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Marius Magnus

Master thesis

Resource-use of crucian carp (*Carassius carassius*) in lakes with different predation risk

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Abstract

Predator fish and prey its prey can have considerable effect on fish communities and can affect the behavior of its prey. stable isotope of carbon (d13C) and nitrogen (d15N can provide as a powerful and useful tool for estimating trophic position, littoral reliance and niche width for food webs in freshwater lakes. Twelve crucian carp lakes were sampled in southeast Norway. Three allopatric lakes with no predators, three lakes with Eurasian perch (*Perca fluviatilis*), three brown trout (*Salmo trutta*) and three with northern pike (*Esox lucius*) as top predators. With fish species richness varying from 1 – 7 fish species. I calculated the trophic position, littoral reliance and examined littoral vs pelagic use, and compared the niche width of crucian carp in the four different regimes. I expect, 1; that crucian carp will shift from pelagic resource use to littoral in lakes with predation, 2; that trophic position will be lower in lakes with predation and 3; the niche of crucian carp will be smaller in a more complex system. Results show that piscivore top predators influence littoral use and trophic position for crucian carp, and that the niche width changes in more complex systems. Thus, I conclude that piscivore top predators have an effect the structure and function of crucian carp communities.

Introduction

The composition and dynamics of food web structure has been a central topic in ecological and evolutionary research for decades (Hairston et al. 1960; Polis et al. 1997; Vadeboncoeur et al. 2002; Odum, 2014; Eloranta et al. 2015), such knowledge is also imperative for management and conservation biology (Polis et al. 1997). Small freshwater lakes and ponds are often the subject of ecological studies of ecosystems in general, and for food web structure in particular (Vadeboncoeur et al. 2002). The reason for this is that small lakes and ponds have relatively clear boundaries to the surroundings. In addition, it is quite "easy" to sample from the whole system within these boundaries (Vadeboncoeur et al. 2002). Food webs are generally complex systems with biological, chemical and physical interactions (Schindler & Scheuerell, 2002). Intraspecific competition is when species compete for the same resources and can lead to reduces fitness (Webster & Hixon (2000), and Interspecific interaction between predator fish and its prey can have considerable effect on the structure of fish communities. Firstly, the predator can affect the abundance of its prey (Weber et al. 2012), and secondly, the behavior of its prey when it comes to foraging and habitat choice (Petterson & Brönmark, 1993; Weber et al. 2012). The predatory strategy is also of importance, where e.g. brown trout (trout; *Salmo trutta*) and Eurasian perch (perch; *Perca fluviatilis*) are mainly pelagic predators (Eklöv & Diehl, 1994; Vander zanden et al. 1999) while northern pike (Pike; *Esox lucius*) is mainly hunting its prey in the vegetation in the littoral zone close to shore(Eklöv & Diehl, 1994) Previous studies has shown that there is a pattern in diel habitat use for fish and zooplankton (Romare et al. 2003; Říha et al. 2015). These two studies showed that planktivorous fish and zooplankton had higher abundance in the littoral zone during day and migrated to the pelagic zone during the night, this behavior is often referred to "night offshore migration". The opposite was seen for the predators in these studies. Pike, perch and pikeperch (*Sander lucioperca*) had higher abundance in the littoral zone during night and were less abundant in the pelagic zone during day, but if there is a lack of prey in the preferred zone, predators can forage in other habitats (Vander zanden et al. 1999). The horizontal diel migration is well documentet in European lakes (Bohl, 1980; Brabran & Faafeng, 1993; Romare et al. 2003; Wolter & Freyhof, 2004). The opposite of night offshore migration is "night inshore migration which has also been documented, but this has been seen mostly in rivers (Kubečka & Duncan, 1998; Erös, 2008) and in some lakes (Schulz & Berg, 1987; Jackobsen et al. 2004). The assumed reason for the migration phenomenon is that the predation-prey interaction is light dependent and such a migration reduces the predation risk (Cerri, 1983).

In addition, the mere presence of a predator, can result in adaptive morphology in the prey (Brönmark & Miner, 1992; Weber et al. 2012). Several fish species such as roach (*Rutilus rutilus*), Perch (Eklöv & Jonsson, 2007), bluegill sunfish (*Lepomis macrochirus*) (Chipps et al. 2004) and Crucian carp (*Carassius carassius*) (Brönmark & Miner, 1992; Vøllestad et al. 2014) can vary in body shape, from a shallow bodied to a deep bodied phenotype apparently as a direct- or indirect response to predation (Brönmark & Miner, 1992; Chipps et al. 2004; Eklöv & Jonsson, 2007; Vøllestad et al. 2014). Typically for the Crucian carp is that the species is often more abundant and use the pelagic habitat more frequently in lakes without predators, on the other hand Crucian carp is often less abundant and live closer to the shore and vegetation in lakes with predator fish present (Holopainen et al. 1997). These predator-prey interactions give rise to the question if predators force the Crucian carp to change its niche, as seen with other fish species (Ingram et al. 2012).

The term "niche" has been used widely in the ecological literature and is described in many different ways, and do not have a standardized definition (Jiménez-Valverde et al. 2011). Grinnellian niche is the sum of the habitat requirements and behaviors that allows a species to live and reproduce itself (Grinnell, 1917; Soberón, 2007). Eltonian niche of a species is the sum of all interactions a species has in its trophic position, meaning the role a species has in a community (Elton, 1927; Leibold, 1995; Layman et al. 2007). Hutchinson niche focused more on the environment, defining that a niche should comprise the resources needed for a species to survive (Hutchinson, 1957; Jackson & Overpeck, 2000). In general, the niche definition is used to describe the environmental requirements of a species on one side, and on the other hand it refers to a place within the environment that has the potential to support a species (Pulliam, 2000). Regardless of this, however, the niche as a concept is often used by ecologists to address and answer research questions related to resource use. Traditionally one has used stomach analyses to assess ecological niche (Bearhop et al. 2004). In this regard, stable isotope analysis is a complementary tool that can be very useful for studies of community structure (Post, 2002; Newsome et al. 2007). Here, niche space (resource and habitat use), is the description of the ecological space that is occupied by a species (Bearhop et al. 2004; Newsome et al. 2007).

In more detail, Isotopes are elements with the same number of protons, but with different number of neutrons. Nature is composed almost entirely of isotopes that are stable. There are 83 elements that have stable isotopes (Lederer, 1980). The main elements of major biological importance are hydrogen, nitrogen, carbon, phosphorus and oxygen. Nitrogen have two stable isotopes: d14N and d15N whereas both have 7 protons but differ with seven and eight neutrons in the nucleus (Schoeller, 1999). Carbon has two stable isotopes, d12C and d13C, both have six protons, but differ with six and seven neutrons (Lederer 1980). Although stable isotopes of carbon and nitrogen have exceedingly similar chemical properties with their elements (C & N), they are not identical, with a difference in mass for the stable isotopes results in a slightly difference in kinetics and bond energy (Schoeller, 1999). Stable nitrogen and carbon isotopes are especially interesting in dietary studies because stable isotope analysis reveals small amounts of dietary patterns, the reason for this is that isotope patterns are passed on through the food chain with some secondary fractionation; e.g bone and tissue are constantly remodeled during life and is built from the compartments obtained from the food that is consumed. Thus, both stable nitrogen (d15N) and stable carbon isotopes (d13C) can be used as ecological tracers to help identify the source of food of the studied organism (Lee-Thorp et al. 1989; Schwarcz & Schoeninger, 1991).

Stable isotopes analysis has become a common tool in addressing both structure and dynamics of ecological communities. Examples on this is Vander Zanden et al. (1997), Post et al (2000) and Post (2003) that used stable nitrogen and carbon isotope to estimate trophic positions on fish in freshwater lakes. Vander Zanden et al. (1999) and Post (2003) that used stable isotopic analyses (hereafter SIA) to study niche shift in largemouth bass. Stable isotopes provide us with continuous and replicable data (given standardization of baseline values of prey sources across study units) that will provide information of food-web links to the top predator (Vander Zanden, 1999; Post et al. 2000; Post, 2003) and this can be done by using the difference expressed in stable isotope ratio measured in nitrogen (d15N) and carbon (d13C) (Post, 2003; Layman et al. 2007).

Studying stable nitrogen isotopes is a good tool to assess trophic positions because nitrogen has an average enrichment of +\- 3,4 % for each trophic level and stable carbon isotope changes approximately with less than 1% for each trophic transfer (Peterson & Fry, 1987; Vander Zanden et al. 1999; Post et al. 2000; Layman et al. 2007). Stable carbon isotope are useful for identifying the source of production for the consumers (Vander Zanden et al. 1999) since the tissue of the consumer is closely linked with their diet (Jackson et al. 2011), and therefore stable carbon isotope can be used to examine the bionomic elements (the study of an organism and it relation to its environment) of a species niche, e.g using stable isotopes values of d13C or d12C to examine a consumers reliance on primary producers between photosynthetic pathways (France, 1995; Post et al. 2000; Elorenta et al. 2015). In this regard littoral areas provide algae, detritus, and benthic macro invertebrates while pelagic provide more plankton, and these organisms can be used to examine the littoral and pelagic reliance of fish by using stable isotopes as a tool (France, 1995; Post et al. 2000; Post, 2003).

The littoral and pelagic production in lakes with regard to primary and secondary production typically depends on trophic status which is the total biomass of different organisms, lake morphometry (the shape or form of a lakes body), watercolor which is an indicator on the input of nutrients, algae growth and water quality (Vadebonceur et al. 2003, 2008; Althouse et al. 2014). The primary production in a lake can be divided into benthic and pelagic primary production. The benthic primary production can be an important source to the animals living in littoral zone and contribute to the total production within the lake (Vadeboncoeur et al. 2001). Previous work using stable isotopes show that littoral production can be the main source of energy for generalist fish species in oligotrophic clear water lakes throughout the year (Elorenta et al. 2013). However, the organisms that inhabit the pelagic habitats include microscopic bacteria, viruses, protozoa, phytoplankton, zooplankton and different life stages of insects beside from fish, but the planktonic organisms are the main inhabitants and is the main source of energy in the pelagic habitats. The difference in horizontal and vertical dimensions in pelagic habitats can be relative different, with the horizontal dimension being relative homogenous and vertical dimension can be substantial heterogeneous with the physical, chemical, and thermal stratification (Schindler & Scheuerell, 2002). Lakes also get nutrient input from fertilizer runoff, litter fall, shore vegetation and watershed from soil (Polis et al. 1997), meaning terrestrial, littoral, and pelagic nutrients play an important role for all consumers within a lake (Vander Zanden et al. 2011). Planktivorous and piscivorous fish can use the resources available in both the littoral and pelagical , thus linking these ecological systems through inter-habitat omnivory (Shindler & Scheuerell, 2002). This habitat linkage by generalist fish top predators has previously been shown to have an impact on the productivity, community, and the structure of the food web (Polis et al. 1997; Rooney & McCann, 2012). Further, littoral and pelagic pathways may also affect species richness within a lake (Barbour & Brown, 1974), and increased fish species may lead to increased competition and predation, which may cause a niche shift by the top predators (Vander Zanden, 1999). Therefore, lake productivity and fish species richness can have a strong and complex influence on functions in an ecosystem and the energy flow pathways (Schindler & Smol, 2006).

The main aim of my study was to investigate different hypothesis on crucian carp about trophic position and niche width and littoral reliance, with regard to lakes with different predation risk from low to high ; (three allopatric lakes and nine sympatric, with the combination of three lakes with Perch as top predator, three with Trout as top predator and finally three with Pike as top predator) in Southeastern Norway. These different predation regimes have been compared with and without predation, to find if there is a difference between the different regimes. Here, stable carbon and nitrogen isotope values were used to define long-term niche use, in terms of littoral reliance and trophic position to calculate trophic niche width of Crucian carp. Further, I examine the littoral and pelagic reliance of Crucian carp to investigate the importance of those two habitats and a principle component analysis was used to determine the productivity in twelve different lakes. I hypothesized that the niche of Crucian carp will be different in lakes with predators than in lakes without predators. Further, I predict that the niche of the Crucian carp was smaller in a more complex system (i.e. in lakes with more species and lakes and higher productivity). In lakes with piscivore predators, I predict that the Crucian carp change from pelagic use to littoral use and that the trophic position of Crucian carp is lower than in lakes without predation duo to refuge from predation and lower d15N values of littoral prey.

Material and methods

Study area and design

The field work was conducted in the southeast of Norway, with a selected total of 12 lakes, consisting of 3 allopatric and 9 sympatric lakes; 3 Crucian carp lakes with no predators, 3 Crucian carp lakes with Perch as top predator, 3 Crucian carp lakes with Trout as top predator, and 3 lakes with Pike as top predator. Lakes varied from forest/swamp, urban and farmland lakes on a gradient from 42-478 meters above sea level. The study lakes varied from low too high in productivity and some lakes consisted only of a littoral zone (0-4 meters), while some had a literal and pelagic zone (> 4 meters). The surroundings were either pine (*Pinus sylvestris*), birch (*Betula spp.*) in the forest and urban areas. In the swamp areas it was peat, grass, birch, and water vegetation were the main characteristics. The urban areas consisted of parks and roads, and the farmland lakes were surrounded by fields. Bugårdsdammen is placed in an urban area. Bjørnmyrdammen, Småvanna and Øvresetertjern are in an intermediate zone close to urban area and forest area. Forkerudstjennet is in an urban/farmland area. Karussputten, Langmyrtjern, Motjennet, Posttjernet and Svartkulp are forest lakes, while Nusttjennet and Stomperudtjernet are located in farmlands (Figure1, Table 3).

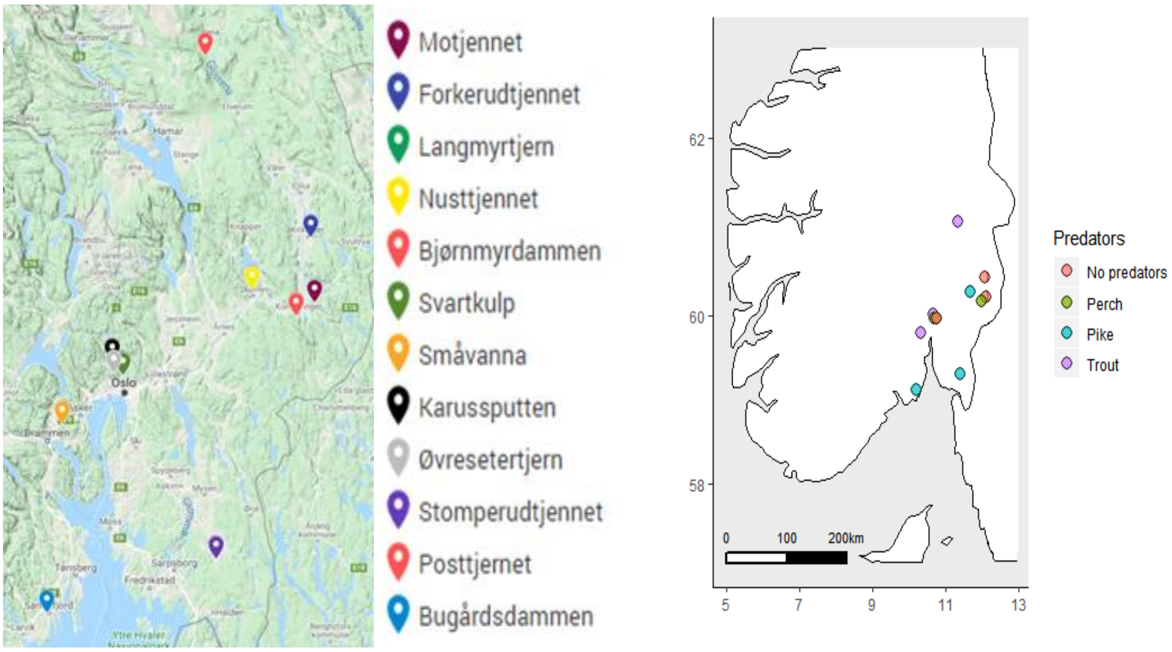

Figure 1. The twelve study lakes from the period 2018 and 2019. The area in focus is southeast Norway. Map to the left shows location and names of the lakes, and the map to the right shows the different piscivores predation regimes.

Data collection

Field work was done in 2018 and 2019 from late May to the end August. Number of fish species caught in each lake varied from 1 – 7 species, with a total of 11 different fish species. Benthic macroinvertebrates (BMI) varied form 3 – 6 groups of different species in each lake, with a total of 10 different BMI species. There were in total 3 different plant types gathered, with 1 – 2 plant species in each lake. Zooplankton varied from 1 – 4 species in each lake, with a total of 6 different groups of species caught. Forkerudtjennet, Langmyrtjern and Motjennet are allopatric lakes, Bjørnmyrdammen, Svartkulp and Øvresetertjern are Perch lakes, Karussputten, Posttjerneet and Småvanna are Trout lakes, Bugårdsdammen, Nustjennet and Stomperudtjernet are pike lakes (Table 2). All fish were sampled from the littoral and pelagic zone with Nordic multi nets (five in each lake) with twelve panels, mesh size from 5 – 55 mm (height of net was 1.5 meters and each panel were 2.5 meters wide) was used to sample the whole lake and each habitat type. Gillnets with small (25mm) and big mesh size (55 mm) was used to increase the chance to get small Crucian carps and predators. Traps were placed in the littoral zone to optimize the chance of getting small Crucian carp in each lake. Number of traps used varied from four to 22 depending on how many times the lake was sampled and how quick we got to targeted minimum of 30 Crucian carp and/or number of small Crucian carps caught. All traps were baited with white bread. Nordic nets and traps were sampled for 1-8 nights depending on how fast we reached the minimum of 30 Crucian carp caught (Table 1). In all lakes, zooplankton was collected with a plankton net with several hauls in the morning in each lake, the plankton net catch was poured into a 1.5L water bottle until it was full, and a sufficient amount was obtained. Benthic macroinvertebrates were caught using a bottom aquatic kick net, plants were sampled by hand. A handheld depth-finder (plastimo echotest 2) were to measure the depth of each lake, depth was measured constantly while rowing in the lake. Temperature and conductivity were measured using a handheld conductivity meter (YSI model 30).

Tabell 1. Fish effort in each of the twelve lakes. Fish effort is shown for Nordic nets.

Lake	Lake type	Fishing effort (#nights)	Top predator
Forkerudstjennet	allopatric	3	No
Langmyrtjern		3	No
Motjennet		2	No
Øvresetertjern	Predator -1	3	Perch
Svartkulp		4	Perch
Bjørnmyrdammen		3	Perch
Karussputten	Pred-2	3	Trout
Småvanna		2	Trout
Posttjernet		3	Trout
Bugårdsdammen	Pred-3	3	Pike
Nusttjennet		8	Pike
Stomperudtjernet		3	Pike

Laboratory methods

Fish caught were measured for total length (cm), body height (cm) (pelvic fin to base of the dorsal fin) and weighed (g). In predator fish the mouth height (mm) and mouth width (mm) were measured. All fish, benthic macro-invertebrates, zooplankton, and plants were identified to species level if possible, if not it got identified to genus level (Table 2). For the stable isotope analysis, a small piece of the dorsal muscle tissue was removed on all fish species, with fish varying from small too big so that the whole range of fish size was represented from each lake. All the samples were stored in -20 degrees Celsius. Altogether the number of fish, zooplankton, plants, benthic macroinvertebrate, and sediment samples analyzed for stable isotopes (SIA) was N=728. In more detail, the total number of tissue samples collected for SIA were; Crucian carp; n=360, piscivore predators; n=151, other fish species; n=76 benthic macroinvertebrates; n=57, plants; n=25, zooplankton; n=34 and sediments; n=25. All samples were dried in a freezer-drier at 40 ° C for > 48 hours and grinded into fine powder. The powder was weighed at 0.5 mg for subsequent SIA. Stable nitrogen and carbon isotope ratios (nitrogen and carbon are expressed as d15N and d13C) were run in an elemental analyzer coupled to a continuous flow isotope ratio mass spectrometer to get stable nitrogen (d15N) and carbon (d13C) (Post et al. 2000; Eloranta et al. 2015). This was done in the Stable Isotopes in Nature Laboratory (SINLAB) in New brunswick, Canada.

Table 2. This shows the different fish, benthic macroinvertebrates, plants and zooplankton species caught and picked in twelve lakes during the field work of summer 2018 and 2019 in South-Eastern Norway.

Lake	Lake type	Fish species caught.	BMI caught	Plants	Zooplankton
Forkerudstjennet	Allopatric	Crucian carp (*Carassius carassius*)	Backswimmers (*Notonectidae sp.*), Mayflies, Chironomids (*Chironomidae sp.*), Damselflies (*Zygoptera sp.*)	Pondweed (*Potamogetonaceae sp.*), Water lily (*Nymphaeaceae sp.*)	Bosminidae, Cladocera
Langmyrtjern	Allopatric	Common minnow (*Phoxinus phoxinus*), Crucian carp (*Carassius carassius*)	Chironomids (*Chironomidae sp.*), Damseflies (*Zygoptera sp.*), Dragonflies (*Anisoptera sp.*)	Pondweed (*Potamogetonaceae sp.*), Water lily (*Nymphaeaceae sp.*)	Daphnia, Cladocera
Motjennet	Allopatric	Crucian carp (*Carassius carassius*)	Chironomids (*Chironomidae sp.*), Damseflies (*Zygoptera sp.*), Dragonflies (*Anisoptera sp.*)	Pondweed (*Potamogetonaceae sp.*), Water lily (*Nymphaeaceae sp.*)	Cladocera, Cyclopoida
Bjørnmyrdammen	Predator - 1	Tench (*Tinca tinca*), Perch (*Perca fluviatilis*), Crucian carp (*Carassius carassius*)	Backswimmers (*Notonectidae sp.*), Caddisflies (Trichoptera sp.), Chironomids (*Chironomidae sp.*), Damselflies (*Zygoptera sp.*)	Pondweed (*Potamogetonaceae sp.*), Water lily (*Nymphaeaceae sp.*)	Bosminidea, Cladocera, Daphnia, Copepods
Svartkulp	Predator - 1	Common minnow (*Phoxinus phoxinus*), Trout (*Salmo trutta*), Perch (*Perca fluviatilis*), Crucian carp (*Carassius carassius*)	Caddisflies (Trichoptera sp.), Damseflies (*Zygoptera sp.*), Mayflies (*Ephemeroptera sp.*), Dragonflies (*Anisoptera sp.*)	Bogbean (*Menyanthes sp.*), Water lily (*Nymphaeaceae sp.*)	Daphnia, Cladocera

Øvresetertjern	Predator - 1	Perch (*Perca fluviatilis*), Trout (*Salmo trutta*), Crucian carp (*Carassius carassius*)	Caddisflies (Trichoptera sp.), Damseflies (*Zygoptera sp.*), Mayflies (*Ephemeroptera sp.*), Water louse (*Asellus aquaticus*)	Water lily (*Nymphaeaceae sp.*)	Daphnia, Calanoida, Copepods
Karussputten	Predator - 2	Trout (*Salmo trutta*), Crucian carp (*Carassius carassius*)	Dragonflies (*Anisoptera sp.*), Caddisflies (Trichoptera sp.), Chironomids (*Chironomidae sp.*), Damflies (*Zygoptera sp.*), Mayflies (*Ephemeroptera sp.*)	Pondweed (*Potamogetonaceae sp.*), Water lily (*Nymphaeaceae sp.*)	Bosminidae, Cladocera
Posttjernet	Predator - 2	Trout (*Salmo trutta*), Common minnow (*Phoxinus phoxinus*), Crucia carp (*Carassius carassius*)	Chironomids (*Chironomidae sp.*), Damselflies (*Zygoptera sp.*), Dragonflies (*Anisoptera sp.*), Mayflies (*Ephemeroptera sp.*), Oligochaetes sp.	Pondweed (*Potamogetonaceae sp.*), Water lily (*Nymphaeaceae sp.*)	Daphnia, Bosminidae, Cladocera, Calanoida
Småvanna	Predator - 2	Trout (*Salmo trutta*), Common minnow (*Phoxinus phoxinus*), Crucian carp (*Carassius carassius*)	Chironomids (*Chironomidae sp.*), Damseflies (*Zygoptera sp.*), Dragonflies (*Anisoptera sp.*), Mayflies (*Ephemeroptera sp.*), Oligochaetes sp., Snail (*Mollusca sp.*)	Bogbean (*Menyanthes sp.*), Water lily (*Nymphaeaceae sp.*)	Bosminidae, Calanoida
Bugårdsdammen	Predator 3	Perch (*Perca fluviatilis*), Pike (*Esox Lucius*), Crucian carp (*Carassius carassius*)	Backswimmers (*Notonectidae sp.*), Caddisflies (Trichoptera sp.), Chironomids (*Chironomidae sp.*), Diving beetle (*Dytiscidae* sp.), Snail (*Mollusca sp.*)	Bogbean (*Menyanthes sp.*), Pondweed (*Potamogetonaceae sp.*)	Daphnia, Cladocera, Cyclopoida, Calanoida
Nusttjennet	Predator 3	Common bream (*Abramis brama*), Common roach (*Rutilus rutilus*), Alburnus	Backswimmers (*Notonectidae sp.*), Damseflies (*Zygoptera sp.*), Diving	Pondweed (*Potamogetonaceae*	Daphnia, Cladocera, Cyclopoida

		sp., Perch (*Perca fluviatilis*), Pike (*Esox Lucius*), Crucian carp (*Carassius carassius*)	beetle (*Dytiscidae* sp.), Dragonflies (*Anisoptera sp.*), Oligochaetes sp.	*sp.*), Water lily (*Nymphaeaceae sp.*)	
Stompertudtjernet	Predator 3	Alburnus sp., Common bream (*Abramis brama*), Common roach (*Rutilus rutilus*), Common rudd (*Scardinius erythrophthalmus*), Perch (*Perca fluviatilis*), Pike (*Esox Lucius*), Crucian carp (*Carassius carassius*)	Chironomids (*Chironomidae sp.*), Damseflies (*Zygoptera sp.*), Caddisflies (Trichoptera sp.), Snail (*Mollusca sp.*), Water louse (*Asellus aquaticus*)	Algae, Water lily (*Nymphaeaceae sp.*)	Bosminidae, Cladocera, Cyclopoida

Environmental measurements

Different variables were used in the environmental measurements; mean air temperature (°C) and were calculated from 2010 – 2019 (June – September), weather data is available on yr.no. Lake area (km^2) was obtained from norgeskart.no for each lake. Max depth (m) was measured in the field in each lake using a handheld depth-finder. Altitude (meters above sea level) was obtained from public information on each lake. Secchi depth (m) is measured depth with a 20 cm diameter white disk. Water clarity by using the Forel-Ule scale index, this is a method to approximately determine the color of the water bodies. Littoral area of the lakes (%) from 0 – 100%, whereas 0% is no littoral area in a lake, and 100% is that a lake only have littoral areas, and this was estimated from field measurements in each lake, using a handheld depth-finder with littoral area being down to 3 meters. Emergent plants were measured using maps of the lakes and a line was drawn around the areas where there were plants. This gave us a coverage of emergent plants in percentage within the lake. Specific conductivity obtained from measured conductivity in the lakes. Specific conductivity was calculated with the following formula; measured 7conductivity/1+0.2*measured temperature in the lakes**.** Land use on a scale from 1 -3. Land use is based on where the lakes are geographically and the impact from the surrounding area around the lake. Forest lakes have 1 because it has little impact from human use and farmland lakes have 3 due to high level of impact from human use. Number of species is amount of fish species caught in each lake. Total nitrates (µg/l) and total phosphates (µg/l) was measured from water samples taken from each lake. Some of the variables describing the environment of the lakes are strongly correlated and because of this it is useful to use a linear combination to sum up the information these variables provide. Thus, a principal component analysis (PCA) was used to determine characteristics and productivity of the study lakes. Environmental measurements and principal component analysis are based on the method used by Hayden et al (2017).

Statistical analyses

In Motjennet there was an error in the isotope values for zooplankton. The isotope values for the littoral and pelagic baselines were very close, and it was not possible to distinguish them were, and because of that the values were not valid (the error could derive from sampling of zooplankton in Motjennet). Thus, isotope values for zooplankton from Posttjernet was used. This lake was chosen due to its similarity from the principle component analysis (PC1).

A mixed model was used to calculate littoral reliance from the baseline values extract from stable isotope analysis in R. With the following formula; Littoral reliance = (d13Ccorr – d13Cpel) / (d13Clit – d13Cpel). Whereas d13Ccorr is the corrected values of d13C of Crucian carp. The reason for correcting these values are due to make sure that the d13C values are not affected by lipids (Post et al. 2000; Eloranta et al. 2015). d13Cpel is the carbon values of zooplankton and d13Clit is the values of benthic macroinvertebrates (Vander Zanden et al. 2011) Littoral reliance was used to calculate the reliance of all organisms (± SD). Niche width of Crucian carp was measured by using the trophic position of Crucian carp and littoral reliance values as coordinates for the isotopic niche. A Bayesian ellipse of SIBER was added with a confidence ellipse of 95%. The niche width then is determined by the resource use (littoral vs pelagic use) of Crucian carp (Layman et al. 2007).

Further on Trophic position was calculated with following formula; Trophic position = TP of baseline 1 + (d15N of consumer - (d15N of base * contribution of littoral reliance + d15N littoral values * (1 – littoral reliance))) / fractionation of d15N (Post et al. 2000; Post 2002),and was used to calculate the trophic position all organisms (± SD).

Catch per unit effort (CPUE) was calculated with the following formula: (CPUE = ind/N/h) where ind is the number of fish caught, N is number of Nordic multi nets (with a minimum of five nets for each lake) and h are the number of hours the Nordic nets were in the water (Appelman, 2015). In the final model, both the CPUE values of Crucian carp and predators were used.

Finally, several linear mixed models with random effect. The twelve study lakes were used as random effect, with random effect being: random intercept. Choosing random intercept on lakes, takes account for the different variance in each lake. The linear mixed models were compered to find the best models to explain Littoral reliance and trophic position. A model selection was used based on Akaike`s Information Criterion (AIC) and removal of none significant variables. An ANOVA-test was used to compare models to check if the decrease was significant (Table 6, 7). Model assumptions was checked with residuals vs fitted was checked and criteria were meet.

- The final model for that best explained littoral reliance was: Littoral reliance was: littrel ~ cpue_pred + PC1 + PC2 + max_mouth (Table 6).

Whereas littrel is the littoral reliance of crucian carp, cpue_pred is the catch per effort unit of predators, PC1 and PC2 is the environmental variables and max_mouth is the maximum mouth size of the predator fish in each lake

- The final model that best explained trophic position was: trophicposition ~ total length (Table 7).

Whereas trophicposition is the trophic position of crucian carp, total_length is the total length of crucian carp, which is an indicator of the size.

All analysis was conducted in R statistical computing package: version 3.6.2 (R development core team, 2019). Package ggplot2 was used for the output of graphs and plots. Package GGally was used to check homogeneity and variance of the data and correlation between variables. Further, Reshape2and plyr were used to transform and split data, and SIBER was used to compare communities and groups of the different study lakes. Further lmertest was used to get p-values when choosing a final model to explain littoral reliance and trophic position. A mixed model was used to estimate the relative contribution of resource use to the diet of all species. The model takes into account the mean of the baselines (raw isotopic values of littoral vs pelagic resources) to standardize consumers values in isotopic space (Post, 2000)

Results

This table shows the variables used in the PCA. All variables except Lake type, Predation, Latitude, Longitude and LandUse(type) that was not used. These variables are in the table to better understand location and which type of lake the different study lakes are (Table 2, Figure 3). PC1 and PC2 are the results of the different variables used in the PCA to explain productivity in the lakes with a negative number representing lower productivity and a positive number means higher productivity. The first two axes of the PCA of lake environment and characteristics explained 63% of the variation in the dataset Table 3, Figure 2). PC1 explained 48.3% of the variation, was inversely related to land use, littoral area and number of species. The most productive lakes are farmland lakes (highest positive number), and the least productive lakes are forest lakes. While PC2 explained 14.7% (Table 3).

Table 3. Lake characteristics of the 12 study lakes. Measured variables are Area (km2), max depth (m), altitude (meters above sea level), seechi disc depth (m) Water clarity (FU), Littoral area (%), emergent plants (%), specific conductivity, air temperature (°C) Land use (LU) and number of species, TotN is total nitrates and TotP is total phosphates. Positive PC values indicate productive lakes, higher (positive) number means more productive lake and negative values indicate lakes that are less productive. Latitude, Longitude, type of land use and predation were not included in the principal component analysis.

			Predation	Lat	Long	Area	MaxDepth	Altitude	SecchiD	FU	LittoralArea	EmergentPlants	SpecCond	AirTemp	LU	LandUse	NumberSpecies	TotN (µg/l)	TotP (µg/l)	PC1	PC2
No.	Lake	Lake type	(species)	(°N)	(°E)	(km2)	(m)	(m a.s.l)	(m)	(Forel ule scale)	(%)	(%)		(°C)	(1-3	(Type)	(1-7)			(48,3%)	(14,7%)
1	Forkerudstjennet	Allopatric	None	60.453	12.078	0.0124	2.2	152.4	0.45	17.5	100	30	82.74	14.56	1.5	Farmland/Urban	1	1985	82	1.3801087	-0.6470256
2	Langmyrtjern	Allopatric	None	59.974	10.747	0.003	5	206	1	19	70	28	54.32	15.69	1	Forest	2	702	20	-1.124997	-0.0149534
3	Motjennet	Allopatric	None	60.228	12.105	0.0094	11.3	166.5	3	20	41	36	11.37	14.29	1	Forest	1	688	23	-2.8999997	1.15629657
4	Bjørnmyrdammen	Predator - 1	Perch	60.182	11.977	0.021	3.5	256	0.4	21	80	63	24.93	14.84	1.5	Forest/Urban	3	672	26	0.1266831	1.09004537
5	Svartkulp	Predator - 1	Perch	59.976	10.739	0.058	10	202	1.2	19	66	16	30.07	15.69	1	Forest	4	550	13	-1.3190931	1.3565619
6	Øvresetertjern	Predator - 1	Perch	59.983	10.672	0.0305	3.5	478	1.7	17	84	14	109.1	14.83	1.5	Forest/Urban	3	446	13	-1.0236521	-1.4349937
7	Karussputten	Predator - 2	Trout	60.023	10.662	0.0025	4.6	356	2	15	53	40	178	13.16	1	Forest	2	361	9	-1.435989	-2.4717068
8	Posttjernet	Predator - 2	Trout	61.076	11.329	0.0172	11	270.8	2.5	19	26	15	24.29	12.95	1	Forest	3	312	8	-3.2363899	0.82779888
9	Småvanna	Predator - 2	Trout	59.802	10.309	0.005	3.8	222.3	1.8	21	70	35	114.61	15.24	1.5	Forest/Urban	3	616	14	-0.856809	-0.1752556
10	Bugårdsdammen	Predator - 3	Pike	59.131	10.195	0.0504	2	42	1.5	14	100	27	129.42	15.48	2	Urban	3	980	54	1.6465566	-1.1416167
11	Nusttjennet	Predator - 3	Pike	60.277	11.661	0.11	1.5	131	0.4	19	100	55	49.6	14.35	3	Farmland	6	1090	164	4.0010348	2.19628017
12	Stomperudtjernet	Predator - 3	Pike	59.324	11.404	0.0375	1.5	103.4	0.4	15	100	70	185.98	14.22	3	Farmland	7	1660	146	4.7425465	-0.7414312

In the principal analyses of all the environmental values PC1 explained 48.3% of the variance. Here, PC1 most correlated with LU (0.37), Littoral area (0.35), number of species (0.28), TotN (0.29) and TotP (0.36) (to the right side of figure 2). To the other direction (to the left side of figure 2) it is secchi depth (- 0.31) and max depth (- 0.31). The variables LU, Littoral area, and number of species for PC1 gets higher positive values and are associated with productivity and with secchi depth and max depth PC1 get lower negative values and are associated with lower productivity. PC2 which explained 14.7% of the variance, was most correlated with SpecCond (0.60) (to the right side of figure 2), and is associated with productivity, to the other direction (the left side of figure 2) it is Forel-ule (- 0.53) and AirTemp (- 0.31) and is associated with lower productivity. PC2 get higher positive values SpecCon and with Forel-ule and AirTemp PC2 gets lower negative values. PC1 and PC2 in the table on the left-hand side show how much each of the variables used in the PCA weighed for each of the PC1 and PC2.

	PC1	PC2
Area	0.24139	0.35233
MaxDepth	-0.31987	-0.21642
Altitude	-0.21622	0.25824
SecchiD	-0.31686	0.14800
FU	-0.15553	-0.53763
LittoralArea	0.35225	0.00557
EmergentPlants	0.26214	-0.01768
SpecCond	0.17276	0.60893
AirTemp	0.06795	-0.31733
LU	0.37278	-0.01653
NumberSpecies	0.28212	-0.07959
TotN..µg.l.	0.29907	0.00011
TotP..µg.l.	0.36445	-0.08216

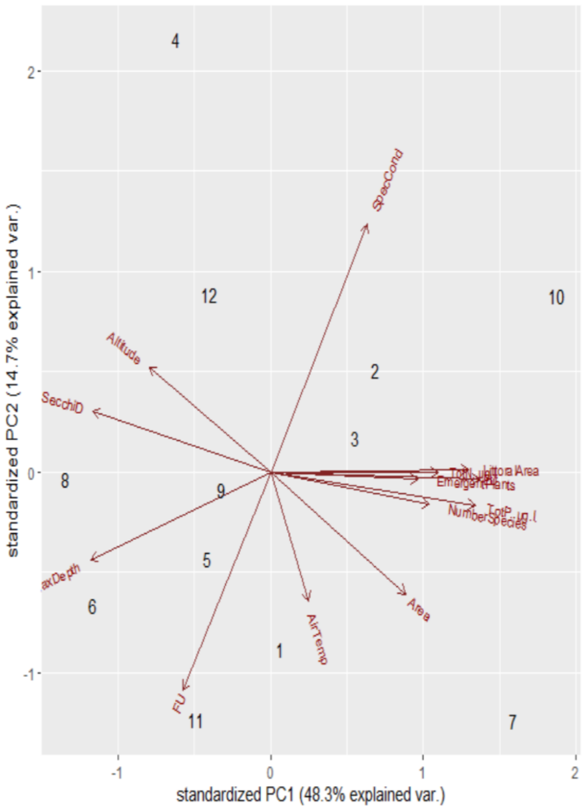

Figure 2. Results of principle components analysis with PC1(48,3%) and PC2 (14,7%). Table on the left shows the pc values from the analysis. Variables with negative numbers are associated little productivity and variables with positive numbers is associated with higher productivity for the lakes. Figure on the right shows variables as a plot and the numbers 1 -12 is the twelve study lakes (Lake number and lake names can be seen in table 2). Lakes to the right in the plot are lakes with higher productivity and lakes on the left are less productive. Lake information and values can be seen in table 1.

The stable isotope values varied between lakes and organisms (Figure 3). Here, the mean d13C and d15N values for the whole system (minus plants and sediments) was as follows, with the first line for allopatric lakes (no predators, second line is Perch lakes, third line is the Trout lakes, and the last line is the Pike lakes.

Forkerudstjennet d13C = - 31.8 ± SD 2.3 and d15N = 8.4 ± SD: 3.1, Langmyrtjern d13C = - 33.5 ± SD: 2.6 and d15N = 3.7 ± SD: 2.3, Motjennet d13C = - 32.3 ± SD: 2.5 and d15N = 3.7 ± SD: 3.8.

Bjørnmyrdammen d13C = - 31.8 ± SD: 1.9 and d15N = 5.2 ± SD: 2.0, Svartkulp d13C = - 32.1 ± SD: 1.9 and d15N = 5.2 ± SD: 2.4, Øvresetertjern d13C = 27.9 ± SD: 1.1 and d15N = 6.8 ± SD 2.5.

Karussputten d13C = 33.2 ± SD: 2.9 and d15 = 2.9 ± SD: 2.7, Posttjernet d13C = - 33.7 ± SD: 2.2 and d15N = 5.5 ± SD: 2.3, Småvanna d13C = - 35.0 ± SD: 3.0 and d15N = 7.7 ± SD: 2.9.

Bugårdsdammen d13C = - 29.6 ± SD: 1.7 and d15N = 8.5 ± SD: 1.9, Nusttjennet d13C = -32.0 ± SD: 2.2 and d15N = 9.7 ± SD: 2.7, Stomperudtjernet d13C = - 31.6 ± SD: 1.5 and d15N = 12.9 ± SD: 2.1.

Figure 3. Raw stable isotope signatures (d13C and d15N) of the whole ecosystem (minus sediments and plants) for the twelve study lakes for the two summer periods 2018 and 2019. Crucian carp is green triangles, blue triangles is piscivore predators (pisc) and yellow triangles is other herbivore fish (con). Each triangle is a single fish. Zooplankton(ZPL) is Pink squares and benthic macro invertebrates (BMI) are red circles. The study lakes are in order of the predation regimes, first row is allopatric lakes, row two is Perch lakes, row three Trout lakes and row for is the Pike lakes. Carbon values show open water vs near shore. Open water is the most negativ (to the left) and near shore is the least negative (to the right).

The estimated trophic position of the crucian carp varied somehow among all the 12 lakes. The mean trophic position varied in the different lakes, and trophic position varied among the population within a lake (Figure 4) Here, the mean trophic position of Crucian carp is as follows, with the first line for allopatric lakes (no predators), second line is Perch lakes, third line is the Trout lakes, and the last line is the Pike lakes.

The value mean trophic position and Standard deviation shows that the expected value (the mean) is close to the mean of Crucian carp. I.e. the standard deviation (SD) as a number tells us how the measurement of a group is spread out from the mean (the expected value) With a low SD it tells that most of the numbers are close to the mean(in this case, Crucian carp as a group is close to the mean trophic position of Crucian carp).

Forkerudstjennet = 2.0 ± SD: 0.4, Langmyrtjern = 1.8 ± SD: 0.3, and Motjennet = 2.1 ± SD: 0.2.

Bjørnmyrdammen = 2.2 ± SE: 0.1, Svartkulp = 1.9 ± SD: 0.1, and Øvresetertjern = 2.1 ± SD: 0.2.

Karussputten = 1.6 ± SD: 0.1, Posttjernet = 2.2 ± SD: 0.1, Småvanna = 2.1 ± SD: 0.3.

Bugårdsdammen = 1.9 ± SD: 0.2, Nusttjennet = 1.4 ± SD: 0.1, and Stomperudtjernet = 2.1 ± SD: 0.4.

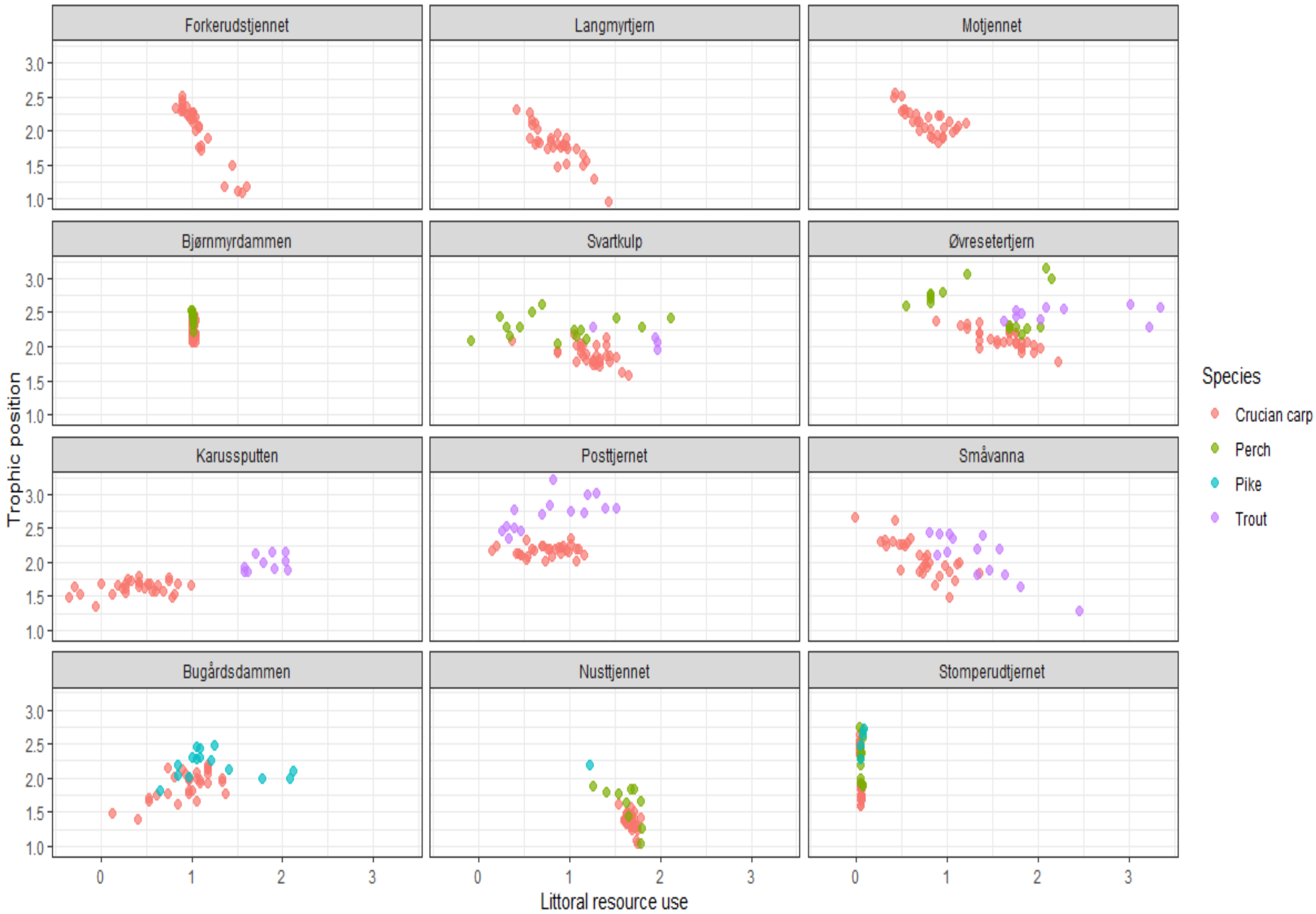

Figure 4. Stable isotope analysis of the organization of the 4 species (Crucian carp, Pike, Perch and Trout) in their trophic position vs littoral reliance. Littoral reliance is the proportion of carbon that comes from the littoral zone. If littoral reliance is between 0 - 1 it means that the fish population is foraging in the littoral zone, 1 – 2 mean that the population is using both littoral and pelagic and if the value is 2 - 3 it means the population is foraging in the littoral zone. Each dot is an individual fish in the twelve study lakes and the study lakes are in order of the predation regimes, first row is allopatric lakes, row two is Perch lakes, row three Trout lakes and row for is the Pike lakes.

With regards to trophic position for Crucian carp in the different lakes. I found that trophic position of Crucian carp is higher in less productive lakes and that the trophic position decreases in more productive lakes (Figure 5). With the results of a linear model, I found a negative correlation between trophic position and PC1 values of Crucian carp in the twelve study lakes ($F_{1,358}$ = 23.79, p= <0.001, intercept ± SE: 1.953005 ± 0.016870, slope ± SE: - 0.038466 ± 0.007886, R^2 = 0.0623). PC1 explained 6% of the variance of trophic position of Crucian carp. In more productive lakes Crucian carp has lower trophic position.

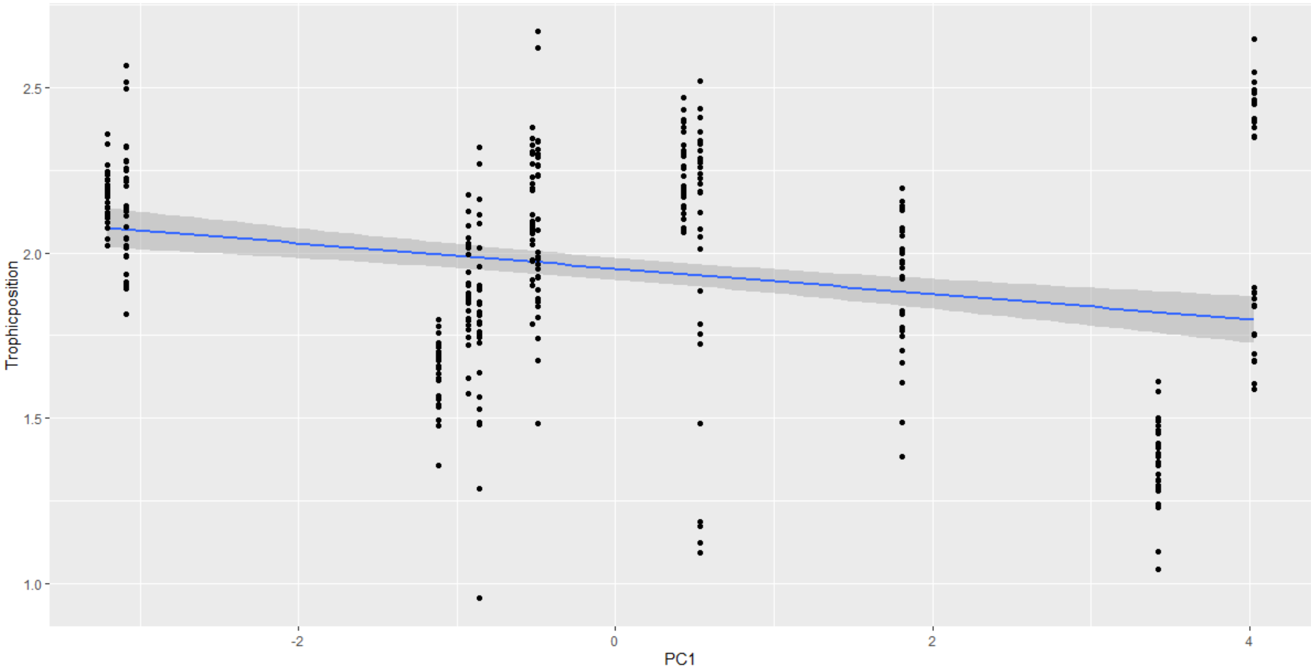

Figure 5. Trophic position of Crucian carp vs environmental variables (PC1) in the twelve study lakes. 95% confident interval is shown as dark grey around the line. Plot is showing that Crucian carp has a lower trophic position with in more productive lakes.

The isotopic width varied among the lakes. More complex lakes (number of species) had smaller niche width and total area (TA) of the niche was smaller (Figure 6, 7, Table 4). Bjørnmyrdammen had a TA of 0.01409, Nusttjennet; 0.06534 and Stomperudtjernet had a TA of 0.0380. Nusttjennet and Stopmperudtjernet were both Pike lakes and were the most complex lakes, with most fish species (Table 2), also the most productive lakes (Table 3). Bjørnmyrdammen was the fifth most productive lake, with 3 different fish species. In all three lakes there were intraspecific competition for the same resources.

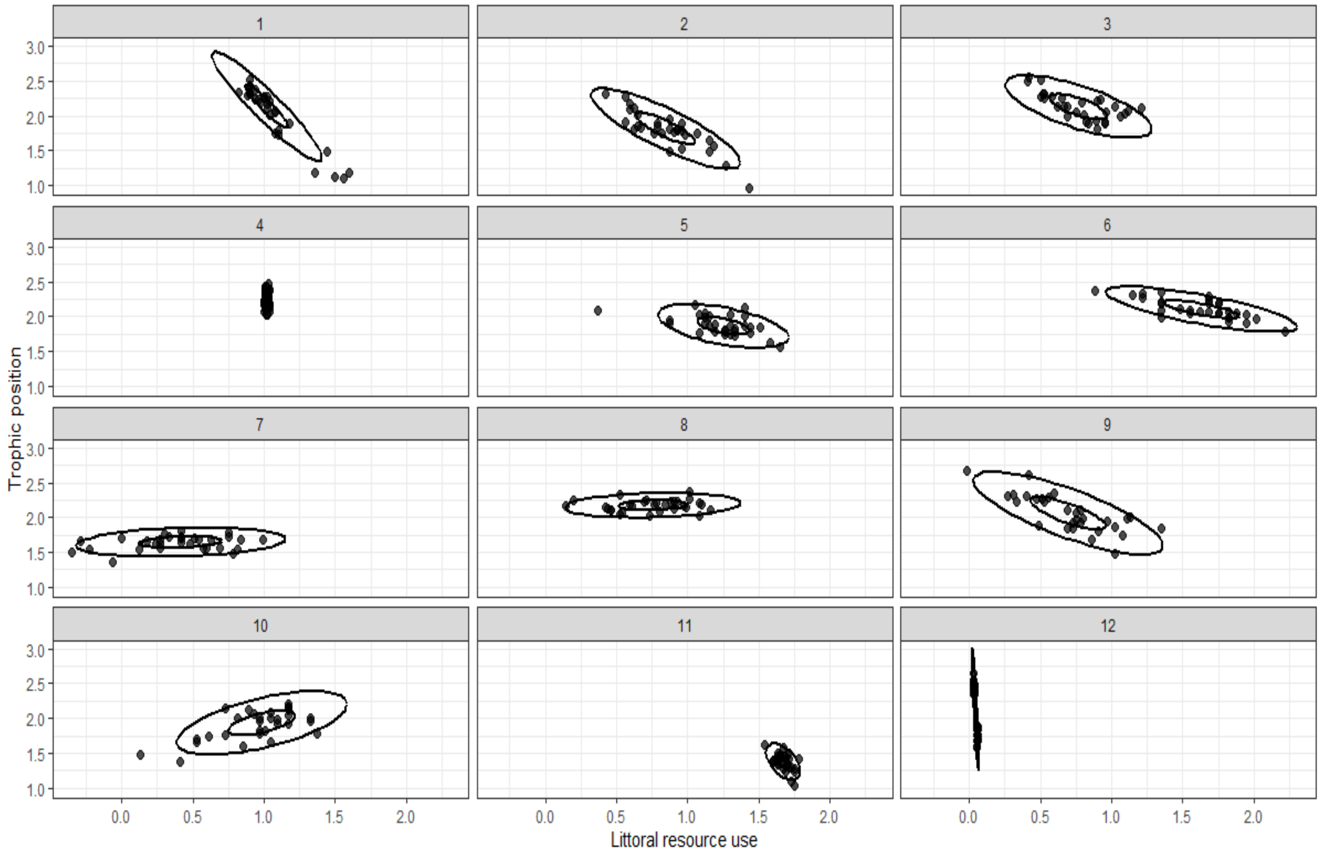

Figure 6. Isotopic niche width plot for Crucian carp (black dots). Confidence of ellipse is shown as 95%. Study lakes are in order of the predation regimes, first row is allopatric lakes, row two is Perch lakes, row three Trout lakes and row for is the Pike lakes. Littoral resource use is the proportion of carbon that comes from the littoral zone. If littoral reliance is 0 -1 it means that the fish population is feeding in the littoral zone, 1 – 2 mean that the crucian carp is using both littoral and pelagic areas and if the value is 2 – 3 it means the population is foraging in the pelagic. Each dot is an individual fish in the twelve study lakes.

This is the result of a Bayesian SIBER ellipse (Table 4, Figure 6, 7)This function loops over the Crucian carp within each community and calculates the convex hull total area, Standard Ellipse Area (SEA) and its corresponding small sample size corrected version SEAc based on the maximum likelihood estimates of the means and covariance matrices of each group.

Table 4 Result of a Bayesian SIEBER ellipse (95%) of TA is the total area of the ellipse in figure 1.

	Forkerudstjennet	Langmyrtjern	Motjennet	Lake type	Predator
TA	0.27313	0.35216	0.24395	Allopatric	None
SEA	0.08467	0.10500	0.09611	Allopatric	None
SEAc	0.08770	0.10875	0.09954	Allopatric	None
	Bjørnmyrdammen	Svartkulp	Øvresetertjern		
TA	0.01409	0.34230	0.32014	Predator - 1	Perch
SEA	0.00483	0.09345	0.08815	Predator - 1	Perch
SEAc	0.00500	0.09679	0.09130	Predator - 1	Perch
	Karussputten	Posttjernet	Småvanna		
TA	0.38689	0.24919	0.63270	Predator - 2	Trout
SEA	0.10071	0.06836	0.16051	Predator - 2	Trout
SEAc	0.10430	0.07081	0.16624	Predator - 2	Trout
	Bugårdsdammen	Nusttjennet	Stomperudtjernet		
TA	0.53641	0.06534	0.01380	Predator - 3	Pike
SEA	0.14604	0.01776	0.00595	Predator - 3	Pike
SEAc	0.15126	0.01839	0.00617	Predator - 3	Pike

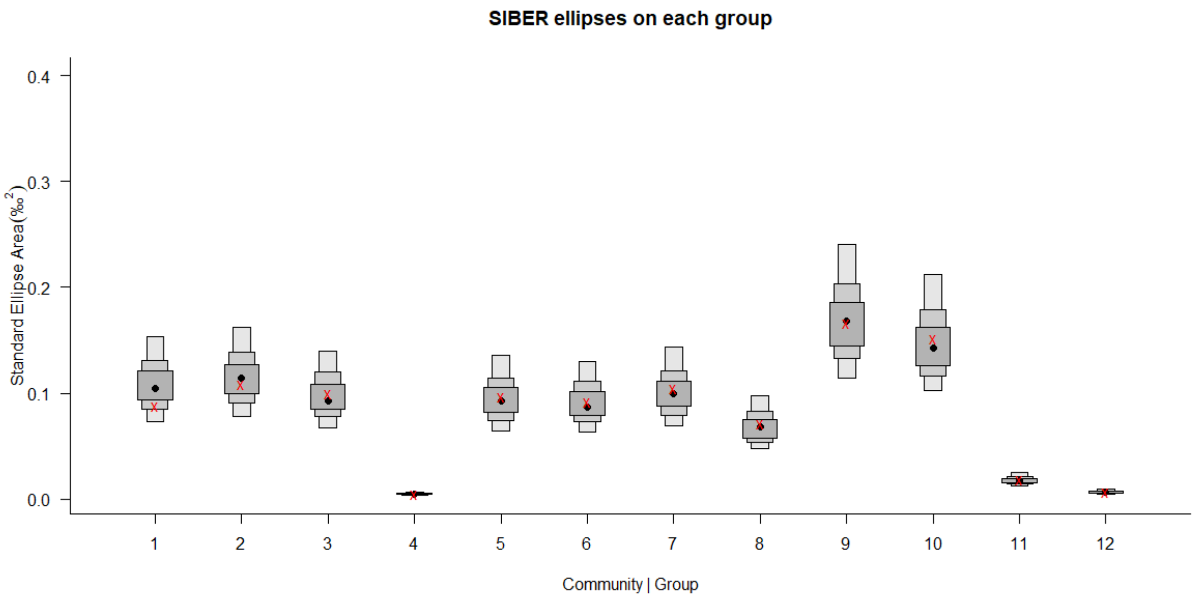

Figure 7. Bayesian SIBER ellipse plot showing the confidence intervals of the standars ellipse area of the core of the isotophic niche for crucian carp between the twelve study lakes. The black dots are showing the mean standard ellipse area for each group. Red crosses represent their mode. Boxes represent 95, 75 and 50 % confidence intervals from dark to light grey. Lakes are in the different predation regimes. The three first are the allopatric lakes without piscavore predators, 4,5 and 6 are the Perch lakes, 7,8 and 9 are the Trout lakes, and 10,11 and 12 are the three Pike lakes.

With regard to Total area (of the convex hull) and environmental variables (PC1). The total area of the niche width for crucian carp become smaller with higher lake productivity. With the result from a linear model, I found a negative correlation between total area of the niche width for crucian carp with higher productivity in the twelve study lakes ($F_{1,358}$ = 75.74, p= <0.001, intercept ± SE: 0.285842 ± 0.008786, slope ± SE: -0.031920 ± 0.003668, R^2 = 0.1746). This result indicates that the width of the niche for crucian carp is smaller with higher predation risk and in more complex systems. (Figure 8).

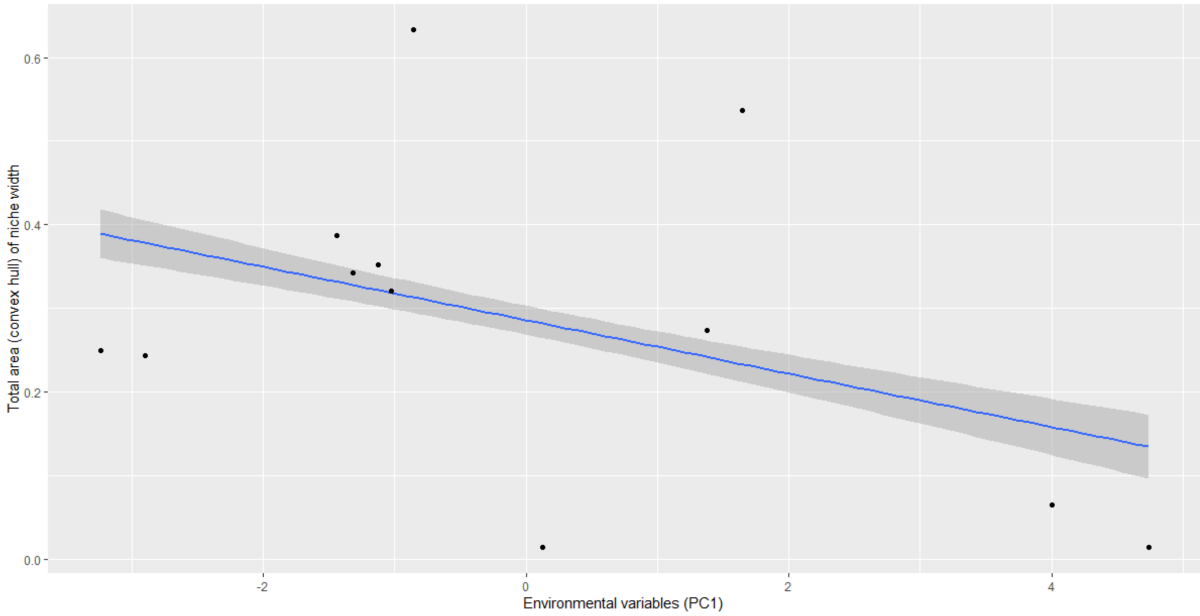

Figure 8. Shows the correlation between Total area (the convex hull) of the niche width for crucian carp and environmental variables (PC1) for the twelve study lakes. The total area of the niche is smaller in more productive lakes.

With regard to standard ellipse (SEA) and environmental variables (PC1). SEA of the niche width for crucian carp become smaller with higher lake productivity. With the result from a linear model, I found a negative correlation between total area of the niche width for crucian carp with higher productivity in the twelve study lakes ($F_{1,358}$ = 105.2, p= <0.001, intercept ± SE: 0.0809617 ± 0.0022266, slope ± SE: -0.0095334 ± 0.0009295, R^2 = 0.2271). This result indicates that the width of the niche for crucian carp is smaller with higher predation risk and in more complex systems. (Figure 9).

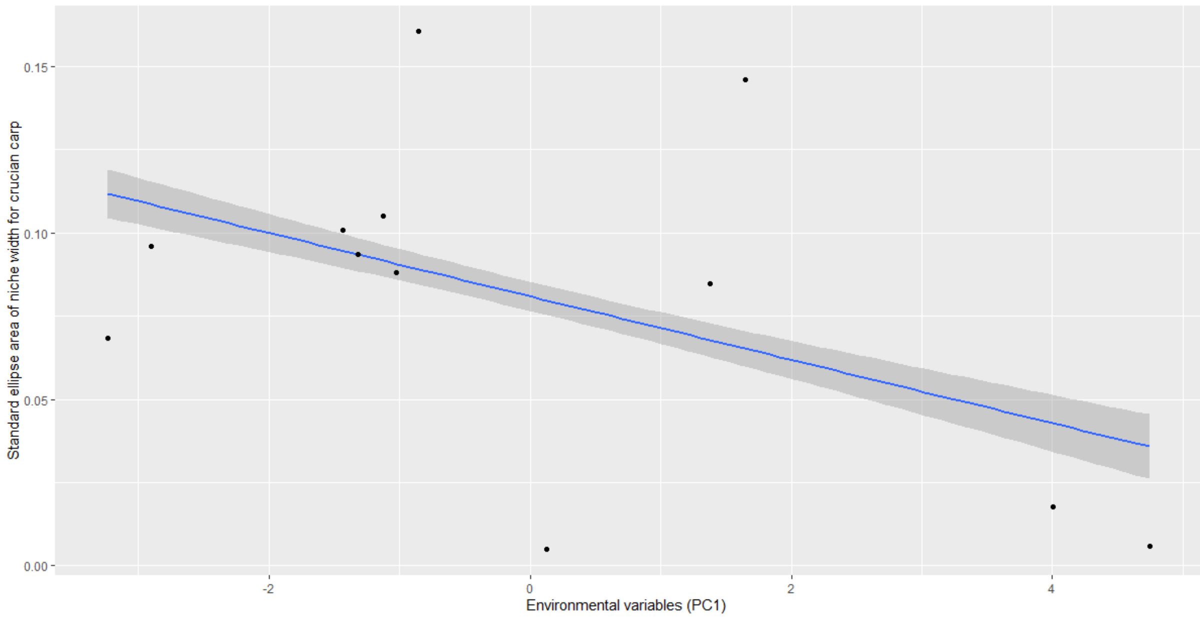

Figure 9. Shows the correlation between Standard ellipse area of the niche width for crucian carp and environmental variables (PC1) for the twelve study lakes. Standard ellipse area is smaller in lakes with higher productivity.

With regard to littoral reliance variance, bigger Sized Crucian carps used littoral habitat or areas closer to the littoral zone. Smaller sized Crucian carp used more the pelagic area (Figure 10). With the result from a linear model, I found a positive correlation between littoral reliance and size of Crucian carp in the twelve study lakes ($F_{1,358}$ = 70.58, p= <0.001, intercept ± SE: 0.462949 ± 0.059647, slope ± SE: 0.023578 ± 0.002806, R^2 = 0.1647).

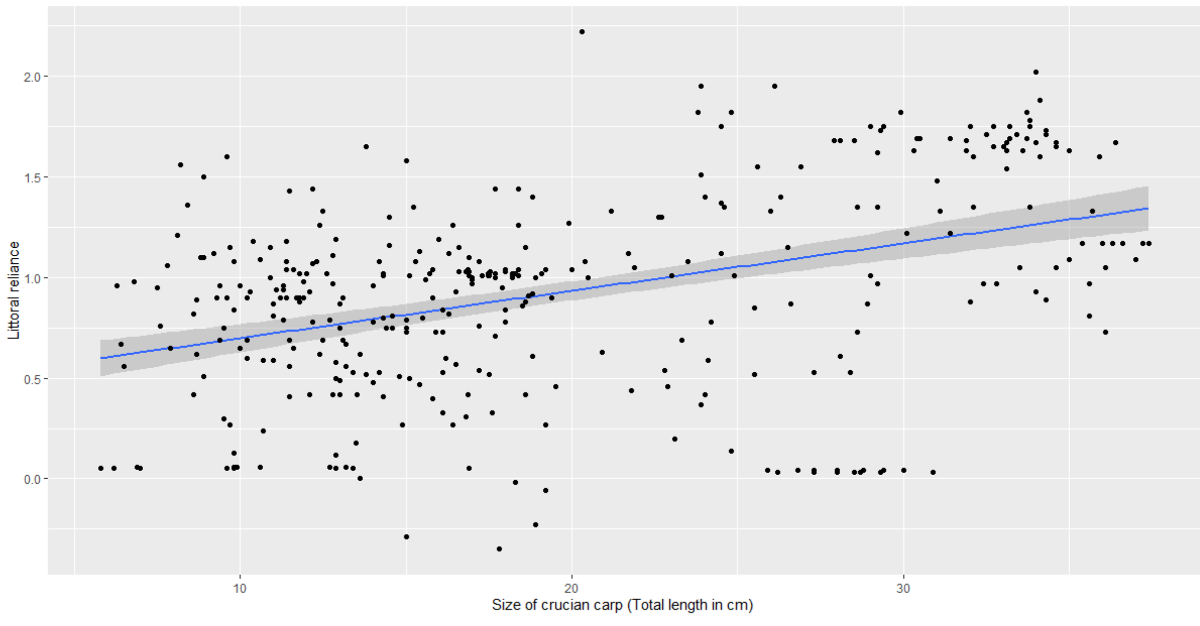

Figure 10. Relationship between littoral reliance and size of Crucian carp (total length in cm) in the twelve study lakes. 95% confindent interval is shown as dark grey around the line. Plot is showing that Crucian carp that is larger in size use littoral habitats while small sized Crucian carp use pelagic habitats.

This is a result from a linear model testing the d15N values vs the lake productivity. The results show that there is an enrichment in d15N in lakes with higher productivity. With the results from a linear model I found a positive correlation between mean d15N and PC1 from the environmental variables ($F_{1,358}$ = 639.3, p= <0.001, intercept ± SE: 7.46755 ± 0.09044, slope ± SE: 1.06897 ± 0.04228, R^2 = 0.641). There is an enrichment in nitrogen with higher productivity (Figure 11).

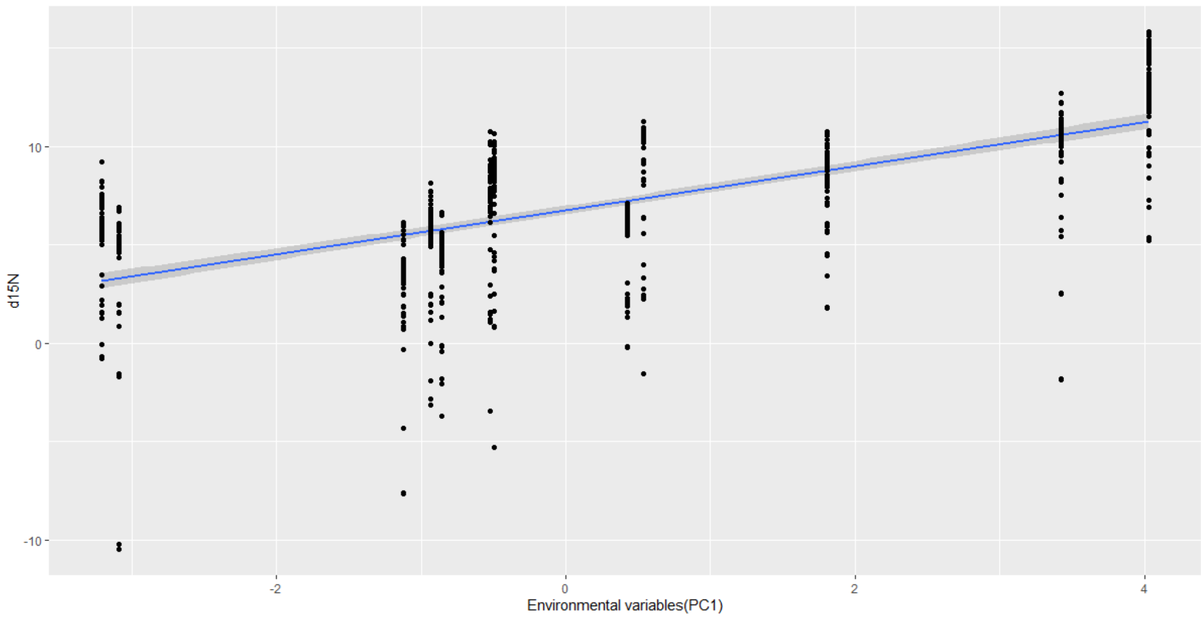

Figure 11. d15N values of the whole system for each of the twelve study lakes vs environmental variables (PC1) for the twelve study lakes. 95% confident interval is shown as dark grey around the line. Plot is showing that there is an enrichment in nitrogen with higher lake productivity. PC1 values can be seen in figure 1.

This is a result from a linear model testing the d15N values vs the total nitrates in each of the twelve study lakes. The results show that there is an enrichment in d15N in lakes with higher productivity. With the results from a linear model I found a positive correlation between mean d15N and total nitrates (µg/l) for the twelve study lakes ($F_{1,726}$ = 395.6, p= <0.001, intercept ± SE: 3.12246 ± 0.23378, slope ± SE: 0.00470 ± 0.00024, R^2 = 0.353. There is an enrichment in stable nitrogen carbon with higher nitrates level within the twelve study lakes (Figure 12).

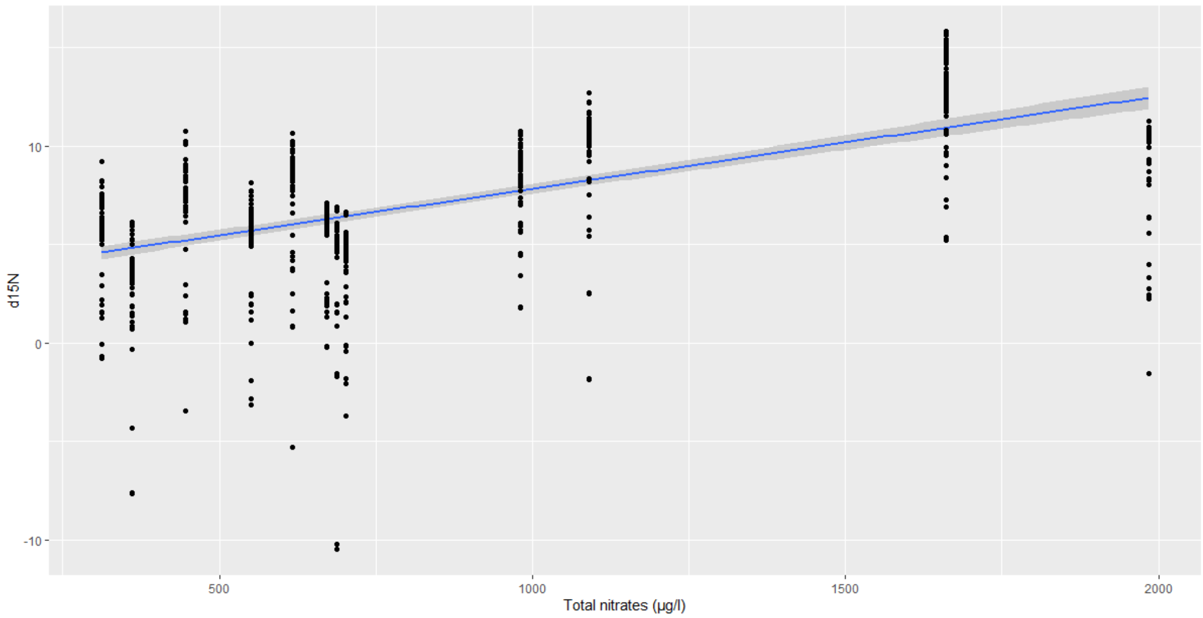

Figure 12. d15N values of the whole system for each of the twelve study lakes vs the total nitrates for the twelve study lakes. 95% confident interval is shown as dark grey around the line. Plot is showing that there is an enrichment in nitrogen with higher levels of nitrates.

In regard to stable carbon isotope (d13C) and lake productivity showed a positive correlation in the twelve study lakes. With the result of a linear model I found a positive correlation between mean d13C and PC1 from the environmental variables. ($F_{1,358}$ = 38.22, p= <0.001, intercept ± SE: -32.60949 ± 0.11709, slope ± SE: 0.33840 ± 0.05474, R^2 = 0.09647). There is an enrichment in carbon with higher productivity (Figure 13).

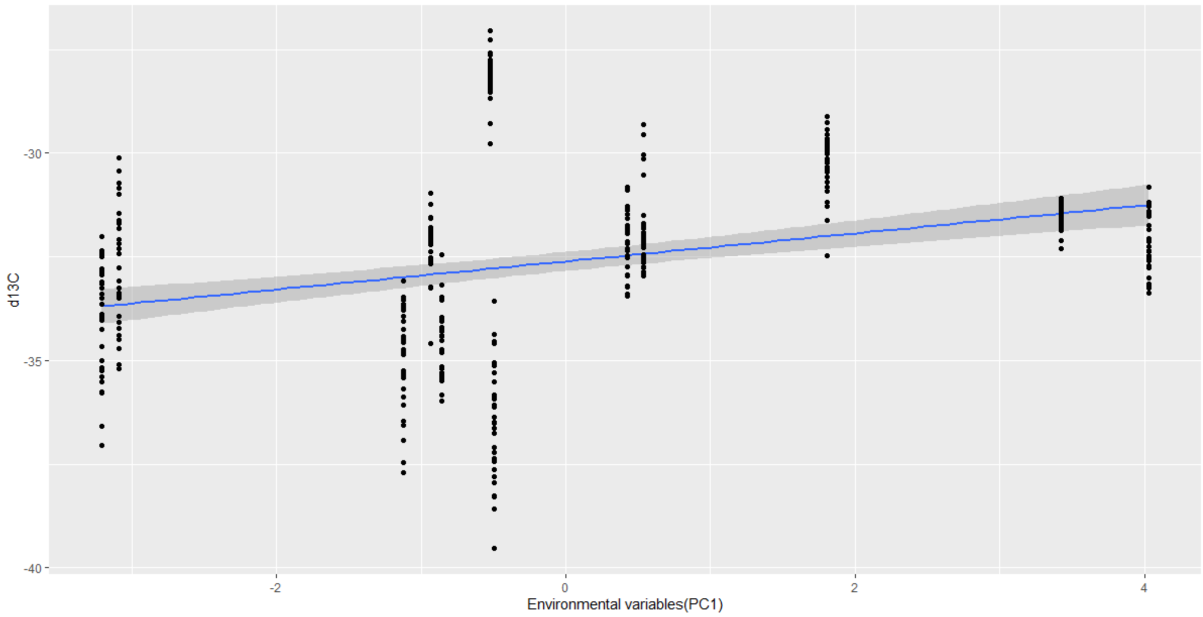

Figure 13. d13C values for the whole system for each of the twelve study lakes vs environmental variables (PC1) for the twelve study lakes. 95% confident interval is shown as dark grey around the line. Plot is showing that there is an enrichment in carbon with higher lake productivity.

CPUE was calculated from the Nordic multi-nets. CPUE was calculated with following formula: CPUE = ind/N/h. CPUE of Crucian carp and the predators show how many fish was approximately caught every hour the Nordic multi-nets were in the water. Thus, a high number indicates a high abundance of fish and a low number indicated less abundance. In the allopatric lakes (without predators) there is a higher CPUE then in the different predation regimes, except in Langmytjern were there was a lower CPUE than in Bjørnmyrdammen (Table 5).

Table 4. Catch per effort for Nordic nets for the twelve study lakes for the period May – August in 2018 and 2019.

Lake	CPUE Crucian	CPUE Predators	Top predator
Forkerudtjennet	10.63	0.00	No
Langmyrtjern	1.38	0.00	No
Motjennet	6.24	0.00	No
Bjørnmyrdammen	2.11	0.41	Perch
Svartkulp	0.30	1.07	Perch
Øvresetertjern	0.28	1.64	Perch
Karussputten	0.79	0.13	Trout
Posttjernet	0.13	0.65	Trout
Småvanna	0.77	0.23	Trout
Bugårdsdammen	0.10	0.78	Pike
Nusttjennet	0.34	0.12	Pike
Stomperudtjernet	0.29	0.14	Pike

A linear mixed model with the different lakes as random effect was used to find the final model that best explain littoral reliance for crucian carp in the twelve study lakes. Results is based on a backward regression method; variables were removed if they were not significant. The different models were based on the lowest AIC value. An ANOVA-test was used to compare the different models to check if the decrease of a variable was significant. When the final model was found, I used ANOVA-test to test if random effect (lakes) was significant or not, and random effect was better. (In the appendix the different models can be seen) the final model to best explain littoral reliance was CPUE of the predators, PC1, PC2 and the max mouth size of the predators, with the twelve study lakes as random effect (Table 6).

Table 5. The final model that best explained littoral reliance for crucian carp in the twelve different study lakes.

```
Linear mixed model fit by maximum likelihood . t-tests use
  Satterthwaite's method [lmerModLmerTest]
Formula: littrel ~ cpue_pred + PC1 + PC2 + max_mouth + (1 | Lake)
   Data: df

     AIC      BIC   logLik deviance df.resid
    34.9     62.1    -10.5     20.9      353

Scaled residuals:
    Min      1Q  Median      3Q     Max
-3.6873 -0.4836 -0.0016  0.4690  2.7735

Random effects:
 Groups   Name        Variance Std.Dev.
 Lake     (Intercept) 0.05999  0.2449
 Residual             0.05519  0.2349
Number of obs: 360, groups:  Lake, 12

Fixed effects:
            Estimate Std. Error       df t value Pr(>|t|)
(Intercept)  1.01167    0.14486 12.00000   6.984 1.47e-05 ***
cpue_pred    0.86543    0.19479 12.00000   4.443 0.000803 ***
PC1          0.12835    0.04772 12.00000   2.690 0.019676 *
PC2          0.12033    0.05731 12.00000   2.100 0.057567 .
max_mouth   -0.01028    0.00358 12.00000  -2.870 0.014080 *
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
          (Intr) cp_prd PC1    PC2
cpue_pred  0.128
PC1        0.506  0.596
PC2       -0.237 -0.053 -0.166
max_mouth -0.745 -0.635 -0.765  0.241
```

A linear mixed model with the different lakes as random effect was used to find the final model that best explain littoral reliance for crucian carp in the twelve study lakes. Results is based on a backward regression method; variables were removed if they were not significant. The different models were based on the lowest AIC value. An ANOVA-test was used to compare the different models to check if the decrease of a variable was significant. When the final model was found, I used ANOVA-test to test if random effect (lakes) was significant or not, and random effect was better. (In the appendix the different models can be seen) the final model to best explain littoral reliance was CPUE of the predators, PC1, PC2 and the max mouth size of the predators, with the twelve study lakes as random effect (Table 7).

Table 7. The final model that best explained Trophic position of crucian carp in the twelve study lakes.

```
Linear mixed model fit by maximum likelihood . t-tests use
  Satterthwaite's method [lmerModLmerTest]
Formula: trophicposition ~ Total_lenght + (1 | Lake)
   Data: df

     AIC      BIC   logLik deviance df.resid
   -78.4    -62.9     43.2    -86.4      356

Scaled residuals:
    Min      1Q  Median      3Q     Max
-4.3165 -0.4704  0.0574  0.5300  2.7099

Random effects:
 Groups   Name        Variance Std.Dev.
 Lake     (Intercept) 0.11747  0.3427
 Residual             0.03964  0.1991
Number of obs: 360, groups:  Lake, 12

Fixed effects:
              Estimate Std. Error        df t value Pr(>|t|)
(Intercept)  1.484e+00  1.100e-01 1.702e+01  13.489 1.62e-10 ***
Total_lenght  2.413e-03 3.600e+02   9.992  < 2e-16 ***
0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:
            (Intr)
Total_lnght -0.427
```

Discussion

I found a clear difference in littoral vs pelagic resource use, and in niche width for the Crucian carp in the twelve study lakes. Crucian carp shifted from pelagic to littoral use with increasing body size. This illustrates that piscivores predator fish influence habitat and resource use for the Crucian carp (Holopainen et al. 1997). Further on in more complex lakes, there was a clear difference in niche with. Showing that in multispecies fish communities the niche of Crucian carp decreases. This can be due to more competition for same habitat and resources. I did not find a difference in trophic position in the different predation regimes. Hence the presence of predators did not affect the trophic position of Crucian carp. The results from the PCA showed that number of species, land use and littoral area, were important factors for lake productivity for the twelve study lakes, and with higher productivity there was a higher biodiversity then in lakes with lower productivity.

PC1 values from the principle components analysis (which explained 48.3% of variation) shows that the number of species, land use and littoral area, total nitrates and total phosphates were the most important variables for productivity within the twelve study lakes. The number of species was correlated with the trophic status of a lake. Trophic status is the total biomass of organisms in a lake, and with higher number of fish means more biomass within a lake to support greater number of fish/multispecies community. With precipitation and land use intensification the nutrient input from terrestrial environments increases, which is resulting in higher levels of dissolved organic matter and higher productivity. The input can affect algae growth and quality of the water, such as eutrophication of a lake (Hayden et al. 2017). My results correspond with previous studies done on freshwater lakes in Finland, Greenland and North America (Vadebonceur et al. 2003, 2008; Althouse et al. 2014; Hayden et al. 2017). These studies also showed that intensification of land use and increase in total biomass has a positive effect on productivity. Ten of my twelve study lakes had bigger littoral area than pelagic area and were mainly shallow lakes. A previous study by Elorenta et al. (2013) showed that the littoral habitat can be the main source of energy in lakes throughout the year. Vadeboncoeur et al. (2001) found out that benthic littoral production contributes for the whole production within a lake. A study on boreal small lakes done by Vesterinen et al. (2016) also showed the importance of littoral production in humic boreal lakes. A large-scale study on lakes across the world gained knowledge that most lakes are shallow lakes, consisting of larger littoral zones. (Wetsel, 1990; Messager et al. 2016) and there are more species to be found in littoral habitats (Schindler & Scheuerell, 2002). With higher production level within a lake there is an enrichment of nitrogen and carbon. In my study lakes, littoral area, number of species and land use intensity was the most important factors for lake productivity, and this corresponds with previous studies done in Finland, North America and Greenland, and thus my results strengthen previous findings on the topic of lake productivity.

There was considerable variation in both d13C and d15N within each of the twelve study lakes. Stable isotopes ratio in different organisms is an integration of the different food resources that have been accumulated over a time certain time period (Kilham et al. 2009; Layman et al. 2012). My results show that higher d15N values is an important factor for trophic status and productivity in the twelve study lakes. Lakes that are more complex in both trophic status and in productivity have higher d15N values for the whole system. There was also an enrichment in d15N with higher levels of nitrates within lakes. A previous study done in 60 different shallow lakes in Poland and UK, showed that d15N and especially nitrates is an important indicator for productivity and species richness in lakes (James et al. 2005). Stomperudtjernet and Nusttjennet was the most productive lakes situated in farmlands, and in these two lakes the whole system has an enrichment in d15N and total nitrates, and on the other hand, the less productive lakes have lower d15N and nitrate values. My results correspond with previous studies, which show that nitrogen and nitrate availability is an important indicator and factor for freshwater communities, it is often determining factor for trophic status and species richness within a lake (Smith, 2003; James et al. 2005; Beversdorf et al. 2013). While carbon is integrated in the diet (Peterson & Fry, 1987) since the tissue of the consumer is closely linked with their diet, d13C can be used to identify resources used by a consumer (Jackson et al. 2011). In almost all study lakes Crucian carp is closer linked with BMI then with zooplankton, except in Nusttjennet, Øvresetertjern and Svartkulp crucian carp is more in the middle with a close link to both zooplankton and BMI. In regard to the importance of d15N and total nitrates in the twelve study lakes. there was an enrichment in both in more productive lakes and in more complex lakes. My result strengthens previous studies showing that d15N and total nitrates are an importance indicator for lake productivity and species richness.

My results show that bigger sized Crucian carp use area closer to littoral habitats and smaller Crucian carp use the pelagic habitat more. With size there is a shift from pelagic to littoral with increasing size. A reason for this is can be that increased size can result in increased drag and reduced swimming speed, while a smaller sized fish may have less drag and higher burst speed. Meaning that a larger fish seeks refuge in the vegetation to avoid encounters with predators, and smaller fish relies on their burst speed and movement ability while foraging plankton in the pelagic habitats. Such morphological traits have been seen in crucian carp and other species, were movement ability, reduced speed, and increased drag with size Which Brönmark & Miner (1992) found out in a field experiment and a laboratory experiment, that in the presence of pike the crucian carp developed deeper bodies, and a result of a deeper body the swimming ability got reduced and the it resulted in an increased drag. Another example, Langerhans et al (2004) saw that mosquito fish (*Gambusia affinis*) in lakes with predators developed deeper bodies, but with increased size the drag increased, and the speed reduced. A study in Finland on Crucian carp in allopatric and sympatric lakes done by Holopainen et al. (1997) showed that in allopatric lakes the Crucian carp often are more abundant and use the pelagic habitat more frequently in lakes without predators, on the other hand Crucian carp is often less abundant and live closer to the shore and vegetation in lakes with predator fish present, the same study also saw that Crucian carp were smaller in size in predator free lakes and on the other hand, the Crucian carp developed deeper bodies and were usually less abundant and were restricted in the vegetated areas in the littoral zone close to shore in sympatry with piscivore predators. This corresponds with the results in my study. The results based on littoral and pelagic reliance in this study strengthens and shows that top predators play a fundamental role in connecting littoral and pelagic habitats and also food web compartments as it has been shown in previous studies done by Vadeboncoeur et al. (2002) and Schindler & Scheuerell (2002).

My results did not show that the Crucian carp population shifted from pelagic use to littoral, but rather a shift with increased size. Looking closer into Stomperudtjernet which was the most productive lake and housed a total of six different fish species and Pike is the top predator, in

Stomperudtjernet crucian carp was only feeding in the littoral habitats even though results showed that smaller size Crucian carp foraged more in the pelagic areas. On the other hand, in Nusttjennet had the most fish species with seven different fish species caught. Nusttjennet was the biggest lake in this study and was a lot bigger than Stomperudtjernet, but in Nusttjennet Crucian carp were only foraging in both littoral and pelagic habitats with closer relations to pelagic. I can only speculate in what are the reasons why in both Nusttjennet and Stomperudtjernet the whole population was clustered in the same place, but previous study done by Vander Zanden et al (1999) and Vander Zanden et al. (1999) showed that increased fish species diversity can lead to a change of intermediate consumers within a lake, but not only that, it may also lead to an increased competition between consumers and with this lake size is a strong and complex influence to the lake ecosystem and the energy flow pathways. In light of the above, predation changed the niche of Crucian carp to littoral from pelagic. With increasing size, the Crucian carp foraged closer to shore. In some lakes with predation Crucian carp was foraging in the pelagic habitats in lakes with predator fish presence, showing that there are other factors that can be of importance for a change in resource use. With the knowledge above can it rather be that in multispecies community such as Nusttjennet and Stomperudtjernet increased competition and species richness changed forage behavior for crucian carp since these were the lakes with the most species, thus the complexity of Nusttjennet and Stomperudtjernet affected the habitat use for the crucian carp population.

The width of the niche was smaller in more complex systems. Nusttjennet and Stomperudtjernet was by far the two most productive lakes and housed seven (Stomperudtjernet) and six (Nusttjennet) different fish species. Both lakes had a max depth of 1.5 meters and Stomperudtjernet had the most plant cover, and Nusttjennet third most plants covering the water surface and both lakes had Pike as top predator. Bjørnmydammen was the fourth most productive lake and had the second most plant cover, with a max depth of 3.5 meters. In Bjørnmyrdammen only three fish species were caught. One out of the three species caught was the Tench *(Tinca tinca)*. Tench eat zooplankton as juveniles and later switch to a broad range of benthic macroinvertebrates (Brönmark, 1994; Specziár et al. 1998). Even though the Tench eat a broad range of benthic macroinvertebrates they specialize on mollusks if available (Brönmark, 1994). Tench is also an invasive species in Norway and has been introduced into many Freshwater lakes (Hesthagen & Sandlund, 2007) and has the second highest gradation (HI) as an alien species from the ecological risk assessment in Norway, because of its impact on native species and the environment it lives in (Biodiversity.no). A previous study done by Brönmark et al (1995) found out that in lakes without piscivore predators the Tench was bigger in size then Crucian carp, and in lakes with piscivore predators the Tench was also bigger than Crucian carp. As mentioned above the niche width was smaller for Stomperudtjernet and Nusttjennet which were complex multispecies communities, and Bjørnmyrdammen even though not as "complex" system as Stomperudtjernet and Nusttjennet, crucian carp and Tench most likely compete for det same food in Bjørnmyrdammen, These three lakes also had in common that there was other fish species that can compete for the same resource with species such as, the Common Rudd (rudd; *Scardinius erythrophthalmus*) and Common bream (bream; *Abramis brama*) and previous studies has shown that the larger bream is benthivores, and forage on organisms on the bottom, but can also feed on plankton (Specziár et al. 1998; Wolnomiejski et al. 2002). While the rudd feed on zooplankton as juvenile but when fully grown the rudd is almost totally herbivore, foraging on algae and plants and live in littoral habitats (Revnne & Jamet, 1991; García-Berthou & Moreno-Amich, 2000). Hence, rudd , bream, Tench and large Crucian carp compete for the same niche, and a study done by Tonn et al (1994) found out that The feeding success, growth, survivorship, and reproductive success of Crucian carps in complex lakes are the products of interspecific interactions rather than the intraspecific interactions or environmental constraints that dominate populations in smaller simpler system, whereas the high-density crucian carp populations in ponds without piscivores are limited by intraspecific competition. With findings from my study and previous studies, it shows that interspecific interactions in complex systems are of great importance, and that interspecific does constrain the crucian carps niche width.

The choice of tissue used in a stable isotope analysis will determine the period for the niche when expressed. This is because different tissue will have different turnover times, and therefor reflect isotopic signatures from the prey consumes at different times (Bearhop et al. 2004). However, I considered muscle tissue to be the most suitable type of tissue in this study, because of the turnover time of the tissue in relations to the time of when the niche is expressed. Muscle tissue reflect the diet of a fish over a period of several months pluss/minus depending on the size of the fish (Hesslein et al. 1993). Hence, the muscle tissue of fish in this study most likely reflect their diet, niche and habitat use in spring and summer months.

Trophic position did not differ for Crucian carp with or without predators, highest mean trophic position for Crucian carp in predator lakes was 2.2 and lowest 1.4 and for lakes absence of predators had highest 2.1 and lowest 1.8. Predator lakes had the highest tropic position and lowest for Crucian carp in the twelve study lakes. Variability in d15N of any of the different types of food used in the baseline, can be responsible for the variation in trophic position of Crucian carp. Variation in d15N in different freshwater river system have in a previous study in Turkey shown to influence the trophic position for the same species in different lakes and rivers (Özdilek & Jones, 2014). In the twelve study lakes in my study there were a variation in d15N and in total nitrates in the different lakes. The more productive lakes had an enrichment in d15N and total nitrates, and in these lakes the trophic position of Crucian carp was lower than in lakes with lower d15N values. The final model that best explained trophic position of crucian carp was the size. Trophic position become higher for crucian carp with bigger size and as mentioned above larger sized crucian carp uses littoral habitats more or closer to the littoral habitat than smaller crucian carps (Holopainen et al. 1997). Diet differences do exist among size classes of crucian carp, with smaller fish forage larger proportions of zooplankton, while larger fish forage more benthic macro-invertebrates (Tonn et al. 1994), this form for prey choice, can be a form for optimal diet, where the consumer will ignore low profitable prey and optimize the overall rate of energy gain (Pulliam, 1974), by changing resource use with size, as seen with the crucian carp (Tonn et al. 1994), and body size is a fundamental determinant of energy flow (Hairston & Hairston 1993). The consumer is often bigger than its prey and thus in trophic position often increases with body size within a given food web (Jennings et al. 2001). Which can be the reason for why trophic position is higher for larger sized crucian carp in my study lakes.

The use of d15N as a tracer to calculate the trophic position of an organism eliminates many of the problems encountered when using diet data to estimate trophic position. D15N represents the major energy flow pathways at lower trophic levels, and gives a time aspect measurement of an organisms trophic position through the temporal and spatial variation in feeding at multiple levels of the food web, and will detect trophic interactions that could otherwise be not observed when using gut content, because gut content can actually differ from the food actually assimilated by an organism (Vander Zanden et al. 1997).

Studies on food webs and community structure are important concepts and a useful tool in illustrating the feeding relations among and between species. Food web and community structure can reveal interspecific and intraspecific interactions and give a broader understanding or give a new perspective on food webs structure, different functions and dynamics in an ecosystem, such as energy transfer in an ecosystem. These results can be used in management to give a more holistic picture of the functions in an ecosystem, and thus guide or help nature management when making decisions in the future. Such knowledge is also imperative for management and conservation biology

In future research I recommend a dial study of Crucian carp. In my study I can only discuss and conclude with were the Crucian carp is when it is foraging. I cannot say anything of its habitat use when it is not foraging. It can be that the Crucian carp only forage in a certain habitat but do not use it when it is not foraging, I: e, it can be using a different habitat while not foraging.

Conclusion

With findings from my study and previous studies, it shows that interspecific interactions in complex systems are of great importance, and that interspecific competition does constrain the crucian carps niche width, The results based on littoral vs pelagic use, this study strengthens previous studies and shows that top predators play a fundamental role in resource use of crucian carp. Thus, I conclude that piscivore top predators have an effect the structure and function of crucian carp communities.

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