Associations between body size polymorphism in Arctic charr and benthic invertebrate communities – clues to mechanisms for population differentiation?

Andreas Sund

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Swedish University of Agricultural Sciences, SLU
Department of Wildlife, Fish and Environmental Studies Skogsmästarprogrammet/Masterutbildning
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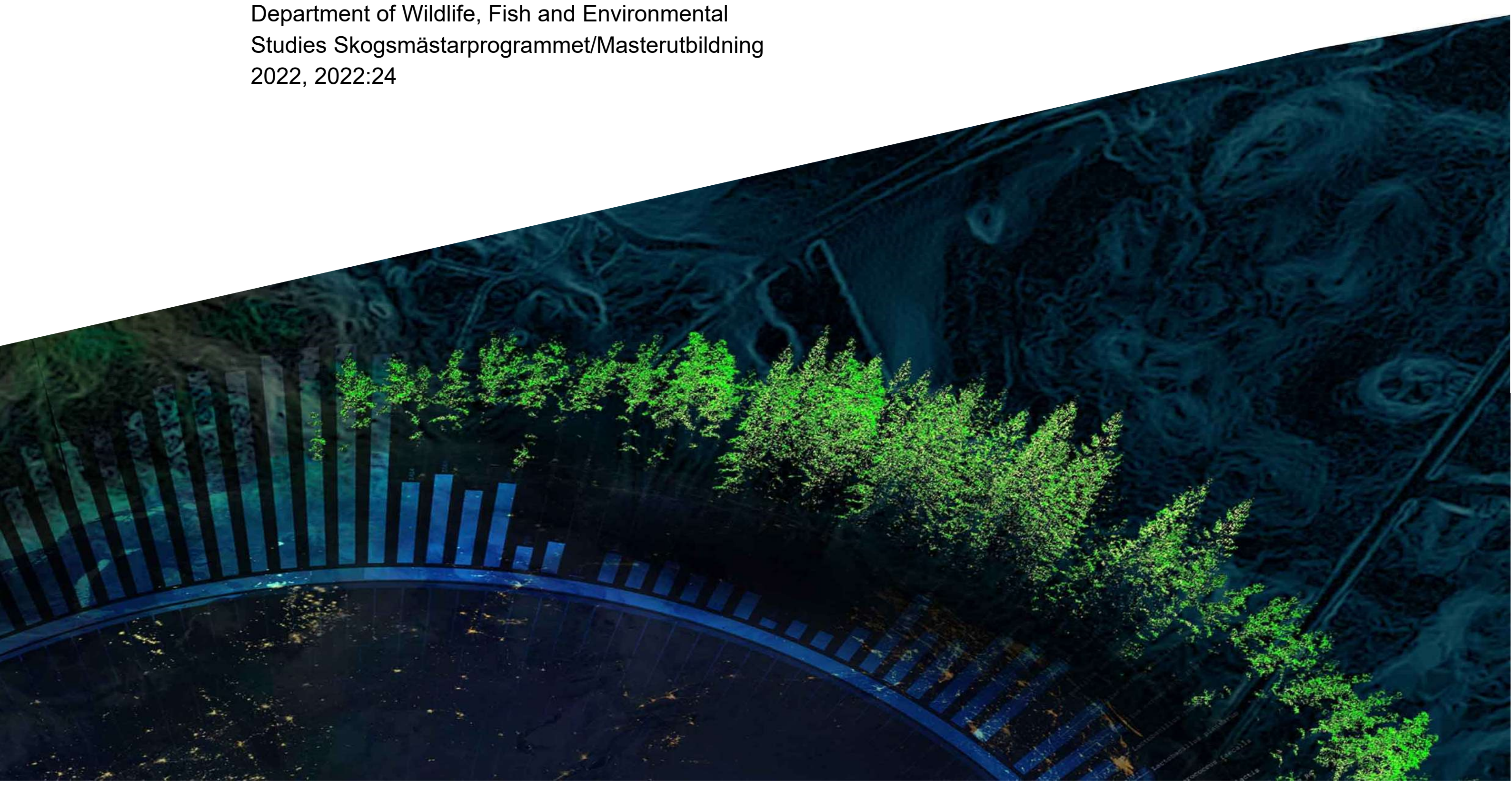

Andreas Sund

Supervisor: Gunnar Öhlund, Swedish University of Agricultural Sciences, SLU
Department of Wildlife, Fish and Environmental Studies
Assistant supervisor: Karin Nilsson, Swedish University of Agricultural Sciences, SLU
Department of Wildlife, Fish and Environmental Studies

Examiner: Petter Axelsson, Swedish University of Agriculture Sciences, SLU

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Swedish University of Agricultural Sciences
Faculty
Department of Wildlife, Fish, and Environmental Studies

Abstract

Many fish populations in the north have divided into coexisting ecotypes that differ in body size. While such polymorphic fish populations have been studied for many years, the understanding of how different types of selection contribute to the formation of dwarf- and giant ecotypes remains limited. Previous findings suggest a positive relationship between body size polymorphism in European whitefish (*Coregonus lavaretus*) and standing biomass of littoral benthic invertebrates. As this observation may hold important clues to the mechanism that underlies body size divergence, it is important to find out if it represents a general phenomenon. In this study, I compare data on biomass and community composition (both estimated using catch data from invertebrate traps) of littoral invertebrates from north-swedish lakes with- and without body size polymorphism in the resident populations of Arctic charr (*Salvelinus alpinus*). In a related follow-up question, I wanted to explore the potential mechanism behind enriched littoral invertebrate communities, i.e., that the habitat specialization associated with body size divergence will cause most Arctic charr to actively avoid feeding on (and thereby supressing) the littoral resource. From this mechanism follows that the standing biomass of littoral invertebrates should be negatively correlated to the degree of littoral benthivory in Arctic charr. I therefore performed stomach content analysis of charr from the lakes of the invertebrate study to test if my invertebrate biomass estimates were correlated to the proportion littoral invertebrates in charr stomach contents. The result of this study reveals no general positive relationship between body size polymorphism in charr and standing biomass of littoral invertebrates. Moreover, Arctic charr preferred to eat zooplankton in all lakes and I found no correlation between littoral invertebrate biomass and the amount of littoral benthic prey found in Arctic charr stomachs. While my results revealed few significant trends overall, my findings still indicate that lakes with polymorphism could be associated with high biomass of predation-sensitive invertebrate taxa. These findings include significantly higher biomass of amphipods and on average (although non-significantly) higher biomass of large-bodied Trichopterans (*Phryganidae* and *Limnephilidae*) in lakes with polymorphism. To determine whether charr polymorphism is indeed associated with enriched littoral invertebrate communities, more studies involving more lakes are needed.

Keywords: Arctic charr, benthic invertebrates, polymorphism.

Table of contents

List of tables

List of figures

1. Background

Many fish populations in the north have divided into large- and small-sized ecotypes. These ecotypes are often specializing on different food resources and many fish species that form dwarf- and giant ecotype pairs are among the classic cases of resource polymorphism (Seehausen and Wagner 2014). In response to differences in habitat- and resource use, ecotypes/species often develop different morphological adaptations (Smith & Skùlason 1996). For instance, dwarfs and giants often develop different numbers of gill rakers to specialize on a certain resource. When feeding on zoobenthos in the littoral, it is advantageous to have sparse gill rakers and when feeding zooplankton in the pelagic zone, dense gill rakers are beneficial (Bolnick et al 2004). Hence, lakes in which species that have developed body size polymorphism represent important study systems for speciation research. While the phenomenon of polymorphism has been studied intensely for several decades, the underlying mechanisms remain poorly understood.

The most suggested mechanisms mediating development of polymorphisms include strong intraspecific competition over food resources and ecological opportunity (Landry et al. 2007; Siwertsson et al. 2010; Gordeeva et al. 2015). Related to ecological opportunity, it is often stated that ecosystem size, i.e., the depth and area of lakes, is important for divergence to occur. Other mechanisms that could trigger polymorphism are presence of cannibals or interspecific predators that may control the division into different ecotypes in the same lake (e.g., Andersson et al 2005, Öhlund et al 2020).

One way to begin to disentangle how ecological drivers can create dwarfs and giants from the same species, is to compare basic biological data from monomorphic and polymorphic lakes. Previous studies have suggested that predation-induced divergence into dwarfs and giants may be associated with high densities of invertebrates in the littoral habitat. The potential mechanism behind this phenomenon is that many fish (i.e., the dwarf ecotype) prioritize survival over growth opportunities, and hence avoid the productive but dangerous littoral zone (Stenman 2014, Öhlund et al 2020). Lowered littoral fish densities would then, in turn, lead to a further increase in invertebrate biomass. Thus, a link between polymorphism and enriched littoral invertebrate resources could potentially suggest that pelagic/profundal habitat specialization (i.e., away from the rich littoral resource) during divergence is mainly related to predator avoidance. Comparing the littoral invertebrate communities between lakes with mono- and polymorphic populations may therefore provide one piece to the complicated puzzle of understanding the ecological mechanism behind the speciation process.

So far, the link between invertebrate densities and body size polymorphism has not been investigated for Arctic charr, a species for which the phenomenon of body size polymorphism is particularly widespread. Larger Arctic charr (*Salvelinus alpinus*) and smaller Arctic charr (*Salvelinus stagnalis*) were long believed to be separate species and were named by Carl von Linné in 1758 after some assistance from his friend and colleague Petrus Artedi. Today, Arctic charr is often considered to be one species, but the literature contains a rich documentation of substantial intraspecific variation that is often related to body size and habitat use (e.g., Gordeeva et al 2015, Knudsen et al 2016, Malmquist et al 1992).

The first purpose of this study is to compare the biomass and composition of littoral benthic invertebrates in lakes hosting either polymorphic or monomorphic populations of Arctic charr. Specifically, I will use catch data (from invertebrate traps) to test the hypotheses that biomass of invertebrates and abundance of predation-sensitive taxa (the latter providing an alternative way of testing for signs of ecological release from littoral benthivory) are positively associated with charr polymorphism. In the second part of the study, I explore the potential mechanism behind enriched littoral invertebrate communities, i.e., that the partial pelagic/profundal habitat specialization typically associated with body size divergence will cause most Arctic char to actively avoid feeding on (and thereby supressing) the littoral resource. From this mechanism follows that the standing biomass of littoral invertebrates should be negatively correlated to the degree of littoral benthivory (i.e., feeding on littoral invertebrates) in Arctic charr. To investigate this corollary, I will test if the littoral invertebrate biomass estimates from my catch data is correlated to the proportion littoral invertebrates in charr stomach contents from the same lakes.

2 Materials and methods

2.1 Study area

The studied lakes are in the western mountain areas of Jämtland. These lakes were chosen with the help of local information from fishermen in the area and experts on the National County Board in Jämtland. Based on various types of existing information (sample fishing data, interviews with county board and local fishers), four of the lakes were classified as polymorphic (i.e., with dwarf and giant charr ecotypes present) and seven as monomorphic (only one charr ecotype present) before the onset of my study. Other species of fish present in the lakes studied are brown trout (*Salmo trutta)* and European minnow (*Phoxinus phoxinus)*. In the lake Rengen, burbot (*Lota lota)* is also present. (Gunnar Öhlund personal information, figure 1).

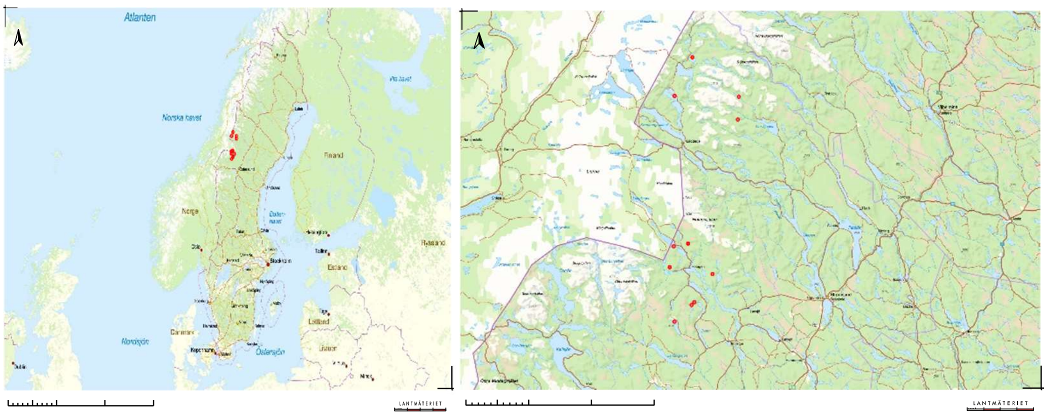

Figure 1. Image of Sweden and a map of western Jämtland County with all lakes studied are marked as red. Lantmäteriet (2022) Jämtland. SWEREF 99 TM, Karta [Kartografiskt material] https://minkarta.lantmateriet.se [2022-05-11]

Table 1. Information about the different lakes: types of data collected (traps= invertebrate catch data using traps, stomach=charr diet data from analysis of stomach contents), putative population structure of Arctic charr (Mono =monomorphic, Poly= polymorphic), area of the lake, maximum depth, and altitude.

Lake	Collected data	Arctic charr population structure	Area (ha)	Depth (m)	Altitude (m.a.s.l.)
Lill-Djupvattnet	traps/stomach	Mono	45	16	450
Stor-Djupvattnet	traps/stomach	Mono	108	38	400
Nedre Härbergsvattnet	traps/stomach	Mono	246	27	550
Åkersjön	traps/stomach	Mono	1200	60	447
Lillsjön	traps/stomach	Mono	70	15	587
Rengen	stomach	Mono	2160	70	350
Blomhöjdsvattnet	traps	Mono	41	15	550
Butjärn	traps/stomach	Poly	36	29	600
Ankarvattnet	traps/stomach	Poly	934	75	448
Bergsjön	traps	Poly	147	29	450
Jormvattnet	traps	Poly	2042	92	347

2.1 Littoral invertebrate study

I collected benthic invertebrates from 10 different lakes: Stordjupvattnet, Lill-djupvattnet, Ankarvattnet, Nedre-Härbergsvattnet, Butjärn, Åkersjön, Lillsjön, Bergsjön, Jormvattnet and Blomhöjdsvattnet (figure 1, table 1). Rengen was excluded from the invertebrate trap study because of unsecure ice-conditions. I planned where in the lake to place the traps by inspecting the Swedish real estate surveying maps online, looking for sheltered shallow areas with soft, bottom substrate. The fieldwork started on the 1st of April after discussions about the ice conditions on the lakes. At that time two weeks with warm temperatures even at night-time had passed so a time window with safe ice-conditions were getting narrow. After considering both the thickness of ice, the ability to move on the ice and the ability to move to the lakes with snowmobiles or skis, we decided to start the fieldwork. We used skis to transport all the gear to the lakes where the fieldwork was carried out. Skiing is far better for the climate and the sensitive fauna in the mountains than a snowmobile. We tried to reduce the miles in the car by planning and carrying out as much fieldwork in an area in a day as possible. These actions reduced the emissions in the atmosphere during this study. When doing a study in biology it is important to leave only footprints and to take only the number of insects needed for the study. In April the reindeers are moved to higher grounds after grazing in low forestlands all winter. In this study we were careful not to disturb the reindeers if we saw any.

The sampling of bottom fauna was performed with a type of insect trap made of a cotton bag designed by Gunnar Öhlund (SLU Umeå). The insect bags were placed on the bottom of the lake, at depths between 0.75- and 2m and between 1- 40 meters from the shoreline. The minimum distance between the traps was 10 meters. The insect bags and a led weight were attached to a string and lowered through a hole in the ice, and the string was secured with a knot around a wooden stick. The insect bags were 15 X 20 cm, and they were baited with dog food from Doggy and green mold cheese from Kvibille to attract the invertebrates. The insect bags were half-filled of its volume with filter plastic fibre allowing many invertebrates to enter the trap without disturbing each other. Pockets of air were completely removed from the bags before they were lowered down into the lakes. After 24 hours, I retrieved the bags and moved all caught invertebrates to a plastic bag marked with sampling date, lake, and bag number. These plastic bags were then stored in a freezer (-18 °C) until the invertebrates were analysed in taxa and length.

Back indoors the catch was studied and identified to the lowest possible taxonomic level. To identify and count the individual invertebrates, a stereomicroscope was used. I then used family-specific equations describing the length-biomass relationships to calculate the biomass of all invertebrate individuals (Benke 1999). This allowed me to calculate the total biomass for each bag and the total biomass per family of invertebrate caught in the lakes. I used a ruler with a millimetre scale to measure the length of the invertebrates. When interpreting and discussing differences in biomass of individual taxa, the large-bodied taxa *Limnephilidae, Phryganeidae* and *Amphipoda* were regarded as predation-sensitive (Carlisle and Hawkins 1998). After analysis, the catch was translocated to a plastic tube with 70% of ethanol for preservation.

2.2 Arctic charr diet study

In total, I analysed stomach content from 304 Arctic charr. These charr originated mainly from nordic gillnet sample fishing performed during 2020 and 2021 in the lakes Ankarvattnet, Butjärn, Lillsjön, Lill-djupvattnet, Nedre Härbergsvattnet, Stor-djupvattnet, Rengen and Åkersjön in Jämtland (figure 1, table 1). Every sample of stomach and content were preserved in ethanol for future research. From the sample fishing protocols (or from the local fishermen), I retrieved information about the length and maturation status of each charr. After the stomachs were defrosted, the weight of the full stomach was noted, stomach contents were removed, and the weight of the empty stomach was noted.

All stomach contents were sorted into the following categories: *Diptera, Trichoptera, Plecoptera, Ephemeroptera, Amphipoda, Copepoda, Cladocera*, Small mussel, fish, mucus or uneatable. Thereafter, the weight of each prey category was noted and given a Prey-ID. Data from the investigation was carefully noted with lake of origin, length of body, species of prey, length of prey and weight of prey. To enable an analysis of foraging habitat for charr, we divided taxonomic groups into putative habitat groups. Hence, during later analysis, *Trichoptera, Plecoptera, Ephemeroptera* and *Amphipoda* were collectively termed littoral invertebrates. *Diptera* and *Sphaeriidae* were grouped as profundal invertebrates and *Copepoda* and *Cladocera* were categorized as pelagic zooplankton.

2.3 Data analysis

From my analysis of the bags, I received estimates on biomass of littoral benthic invertebrates. In addition, I had data on lake area, if there was polymorphism in the lakes, and fish size and diet. Using this data, I wanted to test my two main hypotheses: 1) The biomass of benthic invertebrates and abundance of predation-sensitive taxa are higher in lakes with charr polymorphism, and 2) Invertebrate biomass caught in the littoral traps is positively correlated with proportion of littoral prey found in the diet of charr.

To test my first hypothesis that total standing biomass of littoral benthic invertebrates trapped was associated with polymorphism, I ran a linear model (LM) using the program RStudio (Rx64 4.1.2). In these analyses, I also included lakes size as a predictor as it is known to affect many different ecological processes in lakes (Hein et al 2012, Öhlund et al 2020). To reduce heteroscedasticity, the values of the biomasses were log-transformed. The values of lake area were log-transformed to reduce leverage.

To test my second hypothesis that standing biomass of individual taxa in littoral benthic invertebrates differed between lakes with polymorphic and monomorphic Arctic charr, I ran pair-vise t-tests for each taxa separately. In this analysis, the values of taxa found in less than five lakes were grouped into the category” other”. Then data was transformed using log (x+1) to reduce heteroscedasticity.

As fish diet can be affected by individual size (de Roos & Persson 2013), any sampling bias on fish size between lakes could potentially affect the results of my diet study. To examine if fish size affected the probability that charr had eaten littoral invertebrates, I ran a generalized linear mixed model (GLMM) (Manning 2007). In this analysis, I used the length of fish as fixed factor, lake ID as random factor and if the fish had eaten littoral prey or not (stomachs with littoral prey found= 1, stomachs without littoral prey =0) as a binomial response variable.

To investigate a potential correlation between invertebrate biomass in the traps and proportion of littoral prey found in diet, I used linear regression on logged values.

All results of prey found in the stomachs are presented in the appendix.

3 Results

Composition and biomass of the benthic community in polymorphic and monomorphic lakes

Neither lake area, nor polymorphism was significantly related to the total biomass caught in the traps (based on linear regression analyses, area: t = -1.1, p = 0.311, polymorphism t = 1.016, p=0.339, n=10). Both mean length of invertebrates (figure 2) and mean numbers of invertebrates (figure 3) was slightly higher in polymorphic lakes than monomorphic lakes, but the differences were not significant in either case. However, I found that three out of six invertebrate family taxa differed in biomass depending on if the resident population of Arctic charr in the lake was polymorphic or monomorphic (table 2). For example, *Amphipoda* had ~15 times higher biomass in polymorphic lakes compared to monomophic lakes (P= 0.0003). The average biomass was higher in polymorphic lakes for all three predation-sensitive taxa (*Limnephilidae, Phryganeidae* and *Amphipoda)*, although this difference was significant only for *Amphipoda* (table 2).

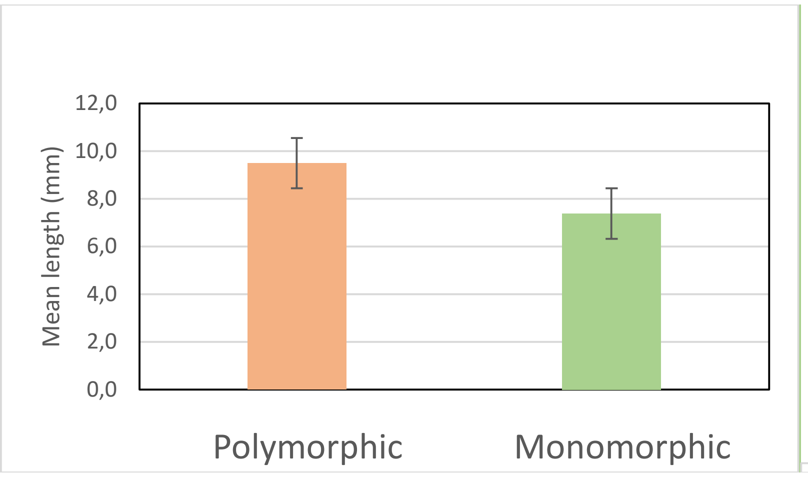

Figure 2. The mean length of invertebrates caught in ten lakes in Jämtland, Sweden, depending on if the resident Arctic charr population was polymorphic (n=4) or monomorphic (n=6). Error bars denote standard error, t = 0.84392, p-value = 0.4232

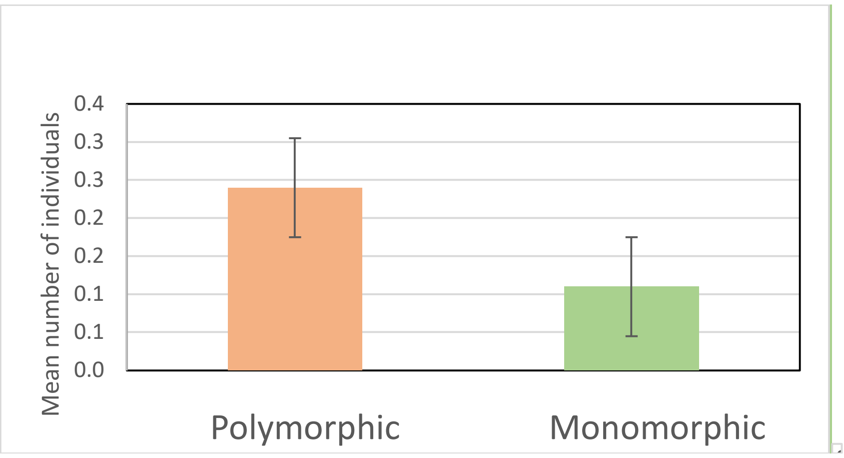

Figure 3. The mean numbers of invertebrates caught in ten lakes in Jämtland, Sweden, depending on if the resident Arctic charr population was polymorphic (n=4) or monomorphic (n=6). Error bars denote standard error, t = 0.51652, p-value = 0.6195.

Table 2. Results of pairwise t-tests, p-value and mean values with standard error comparing biomass of invertebrate taxa collected with traps in lakes with either polymorphic or monomorphic populations of Arctic charr. Taxa that are especially sensitive to high predation pressure (e.g., Carlisle and Hawkins 1998) are marked in bold.

	Polymorphic		Monomorphic		Test statistics	
Taxa	Mean biomass (mg)	SE	Mean biomass(mg)	SE	t-value	p-value
Limnephilidae	0.3400	0.0900	0.1900	0.0700	-1.3300	0.1800
Phryganeidae	0.2700	0.1100	0.0800	0.0600	-1.6000	0.1100
Heptageniidae	0.0300	0.0200	0.1400	0.0400	2.0100	0.0370
Chloroperlidae	0.0100	0.0100	0.0800	0.0400	1.4000	0.1700
Amphipoda	1.7900	0.1200	0.1700	0.0700	4.7000	0.0003
Cladocera	<0.0001	<0.0001	0.0100	0.0040	2.5300	0.0130
Other	0.0030	0.0020	0.0000	0.0000	-1.8000	0.0700

Diet of Arctic charr depending on fish size and invertebrate biomass

The analyzed stomach contents were generally dominated by zooplankton and only 27 out of 304 stomachs contained littoral invertebrates and only one contained fish (Table 3). Lake Butjärn is showing signs of a population of Arctic charr with highly variable diet (table 3). Analyzing the stomach content data, I found no significant relationship between fish length and the occurrence of littoral invertebrates in the diet (GLMM analyses: z-value=0.632, p=0.53, n=304).

Table 3. Proportion of Arctic charr feeding on different categories of prey from littoral, profundal, zooplankton and fish.

Lakes	Poly-/Monomorphic	Littoral	Profun-dal	Zooplank-ton	Fish
Ankarvattnet	Polymorphic	0.05	0.13	0.82	0.02
Butjärn	Polymorphic	0.28	0.36	0.31	0
Lilldjupvattnet	Monomorphic	0.00	0.14	0.56	0
Lillsjön	Monomorphic	0.04	0.18	0.84	0
Nedre härbergsvatt-net	Monomorphic	0.02	0.02	0.61	0
Rengen	Monomorphic	0.00	0.11	0.86	0
Stordjupvattnet	Monomorphic	0.80	0.00	0.60	0
Åkersjön	Monomorphic	0.00	0.00	0.50	0

The association between average biomass of invertebrates caught in the traps and the proportion of littoral prey found in diet of Arctic charr was not statistically significant (linear regression, p =0.09464, n=7, Figure 4).

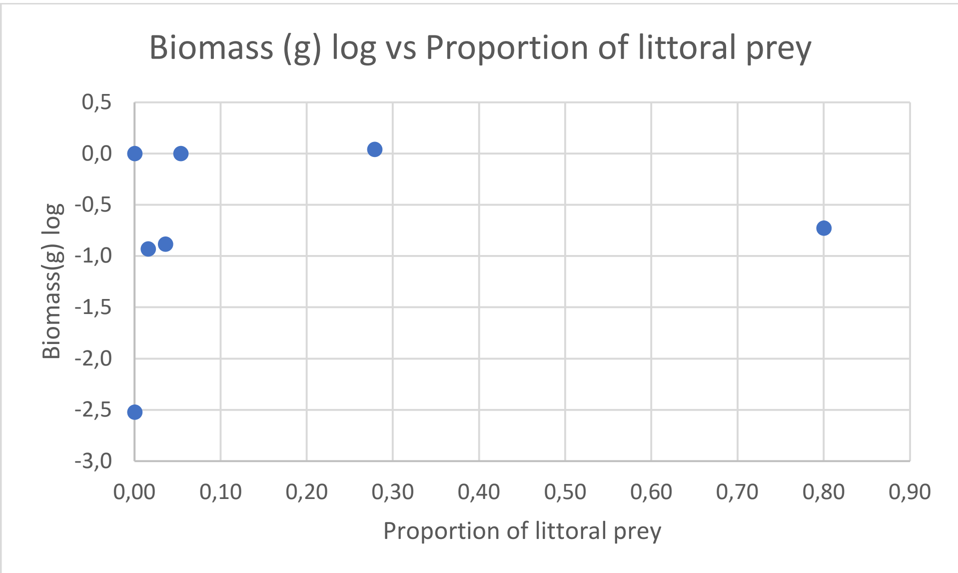

Figure 4. Biomass (g) of invertebrates caught in the bags against average proportion of littoral prey found in the diet of Arctic charr, logged values, p =0.09464, n=7 (lakes studied with both traps and diet)

4 Discussion

4.1 The most important results of this study

My study brings new insights by showing that polymorphic and monomorphic populations of Arctic charr might be associated with invertebrate prey communities that differ in composition. A comparison between mean biomass of individual taxa shows significantly higher biomass of *Amphipoda* in polymorphic lakes (table 2). Although the differences were not significant, the average catches of the Trichopteran families *Limnephilida*e and *Phryganeidae* were also higher in the ecosystems with two morphs of Arctic charr (table 2). These three invertebrate groups are likely to be sensitive to predation (Carlisle and Hawkins 1998) as size of the individuals are relatively large, and they in some cases have a larval stage that spans more than one growing season. Hence, this could indicate that the level of benthivory is higher in monomorphic lakes, where the biomass shows a non-significant trend of being lower than in polymorphic lakes. This indication in my study may support the results of a previous study on the link between whitefish polymorphism and littoral invertebrate biomass (Stenman 2014).

There was no correlation between biomass found in the littoral insect traps and proportion of littoral invertebrates found in the Arctic charr stomachs (figure 4). Therefore, this study finds no direct support for the idea that charr avoiding the littoral zone will have a positive effect on the standing biomass of littoral benthic invertebrates. However, the information that could be drawn from this comparison was reduced by the fact that there were low levels of benthivory in my studied charr populations. Hence, this subject will require further studies, ideally involving more lakes and charr diet data spanning larger parts of the growing season

In general, the Arctic charr seems to feed mainly on zooplankton in these lakes. If they search for other prey, they seem to prefer the profundal instead of the littoral in most of the sampled lakes (table 3). Moreover, out of 304 stomachs from Arctic char only 1 contained fish as prey. Hence, my study does not support earlier findings of larger Arctic charr eating fish (Malmquist et al 1992, Jonsson & Jonsson 2001), as many individuals included in my study were large enough (Appendix 2) to be potential fish-eaters and/or cannibals (Andersson 2005).

For resource polymorphism to occur there must be more than one morph existing. In one of the polymorphic lakes included in the diet study, Ankarvattnet, zooplankton were highly dominant in the diet and there were few signs of a resource polymorphism. In the other lake with body size polymorphism, lake Butjärn, a greater diversity in the diet of Arctic charr is revealed (table 3), potentially indicating resource-driven polymorphism. The fishes caught in this lake seems to eat from everything available with some examples of individuals eating 100 % zooplankton or littoral and/or profundal bottom fauna. In fact, Butjärn is the only lake in my study that seems to host a population of Arctic charr eating equally from three different habitats (i.e., profundal invertebrates, littoral invertebrates, and pelagic zooplankton). Supported by both the catches in insect traps and prey found in the stomachs, it seems that the Arctic charr in lake Butjärn uses many habitats (Appendix 1). Ecotypic differentiation into several different habitats has been reported for charr in several lakes, most famously in lake Thingvalavatn that hosts four different morphs of Arctic charr (Malmqvist et al 1992).

I found no correlation that length of the fish relates to diet. This study cannot support earlier studies of juvenile fish feeding on prey in the littoral and dwarfs feeding on prey in the profundal (Knudsen et al 2006; Knudsen et al 2016; Smith & Skúlason 1996). Because data in this study is based mainly on monomorphic lakes it cannot explain why dwarf and juveniles are feeding on different prey. More studies are needed.

4.2 Limitations in this study

The littoral invertebrate study included four lakes with polymorphic charr, and the diet study included only two lakes with polymorphic charr. Ideally, this study should be expanded to include more lakes of both the monomorphic and polymorphic lake categories. Collection of stomachs from Arctic charr should be done in all seasons so all ranges of prey are active. Generally, more polymorphic lakes need to be studied. A better knowledge is needed of exactly where bags should be placed in a lake to study biomass production such as: distance from shore, type of bottom structure and other. In future studies the concentration of zooplankton should be analysed in different ecosystems. How the geographical condition such as depth and type of bottom of the lake influence on the ecosystem should be studied. When adding the trout into the equation we should ask how the different size of individuals of this species affects the ecosystem in a lake with Arctic charr. Another study should answer if a lake can be described as something in between poly- and monomorphic. It has been shown that the interactive segregation between two morphs of whitefish is related to resource competition. Correspondingly, a study of Arctic charr gillrakes in both poly- and monomorphic lakes should be performed to see if they display specialized adaptions to eating zooplankton (Bolnick et al 2004).

4.3 Conclusions

This study could not show any connection between Arctic charr polymorphism, and the biomass of benthic invertebrates. However, large, predation-sensitive groups were more common in lakes with polymorphic charr, which may partly support the idea that biomass of invertebrates is lower in a monomorphic lake than a polymorphic (Stenman 2014). Unlike previous studies (e.g., Malmquist et al (1992) and Knudsen et al (2006), I found no correlation between charr length and choice of prey. The results from stomach content also show that Arctic charrs consumed zooplankton to a large extent, but their diets also included other types of prey. The reason why they choose zooplankton before littoral bottom fauna could be competition or predation. More studies are required.

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Popular science summary

Men and women who like sportfishing, and others of course, are all concerned about climate change. What impact will a new climate have on our way of experiencing nature? What will sportfishing look like in the future? Which species will gain in number, and which one will decrease due to competition and warmer waters? What do we know of the ongoing processes within species? This Master thesis studied the production of bottom fauna with bags and the stomach content from Arctic charr. The results show that the Arctic charr eats a lot of zooplankton. In all lakes studied the zooplankton was the dominating prey. If there are other resources, the Arctic charr will use them like in Butjärn. Butjärn is an extreme lake in many senses. Here we got a jackpot in the insect traps with a high biodiversity of bottom fauna. In the stomach content of Arctic charr we also could see a large variety of insects. Only one fish eating Arctic charr was found. Has polymorphism anything to do with the behaviour of the Arctic charr? How does the ecosystem differ between lakes with or without polymorphs of Arctic charrs? In this study only two lakes with polymorphism were studied on stomach content. The study of biomass production found no statistical proof of the difference between poly- or monomorphism. A larger study is needed. We still don't know much about how this will affect the species over time. Witnesses is talking about warmer waters in extreme summers causing them to migrate. Locals talk about decreasing populations of Arctic charr and increasing populations of salmon trout. More research is needed in this field.

Acknowledgements

Here comes my Master thesis about Arctic charr. For a fisherman like myself it's been a very interesting process. fI go. I have met very cooperative and nice locals all over the west of Jämtland. Thank you all for your kindness! This master thesis would not have come true without a great portion of patience and a lot of support from my wife, Maja Sund. I also like to thank my supervisors Gunnar Öhlund and Karin Nilsson at SLU. My fieldwork would not have been a success without the help from my father-in-law, Jonne Nilsson. He accompanied me in bad weather and with a snowmobile to the fair distant lake Värjaren. I also want to thank Göran Englund who helped me during my difficult times with statistics and the studio R.

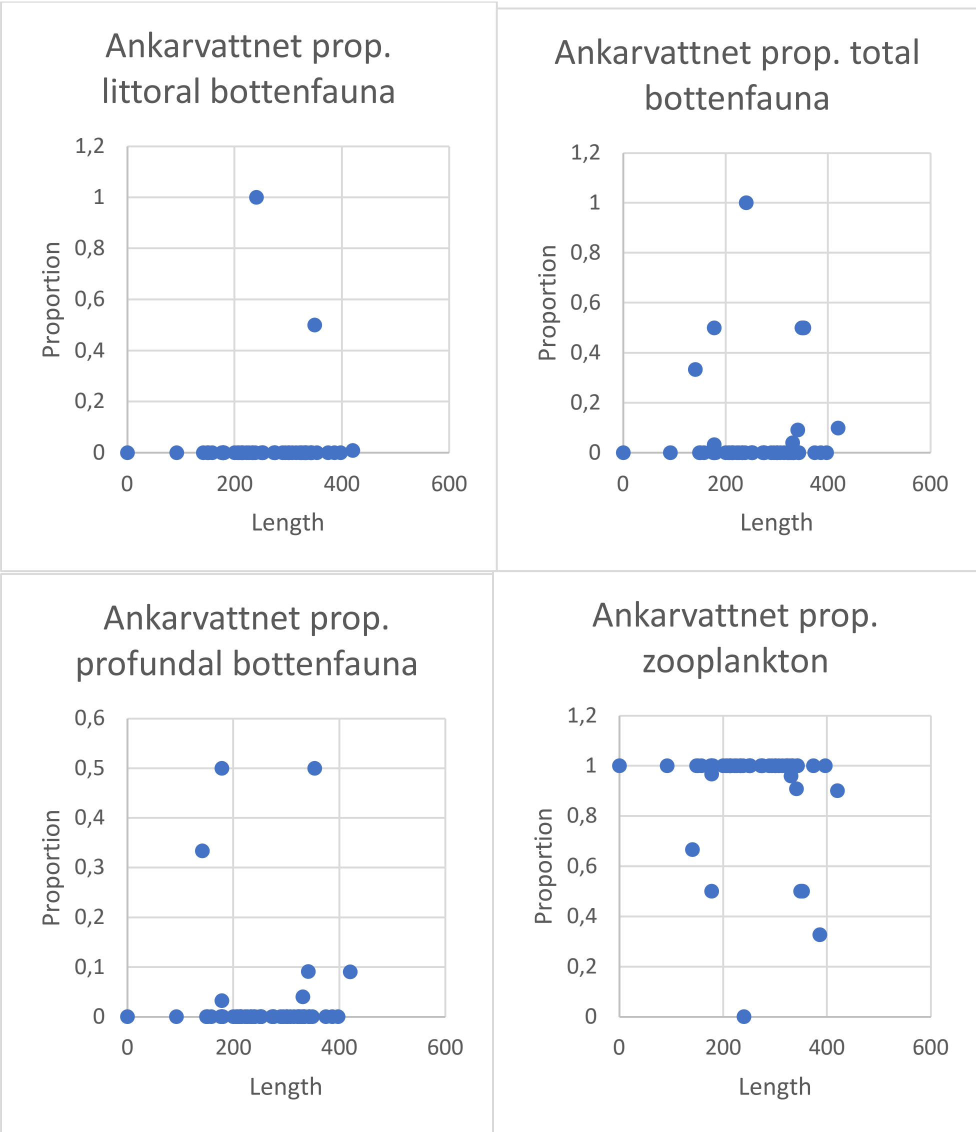
Appendix 1

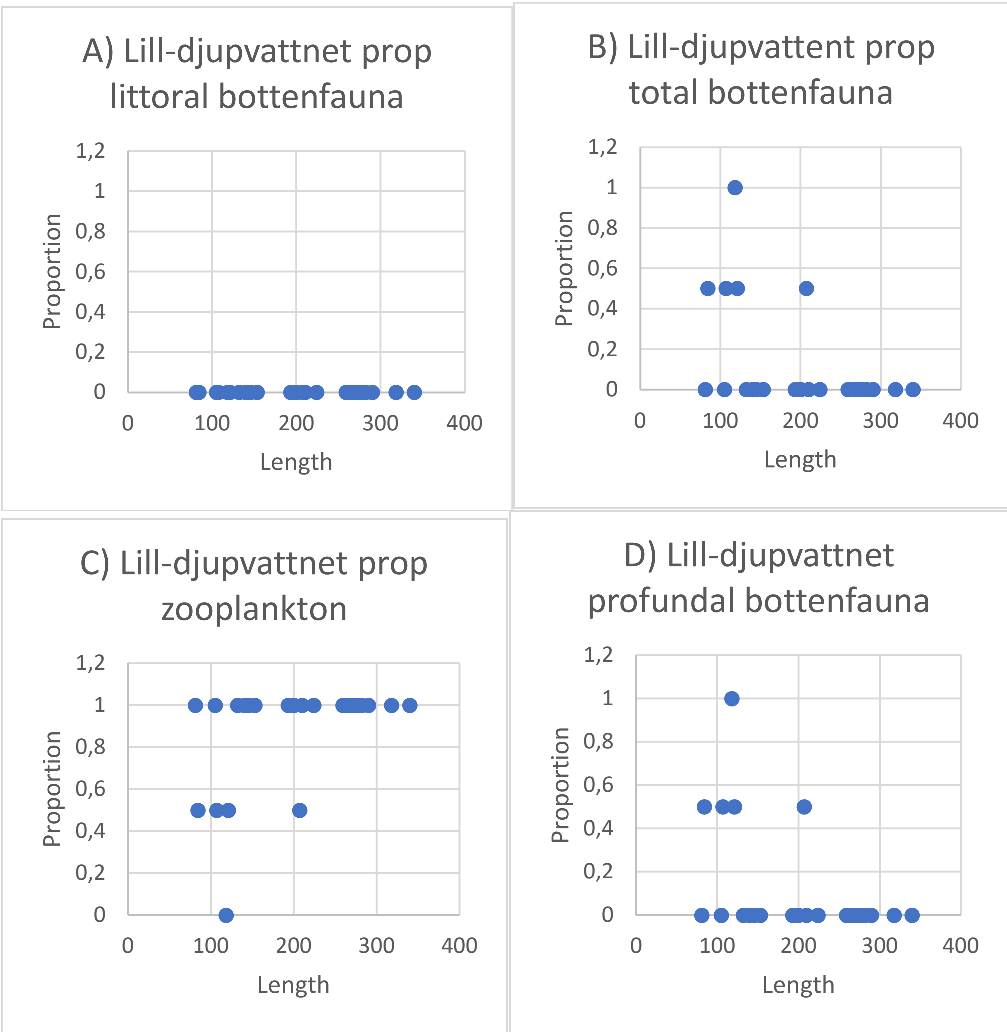
Lake+L18I	Date	Species							Sum Biom
Ankarvatt	2021-04-01	Limnephilidae	Phryganeidae	Heptageniidae	Chloroperlidae	Amphipoda	Zooplankton	Other	(mg)
Sum biomass									**0**
Jorm	2021-04-01								
Sum biomass						68,80			**68,80**
Bodtjärn	2021-04-02								
Sum biomass		153,46	311,49	7,04	1,30	622,67		0,18	**1096,15**
Åkersjön	2021-04-02								
Sum biomass				0,22			0,10	0,00	**0,33**
Lillsjön	2021-04-03								
Sum biomass		11,260	108,989	10,137			0,013		**130,40**
Bergsjön	2021-04-03								
Sum biomass			69,69			85,39	0,03		**155,11**
Stordjupv	2021-04-06								
Sum biomass		2,52	63,15	14,60	8,61	98,08	0,54		**187,50**
Lilldjupva	2021-04-06								
Sum biomass									**0**
Nedre Här	2021-04-11								
Sum biomass		95,89		10,91		10,40	0,26		**117,46**
Värjaren	2021-04-15								
Sum biomass					36,85		1,28	0,01	**38,14**
Blomhöjd	2021-04-17								
Sum biomass				5,62			0,97	0,01	**6,72**

Table of biomass found in bags

Appendix 2

Proportion of different prey found in stomachs of Arctic charrs




A) Lill-djupvattnet prop littoral bottenfauna
Proportion
1,2
1
0,8
0,6
0,4
0,2
0
0
100
200
300
400
Length
B) Lill-djupvattent prop total bottenfauna
Proportion
1,2
1
0,8
0,6
0,4
0,2
0
0
100
200
300
400
Length
C) Lill-djupvattnet prop zooplankton
Proportion
1,2
1
0,8
0,6
0,4
0,2
0
0
100
200
300
400
Length
D) Lill-djupvattnet profundal bottenfauna
Proportion
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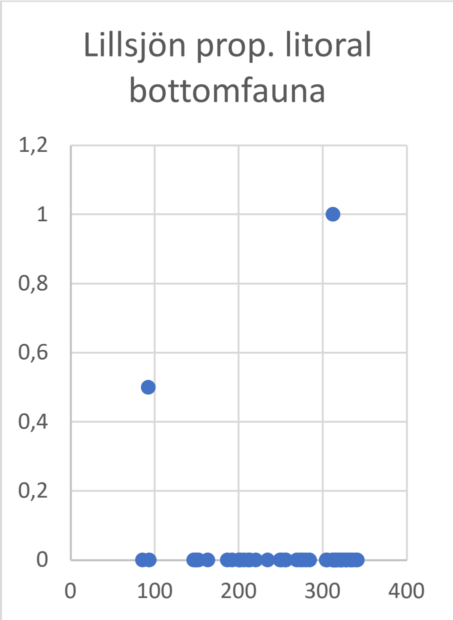
1
0,8
0,6
0,4
0,2
0
0
100
200
300
400
Length


Lillsjön prop. litoral bottomfauna
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0,8
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0,4
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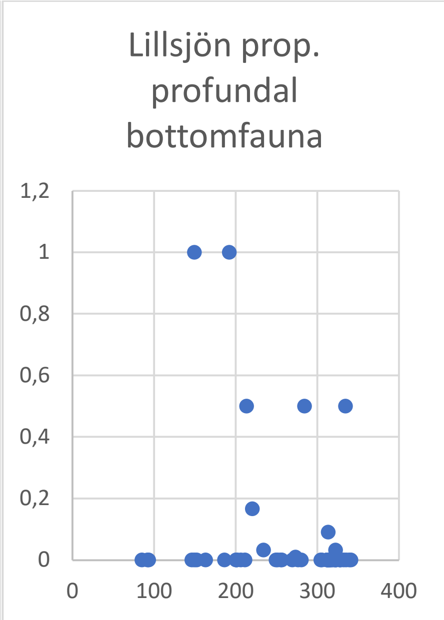
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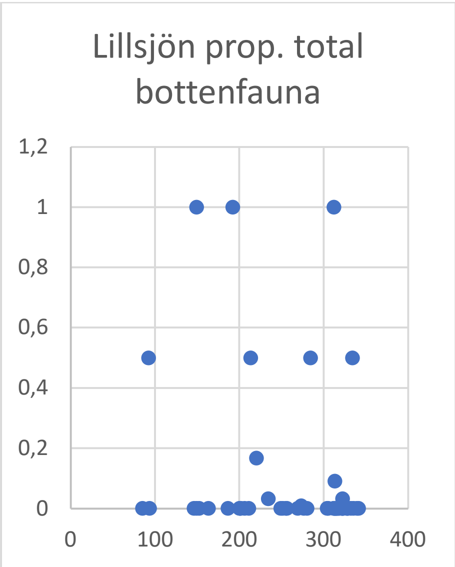
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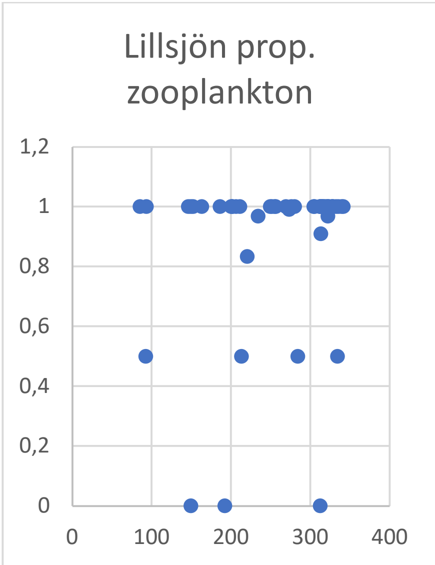
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0,4
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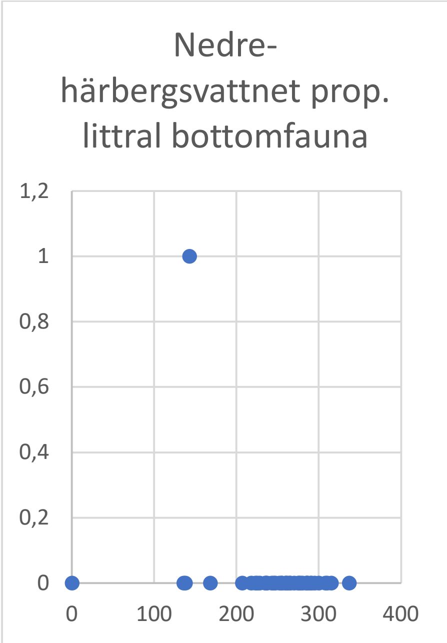
100
200
300
400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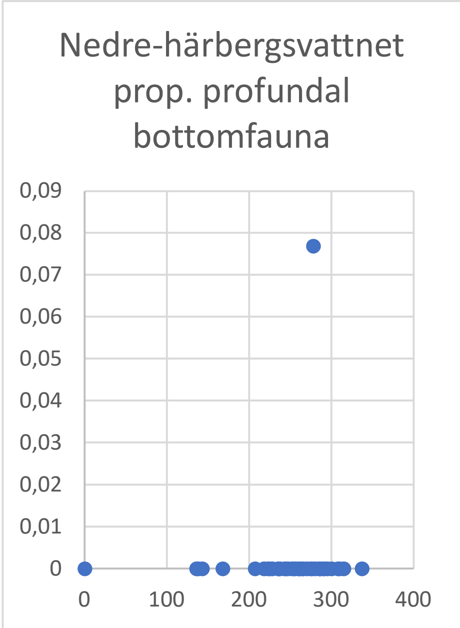
0,4
0,2
0
0
100
200
300
400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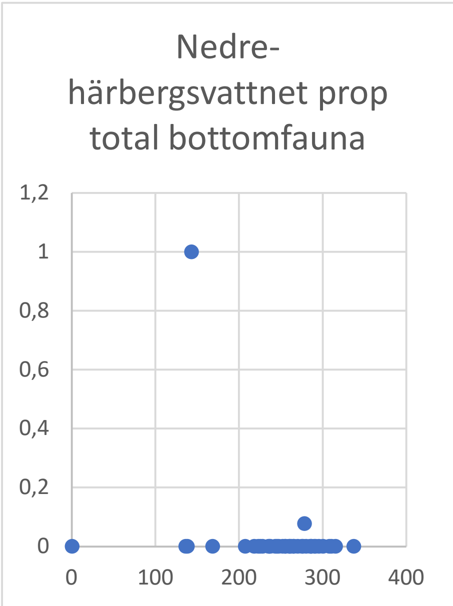
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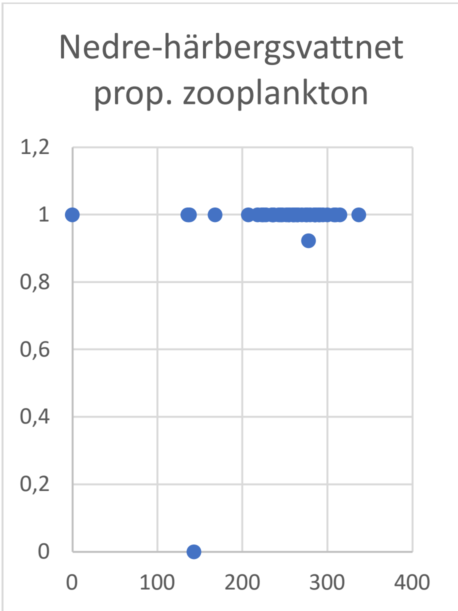
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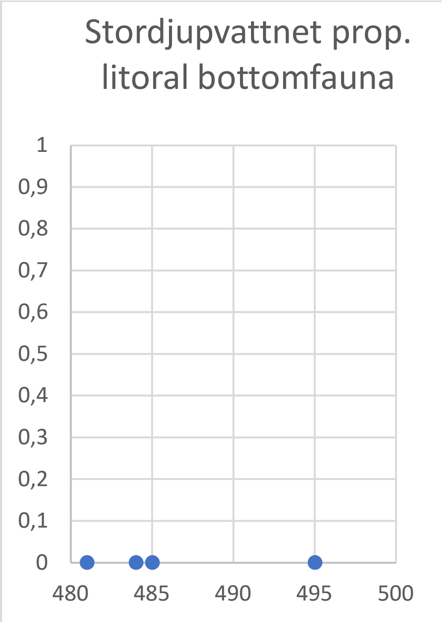
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0
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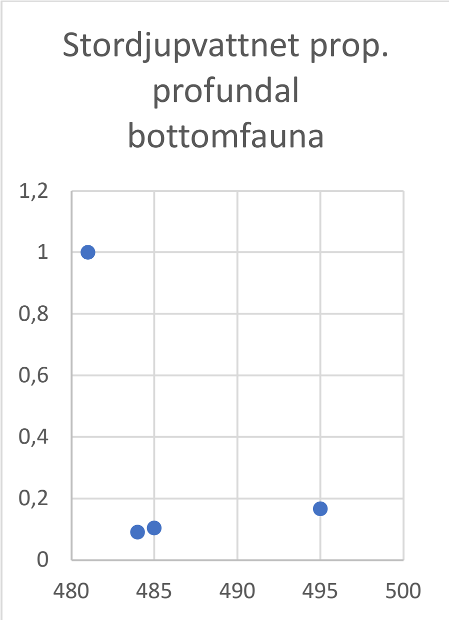
485
490
495
500

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485
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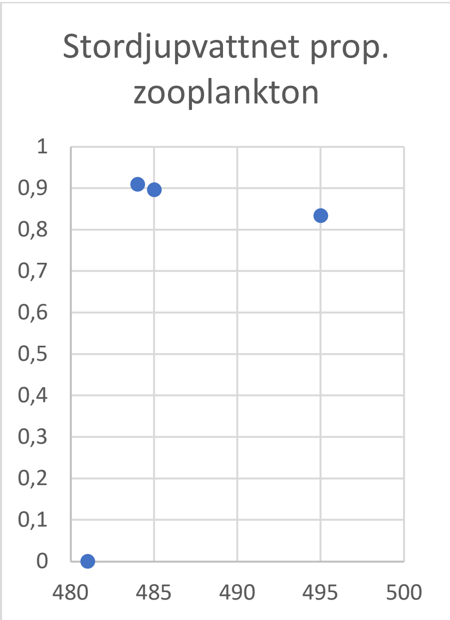
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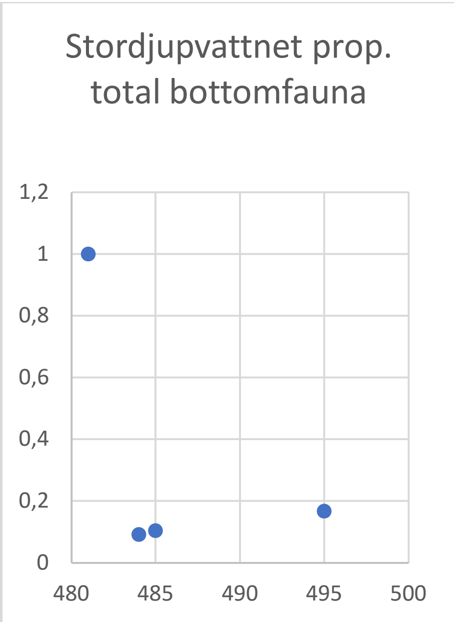
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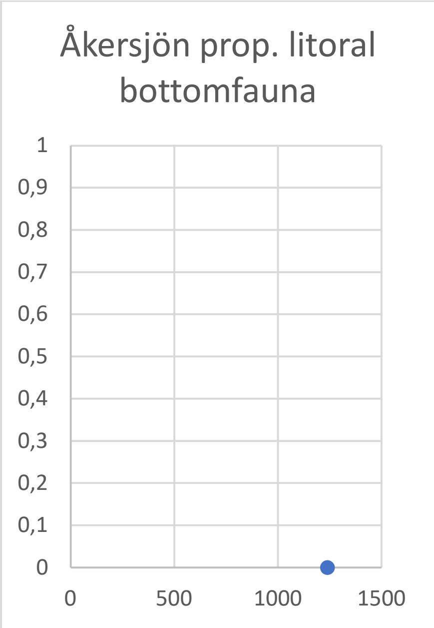
Åkersjön prop. litoral bottomfauna
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0,2
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0
500
1000
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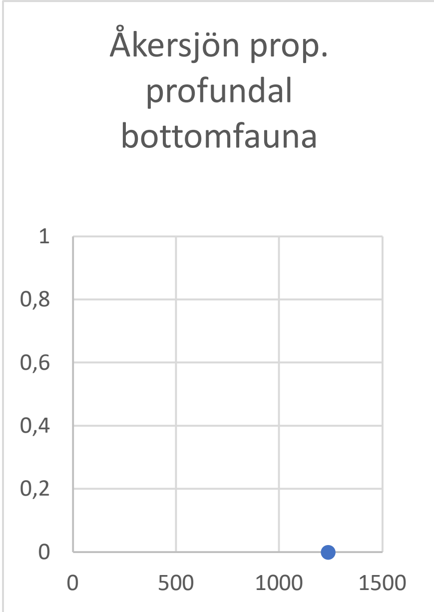
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1
0,8
0,6
0,4
0,2
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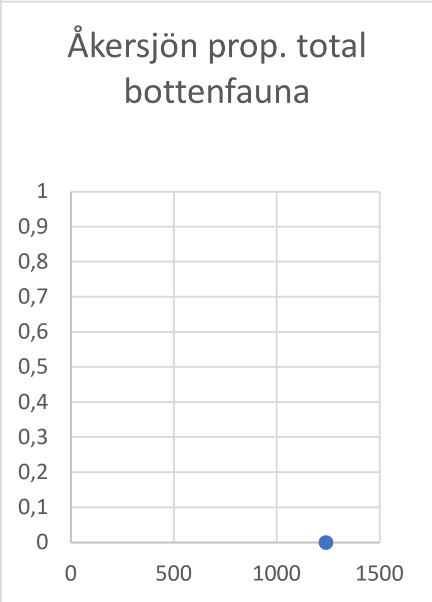
1000
1500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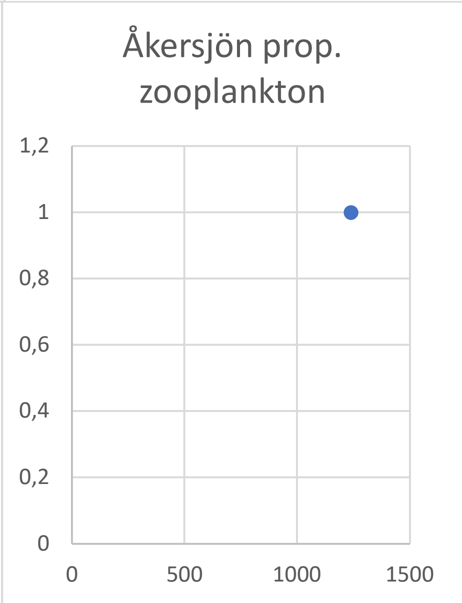
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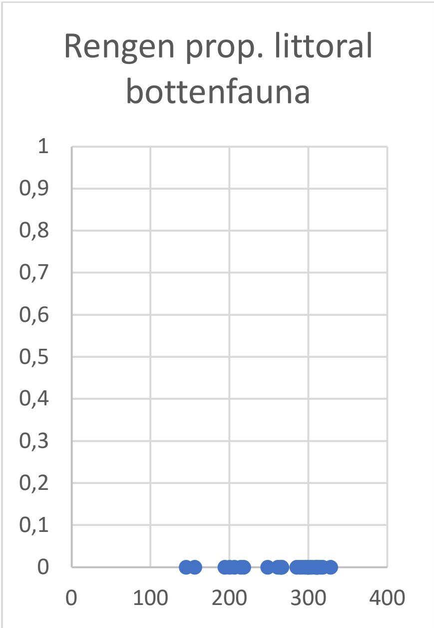
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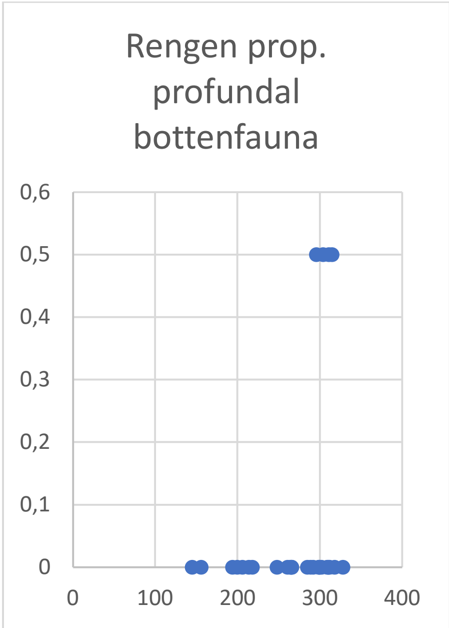
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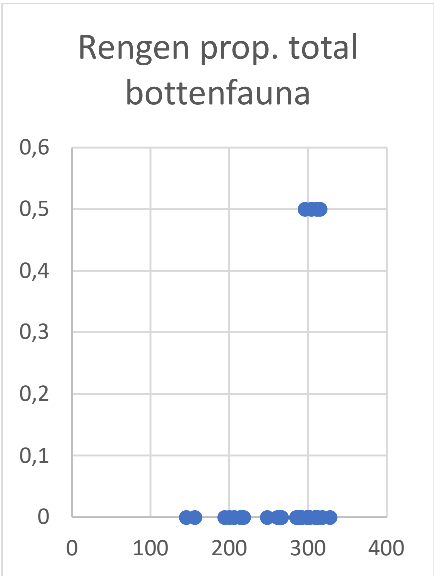
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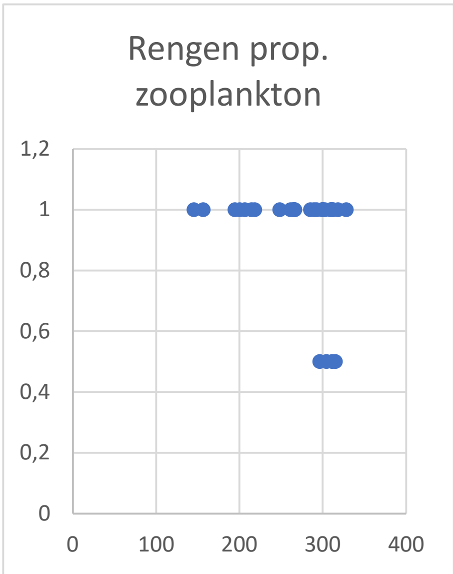
Rengen prop. zooplankton
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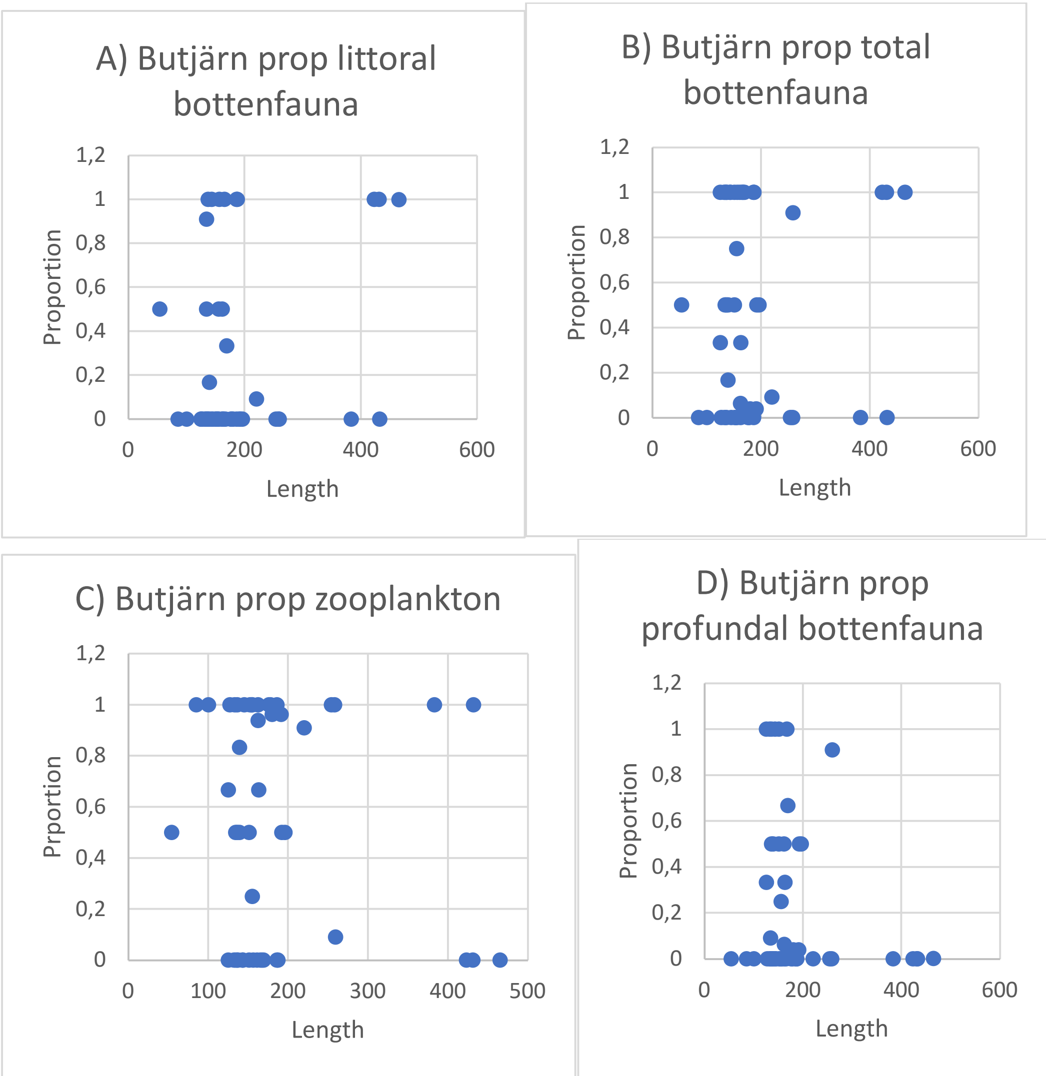

Figures. These figures show the proportion of littoral bottom fauna, proportion of profundal bottom fauna, proportion of total amount of bottom fauna and the proportion of zooplankton. All the content was found in the stomachs of Arctic charr catched in different lakes.

Appendix 3

Figures from Studio R to give an image of statistics.

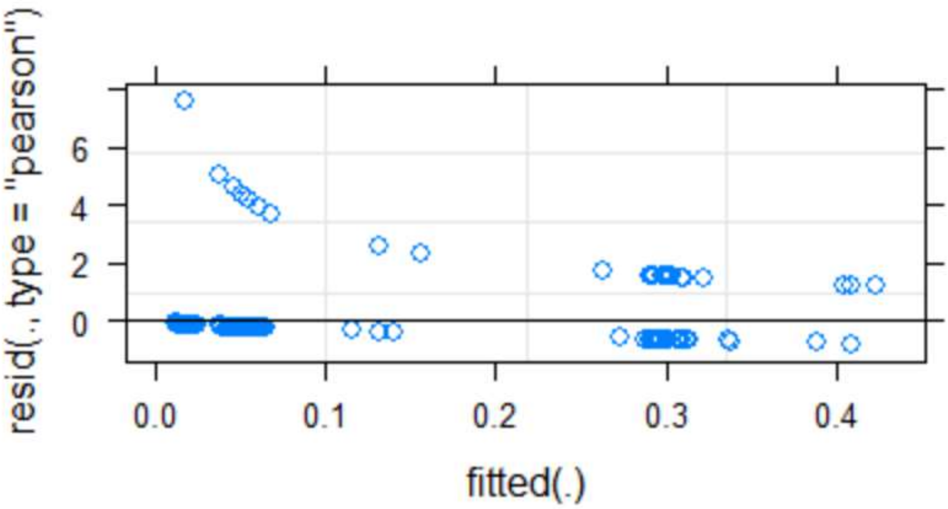

Figure Relationship between occurrence of littoral invertebrates found in diet and fish length

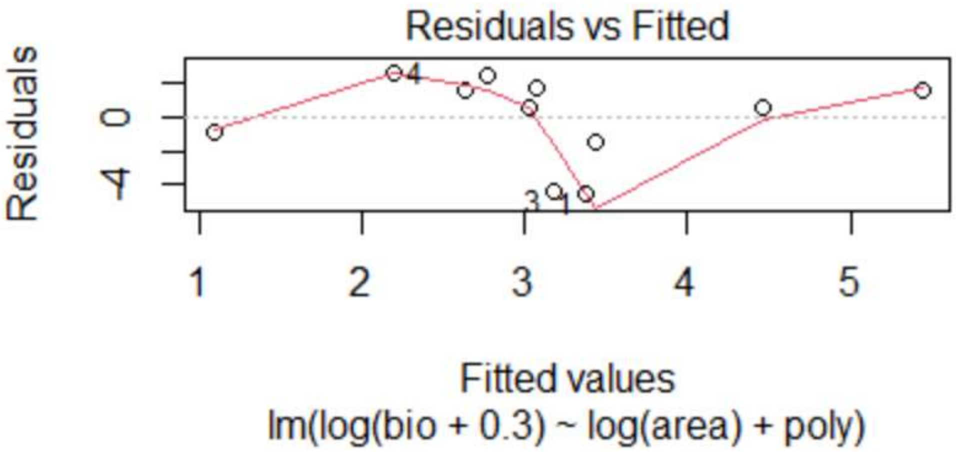

Figure Residuals shows no connection to estimated values of lm(log(bio+0.3)~log(area)+poly) analyses..

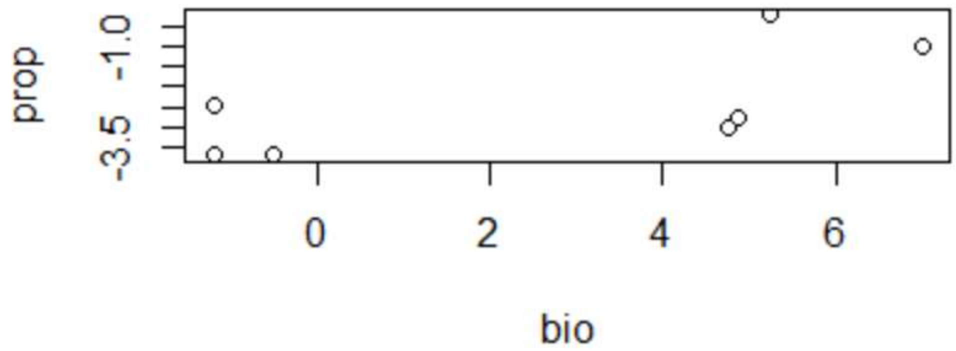

Figure Proportion of littoral prey found in diet against the biomass of invertebrates caught in the traps.

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