appendix figure A1).

Sampling was conducted during the first two weeks of September in all four study years. For the fish sampling, we used multi-meshed floating gillnets set out overnight in the pelagic zone above the deepest part of the lakes. In 2018 and 2019, gillnets were set out one night in each of the lakes Ruskebukta and Tjærebukta, and two nights in Skrukkebukta due to smaller fish catches. The gillnets are 45 m long and 6 m deep. We tied two and two together, giving a total length of 90 m. Each gillnet is separated into nine panels of 5 m each, with mesh sizes 6 mm, 8 mm, 10 mm, 12.5 mm, 15 mm, 18.5 mm, 22 mm, 26 mm, and 35 mm.

The fish were removed from the gillnets shortly after being brought ashore. In the field laboratory, every fish was given an individual number, and the relevant information and samples were collected. We identified the species, and for whitefish also the morph, and measured fork length (mm) and weight (g) and recorded the sex and sexual maturity of all the fish. Only pelagic caught vendace and DR whitefish were addressed in the present study. Stomachs were sampled and conserved in 96% ethanol for later dietary analysis in the university laboratory. Depending on the fish species, we also sampled otoliths, gills, flesh and intestines, and looked for parasites in the stomachs, hearts and flesh, but these materials and data were not utilized in this study.

In all three localities, we sampled zooplankton with a plankton net with mesh size 125 μm. We used standard zooplankton sampling, conducting three vertical hauls at each locality from 15 m depth up to the surface. The plankton net was pulled at a speed of approximately 0.5 m/second. The zooplankton samples were passed into sample containers of 250 ml. 10% of 40% formalin was added to the samples to preserve them, giving a final concentration of 4%.

3.2.1 Catch per unit effort (CPUE)

Catch per unit effort (CPUE) was used as an indicator of relative fish density and calculated for both vendace and DR whitefish for all four years investigated. Due to the small size of the 0+ generation of vendace, it is likely that they to a high degree escaped being caught by the gillnets. Thus, the actual density of this generation is likely not well represented by the CPUE estimates.

In general, the vendace CPUE was much higher in Ruskebukta and Tjærebukta than in Skrukkebukta (figure 2 and appendix figure A2, appendix table A3, A5). In addition, there was a greater variation between the years in Ruskebukta and Tjærebukta, whereas it stayed at approx. the same low level throughout the study in Skrukkebukta. Whitefish CPUE on the other hand, showed a pattern with stable but low CPUE in all three localities throughout the study.

In Ruskebukta, the CPUE of vendace was quite low in 2008 and 2009, before it more than doubled in 2018 and stayed at a similar level in 2019 (figure 2a). In Tjærebukta, vendace also had a quite low CPUE in 2008 (figure 2b). However, the CPUE more than doubled in 2009. In 2018, however, it had decreased to almost the same level as in 2008 and stayed at this level also in 2019. In Skrukkebukta, the vendace CPUE was consistently low throughout the study (figure 2c).

For DR whitefish, CPUE was low in all three localities (figure 3 and appendix A2, appendix table A3, A5). In both Ruskebukta and Tjærebukta, the CPUE was many times lower for DR whitefish than for vendace. In Skrukkebukta, although still at a low level, DR whitefish CPUE was approximately twice as high as the vendace CPUE in 2008 and 2009, whereas it was below half of the vendace CPUE in 2018 and 2019.

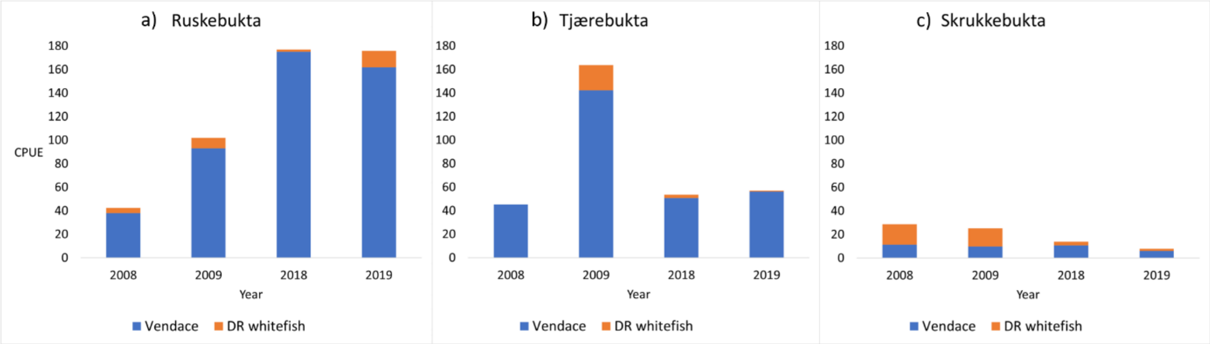

Figure 2: CPUE of vendace and DR whitefish in a) Ruskebukta, b) Tjærebukta and c) Skrukkebukta during the four study years 2008, 2009, 2018 and 2019.

3.2.2 Temperature data

Water temperature data have been retrieved from NVE's automatic temperature logger at the Skogfoss hydropower dam, located more or less halfway between the upper and lower localities. The temperatures were measured at one meter depth on a daily basis since 1991. Average temperatures were calculated from the retrieved data (figure 3, A1). I assume that the water temperatures measured at Skogfoss are representative for the water temperatures in the three lakes I have investigated. A period of three months, from June 15th to September 15th was selected for the study, a time period that includes both the most important growing season for zooplankton (Primicerio and Klemetsen, 1999) and period of field sampling. I used two-sample t-test analyses in the statistical software program "r" to analyze if the body sizes of *Bosmina* spp. and *Daphnia* sp. were affected by temperature variations. In addition to analyzing the effects on body size from the average temperature from June 15th to September 15th, I also selected all days within this period with temperatures >8°C to see if higher temperatures affected the body size. To facilitate more extensive comparisons, I was also given access to data from the complete Pasvik zooplankton time-series in order to analyse possible correlation between the body sizes of *Bosmina* spp. and *Daphnia* sp. and the annual mean water temperatures from 1991 to 2019 (figure A5, table A21).

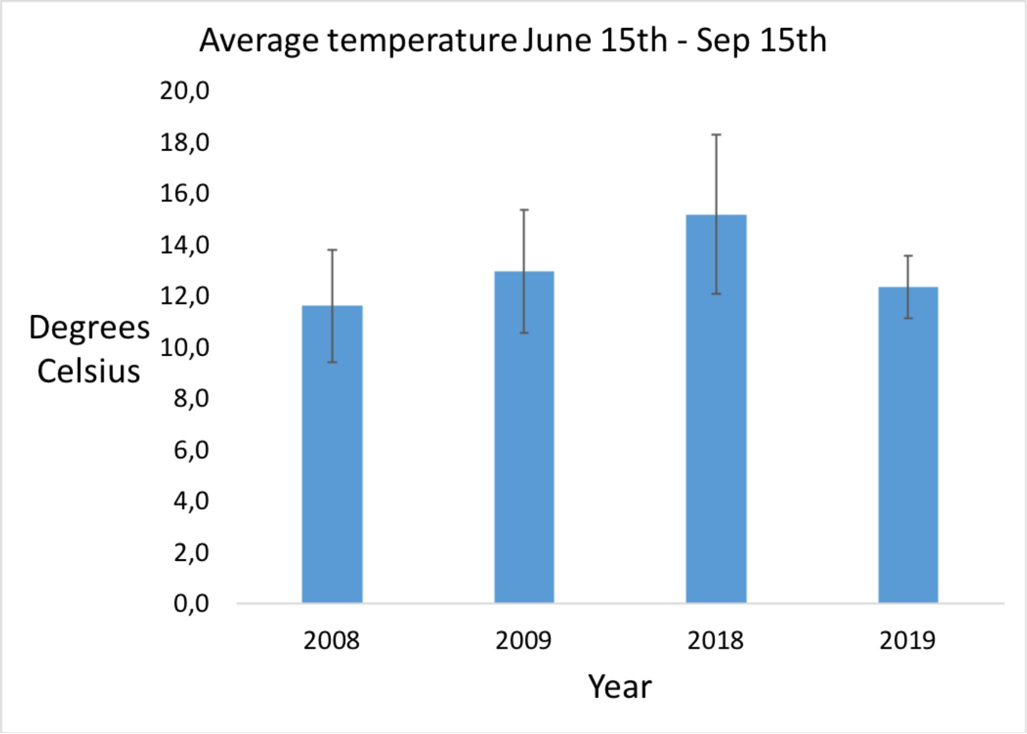

Figure 3: Average water temperature with standard deviation from June 15th to September 15th at the measuring station at Skogfoss for the study years 2008, 2009, 2018 and 2019.

3.3 Laboratory work in Tromsø

In the lab, I analyzed all fish stomachs and zooplankton samples from 2019 (see table 1 for number of stomachs analyzed). I also analyzed the stomachs from 2018 when I was working on my bachelor thesis (Høstmark, 2018). The stomachs and zooplankton samples from 2008 and 2009 were collected and analyzed according to the same procedures as I used, and the data were put at disposal for my study.

For the stomach samples, I used the subjective relative-fullness method (Hyslop, 1980) to determine how much of each prey group the individual fish had eaten. I visually determined the total stomach fullness on a scale from 0 % (empty stomach) to 100 % (full stomach). When analyzing the stomach content of the fish, the different types of prey (n=27) were identified down to species or genus for zooplankton, while zoobenthos were mostly identified down to family level. To better visualize the results, some of the less important prey taxa in the fish diets were combined and registered into categories (n=8, appendix table A2). The prey taxa from the category “other” were very digested and could mostly be identified to genus or family level, but not species level. When organizing the prey taxa into categories, the genus and families identified in “other” could be reorganized into the new categories, thus the category “other” were removed. Every species was assigned a fullness contribution as part of the total fullness of the stomach (Amundsen et al., 2019).

Table 1: The number of fish (n) sampled for stomach content analysis from vendace and DR whitefish in Ruskebukta, Tjærebukta and Skrukkebukta for the four study years (2008, 2009, 2018 and 2019).

		Vendace	**DR whitefish**
Ruskebukta	2008	126	25
	2009	86	22
	2018	45	9
	2019	44	24
Tjærebukta	2008	99	3
	2009	72	24
	2018	35	10
	2019	59	4
Skrukkebukta	2008	133	136
	2009	63	95
	2018	39	25
	2019	64	18

After gently flushing the zooplankton samples for several hours in order to remove the formalin and diluting them with water, the zooplankton were counted and measured. All species were registered and counted until I had at least 100 individuals of the most abundant species (appendix table A1). I took new sub-samples until 100 individuals were reached, while always finishing all the sub-samples, also the last one where 100 individuals were reached. All species were counted, whereas length and clutch size were only measured on *Daphnia* sp. and *Bosmina* spp. In the data analysis, density of the zooplankton was measured as the relative density of zooplankton estimated as number of individuals per vertical net hauls. The density composition of the zooplankton community is expressed as the relative density contribution of each taxa to the total zooplankton density.

When measuring the length of *Bosmina* spp., I measured the total length of the body, without the spine, on 50 individuals (table 2). I registered if they had eggs or ephippia, and if so, how many. After reaching 50 individuals, I kept measuring until I had registered 40 females with eggs in total. For *Daphnia* sp. I measured the length of the head, the body (from top of the head to bottom of the body where the spine starts) and the total length (from top of the head to the end of the spine). The spine length was later calculated by subtracting the body length from the total length. I measured 50 *Daphnia* sp. and registered the sex, if they had eggs or ephippia, and if so, how many. When I had measured 50 individuals I continued until I had 50 females, and then until I had 40 females with eggs or ephippia in total.

I also measured the length of *Bosmina* spp. and *Daphnia* sp. in the stomachs of vendace and DR whitefish in order to compare the size distribution of zooplankton community in the environment with the zooplankton that the fish chose to feed on (table 2 and 3). From each locality, I selected 3-5 vendace and 3-5 DR whitefish stomachs that contained zooplankton that were relatively undigested and could be measured. The measuring of zooplankton from fish stomachs had not been conducted in the 2008 and 2009 sampling, and these two early years could thus not be included in the comparisons of zooplankton sizes in the environment *versus* the stomachs of pelagic vendace and DR whitefish. When analyzing the data from the length measurements of *Bosmina* spp. and *Daphnia* sp. I only used the egg-carrying females, as they are more visible for zooplanktivore fish and thus believed to be thr preferred prey over individuals without eggs (Arts, 1999; Gliwicz, 1981; O'Brien, 1987; Skoglund et al., 2013).

Table 2: Overview of how many individuals (n) of Bosmina *spp. and* Daphnia *sp. from zooplankton samples in the environment that were measured in the study localities Ruskebukta, Tjærebukta and Skrukkebukta in the study years 2008, 2009, 2018 and 2019.*

		***Bosmina* ssp. (with or without eggs)**	***Bosmina* ssp. with eggs**	***Daphnia* sp. (with or without eggs)**	***Daphnia* sp. females**	***Daphnia* sp. females with eggs**
Ruskebukta	2008	59	23	82	79	40
	2009	66	20	78	78	40
	2018	76	42	167	144	68
	2019	82	42	101	96	63
Tjærebukta	2008	50	7	50	44	3
	2009	57	12	70	70	34
	2018	81	46	128	82	42
	2019	93	43	103	85	40
Skrukkebukta	2008	55	8	50	47	6
	2009	80	42	75	68	29
	2018	104	47	108	70	13
	2019	85	42	96	85	44

Table 3: Overview of how many individuals (n) of Bosmina *ssp. and* Daphnia *sp. from fish stomachs that were measured in the study localities Ruskebukta, Tjærebukta and Skrukkebukta in the two latest study years, 2018 and 2019.*

		***Bosmina* ssp. (with or without eggs)**	***Bosmina* ssp. with eggs**	***Daphnia* sp. (with or without eggs)**	***Daphnia* sp. females**	***Daphnia* sp. females with eggs**
Ruskebukta	2018	58	30	33	30	7
	2019	151	56	45	44	11
Tjærebukta	2018	51	22	2	2	1
	2019	122	63	60	55	28
Skrukkebukta	2018	105	52	21	17	1
	2019	202	124	31	30	21

3.4 Data analyses

3.4.1 Diet composition

The diet composition of vendace and DR whitefish is measured by using the subjective relative-fullness method in terms of percent prey abundance, defined as the percentage of total stomach contents in all predators comprised by each given prey type (Hyslop, 1980; Amundsen et al., 2019).

The percent prey abundance (A_i) of each prey type was calculated from their presence and fullness in the stomachs:

$A_i = (\Sigma S_i / \Sigma S_t) \times 100$,

Where S_i is the stomach fullness of prey type *i* in the stomachs and S_t is the total stomach fullness of all fish in a population.

3.4.2 Niche width

For calculating the niche width, I used Levins' index (Krebs, 2016):

$$B = 1/\Sigma p_i^2,$$

Where B = Levins' measure for niche width, and p_i = proportion of individuals using resource type *i*.

3.4.3 Diet similarity

To explore the diet similarities between vendace and whitefish, and among the lake localities for the two fish species, the diet similarity was calculated by using Schoener's index (Schoener, 1970):

$$D = 100\left(1 - 0.5 \times \Sigma\left|p_{xi} - p_{yi}\right|\right), i = 1, 2, \ldots, n$$

where p_{xi} and p_{yi} are the frequencies of prey type *i* in fish species x and y, respectively, and n = the number of prey types. D = 0 means there is no overlap between the diets and D = 100 means the diets are of identical composition (Schoener, 1970). Wallace (1981) argued that it is unlikely that two assumed identical individuals from the same population will have the exact same diet. There will be random events causing some differences. Therefore, he concluded that an overlap with > 60 % between two individuals/species is biologically significant (Wallace, 1981). Thus, I define the degree of diet overlap as < 40 % = modest diet similarity, 40 % - 60 % = intermediate diet similarity, > 60 % = significant diet similarity.

4 Results

4.1 Zooplankton density

The total zooplankton densities varied largely among the localities and study years, with the highest densities observed in Ruskebukta and Tjærebukta, whereas Skrukkebukta generally had the lowest densities (figure 4, appendix figure A2, A3, and appendix table A4). The density variations among localities and years were chiefly due to large fluctuations in the densities of *Bosmina* spp. and *Daphnia* sp., and to some extent also cyclopoid copepods.

In Ruskebukta, the total zooplankton density largely varied over the sampled years, being low in 2008 and 2018 and high in 2009 and 2019 (figure 4a, appendix A2a and A3a). These changes were largely due to great variations in the density of *Daphnia* sp. The density of *Bosmina* ssp. was in contrast low and other cladocerans were almost non-existent in the zooplankton samples over the four study years. Cyclopoid copepods had highest densities in the first two study years, and both cyclopoid and calanoid copepods had their peaks in 2009, whereas their densities were low in the last two study years.

In Tjærebukta, the total zooplankton density was high in 2008 and 2019 and low in 2009 and especially in 2018 (figure 4b, appendix A2b and A3b). As for Ruskebukta, these variations were driven by the *Daphnia* sp. density, which was high in 2008 and 2019 and low in the other two years. *Bosmina* spp. had a relatively high density in 2008, but low in the other three study years, whereas other cladocerans and copepods consistently had very low densities.

In Skrukkebukta, the total zooplankton density was relatively high in 2008 and quite low in the other years (figure 4c, appendix A2c and A3c) but showed in general smaller variations than in the other two lakes. In contrast to the dominance of D*aphnia* sp. in Ruskebukta and Tjærebukta, the densities of *Bosmina* spp. and *Daphnia* sp. showed similar levels and patterns in Skrukkebukta. Both were most abundant in 2008. Other cladocerans and the copepods had relatively low densities in all years, except for a slight peak in cyclopoid copepods in 2018.

For a detailed density account of all species and their various life stages, see appendix figure A3 and appendix table A4, in the supplementary information.

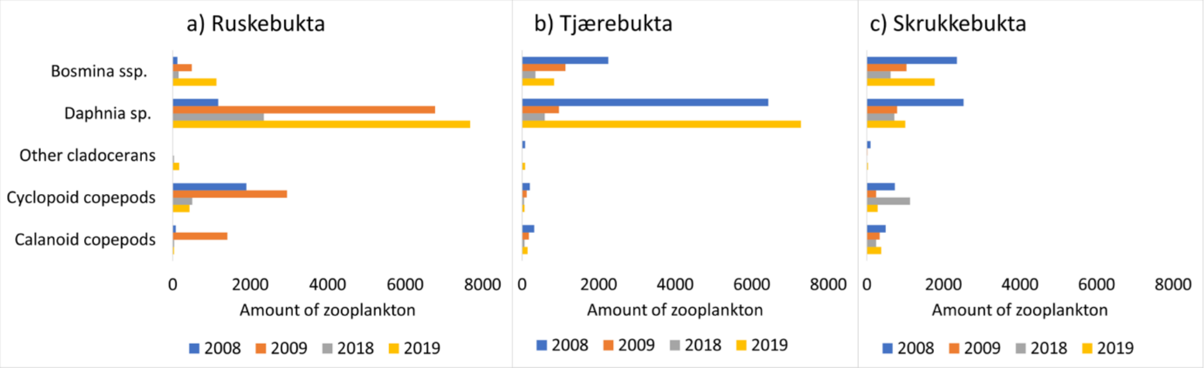

Figure 4: Overview of the mean densities of zooplankton in a) Ruskebukta, b) Tjærebukta and c) Skrukkebukta over the four years investigated (2008, 2009, 2018 and 2019).

4.2 Zooplankton community composition

The zooplankton composition varied among the localities (figure 5, appendix A4). While *Daphnia* sp. made a large contribution to the zooplankton community in all three lakes, *Bosmina* spp. and the copepods showed greater variation between the localities, whereas other cladocerans mostly had insignificant contributions.

In Ruskebukta, the zooplankton composition was dominated by cyclopoid copepods (58 %) and *Daphnia* sp. (36 %) in 2008 (figure 5a). The following three study years the contribution of cyclopoid copepods decreased gradually to 4.6 % in 2019, whereas *Daphnia* sp. was by far the dominating species in 2009, 2018 and 2019 with > 50 % in all three years.

In Tjærebukta, *Daphnia* sp. and *Bosmina* spp. dominated the lake throughout the study, while cyclopoid copepods, calanoid copepods and other cladocerans only constituted a small part of the zooplankton composition (figure 5b). In most years, *Daphnia* sp. was by far the dominant of the two cladocerans, constituting > 50 % the zooplankton community, except in 2009, when *Bosmina* spp. had a small domination over *Daphnia* sp.

Bosmina spp. and *Daphnia* sp. dominated the zooplankton community in Skrukkebukta as well (figure 5c), except in 2018 when cyclopoid copepods constituted a large part of the zooplankton composition and dominated over *Bosmina* spp. and *Daphnia* sp. The relative contribution of *Bosmina* spp. was generally larger in Skrukkebukta than in Tjærebukta and consistently much larger than in Ruskebukta.

For a detailed zooplankton composition account of all species and their various life stages, see figure appendix A4 and appendix table A5, in the supplementary information.

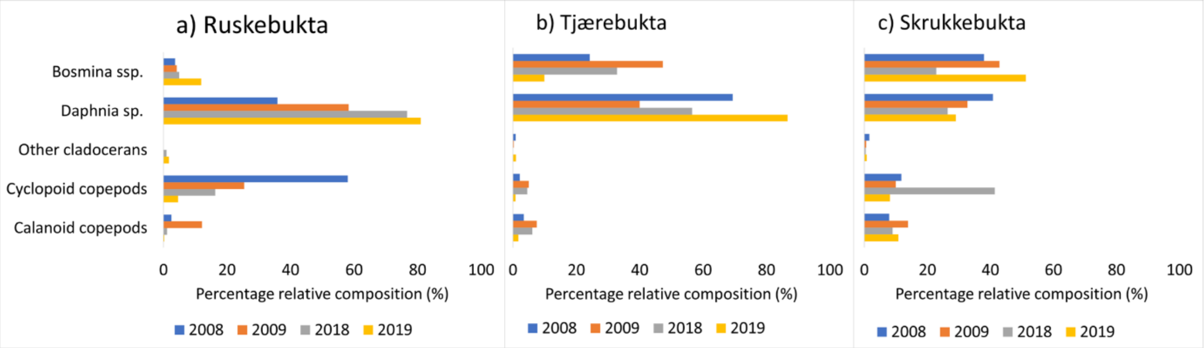

Figure 5: Relative composition (%) of the zooplankton communities in the three localities a) Ruskebukta, b) Tjærebukta and c) Skrukkebukta over the four years investigated (2008, 2009, 2018 and 2019). Nauplius larvae are not included.

4.3 Prey abundance

4.3.1 Vendace

Vendace in Ruskebukta fed on different prey types than in Tjærebukta and Skrukkebukta (figure 6). In Tjærebukta and Skrukkebukta, the vendace diet was consistently dominated by *Bosmina* spp., whereas in Ruskebukta vendace predominantly fed on other organisms like surface insects, insect pupae, and benthic invertebrates (*Eurycecus lamellatus*, appendix table A6), and in 2008, also fish (nine-spined sticklebacks).

More specifically, in 2008 and 2009 the vendace diet in Ruskebukta was dominated by the surface insects/insect pupae prey category (59 % and 45 %, respectively, figure 6a). However, in 2008 also fish constituted a large part of the vendace diet, while in 2009 *Bosmina* sp. and large cladocerans were more commonly represented. In 2018, benthic invertebrates, surface insects and *Daphnia* sp. constituted similar parts of the vendace diet in Ruskebukta (from ~25 to ~28 % each), whereas in 2019, *Bosmina* spp., surface insects/insect pupae and large cladocerans dominated. In terms of the niche width of vendace in Ruskebukta, it was relatively low in 2008 and 2019 (Levins' index: 3.0 and 3.3, respectively), and high in 2009 and especially high in 2018 (Levins' index: 4.7 and 6.7, respectively; figure 7, appendix table A7).

In Tjærebukta, cladocerans dominated the vendace diet in all four years and *Bosmina* spp. was by far the dominant taxa among the cladoceran prey groups (figure 6b). The *Bosmina* spp. dominance was at its lowest in 2008 (39.2 %), when it was closely followed by *Daphnia* sp., and calanoid and cyclopoid copepods. In the last three study years, *Bosmina* ssp. constituted > 70 % of the vendace diet. The niche width was 3.8 in 2008 in Tjærebukta, and thus higher than in Ruskebukta, whereas in the other three years the index values for vendace were mostly below 2.0 and thus distinctly lower than in Ruskebukta (figure 7, appendix table A7).

Also in Skrukkebukta, the vendace diet was dominated by *Bosmina* spp. all four years. Like in Tjærebukta, the *Bosmina* spp. dominance was at its lowest in 2008 (33.3 %), closely followed by cyclopoid copepods and *Daphnia* sp. In 2009, 2018 and 2019, *Bosmina* spp. constituted 65 % to 85 % of the vendace diet. The niche width in Skrukkebukta were similar to Tjærebukta, with an index value of 4.0 in 2008 and mostly below 2.0 in the other three years, and thus distinctly different from Ruskebukta (figure 7, appendix table A7).

4.3.2 DR whitefish

In Ruskebukta in 2008, the diet of DR whitefish was dominated by benthic invertebrates (mainly *Eurycecus lamellatus*, figure 6a, appendix table A6), fish and surface insects. In the last three study years, surface insects/insect pupae constituted more than 50 % of the prey abundance, followed by benthic invertebrates as the second most important prey group. Only in 2019, the cladoceran prey groups gave a notable contribution to the DR whitefish diet in Ruskebukta, when both *Bosmina* spp. and large cladocerans had a prey abundance of 10.9 % each (21.8 % in total). The niche width varied moderately between 3.0 and 3.7 (figure 7, appendix table A7).

In Tjærebukta, cladocerans dominated the DR whitefish diet in all years, except for 2018, when insect pupae dominated, constituting 58 % (figure 6b). In 2008, DR whitefish fed almost exclusively on *Bosmina* spp. and *Daphnia* sp. (46.5 % and 45.7 %, respectively). In 2009 and 2019, they also fed on large cladocerans, in addition to *Bosmina* spp. and *Daphnia* sp. The niche width was at a low level in 2008 and 2009 (2.4 and 2.2, respectively) and somewhat higher in 2018 (3.8) and 2019 (3.3) (figure 7, appendix table A7).

In Skrukkebukta, the DR whitefish diet looked similar to the vendace diet, consistently being dominated by *Bosmina* spp., which constituted more than 50 % of the prey abundance in all four years (figure 6c). The niche width varied between 1.8 and 3.1 in a similar pattern among years as for vendace, but with smaller inter-annual differences (figure 7, appendix table A7).

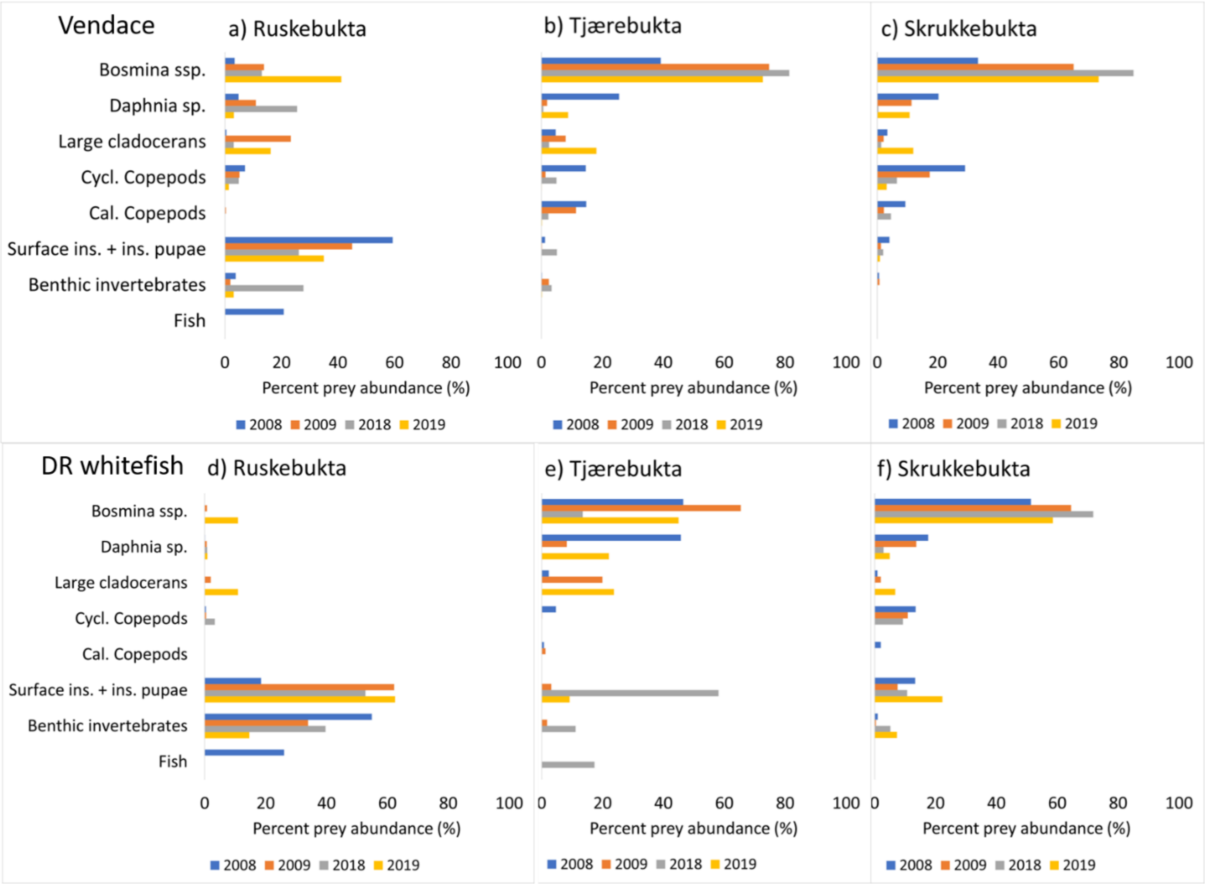

Figure 6: Relative diet composition in terms of percent prey abundance (%) in vendace in a) Ruskebukta, b) Tjærebukta and c) Skrukkebukta and DR whitefish d) Ruskebukta, e) Tjærebukta and f) Skrukkebukta, over the four years (2008, 2009, 2018 and 2019).

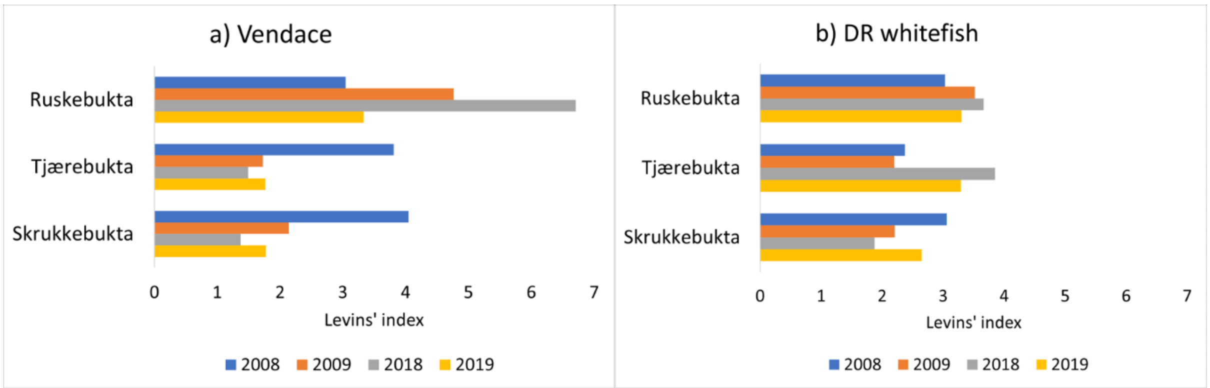

Figure 7: Dietary niche widths in terms of Levin's index in a) vendace and b) DR whitefish, over the study years (2008, 2009, 2018 and 2019) in the three localities Ruskebukta, Tjærebukta and Skrukkebukta.

4.4 Diet similarity between species and among localities

4.4.1 Dietary niche overlap between vendace and DR whitefish

Among the three investigated localities, the lowest dietary overlaps between vendace and DR whitefish were seen in Ruskebukta and partly in Tjærebukta, whereas the highest diet similarity was consistently seen in Skrukkebukta with a significant overlap in all study years (figure 8, appendix table A8). In Ruskebukta, the diet overlap between vendace and DR whitefish showed an increasing trend over the study years with the lowest index value observed in 2008 and the highest in 2019. The dietary differences between the two species were mostly due to a relatively large inclusion of benthic invertebrates in the DR whitefish diet, whereas vendace in contrast partly fed on zooplankton.

In Tjærebukta, the diet overlap was high and significant (i.e. >60 %) in the first two years, whereas the overlap was very low in 2018 and relatively high again in 2019 (figure 8). The high overlap values were related to a dominance of *Bosmina* spp. and in 2008 also *Daphnia* sp. in the diet of both species. The low overlap values in 2018 was related to a dominance of surface insects/insect pupae (mostly chironomidae pupae and unidentified species of insect larvae/pupae) in the DR whitefish diet while vendace still predominantly fed on *Bosmina* spp.

In Skrukkebukta, vendace and DR whitefish had a high and significant diet overlap (>60 %) in all four years. In 2008, the high diet overlap was related to a varied but similar zooplankton diet where both fish species fed on *Bosmina* spp., *Daphnia* sp. and cyclopoid copepods. For the three years, the high dietary overlap was predominantly a result of both fish species specializing on *Bosmina* spp.

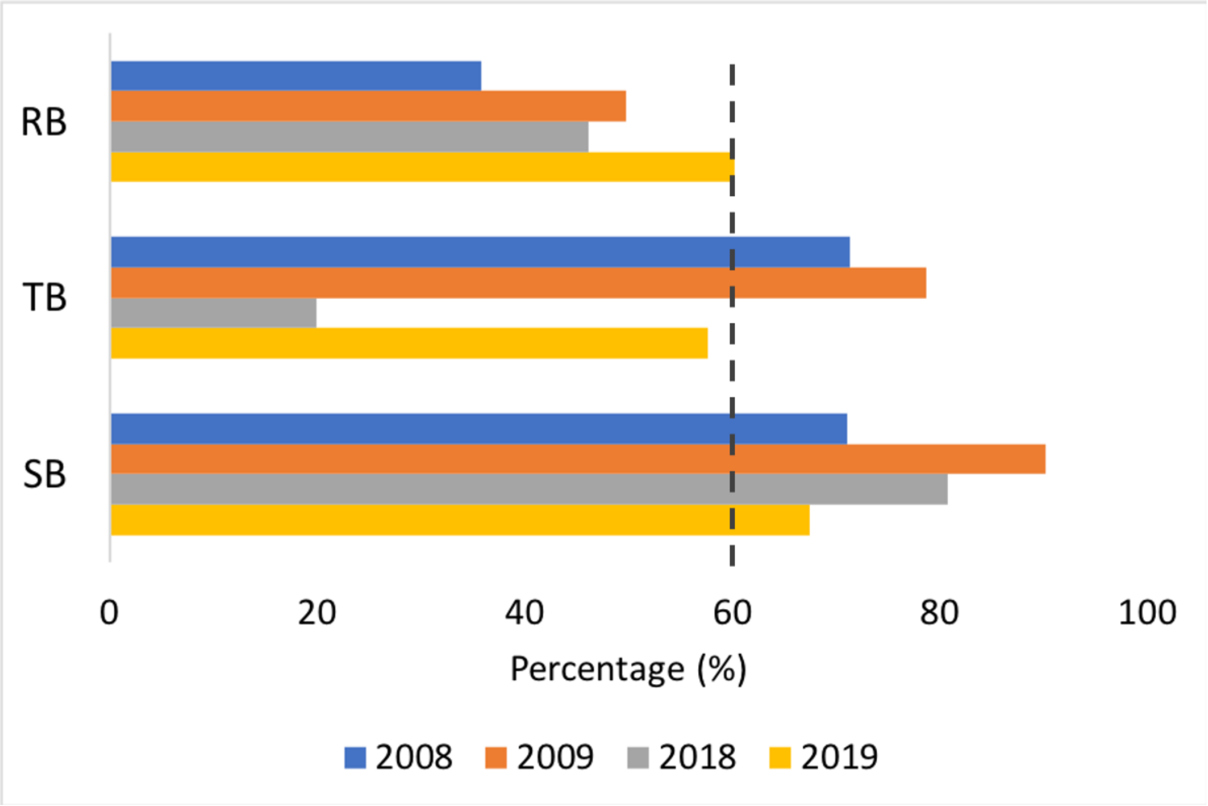

Figure 8: Diet overlap of vendace and DR whitefish over the four study years (2008, 2009, 2018 and 2019) in the three investigated localities (Ruskebukta, Tjærebukta and Skrukkebukta), illustrated by using Schoener's index. The stapled line shows the 60 % limit that indicates when the diet similarity is high (Wallace, 1981).

4.4.2 Comparison among localities

4.4.2.1 Vendace

In general, the vendace diet similarity was high between Tjærebukta and Skrukkebukta, while it was low between Tjærebukta and Ruskebukta, and between Skrukkebukta and Ruskebukta.

Vendace in Tjærebukta and Ruskebukta had a low diet similarity (<25 %) in the first three study years. It was high (>60 %) in 2019 (figure 9a, appendix table A8), at the same time as vendace in Ruskebukta had an enhanced dietary contribution of *Bosmina* spp. and large cladocerans, and thus a diet more similar to vendace in Tjærebukta. In contrast, the diet similarity between vendace in Tjærebukta and Skrukkebukta was high and significant (>60 %) in all study years, reflecting a dominance of *Bosmina* spp. in both localities throughout the study. Between Skrukkebukta and Ruskebukta, the diet similarity showed the same pattern as between Tjærebukta and Ruskebukta; it was mostly low in the first three years and high in 2019. The vendace diet was dominated by *Bosmina* spp. in all four years in Skrukkebukta, as it also was in Ruskebukta in 2019. However, in the other three study years, surface insects/insect pupae dominated the diet in Ruskebukta, resulting in the low diet similarity between the two localities.

4.4.2.2 DR whitefish

In general, the diet similarity of DR whitefish showed the same pattern as for vendace. It was high between Tjærebukta and Skrukkebukta, while it was low between Tjærebukta and Ruskebukta, and between Skrukkebukta and Ruskebukta. However, the pattern was not consistent throughout the study period, and 2018 deviated from the general pattern.

The diet similarity of DR whitefish between Tjærebukta and Ruskebukta was low (<40 %) in the first two years and in 2019, while it was high (>60 %) in 2018 (figure 9b, appendix table A8). The diet of DR whitefish in Ruskebukta was dominated by surface insects/insect pupae, benthic invertebrates and fish in all four years, while in Tjærebukta these prey groups dominated only in 2018, resulting in the high diet similarity index. The diet similarity between DR whitefish in Tjærebukta and Skrukkebukta showed a pattern that was completely opposite to Tjærebukta and Ruskebukta, being high in all years expect for 2018, when it was low. The high diet similarity in the first three study years was due to the diet in both localities being dominated by *Bosmina* spp. In 2018 in contrast, the diet of DR whitefish in Tjærebukta had changed to a domination of insect pupae, benthic invertebrates and fish, resulting in the low diet similarity (appendix table A6). Between Skrukkebukta and Ruskebukta, the diet similarity of DR whitefish was low in all investigated years. This was due to the dietary dominance of *Bosmina* spp. in all study years in Skrukkebukta, whereas *Bosmina* spp. never dominated in Ruskebukta.

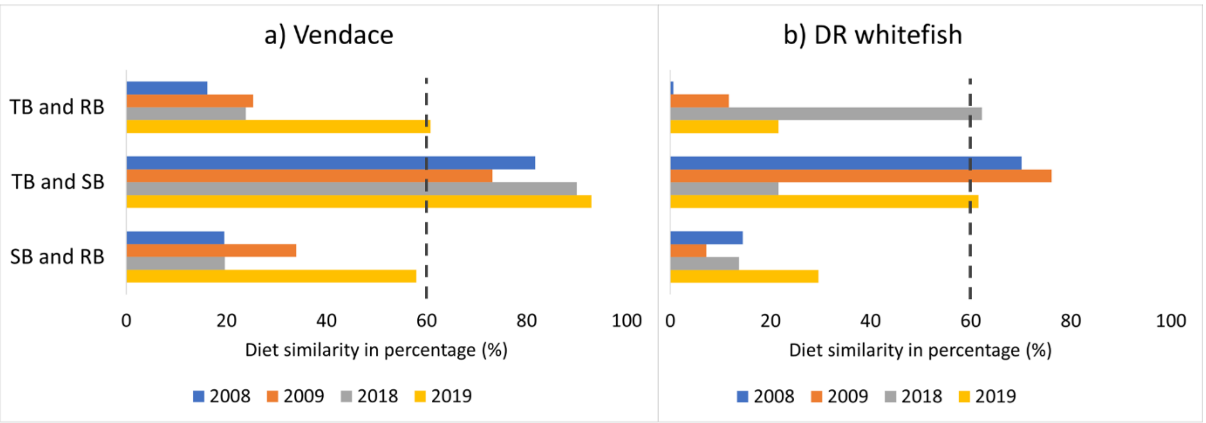

Figure 9: Diet similarity of a) vendace and b) whitefish between Ruskebukta (RB), Tjærebukta (TB) and Skrukkebukta (SB), over the four study years (2008, 2009, 2018 and 2019), illustrated by using Schoener's index. The stipled line shows the 60 % limit that indicates when the diet similarity is high (Wallace, 1981).

4.5 Zooplankton body size

Any differences observed in body sizes of *Bosmina* spp. and *Daphnia* sp. were greater between the lakes than between the years within each lake. In 2018 and 2019, *Bosmina* spp. in the environment were at similar sizes in all three lakes, whereas differences between the lakes could be seen from the stomachs, where they were smallest in Ruskebukta in both 2018 and 2019 and biggest in Tjærebukta in 2018 and in Skrukkebukta in 2019 (two-sample t-test; $p<0.05$, appendix table A19). Both in 2018 and 2019, *Daphnia* sp. carapace length was smallest in Ruskebukta and biggest in Skrukkebukta in both environment and stomachs. In the environment the differences were significant in both 2018 and 2019 for the three lake comparisons (two-sample t-test; $p<0.05$, appendix table A19), except between Tjærebukta and Skrukkebukta in 2018. In the stomachs however, the differences were only significant in 2019, for all three comparisons.

Bosmina spp. body size in the environment showed similar patterns throughout the study in the three study lakes, with an average body size ranging from 0.39 mm to 0.47 mm (figure 10, appendix table A9, A20). In all lakes, the body size decreased from 2008 to 2009. The opposite pattern was evident in 2018 when body sizes increased, which it also did in 2019. The body size of female egg-carrying *Daphnia* sp. showed greater variations in the environment than *Bosmina* spp. did (figure 10, appendix table A12, A20). The body size of *Daphnia* sp. decreased from 2008 to 2009 in all three localities. In Ruskebukta and Tjærebukta, the body size in 2008 was the largest in the study, whereas in Skrukkebukta the body size increased and was largest in 2019.

The body size of *Bosmina* spp. was bigger and significant in the stomachs of the fish than in the environment in both 2018 and 2019 in all three localities, except for Ruskebukta and Skrukkebukta 2018 (two-sample t-test; $p<0.05$; figure 11a, appendix table A9, A10, A11). Additionally, in all three localities, *Bosmina* spp. was significantly bigger in 2019 than in 2018 in both the environment and in the stomachs and in all the lakes (two-sample t-test; $p<0.05$, appendix table A15), except for in the environment in Ruskebukta (two-sample t-test; $p<0.05$). The carapace body size of female egg-carrying *Daphnia* sp. was only significantly bigger in the environment than in the stomachs in Ruskebukta 2019 (two-sample t-test; $p<0.05$, figure 11b, appendix table A12, A13, A14). In Ruskebukta, the carapace length of female egg-carrying *Daphnia* sp. was significantly bigger in 2018 than in 2019, in both environment and stomachs (two-sample t-test; $p<0.05$). In Tjærebukta, it was significantly bigger in 2019 than 2018 only in the stomachs, whereas in Skrukkebukta, only in the environment (two-sample t-test; p<0.05, appendix table A15). I was given access to analyses of the correlation between *Bosmina* spp. and *Daphnia* sp. and the annual mean water temperatures from 1991 to 2019 (appendix figure A5, appendix table A16, A17, A18, A21), which did not show an impact on the body sizes from water temperatures.

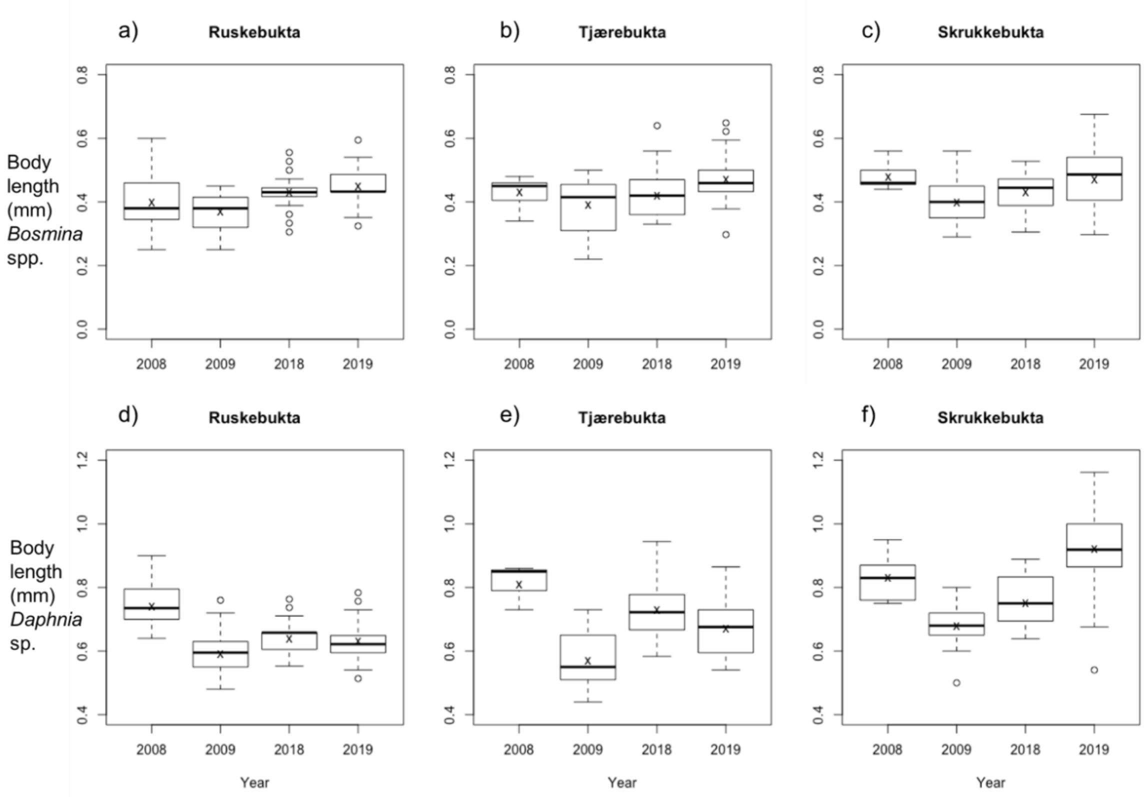

Figure 10: Boxplot of the observed body length of Bosmina *spp. (a, b and c) and female egg-carrying* Daphnia *sp. (d, e and f) in the environment, where x marks the average, the solid line is the median, the box represents 50% of the observations whiskers represents 95% of observations and dots are outliers, for the localities Ruskebukta, Tjærebukta and Skrukkebukta in all study years (2008, 2009, 2018 and 2019).*

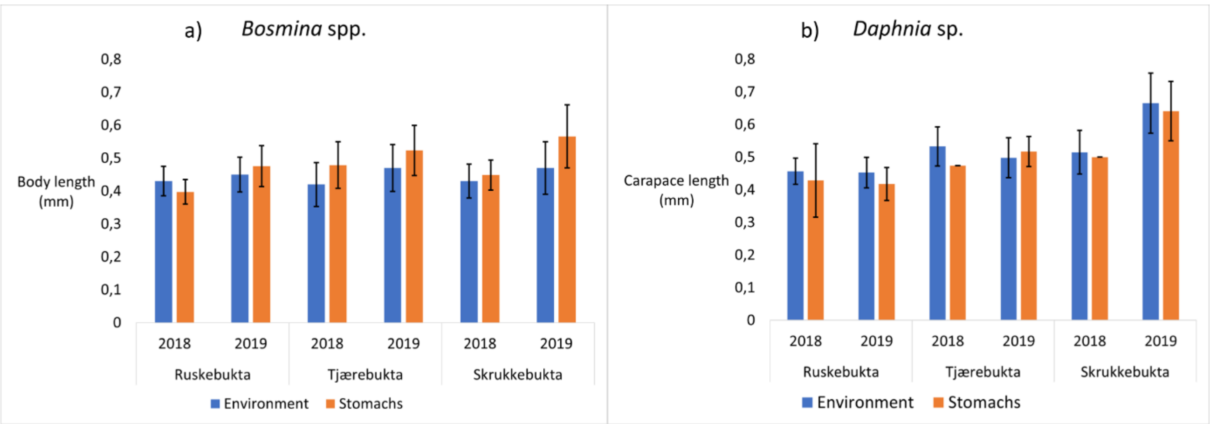

Figure 11: Average body length of a) Bosmina *spp. and average carapace length of b) female egg-carrying* Daphnia *sp. in the environment and in the stomachs of the fish, with standard deviation, from Ruskebukta, Tjærebukta and Skrukkebukta in 2018 and 2019.*

5 Discussion

A key finding of the present study was that the zooplankton communities and the fish diets in Tjærebukta and Skrukkebukta looked similar to each other in all study years, as opposed to in Ruskebukta, which seemed to be much more affected by the vendace invasion. In Ruskebukta, predation from vendace had almost depleted *Bosmina* spp., whereas in Tjærebukta and Skrukkebukta, *Bosmina* spp., together with *Daphnia* sp., had large contributions to the zooplankton communities and both fish species could to a larger degree feed on the cladocerans. The body sizes of *Bosmina* spp. and *Daphnia* sp. did not appear to be affected by the inter-annual temperature changes, but rather by the predation pressure they have been exposed to since the invasion took place.

As expected, cladoceran zooplankton showed a large contribution to the zooplankton community in Skrukkebukta throughout the study. For Ruskebukta and Tjærebukta, the expectation that the cladocerans would have smaller densities and a lower contribution to the zooplankton composition was not fullfilled. In Tjærebukta, the zooplankton community was similar to Skrukkebukta, with both lakes for the most part being dominated by *Bosmina* spp. and *Daphnia* sp. Also in Ruskebukta the zooplankton community was dominated by cladocerans throughout the study, except in 2008 when cyclopoid copepods dominated. However, in contrast to Skrukkebukta and Tjærebukta, *Daphnia* sp. was the only dominating cladoceran species in Ruskebukta, whereas the contribution of *Bosmina* spp. was small. *Daphnia cristata,* which is the common daphnid species in Pasvik (Amundsen et al., 2009), is known to coexist with zooplanktivorous fish (Hamrin, 1983). This species is narrow and transparent (*Artsdatabanken*, 2016), which probably allows for them to easier avoid being seen by predators and when eaten, even escape through the fish gills (Pijanowska, 1992). *Daphnia cristata*, together with cyclopoid copepods and rotifers, are commonly dominating the zooplankton community in vendace dominated lakes (Hamrin, 1983; Løvik and Kjellberg, 2003). *Bosmina* spp. is in contrast known to be the favorite prey of vendace (Hall, 1982; O'Brien, 1987; Hammar, 1988), and it has previously been demonstrated that the invasion of vendace into the Pasvik watercourse had a strong impact on the *Bosmina* spp. population in Ruskebukta, which has been strongly reduced (Bøhn and Amundsen, 1998; Amundsen et al., 2009). This is supported by the low densities of *Bosmina* spp. in comparison to *Daphnia* sp. found in Ruskebukta in the present study. Skrukkebukta, and to a certain degree also Tjærebukta, had equal densities of *Bosmina* spp. and *Daphnia* sp. Skrukkebukta has not experienced the same densities of vendace as in the upper localities (fig. 2; Amundsen et al., 1999, 2019), and the vendace density was also generally much higher in Ruskebukta than in Tjærebukta. The cladoceran species has thus been exposed to a smaller predation pressure from vendace in Skrukkebukta and partly Tjærebukta, which has allowed for a higher survival rate among the larger individuals and preferred cladoceran species like *Bosmina* spp. (Bøhn and Amundsen, 1998; Amundsen et al., 2009). Also Liso et al. (2013) found the zooplankton community in Tjærebukta to be more similar to Skrukkebukta than to Ruskebukta, and concluded that the predation pressure from vendace and DR whitefish has been much stronger in Ruskebukta, making the cladocerans, and in particular *Bosmina* spp., a scarce resource there. Vendace seem to prefer feeding on *Bosmina* spp. even when the species is scarce and there are other potential prey items available (Northcote and Hammar, 2006). For example, in the Swedish lake Mälaren, vendace chose to feed on *Bosmina longispina* even in late summer/autumn when the numbers of *Bosmina* spp. had been greatly reduced (Northcote and Hammar, 2006). This underlines how the high densities of vendace in Ruskebukta can impose a greater predation pressure on the zooplankton, in comparison to the other two investigated lakes. A decrease in zooplankton densities after the introduction of an efficient zooplanktivorous fish has also been documented in several other studies (e.g., Brooks and Dodson, 1965; Reif and Tappa, 1966; Galbraith, 1967; Hall et al., 1970; Lazzaro, 1987) and shows how a preferred prey can be highly vulnerable to a new and specialized predator, as also revealed in the present study.

As expected, cladoceran zooplankton dominated the diets of both vendace and DR whitefish in Skrukkebukta in all four study years, with *Bosmina* spp. as the preferred species. In Ruskebukta, the results were also as expected, as DR whitefish fed predominantly on benthic invertebrates and surface insects. For Tjærebukta, however, this hypothesis must be rejected. There, the diet of both vendace and DR whitefish were dominated by cladoceran zooplankton and were more similar to the diet in Skrukkebukta (except in 2018 when benthic invertebrates and surface insects dominated the DR whitefish diet in Tjærebukta). In both Skrukkebukta and Tjærebukta, the high dietary overlap between vendace and DR whitefish and the relative high densities of *Bosmina* spp. in all study years, suggest that there was moderate interspecific competition between the two fish species for food resources. However, even though the fish diets and zooplankton densities were similar in Tjærebukta and Skrukkebukta, it must be pointed out that the fish densities were not. In Tjærebukta, the CPUE of DR whitefish was much lower than vendace and, in this regard, more similar to Ruskebukta, which had similar fish densities. Gjelland et al. (2007) argued that vendace and DR whitefish in Skrukkebukta had segregated into different microhabitats along the depth gradient, where vendace occupied the epipelagic microhabitat (0-6 m) and the DR whitefish persisted in high numbers at intermediate depths (6-16 m). Furthermore, the densities of *Bosmina* spp. seem to have been high enough to sustain both fish species (Gjelland et al., 2007). It is possible that the segregation into microhabitats have persisted through my study as well, and in combination with a higher cladoceran density and a relatively low CPUE of both vendace and DR whitefish, contribute to the observed coexistence between vendace and DR whitefish in Skrukkebukta. A segregation along the depth gradient has not been investigated in Tjærebukta, but the low CPUE values of DR whitefish in comparison to vendace suggests little coexistence between the two fish species there.

The pelagic zone in the upper localities, and especially in Ruskebukta, has been dominated by vendace since the very beginning of the invasion (Bøhn and Amundsen, 2001; Gjelland et al., 2007). A shift in the DR whitefish diet from zooplankton to surface insects and benthic prey has previously been documented for Ruskebukta and concluded to be a response to the vendace grazing down the zooplankton community (Bøhn and Amundsen, 2001; Gjelland et al., 2007; Liso et al., 2013). Additionally, fish was found in the diets of both vendace and DR whitefish in Ruskebukta in 2008, even though this is not a common prey for any of the two fish species diets (Hall, 1982; O'Brien, 1987; Hammar, 1988). 2008 was also the year of the present study when the cladocerans in Ruskebukta species had the lowest densities and made the smallest contributions to the zooplankton composition and to the vendace prey abundance. Liso et al. (2011, 2013) studied the vendace and DR whitefish diets in 2008 from the same three lakes as in the present study and concluded that the fish occurrence in the diets in Ruskebukta was a consequence of extreme food resource limitation. It was further concluded that vendace, even though being a zooplanktivorous specialist, has the ability to adapt to a broader niche width when times are desperate and thus is more flexible in diet choice than previously assumed (Liso et al., 2011). It is possible that the suggestive extreme food resource limitation in Ruskebukta in 2008 is the result of a very strong 0+ vendace generation, even though this is not reflected in the CPUE. The youngest vendace generation is likely so small that most of them escaped the gill nets, and it is therefore plausible that the CPUE results do not reflect the actual fish densities in the lakes. Hence, in 2008 the abundance of the 0+ generation may likely have been big enough to have a major impact on the zooplankton community.

It has in previous studies been pointed out that reduced niche overlap between vendace and DR whitefish in the Pasvik watercourse and especially Ruskebukta, should be regarded as an evidence for competition (Bøhn and Amundsen, 2001; Liso, 2010). The competitive exclusion principle states that two species competing for the same resources should not be able to coexist, since one of the species will have an advantage over the other and the weaker species will either be excluded, or go through a niche shift and change its resource use (Gause, 1934; Molles, 2002). Vendace is considered a zooplankton specialist with a narrow diet spectrum and habitat range, and a greater competitor for zooplankton than DR whitefish (Northcote and Hammar, 2006; Sandlund et al., 2013). Whitefish is considered a generalist and its diet can include a wide array of prey items, although the DR whitefish morph prefer crustacean zooplankton (Sandlund et al., 2010). DR whitefish also has the ability to change its diet to benthic invertebrates when times are scarce and thus has a wider fundamental niche than vendace (Northcote and Hammar, 2006; Sandlund et al., 2010; Sandlund et al., 2013). In Ruskebukta, where the preferred prey resource has become scarce, the wider fundamental niche of DR whitefish has made it possible to change its realized niche in order to reduce the interspecific competition with vendace. However, the exclusion from its original realized niche has led to a strong decline in population density in Ruskebukta (Bøhn et al., 2008; Amundsen et al., 2019).

In contrary to what I expected, the differences in body sizes of *Bosmina* spp. and *Daphnia* sp. could not be correlated to the inter-annual temperature variations in any of the three lakes investigated. It is important to point out that *Bosmina* spp. has a generation time of 10-20 days (Urabe, 1991) and *Daphnia* sp. 10-30 days (Ebert, 2005). This means that during the sampling for the present study, there has already been multiple generations that have lived and reproduced and the measured body sizes from September might not be representative for the population. This represents a source of error in the analyses that looks for a correlation between the September body sizes and the water temperatures measured over a period of three months in summer. However, analyses of time-series data on cladoceran body size and water temperatures from 1991 to 2019 supports that there is no correlation between the body sizes of *Bosmina* spp. and *Daphnia* sp. and inter-annual temperature variations (figure A5, table A21). Further, the differences in *Bosmina* spp. and *Daphnia* sp. body size were bigger between the lakes than they were between the study years, especially for *Daphnia* sp. *Bosmina* spp. was also consistently bigger in the fish stomachs than in the environment throughout the study in all the lakes (except in Ruskebukta in 2018), which supports the assumption that vendace imposes a great size-selective pressure on the bigger *Bosmina* spp. The same differences between fish stomachs and the environment could not be seen in the body size of *Daphnia* sp., which were similar or bigger in the environment, confirming the assumption that *Bosmina* spp. is the preferred prey of vendace. It has been suggested that temperature is one of the main determinants of growth in cladoceran species (Gillooly and Dodson, 2000; Hart and Bychek, 2011; Havens et al., 2015). However, even though temperature can have strong effects on zooplankton, predation has been suggested to have an "over-riding influence on body size selection" (Hart and Bychek, 2011). As previously discussed, the predation pressure from vendace is higher on the zooplankton in the upper localities than in the lower, and these differences in predation pressure provides a better explanation for the differences in body size than the inter-annual temperatures do. Predation is believed to be the primary determinant of zooplankton size structure at both the individual and community level (Hall, 1982), and a study conducted in Lake Pyhäjärvi, Finland, concluded that vendace has the potential to influence the population dynamics of its main prey species (Helminen et al., 1990). It has previously been documented that the larger cladoceran species, both among *Bosmina* and *Daphnia*, disappeared from the watercourse after the vendace invasion (Amundsen et al., 1999, 2009). The smaller species that remained and have coexisted with the predators, have been exposed to a great selection pressure, and a reduction in body size of *Bosmina* spp. has been documented in Ruskebukta (Amundsen et al., 2009), which the present study supports. Predators select for the bigger and more visible zooplankton and a higher mortality and reduction in body size are direct effects from the predation (Lynch, 1977; O'Brien, 1987; Dodson, 1988; Havens et al., 2015). In the Pasvik watercourse, this particularly seems to apply for *Bosmina* spp., which by far was the most commonly selected zooplankton prey and apparently also suffered from a strong size-selective impact from the vendace predation. The larger but more transparent and narrow *Daphnia* sp. had on the other hand a modest contribution to the diets of both vendace and DR whitefish, and possibly also suffered less from any size-selective predation.

In conclusion, there was a high level of interspecific competition between vendace and DR whitefish in Ruskebukta and Tjærebukta. The downgrazing of cladocerans, and mainly *Bosmina* spp., has forced not only DR whitefish, but to a certain degree also vendace, to feed on other types of prey and thus shift its realized niche. In Tjærebukta, DR whitefish has not shifted its realized niche, but have instead almost been eliminated from the locality due to interspecific competition with vendace. In Skrukkebukta, the preferred zooplankton prey

Bosmina spp. had higher densities than in Ruskebukta and the two fish species could coexist with a large niche overlap especially from a common utilization of this prey type. Further, I conclude that the body sizes of *Bosmina* spp. and *Daphnia* sp. were not correlated to inter-annual temperature variations. The predation pressure they were exposed to appeared to override any effects from the inter-annual temperature variations. To avoid sources of error in future studies, I recommend that zooplankton sampling is conducted on a weekly basis throughout the period that temperatures are collected from. Siwertsson (2004) concluded that the vendace invasion into the Pasvik watercourse has had a strong impact on zooplankton composition, demography, life-history, and morphology in its native prey community, and that biological invasion can develop differently even within the same watercourse. The Pasvik watercourse exemplifies how difficult it can be to predict the outcome of a biological invasion (Heger and Trepl, 2003), by the two fairly different situations that have developed in the upper and lower localities. My study supports the conclusion of Siwertsson (2004) and emphasizes the importance of good management strategies to avoid invasions of alien species into ecosystems where they do not naturally occur, and where they can drastically alter the demography and population development of native species (Strayer, 2010; Engel et al., 2011; Seebens et al., 2017).

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7 Appendix

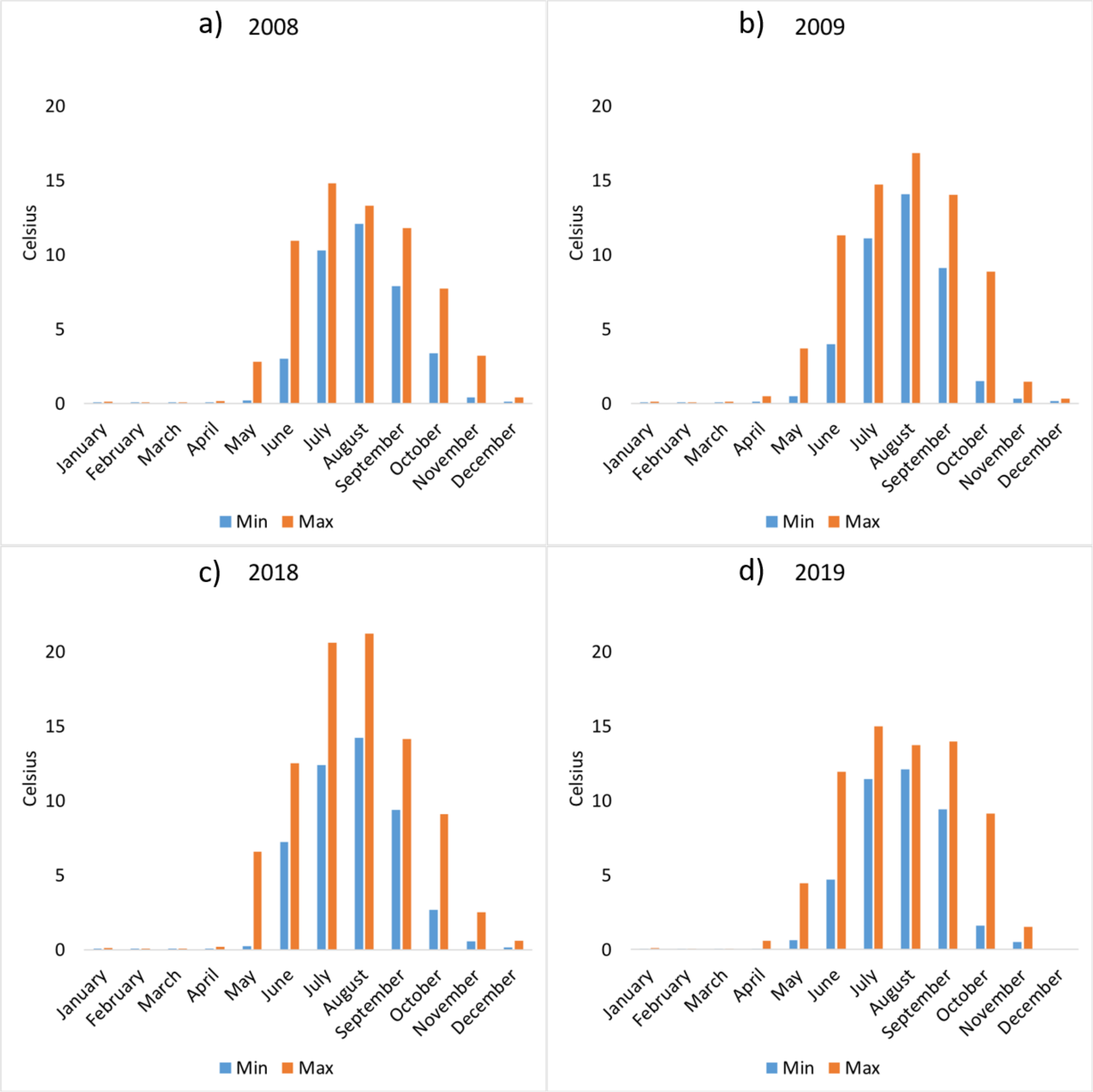

Figure A1: Maximum and minimum water temperatures from every month in the years a) 2008, b) 2009, c) 2018 and d) 2019, measured at Skogfoss.

Table A1: Zooplankton categories that were identified and counted in the zooplankton samples from Ruskebukta, Tjærebukta and Skrukkebukta in the study years 2008, 2009, 2018 and 2019.

***Bosmina* ssp.**
***Bosmina* with eggs**
***Bosmina* with ephippia**
***Daphnia* sp. female**
***Daphnia* with eggs**
***Daphnia* with ephippia**
***Daphnia* sp. male**
D. galeata
***D. galeata* with eggs**
Holopedium gibberum
***H. gibberum* with eggs**
Nauplii
Cyclopoid copepods C1-C3
Cyclopoid copepods C4-C5
***Cyclops scutifer* female**
***Cyclops scutifer* male**
***Mesocyclops leucartii* female**
***Mesocyclopos leucartii* male**
Calanoid copepods C1-C3
Calanoid copepods C4-C5
***Eudiaptomus graciloides* female**
***Eudiaptomus graciloides* male**
***Heterocope appendiculate* female**
***Heterocope appendiculate* male**
Leptodora kindtii
Polyphemus pediculus
Daphnia quadrangular

Table A2: The categories used for presentation of percent prey abundance.

Category	**Species**
***Bosmina* ssp.**	
***Daphnia* sp.**	
Large cladocerans	*Bythotrephes* sp. *Polyphemus pediculus* *Leptodora kindtii* *Holopedium gibberum* Unidentified zooplankton
Cyclopoid copepods	
Calanoid copepods	
Surface insects + insect pupae	Surface insects Chironomid pupae Trichoptera pupae Unidentified insects
Benthic invertebrates	Acanthocyclops *Pisidium* sp. *Planorbis* sp. *Valvata* sp. *Eurycecus lamellatus* Ostracods Chironomid larvae Trichoptera larvae with house *Ephemeroptera* larvae *Odonata* larvae Water mites Other
Fish	*Pungitius pungitius* *Perca fluviatilis*

Table A3: CPUE values for vendace and DR whitefish in the localities Ruskebukta, Tjærebukta and Skrukkebukta in the study years 2008, 2009, 2018 and 2019.

Locality	**Year**	**Month**	**Habitat**	**Vendace**	**DR whitefish**
Ruskebukta	2008	9	3	46,17	7,50
Ruskebukta	2009	9	3	69,33	8,67
Ruskebukta	2018	9	3	175,17	1,67
Ruskebukta	2019	9	3	162,00	13,83
Tjærebukta	2008	9	3	45,33	0,00
Tjærebukta	2009	9	3	123,00	16,00
Tjærebukta	2018	9	3	50,17	3,00
Tjærebukta	2019	9	3	54,83	0,67
Skrukkebukta	2008	9	3	14,33	9,00
Skrukkebukta	2009	9	3	14,44	4,44
Skrukkebukta	2018	9	3	15,42	3,83
Skrukkebukta	2019	9	3	6,08	1,67

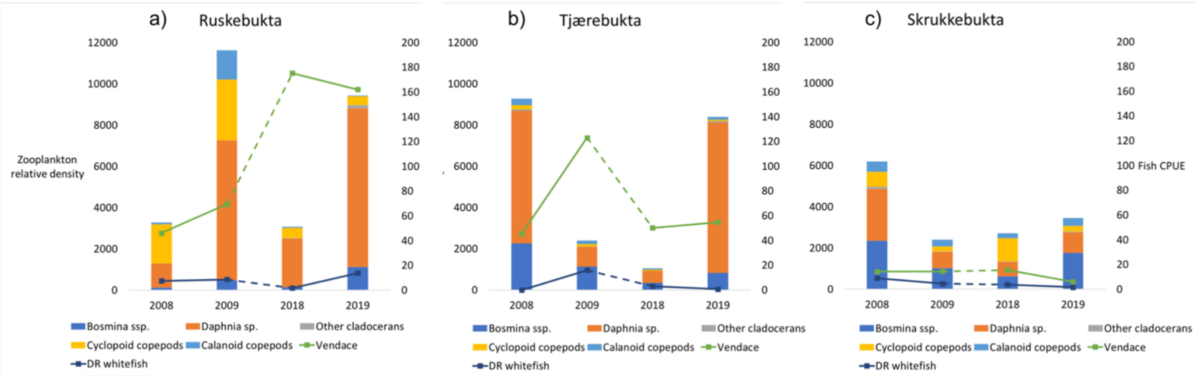

Figure A2: Relative density of fish (CPUE; dots with connecting lines) and zooplankton (number per net haul; bars) over the four study years (2008, 2009, 2018 and 2019) in the three localities: a) Ruskebukta, b) Tjærebukta and c) Skrukkebukta. Nauplius larvae are not included in the zooplankton densities. CPUE (catch per unit effort) is the number of fish caught per 100m^2 gillnet per night. Zooplankton relative density is a number of zooplankton per 15 m vertical plankton net haul.

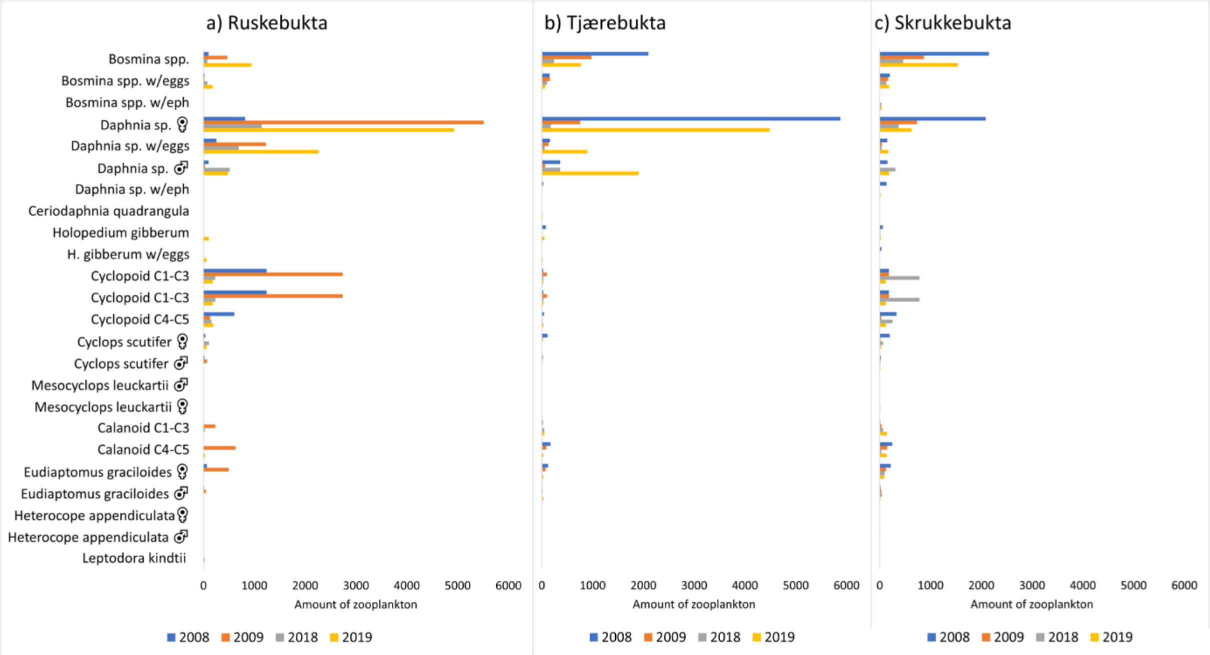

Figure A3: Overview of the densities of zooplankton with all species and life stages in a) Ruskebukta, b) Tjærebukta, c) Skrukkebukta over the four years investigated in the study (2008, 2009, 2018 and 2019).

Table A4: Zooplankton density values for vendace and DR whitefish in Ruskebukta, Tjærebukta and Skrukkebukta in the four study years (2008, 2009, 2018 and 2019).

Locality	Year	Month	Bosmina spp.	B w/eggs	Bosmina w/ephippie	Daphnia sp. ♀	Daphnia sp. w/eggs	Daphnia sp. ♂	Daphnia sp. w/ephippia	Ceriodaphnia quadrangula	Holopedium gibberum	H. gibberum w/eggs	Cyclopoid C1-C3	Cyclopoid C4-C5	Cyclops scutifer ♀	Cyclops scutifer ♂	Mesocyclops leuckartii ♂	Mesocyclops leuckartii ♀	Calanoid C1-C3	Calanoid C4-C5	Eudiaptomus graciloides ♀	Eudiaptomus graciloides ♂	Heterocope appendiculata ♀	Heterocope appendiculata ♂	Leptodora kindtii
Ruskebukta	2008	9	100	20	0	820	253	100	0	0	0	0	1240	607	33	20	0	0	0	0	67	13	0	0	0
Ruskebukta	2009	9	470	20	0	5510	1230	30	0	0	0	0	2740	130	10	70	0	0	230	630	500	50	0	0	0
Ruskebukta	2018	9	75	75	0	1145	690	515	0	5	0	0	230	160	110	0	0	0	25	5	5	0	0	0	25
Ruskebukta	2019	9	945	180	0	4935	2265	480	0	0	105	60	180	195	60	0	0	0	0	30	0	0	0	0	0
Tjærebukta	2008	9	2100	150	0	5880	160	360	30	0	80	0	30	40	110	20	0	0	20	170	120	10	0	0	0
Tjærebukta	2009	9	973	160	0	753	133	67	7	0	0	7	100	0	20	0	0	0	7	87	73	13	0	0	0
Tjærebukta	2018	9	240	104	0	176	56	360	0	0	0	0	32	16	0	0	0	0	48	0	16	0	0	0	0
Tjærebukta	2019	9	768	64	0	4480	896	1904	0	16	48	16	32	32	0	0	0	0	48	32	32	32	0	0	0
Skrukkebukta	2008	9	2150	200	0	2085	150	155	135	0	60	35	180	330	200	20	0	0	10	245	215	15	0	5	0
Skrukkebukta	2009	9	870	160	0	737	43	7	0	0	10	3	180	27	17	17	0	0	37	147	123	27	0	0	0
Skrukkebukta	2018	9	460	129	31	369	37	309	3	0	9	3	783	254	66	6	3	11	66	34	100	43	0	0	0
Skrukkebukta	2019	9	1540	187	40	627	167	187	20	0	20	7	120	120	27	13	0	0	140	133	87	13	0	0	0

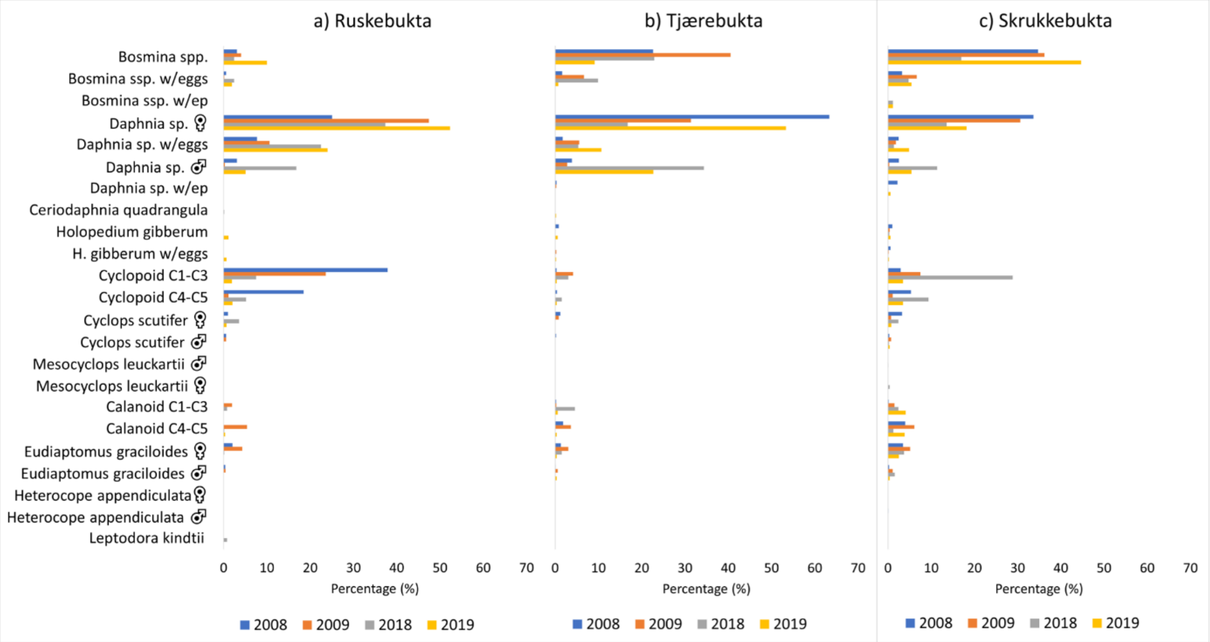

Figure A4: The detailed zooplankton composition account of all species and their various life stages in a) Ruskebukta, b) Tjærebukta and c) Skrukkebukta in the four study years (2008, 2009, 2018 and 2019).

Table A5: Zooplankton composition values (%) for vendace and DR whitefish in Ruskebukta, Tjærebukta and Skrukkebukta in the four study years (2008, 2009, 2018 and 2019).

Locality	**Year**	**Month**	**Bosmina spp.**	**B w/eggs**	**Bosmina w/ephippie**	**Daphnia sp. ♀**	**Daphnia sp. w/eggs**	**Daphnia sp. ♂**	**Daphnia sp. w/ephippia**	**Ceriodaphnia quadrangula**	**Holopedium gibberum**	**H. gibberum w/eggs**	**Cyclopoid C1-C3**	**Cyclopoid C4-C5**	**Cyclops scutifer ♀**	**Cyclops scutifer ♂**	**Mesocyclops leuckartii ♂**	**Mesocyclops leuckartii ♀**	**Calanoid C1-C3**	**Calanoid C4-C5**	**Eudiaptomus graciloides ♀**	**Eudiaptomus graciloides ♂**	**Heterocope appendiculata ♀**	**Heterocope appendiculata ♂**	**Leptodora kindtii**
Ruskebukta	2008	9	3,1	0,6	0,0	25,1	7,7	3,1	0,0	0,0	0,0	0,0	37,9	18,5	1,0	0,6	0,0	0,0	0,0	0,0	2,0	0,4	0,0	0,0	0,0
Ruskebukta	2009	9	4,0	0,2	0,0	47,4	10,6	0,3	0,0	0,0	0,0	0,0	23,6	1,1	0,1	0,6	0,0	0,0	2,0	5,4	4,3	0,4	0,0	0,0	0,0
Ruskebukta	2018	9	2,4	2,4	0,0	37,4	22,5	16,8	0,0	0,2	0,0	0,0	7,5	5,2	3,6	0,0	0,0	0,0	0,8	0,2	0,2	0,0	0,0	0,0	0,8
Ruskebukta	2019	9	10,0	1,9	0,0	52,3	24,0	5,1	0,0	0,0	1,1	0,6	1,9	2,1	0,6	0,0	0,0	0,0	0,0	0,3	0,0	0,0	0,0	0,0	0,0
Tjærebukta	2008	9	22,6	1,6	0,0	63,4	1,7	3,9	0,3	0,0	0,9	0,0	0,3	0,4	1,2	0,2	0,0	0,0	0,2	1,8	1,3	0,1	0,0	0,0	0,0
Tjærebukta	2009	9	40,6	6,7	0,0	31,4	5,6	2,8	0,3	0,0	0,0	0,3	4,2	0,0	0,8	0,0	0,0	0,0	0,3	3,6	3,1	0,6	0,0	0,0	0,0
Tjærebukta	2018	9	22,9	9,9	0,0	16,8	5,3	34,4	0,0	0,0	0,0	0,0	3,1	1,5	0,0	0,0	0,0	0,0	4,6	0,0	1,5	0,0	0,0	0,0	0,0
Tjærebukta	2019	9	9,1	0,8	0,0	53,3	10,7	22,7	0,0	0,2	0,6	0,2	0,4	0,4	0,0	0,0	0,0	0,0	0,6	0,4	0,4	0,4	0,0	0,0	0,0
Skrukkebukta	2008	9	34,7	3,2	0,0	33,7	2,4	2,5	2,2	0,0	1,0	0,6	2,9	5,3	3,2	0,3	0,0	0,0	0,2	4,0	3,5	0,2	0,0	0,1	0,0
Skrukkebukta	2009	9	36,2	6,7	0,0	30,7	1,8	0,3	0,0	0,0	0,4	0,1	7,5	1,1	0,7	0,7	0,0	0,0	1,5	6,1	5,1	1,1	0,0	0,0	0,0
Skrukkebukta	2018	9	16,9	4,7	1,2	13,6	1,4	11,4	0,1	0,0	0,3	0,1	28,8	9,4	2,4	0,2	0,1	0,4	2,4	1,3	3,7	1,6	0,0	0,0	0,0
Skrukkebukta	2019	9	44,7	5,4	1,2	18,2	4,8	5,4	0,6	0,0	0,6	0,2	3,5	3,5	0,8	0,4	0,0	0,0	4,1	3,9	2,5	0,4	0,0	0,0	0,0

Table A6: Prey abundance values for vendace and DR whitefish in Ruskebukta (RB), Tjærebukta (TB) and Skrukkebukta (SB) in the four study years (2008, 2009, 2018 and 2019).

Lake	Species	Size group	Year	Bosmina spp.	Daphnia sp.	Bythotrep.	Polyph.	Leptodora	Unid. Plankon	holopedium	SUM Large cladocerans	CyclCop	CalCop	Acantocycl.	Eurycercus lamellatus	Muslingkr	SUM benthic crustaceans	Planorbidae	Gjellesnegl	Pisidium sp.	SUM mussels and snails	Surface insects	ChirPup	Unid. Insect larvae	SUM urface insects + insect pupae	Trichoptera pupae	ChirLarv	trich. With house	Trich. w/o house	Ephemeroptera larvae	Hydracarina	Odonata larvae	Araneae	SUM benthic larvae	Unid. Fish	Perch	SUM fish	unidentified
RB	Vendace	Total	2008	3,2	4,5	0,0	0,0	0,0	0,4	0,0	0,5	6,6	0,0	1,7	1,1	0,0	1,1	0,0	0,0	0,0	0,0	52,7	0,1	2,4	55,2	0,3	0,0	0,0	0,0	0,0	0,8	0,0	0,0	0,8	19,5	0,0	19,5	6,3
RB	Vendace	Total	2009	13,9	10,9	0,0	23,0	0,0	0,2	0,2	23,3	5,1	0,4	0,0	1,0	0,8	1,8	0,0	0,0	0,0	0,0	33,2	11,3	0,5	45,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0	0,1	0,0	0,0	0,0	0,0
RB	Vendace	Total	2018	12,7	24,7	0,0	0,0	0,0	3,0	0,0	3,0	4,7	0,0	0,0	13,7	6,0	19,7	0,0	0,0	0,0	0,0	0,0	0,7	5,0	5,7	19,6	6,7	0,0	0,0	0,0	0,5	0,0	0,0	7,2	0,0	0,0	0,0	3,0
RB	Vendace	Total	2019	41,2	3,2	0,0	0,0	0,0	0,8	15,4	16,2	1,4	0,0	0,0	1,3	0,0	1,3	0,0	0,0	0,0	0,0	2,2	0,4	0,0	2,6	32,4	0,2	0,0	0,0	0,0	0,0	0,0	1,6	1,8	0,0	0,0	0,0	0,0
RB	Whitefish	Total	2008	0,0	0,1	0,0	0,0	0,0	0,0	0,0	0,0	0,4	0,0	1,0	0,5	0,0	0,5	0,0	0,3	0,7	1,0	12,3	0,7	3,0	16,0	2,5	0,0	0,0	0,0	0,0	52,4	0,0	0,0	52,4	17,8	8,2	26,0	0,1
RB	Whitefish	Total	2009	0,8	0,7	0,0	2,0	0,0	0,0	0,0	2,0	0,5	0,0	0,0	3,6	0,3	4,0	0,0	0,0	3,3	3,3	48,2	14,1	0,0	62,2	0,0	0,7	5,0	0,0	0,0	15,6	0,0	5,4	26,6	0,0	0,0	0,0	0,0
RB	Whitefish	Total	2018	0,0	0,8	0,0	0,0	0,0	0,0	0,0	0,0	3,3	0,0	0,0	26,2	1,0	27,2	0,0	0,0	5,2	5,2	1,6	2,5	4,4	8,5	44,3	2,1	2,0	0,0	0,0	0,5	2,6	0,0	7,2	0,0	0,0	0,0	0,0
RB	Whitefish	Total	2019	10,9	0,9	0,0	0,0	0,0	0,0	10,9	10,9	0,0	0,0	0,0	13,5	0,0	13,5	0,0	0,0	0,0	0,0	6,9	5,4	0,0	12,2	50,3	0,0	0,0	0,0	0,0	0,0	0,0	1,2	1,2	0,0	0,0	0,0	0,0
TB	Vendace	Total	2008	39,2	25,5	0,1	1,2	0,0	3,4	0,0	4,7	14,6	14,7	0,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	1,1	0,1	0,0	1,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1
TB	Vendace	Total	2009	74,8	1,9	0,3	7,7	0,0	0,0	0,0	8,0	1,4	11,4	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0	0,1	0,1	2,2	0,2	0,0	0,0	0,0	0,0	0,0	2,4	0,0	0,0	0,0	0,0
TB	Vendace	Total	2018	81,4	0,6	0,0	0,0	0,0	2,5	0,0	2,5	4,9	2,3	0,0	0,1	0,0	0,1	0,0	0,0	0,0	0,0	0,0	5,0	0,0	5,0	0,0	2,5	0,6	0,0	0,0	0,0	0,0	0,0	3,1	0,0	0,0	0,0	0,0
TB	Vendace	Total	2019	72,7	8,8	0,0	0,0	0,0	0,9	17,2	18,1	0,1	0,1	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0	0,0	0,0	0,0	0,0	0,1	0,0	0,0	0,0	0,0
TB	Whitefish	Total	2008	46,2	45,4	0,8	1,5	0,0	0,0	0,0	2,3	4,6	0,8	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,8
TB	Whitefish	Total	2009	63,7	8,4	2,3	12,9	0,0	1,1	0,0	16,3	0,2	1,3	0,0	0,1	0,0	0,1	0,0	0,0	0,0	0,0	0,9	1,3	0,9	3,0	0,2	1,8	0,0	0,0	0,0	0,0	0,0	0,5	2,3	0,0	0,0	0,0	0,0
TB	Whitefish	Total	2018	13,5	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	5,8	0,0	5,8	0,0	0,0	0,0	0,0	1,9	3,8	7,7	13,5	44,6	3,8	0,0	0,0	0,0	0,0	1,5	0,0	5,4	17,3	0,0	17,3	0,0
TB	Whitefish	Total	2019	45,0	22,1	0,0	0,0	0,0	20,8	2,9	23,8	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	9,2	0,0	0,0	9,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
SB	Vendace	Total	2008	33,3	20,3	0,0	0,4	0,0	2,6	0,3	3,3	29,1	9,3	0,5	0,0	0,0	0,0	0,0	0,0	0,0	0,0	3,7	0,0	0,3	4,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,2
SB	Vendace	Total	2009	65,1	11,3	0,0	2,1	0,0	0,0	0,0	2,1	17,4	2,2	0,0	0,3	0,1	0,3	0,0	0,0	0,0	0,0	1,1	0,0	0,1	1,2	0,0	0,3	0,1	0,0	0,0	0,0	0,0	0,0	0,4	0,0	0,0	0,0	0,0
SB	Vendace	Total	2018	84,9	0,3	0,0	0,0	0,0	1,2	0,1	1,3	6,5	4,5	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	1,2	0,0	0,0	1,2	0,8	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
SB	Vendace	Total	2019	73,4	10,7	0,6	0,0	0,0	0,4	11,0	11,9	3,2	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,8	0,0	0,0	0,8	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0,0
SB	Whitefish	Total	2008	51,2	17,6	0,0	0,8	0,0	0,0	0,1	1,0	13,4	2,0	0,1	0,1	0,0	0,1	0,0	0,0	0,4	0,4	12,3	0,0	0,9	13,3	0,0	0,0	0,1	0,0	0,3	0,1	0,0	0,0	0,5	0,0	0,0	0,0	0,2
SB	Whitefish	Total	2009	64,5	13,7	0,1	1,8	0,0	0,0	0,1	2,0	10,9	0,1	0,0	0,2	0,0	0,2	0,0	0,0	0,0	0,0	7,6	0,0	0,0	7,6	0,0	0,1	0,0	0,0	0,0	0,0	0,0	0,1	0,3	0,0	0,0	0,0	0,0
SB	Whitefish	Total	2018	71,8	2,9	0,0	0,0	0,0	0,0	0,0	0,0	9,3	0,1	0,0	2,8	0,3	3,1	0,0	0,0	1,1	1,1	7,8	0,6	0,1	8,5	2,2	0,6	0,4	0,0	0,0	0,0	0,0	0,0	1,0	0,0	0,0	0,0	0,0
SB	Whitefish	Total	2019	58,6	4,9	4,3	0,0	0,0	0,0	2,5	6,8	0,0	0,0	0,0	0,2	0,0	0,2	0,6	0,0	0,4	1,0	14,1	0,8	0,0	14,9	7,4	0,0	6,1	0,0	0,0	0,0	0,0	0,0	6,1	0,0	0,0	0,0	0,0

Table A7: Exact values for dietary width in terms of Levins' index for vendace and DR whitefish in Ruskebukta, Tjærebukta and Skrukkebukta over the four study years (2008, 2009, 2018 and 2019).

Locality	Year	Vendace	Whitefish
Ruskebukta	2008	3,0	3,0
Ruskebukta	2009	4,8	3,5
Ruskebukta	2018	6,7	3,7
Ruskebukta	2019	3,3	3,3
Tjærebukta	2008	3,8	2,4
Tjærebukta	2009	1,7	2,2
Tjærebukta	2018	1,5	3,8
Tjærebukta	2019	1,8	3,3
Skrukkebukta	2008	4,0	3,1
Skrukkebukta	2009	2,1	2,2
Skrukkebukta	2018	1,4	1,9
Skrukkebukta	2019	1,8	2,6

Table A8: Exact values of dietary niche overlap between Ruskebukta (RB), Tjærebukta (TB) and Skrukkebukta (SB) over the four study years (2008, 2009, 2018 and 2019, illustrated by Schoeners' index.

		2008	**2009**	**2018**	**2019**
Between species (%)	**RB**	35,9	49,8	46,1	60,2
	TB	71,4	78,6	19,9	57,6
	SB	71,1	90,1	80,8	67,4
Between localities – vendace (%)	**TB and RB**	16,2	25,3	23,9	60,8
	TB and SB	81,7	73,2	90,0	92,9
	SB and RB	19,6	33,9	19,7	57,9
Between localities – whitefish (%)	**TB and RB**	0,6	11,7	62,2	21,6
	TB and SB	70,2	76,1	21,6	61,5
	SB and RB	14,5	7,2	13,7	29,6

Table A9: Average body length (mm) of Bosmina spp. in the environment and in the stomachs of the sampled fish in Ruskebukta, Tjærebukta and Skrukkebukta over the four study years (2008, 2009, 2018 and 2019). In the fish stomachs, body lengths were only measured in 2018 and 2019.

		2008	2009	2018	2019
Environment	Ruskebukta	0,40	0,37	0,43	0,45
	Tjærebukta	0,43	0,39	0,42	0,47
	Skrukkebukta	0,48	0,40	0,43	0,47
Stomachs	Ruskebukta	-	-	0,04	0,05
	Tjærebukta	-	-	0,07	0,07
	Skrukkebukta	-	-	0,05	0,08

Table A10: Average body length of Bosmina *spp. in the environment and in the stomachs of the sampled fish in 2018 and 2019 with standard deviation in Ruskebukta, Tjærebukta and Skrukkebukta.*

	Ruskebukta		Tjærebukta		Skrukkebukta	
	2018	**2019**	**2018**	**2019**	**2018**	**2019**
Environment	0,43	0,45	0,42	0,47	0,43	0,47
Stomachs	0,40	0,48	0,48	0,52	0,45	0,57
st.dev env.	0,04	0,05	0,07	0,07	0,05	0,08
st.dev sto.	0,04	0,06	0,07	0,08	0,05	0,10

Table A11: p-value, df and t-results from two-sample t-tests between average length of Bosmina *spp. in the environment and in the stomachs of the sampled fish in 2018 and 2019 in Ruskebukta, Tjærebukta and Skrukkebukta.*

		2018	2019
p-value	Ruskebukta	0,001	0,040
	Tjærebukta	0,002	0,001
	Skrukkebukta	0,054	0,000
df	Ruskebukta	70	95
	Tjærebukta	66	104
	Skrukkebukta	97	166
t	Ruskebukta	-3,34	2,08
	Tjærebukta	3,26	3,29
	Skrukkebukta	1,95	5,70

Table A12: Average lengths of female egg-carrying Daphnia *sp. and of all* daphnia *sp. in the environment of the study lakes Ruskebukta, Tjærebukta and Skrukkebukta for all study years (2008, 2009, 2018 and 2019) with standard deviation for 2018 and 2019, which are the two years when body lengths were measurements in the stomachs as well.*

				Helmet length (mm)	**Body length (mm)**	**Carapace length (mm)**	**Total length (mm)**	**Spine length (mm)**
Female egg-carrying *Daphnia* sp.	**Ruskebukta**	**2008**	**Length**	0,20	0,74	0,55	1,13	0,39
		2009	**Length**	0,15	0,59	0,45	0,99	0,40
		2018	**Length**	0,18	0,64	0,46	1,02	0,38
			St.dev	0,02	0,05	0,04	0,09	0,05
		2019	**Length**	0,18	0,63	0,45	0,99	0,36
			St.dev	0,02	0,06	0,05	0,08	0,05
	Tjærebukta	**2008**	**Length**	0,23	0,81	0,59	1,15	0,36
		2009	**Length**	0,14	0,57	0,43	0,87	0,29
		2018	**Length**	0,20	0,73	0,53	1,13	0,40
			St.dev	0,03	0,07	0,06	0,10	0,05
		2019	**Length**	0,17	0,67	0,50	1,04	0,38
			St.dev	0,02	0,08	0,06	0,10	0,06
	Skrukkebukta	**2008**	**Length**	0,21	0,83	0,63	1,22	0,39
		2009	**Length**	0,17	0,68	0,51	1,05	0,37
		2018	**Length**	0,24	0,75	0,51	1,18	0,43
			St.dev	0,03	0,08	0,07	0,16	0,10
		2019	**Length**	0,25	0,92	0,67	1,39	0,48
			St.dev	0,03	0,12	0,09	0,16	0,08
All *Daphnia* sp.	**Ruskebukta**	**2008**	**Length**	0,18	0,67	0,49	1,03	0,36
		2009	**Length**	0,15	0,54	0,39	0,89	0,35
		2018	**Length**	0,17	0,57	0,40	0,90	0,33
			St.dev	0,03	0,09	0,08	0,16	0,09
		2019	**Length**	0,17	0,58	0,41	0,92	0,34
			St.dev	0,02	0,09	0,08	0,14	0,08
	Tjærebukta	**2008**	**Length**	0,19	0,72	0,53	1,05	0,35
		2009	**Length**	0,14	0,56	0,42	0,81	0,25
		2018	**Length**	0,18	0,64	0,46	1,00	0,37
			St.dev	0,03	0,11	0,09	0,14	0,06
		2019	**Length**	0,16	0,59	0,43	0,93	0,33
			St.dev	0,02	0,11	0,09	0,16	0,07
	Skrukkebukta	**2008**	**Length**	0,21	0,80	0,59	1,18	0,38
		2009	**Length**	0,16	0,64	0,48	0,99	0,35
		2018	**Length**	0,21	0,66	0,45	1,02	0,36
			St.dev	0,05	0,12	0,09	0,17	0,08
		2019	**Length**	0,22	0,77	0,55	1,19	0,41
			St.dev	0,04	0,19	0,15	0,25	0,09

Table A13: Average lengths of female egg-carrying Daphnia *sp. and of all* daphnia *sp. in the fish stomachs from the study lakes Ruskebukta, Tjærebukta and Skrukkebukta for 2018 and 2019, with standard deviation.*

				Helmet (mm)	**Body (mm)**	**Carapace (mm)**	**Total (mm)**	**Spine (mm)**
Female egg-carrying *Daphnia* sp.	**Ruskebukta**	**2018**	**Length**	0,18	0,61	0,43	0,89	0,27
			st.dev	0,02	0,12	0,11	0,10	0,11
		2019	**Length**	0,18	0,59	0,42	0,94	0,34
			st.dev	0,02	0,06	0,05	0,10	0,07
	Tjærebukta	**2018**	**Length**	0,24	0,71	0,47	1,08	0,37
			st.dev	0,00	0,00	0,00	0,00	0,00
		2019	**Length**	0,18	0,70	0,52	0,99	0,29
			st.dev	0,03	0,05	0,05	0,09	0,06
	Skrukkebukta	**2018**	**Length**	0,13	0,63	0,50	1,03	0,39
			st.dev	0,00	0,00	0,00	0,00	0,00
		2019	**Length**	0,25	0,89	0,64	1,33	0,44
			st.dev	0,03	0,09	0,09	0,16	0,14
All *Daphnia* sp.	**Ruskebukta**	**2018**	**Length**	0,17	0,55	0,37	0,84	0,29
			st.dev	0,02	0,09	0,08	0,10	0,07
		2019	**Length**	0,17	0,56	0,39	0,85	0,30
			st.dev	0,03	0,08	0,06	0,12	0,06
	Tjærebukta	**2018**	**Length**	0,20	0,66	0,46	1,01	0,36
			st.dev	0,04	0,05	0,01	0,07	0,01
		2019	**Length**	0,17	0,68	0,51	0,98	0,29
			st.dev	0,03	0,07	0,06	0,10	0,06
	Skrukkebukta	**2018**	**Length**	0,18	0,63	0,46	0,95	0,33
			st.dev	0,04	0,10	0,08	0,13	0,05
		2019	**Length**	0,25	0,90	0,65	1,32	0,43
			st.dev	0,04	0,10	0,10	0,15	0,12

Table A14: p-value, df and t-results from two-sample t-tests between average lengths of Daphnia *sp. in the environment and in the stomachs of the sampled fish in 2018 and 2019 in the study localities Ruskebukta, Tjærebukta and Skrukkebukta.*

Helmet length (mm)		**2018**	**2019**
p-value	Ruskebukta	0,66	0,81
	Tjærebukta	0,15	0,13
	Skrukkebukta	0,00	0,92
df	Ruskebukta	73,00	72,00
	Tjærebukta	41,00	60,00
	Skrukkebukta	12,00	63,00
t	Ruskebukta	0,44	-0,24
	Tjærebukta	-1,45	-1,53
	Skrukkebukta	3,79	0,10
Body length (mm)		**2018**	**2019**
p-value	Ruskebukta	0,18	0,81
	Tjærebukta	0,81	0,11
	Skrukkebukta	0,19	0,40
df	Ruskebukta	73,00	72,00
	Tjærebukta	41,00	60,00
	Skrukkebukta	12,00	63,00
t	Ruskebukta	1,34	-0,24
	Tjærebukta	0,24	-1,62
	Skrukkebukta	1,40	0,85
Carapace length (mm)		**2018**	**2019**
p-value	Ruskebukta	0,18	0,03
	Tjærebukta	0,34	0,21
	Skrukkebukta	0,84	0,33
df	Ruskebukta	73,00	72,00
	Tjærebukta	41,00	60,00
	Skrukkebukta	12,00	63,00
t	Ruskebukta	1,36	2,22
	Tjærebukta	0,97	-1,26
	Skrukkebukta	0,21	0,99
Total length (mm)		**2018**	**2019**
p-value	Ruskebukta	0,00	0,07
	Tjærebukta	0,66	0,04
	Skrukkebukta	0,39	0,18
df	Ruskebukta	73,00	72,00
	Tjærebukta	41,00	60,00
	Skrukkebukta	12,00	63,00
t	Ruskebukta	3,39	1,86
	Tjærebukta	0,45	2,06
	Skrukkebukta	0,90	1,37
Spine length (mm)		**2018**	**2019**
p-value	Ruskebukta	0,00	0,34
	Tjærebukta	0,56	0,00
	Skrukkebukta	0,74	0,23
df	Ruskebukta	72,00	72,00
	Tjærebukta	41,00	60,00
	Skrukkebukta	12,00	63,00
t	Ruskebukta	4,43	0,96
	Tjærebukta	0,56	5,05
	Skrukkebukta	0,33	1,21

Table A15: p-value, df and t-results from two-sample t-tests between 2018 and 2019 in the environment and stomachs for Bosmina *spp. and* Daphnia *sp. in Ruskebukta, Tjærebukta and Skrukkebukta. T-tests for* Daphnia *sp. includes both total body length and* the *carapace length.*

		***Bosmina* spp.**		***Daphnia* sp. (total length)**		***Daphnia* sp. (carapace length)**	
		environment	stomachs	environment	stomachs	environment	stomachs
p-value	Ruskebukta	0,078	0,000	0,016	0,475	0,598	0,795
	Tjærebukta	0,000	0,019	0,000	0,627	0,003	0,233
	Skrukkebukta	0,003	0,000	0,108	0,000	0,097	0,000
df	Ruskebukta	82	83	129	15	129	16
	Tjærebukta	87	83	127	42	127	42
	Skrukkebukta	87	176	148	41	148	51
t	Ruskebukta	-1,784	-6,192	2,449	-0,374	0,528	0,264
	Tjærebukta	-3,670	-2,395	4,317	0,489	2,998	-1,211
	Skrukkebukta	-3,044	-8,435	-1,619	-6,117	-1,672	-6,235

Table A16: p-value and intercept result from linear regression-testing of Bosmina *spp. body length (mm) against all factors within my dataset, in all four years (2008, 2009, 2018 and 2019).*

		Total body size Daphnia sp.	**Carapace size Daphnia sp.**	**Bosmina sp. Co tribution in zooplankton**	**Daphnia sp. Contribution in zooplankton**	**Bosmina spp. Contribution in zooplankton**	**Daphnia ps. Contribution in zooplankton**	**CPUE vendace**	**CPUE whitefish**	**Bosmina spp. In vendace diet**	**Daphnia sp. In vendace diet**	**Bosmina spp. In whitefish diet**	**Daphnia sp. In whitefish diet**	**Number of days with >8°C**	**Temperatures >8°C**	**°C Jul15th-sep15th**
p-value	**2008**	0,176	0,841	-0,437	0,111	0,879	0,040	0,729	0,147	0,521	0,464	0,673	0,200	NA	0,196	0,696
	2009	0,107	0,198	0,165	0,276	0,201	0,438	0,744	0,642	0,166	0,431	0,253	0,533	NA	0,119	0,067
	2018	0,208	0,223	0,064	0,374	0,563	0,072	0,201	0,084	0,306	0,326	0,221	0,509	NA	0,007	0,008
	2019	0,110	0,012	0,283	0,050	0,111	0,142	0,385	0,626	0,571	0,425	0,404	0,866	NA	0,778	0,632
Intercept	**2008**	0,683	0,395	0,501	0,538	0,473	0,636	0,510	0,383	0,517	0,535	0,494	0,515	0,500	0,295	0,401
	2009	0,467	0,462	0,476	0,394	0,445	0,349	0,426	0,436	0,451	0,384	0,441	0,433	0,440	0,321	0,319
	2018	0,368	0,377	0,401	0,473	0,419	0,503	0,470	0,373	0,408	0,459	0,425	0,428	0,417	0,492	0,500
	2019	0,407	0,387	0,238	0,622	0,372	0,683	0,556	0,519	0,261	0,321	0,349	0,495	0,405	0,476	0,492

Table A17: p-value and intercept result from linear regression-testing of all Daphnia *sp. body lengths (mm) against temperature data, in all four study years (2008, 2009, 2018 and 2019).*

		***Daphnia* sp. (total length)**		***daphnia* sp. (carapace length)**	
		Temperatures >8°C	**All temperatures Jul15th - Sep15th**	**Temperatures >8°C**	**All temperatures Jul15th - Sep15th**
p-value	2008	0,669	0,883	0,355	0,797
	2009	0,045	0,668	0,539	0,445
	2018	0,891	0,628	0,929	0,307
	2019	0,104	0,051	0,107	0,12
Intercept	2008	1,098	1,135	0,62	0,548
	2009	1,146	1,115	0,429	0,429
	2018	1,063	1,072	0,483	0,504
	2019	0,859	0,82	0,377	0,375

Table A18: p-value and intercept result from linear regression-testing of all Bosmina *spp. and* Daphnia *sp. body lengths (mm) against temperature data and CPUE of vendace and DR whitefish, independently of the study years.*

		Temperatures > 8°C	**All temperatures**	**CPUE vendace**	**CPUE whitefish**
p-value	*Bosmina* spp.	0,534	0,610	0,988	0,838
	Daphnia sp. (total length)	0,000	0,000	0,889	0,166
	Daphnia sp. (carapace length)	0,000	0,002	0,407	0,784
Intercept	*Bosmina* spp.	0,419	0,422	0,416	0,410
	Daphnia sp. (total length)	0,887	0,891	1,149	1,100
	Daphnia sp. (carapace length)	0,410	0,432	0,512	0,556

Table A19: p-value, df and t-results from two-sample t-tests comparing the lakes (Ruskebukta, Tjærebukta and Skrukkebukta), both in the environment and in the fish stomachs for Bosmina *spp. and* Daphnia *sp. T-tests for* Daphnia *sp. includes both the total body length and the carapace length. In both Tjærebukta and Skrukkebukta in 2018, it was only found one individual of* Daphnia *sp. in the fish stomachs, therefore statistical analyses between these two lakes was not possible in this year.*

		Bosmina spp.				**Daphnia sp. (total length)**				**Daphnia sp. (carapace length)**			
		environment		**stomachs**		**environment**		**stomachs**		**environment**		**stomachs**	
		2018	**2019**	**2018**	**2019**	**2018**	**2019**	**2018**	**2019**	**2018**	**2019**	**2018**	**2019**
p-value	Ruskebukta VS Tjærebukta	0,378	0,085	0,000	0,000	0,000	0,003	0,195	0,140	0,000	0,000	0,740	0,000
	Ruskebukta VS Skrukkebukta	0,837	0,145	0,000	0,000	0,000	0,000	0,335	0,000	0,000	0,000	0,602	0,000
	Tjærebukta VS Skrukkebukta	0,482	0,894	0,036	0,002	0,136	0,000	-	0,000	0,367	0,000	-	0,000
df	Ruskebukta VS Tjærebukta	86	83	50	116	108	101	5	31	108	101	6	31
	Ruskebukta VS Skrukkebukta	87	82	80	179	79	105	5	30	79	105	6	30
	Tjærebukta VS Skrukkebukta	91	83	72	187	53	82	-	41	53	82	-	41
t	Ruskebukta VS Tjærebukta	0,887	-1,746	-5,235	-3,652	-5,539	-3,089	-1,495	-1,516	-7,927	-4,196	-0,348	-5,461
	Ruskebukta VS Skrukkebukta	0,206	-1,471	-5,115	-6,400	-5,081	-17,165	-1,068	-7,317	-4,17	-15,527	-0,551	-7,330
	Tjærebukta VS Skrukkebukta	-0,706	0,134	2,142	-3,071	-1,513	-11,731	-	-8,697	0,911	-9,599	-	-5,539

Table A20: p-value, df and t-results from two-sample t-tests comparing body lengths (mm) of Bosmina *spp. and* Daphnia *sp. in the environment in 2008 with each of the three other study years, in the three lakes investigated.*

		***Bosmina* spp. body length**			***Daphnia* sp. total length**			***Daphnia* sp. carapace length**		
		Ruskebukta	**Tjærebukta**	**Skrukkebukta**	**Ruskebukta**	**Tjærebukta**	**Skrukkebukta**	**Ruskebukta**	**Tjærebukta**	**Skrukkebukta**
p-value	**2008 vs. 2009**	0,172	0,293	0,001	0	0,044	0,001	0	0,001	0
	2008 vs. 2018	0,077	0,756	0,014	0	0,796	0,69	0	0,142	0,006
	2008 vs. 2019	0,008	0,113	0,821	0	0,18	0,024	0	0,021	0,363
df	**2008 vs. 2009**	41	17	48	75	34	32	78	35	32
	2008 vs. 2018	63	51	53	104	42	16	106	43	16
	2008 vs. 2019	63	48	48	99	40	47	101	41	47
t	**2008 vs. 2009**	1,391	1,086	3,506	7,715	2,093	3,514	8,328	3,776	4,575
	2008 vs. 2018	-1,797	0,313	2,538	6,311	0,26	0,406	9,686	1,494	3,168
	2008 vs. 2019	-2,76	-1,617	0,218	8,754	1,366	-2,339	9,186	2,408	-0,919

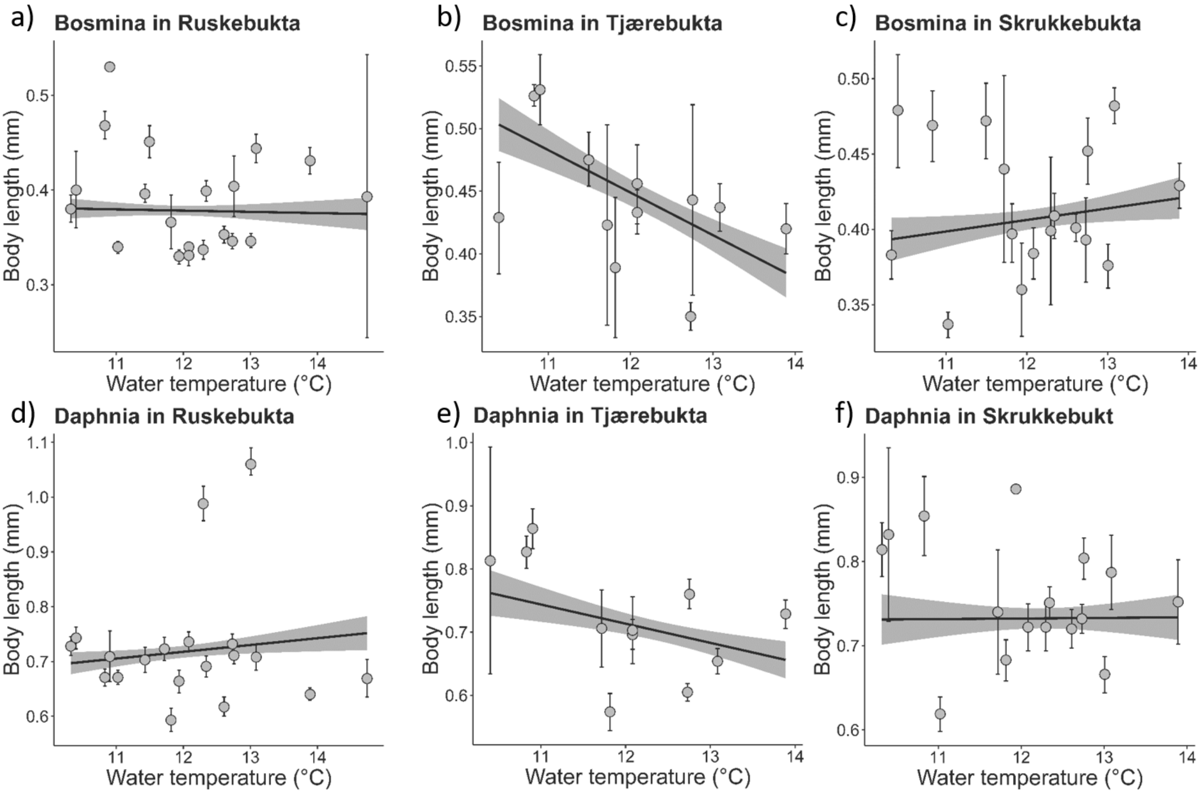

Figure A5: Body length (mm) of Bosmina *spp. in a) Ruskebukta, b) Tjærebukta and c) Skrukkebukta and body length of Daphnia sp. in d) Ruskebukta, e) Tjærebukta and f) Skrukkebukta, dependent on annual mean water temperature (°C) from 1991 to 2019. Grey points represent the mean and the whiskers represents the bootstrapped 95 % confidence interval of the mean, line with shading represents linear regression with standard error.*

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Table A21: Summary results for the linear regression models of mean annual water temperature (°C) and catch per unit effort in the pelagic zone (centered and standardized) on body-length of Bosmina *spp. and* Daphnia *sp. in the lakes Ruskebukta, Tjærebukta and Skrukkebukta from 1991 to 2019.*

Ruskebukta

	Body length Bosmina		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.38	0.38 – 0.38	**<0.001**
Water temperature (summer)	-0.00	-0.01 – 0.00	0.504
CPUEp	0.01	0.01 – 0.02	**<0.001**
Observations	1133		
R^2 / R^2 adjusted	0.028 / 0.026		

	Body length Daphnia		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.72	0.71 – 0.72	**<0.001**
Water temperature (summer)	0.01	0.00 – 0.02	**0.002**
CPUEp	-0.01	-0.02 – -0.00	**0.004**
Observations	907		
R^2 / R^2 adjusted	0.019 / 0.017		

Tjærebukta

	Body length Bosmina		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.44	0.43 – 0.45	**<0.001**
Water temperature (summer)	-0.03	-0.03 – -0.02	**<0.001**
CPUEp	0.01	0.00 – 0.02	**0.041**
Observations	318		
R^2 / R^2 adjusted	0.153 / 0.147		

	Body length Daphnia		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.70	0.69 – 0.71	**<0.001**
Water temperature (summer)	-0.04	-0.05 – -0.03	**<0.001**
CPUEp	-0.03	-0.04 – -0.02	**<0.001**
Observations	310		
R^2 / R^2 adjusted	0.124 / 0.118		

Skrukkebukta

	Body length Bosmina		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.41	0.40 – 0.41	**<0.001**
Water temperature (summer)	0.01	0.00 – 0.01	**0.001**
CPUEp	-0.01	-0.01 – -0.00	**<0.001**
Observations	809		
R^2 / R^2 adjusted	0.025 / 0.023		

	Body length Daphnia		
Predictors	*Estimates*	*CI*	*p*
(Intercept)	0.73	0.72 – 0.74	**<0.001**
Water temperature (summer)	0.00	-0.01 – 0.01	0.463
CPUEp	-0.01	-0.02 – 0.00	0.050
Observations	444		
R^2 / R^2 adjusted	0.009 / 0.004		