The road toward sympatric speciation in whitefish.

The effects of divergent selection on European whitefish (*Coregonus lavaretus*) size and behavior, and effects on zooplankton communities.

William Hatchett
Abstract

For almost every organism there are large gaps in our knowledge about the processes that leads to speciation. The changes an organism undergoes before divergence has occurred have remained a mystery, as it is difficult to say whether or not a species is going to diverge and when. To investigate this unknown the European whitefish (*Coregonus lavaretus*) and the northern pike (*Esox lucius*) were studied, as they produce a repeatable and predictable pattern of speciation in sympatry. To investigate the changes in phenotypes and behaviour in whitefish that precedes divergence, two lake populations were examined, Gräsvattnet and Ringsjön. Gräsvattnet was used as a control, with a population of whitefish but an absence of pike, whereas Ringsjön has a population of whitefish that invaded from Gräsvattnet and a pike population. The presence of pike presumably exerts divergent selection on the whitefish population. Fish and zooplankton were surveyed in both lakes from 1970 to the present day, which allows us to compare how whitefish populations and their resources change in the presence and absence of pike. The results found in Ringsjön show; (1) a change in habitat use, (2) a change in diet from pelagic to benthic, (3) an increase in the relationship between individual body size and diet and (4) a decrease in average size over the course of the study. (1) The presence of pike is believed to have forced the whitefish into the pelagic which could be seen in the result, with an increase in individuals caught in the pelagic. (2) The change in diet is thought to be caused by a resource competition created by individuals being forced to use the pelagic. Although insignificant this led to an overall reduction in zooplankton abundance by almost 40% which could have intensified competition. The resource competition could then have been intensified further by the change in composition of zooplankton relative abundance. (3) The increase in relationship between individual body size and diet is thought to increase due to the resource competition between smaller and larger individuals in the pelagic. Smaller individuals are better competitors than larger individuals for pelagic resource which could have led to the larger individuals switching to a more benthic diet. (4) The decrease in average size is thought to be caused by negative selection for larger individuals. Larger individuals have switched to a more benthic diet, and although the individuals are larger they still face the risk of predation in the littoral zone as they have not outgrown the gape size of the pike. This could have led to the average size reduction that may be the first steps in speciation, and ultimately leading to the divergence of two morphs by sympatric speciation in Ringsjön. In Gräsvattnet over the course of the study there were few and small changes in whitefish size, zooplankton relative abundance in the diet and in the environment. The results in Gräsvattnet could however suggest resource competition for benthic resources. Although resource competition is thought to be an important factor in the speciation of whitefish, without predation pressure no speciation occurs. This result could suggest the importance of predation pressure in the speciation of whitefish.

Key Words: sympatric speciation, selection pressures, divergence, speciation
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1. Introduction and Background

Studying divergence as a whole is often quite problematic, as most empirical studies of divergence can only provide a snapshot of the speciation process. Studies typically focus on systems in an early stage of divergence and assume that selective processes acting at present were also responsible for the initiation of divergence. However, the processes that lead to divergence have never been observed directly. The reason for this is that it difficult to say whether or not a species is going to diverge, making the study of an organism on the road to divergence extremely challenging (Nosil 2012). Sympatric speciation, often defined as evolutionary divergence without physical barriers to gene flow, is the rarest and most controversial form of speciation. It was considered theoretically implausible in the mid 1900’s (Mayr 1963), but more recent theoretical and empirical work has made it a plausible alternative to allopatric speciation. Studying sympatric speciation is challenging as it involves feedbacks between ecological, genetic and behavioural mechanisms or processes (Berlocher & Feder, 2002).

Some of the best examples of speciation in sympatry are found in freshwater fish taxa in post glacial lakes. These fresh water fish taxa form sympatric ecotypes pairs differing in ecology, morphology and reproductive biology. These ecotype pairs typically consist of either large benthic morphs known as giants, or small-bodied pelagic morphs known as dwarfs (Öhlund 2012). The dominating hypothesis for how divergent natural selection can arise in postglacial fish communities suggests that competition for two food sources, benthic macroinvertebrates and pelagic zooplankton, leads to selection on specialisation for one of the two resources. This is thought to be the cause of sympatric speciation and the formation of the giant benthic morph and the dwarf pelagic morph (Martin & Pfennig 2010). However the pike-whitefish system model suggests that without the presence of predation pressure no speciation will occur, making it a vital requirement in regards to speciation. The pike-whitefish model shows that the presence of a large predator, the northern pike (Esox lucius) induces divergence into dwarfs and giants in large lakes and one or the other in smaller lakes (Öhlund 2012).

1.1 Aims and objectives

I study the pike-whitefish system, which is a promising model system for studying in situ sympatric speciation. It has been shown in European whitefish (Coregonus lavaretus) that the presence of pike cause a repeatable and predictable pattern of sympatric speciation (Öhlund 2012). A study of whitefish populations in 358 lakes show, that the presence of pike, a large predator, induces divergence in the whitefish population into giant and dwarf morphs in large and deep lakes, and either one or the other in small lakes. Studies of introduced populations show that the probability of finding the dwarf-giant ecotype pair in large deep lakes reached 50% after only 72 years. This allows us to identify introduced whitefish populations that has not diverged, but have a very high probability to diverge in the near future (Öhlund 2012).

To investigate the changes in behaviour and phenotypes of whitefish that precede divergence, two lakes were examined. The first lake used in this investigation is Gräsvatnet, which has had a population of whitefish since 1974 (Filipsson 1994), however this lake is used as a control as the lake does not have a pike population. The second lake is Ringsjön, which has a population of whitefish that invaded from Gräsvatnet between 1982 and 1986 (Filipsson 1994). Ringsjön also has a pike population which presumably exerts divergent selection on the whitefish population. Both lakes have been surveyed for fish and zooplankton from 1970 to the present day which allows us to investigate the effects of pike presence on the whitefish populations, and their resources before divergence has occurred. Our hypothesis is that there should be minimal change in the Gräsvatnet’s whitefish
population, whereas divergent selection caused by the presence of pike in Ringsjön will produce changes that could ultimately lead to divergence.

2. Materials and methods

2.1 Sampling scheme and sample collection

Olof Filipsson at the Freshwater Research Institute, Drottningholm collected whitefish and zooplankton (Except for Bytetrophes and Leptadora due to lack of population data) from Gräsvattnet and Ringsjön every August in 1970, 1974, 1978, 1982, 1986, 1990, 1994, 2001 and 2013. A standardized set of gill nets (20 benthic nets: 36 x 1.5 m, multi-mesh with mesh sizes 10, 12.5, 16.5, 22, 25, 30, 33, 38, 43, 50, 60, and 75 mm; 36 pelagic nets: 30 x 6 m, single-meshed nets with mesh sizes 12, 16, 18, 20, 24, 28, 36, 48, and 60 mm) was used to estimate catch per unit effort (CPUE) and size distribution of whitefish in benthic and pelagic habitats in both lakes. Each fish was measured to the nearest mm (total length). Fish stomachs and guts were dissected and labelled along with the data collected from the fish. Zooplankton was sampled with a 100 mm-mesh net (diameter 20/25 cm) and using five vertical tows from 25 m depth to the surface. All samples were stored in formaldehyde or a mixture of formaldehyde and calcium carbonate. Before analyses the samples was rinsed with water for several days and then transferred to 70% ethanol through an alcohol gradient of 30%, 50% then finally 70%.

2.2 Sample processing

Pia Bartels at Department of Ecology and Environmental Science, Umeå University, counted, measured, and identified the zooplankton samples using a stereomicroscope. Biomass of zooplankton and invertebrates was calculated using published mass-length relationships (Botrell et al. 1976) and all relative abundances are based on biomass. I made a selection of 40 fish from Ringsjön and 20 from Gräsvattnet from the years 1986, 1990, 1994 and 2001. For each year the population was split according to where they were caught and again into the largest and the smallest fish individuals, an equal number of individuals was then selected, dissected and the content was then removed. The stomach content was identified, counted and measured (up to 30 individuals of each species) using a stereomicroscope.

2.3 Data analysis

The Ivlev’s electivity index was calculated as \( E_i = (p_i - r_i) / (p_i + r_i) \), where \( p_i \) is the relative abundance of prey type \( i \) in the diet and \( r_i \) is the relative abundance in the environment. Relative abundances in the diet \( (p_i) \) was logit transformed using \( p_i = \logit^{-1}(p_i) \) before statistical analyses.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>Gräsvattnet</th>
<th>Ringsjön</th>
<th>1-Pi</th>
<th>1-Pi</th>
</tr>
</thead>
<tbody>
<tr>
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<tr>
<td>Size</td>
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<td>( \beta_2 ) 2.126</td>
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<td>1-Pi</td>
</tr>
<tr>
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<td>( \beta_{1,2} ) 1.389</td>
<td>1-Pi</td>
<td>1-Pi</td>
</tr>
</tbody>
</table>

Table 1. Morphological and geographic data for Gräsvattnet and Ringsjön.

<table>
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<th>1</th>
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<tr>
<td>Size</td>
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<td>( \beta_1 ) 0.4583</td>
<td>1-Pi</td>
<td>1-Pi</td>
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<tr>
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<td>( \beta_{1,2} ) 0.6337</td>
<td>1-Pi</td>
<td>1-Pi</td>
</tr>
</tbody>
</table>

Table 2. Multiple regression models using year of sampling (Time), whitefish size, and their interaction as predictors of logit transformed relative abundances of prey from benthic, pelagic and terrestrial habitats. The number of degrees of freedom for the error term was 89 for Gräsvattnet and 151 for Ringsjön.
3. Results

The average size of the whitefish in Ringsjön dropped by around 50 mm in the first 4 years and dropped by a total of 70 mm over the course of the study (Fig. 1, Ringsjön linear regression: \( t = -5.088, N = 460, p = 5.28 \times 10^{-07} \)). The whitefish in Gräsvatten showed a small but significant increase in average size (Fig. 1, Gräsvatten linear regression: \( t = 2.52, N = 464, p = 0.0121 \)).

In Gräsvatten a larger proportion of individuals were caught in the benthic zone and in Ringsjön there was a large change in proportion over time, with an increase in the pelagic (logistic regression, \( Z = 3.63, p = 2.80 \times 10^{-04} \)). There was a smaller but significant change in proportion over time in Gräsvatten (logistic regression, \( Z = 0.022, p = 4.48 \times 10^{-06} \)) (Fig. 2).

The relative abundance of pelagic, benthic and terrestrial prey in the diet did not change over time in Gräsvatten. (Table 2, Fig. 3). In Ringsjön there were significant changes in the relative abundance of both pelagic and benthic prey over time and a slight significant change in terrestrial prey over time (Table 2 & Fig. 3).

In Gräsvatten there were no significant variation in the diet with whitefish length (Table 2 & Fig. 4), whereas in Ringsjön there was a shift from pelagic to benthic diet with increasing fish size (Table 2 & Fig. 4).

For Ringsjön there was a significant time x size interactions (Table 2). Figure 5 shows that it occurred because the relationship between body size and diet was weak in 1986 and became more pronounced over time.

Fig. 1. Trends in the average size of whitefish in Ringsjön and Gräsvatten over time. Error bars denote standard errors.

Fig. 2. The distribution in percentage of whitefish caught in each habitat over time.

Fig. 3. All sampled individual's stomach content as total relative abundance of benthic, pelagic and terrestrial prey biomass. For 1994 in Gräsvatten there is a smaller pie chart which represents the values obtained when including the data for a single individual who consumed 80% of the total biomass for that year.
In both Gräsvattnet and Ringsjön, *Bythotrephes* or copepods made up a large proportion of the pelagic diet (fig. 6). In Gräsvattnet the rest of the pelagic diet was *Daphnia*, which remained constant over time. In Ringsjön the majority of the diet consisted of *Bosmina* during the study period. Out of the seven zooplankton species found in the pelagic diet only four had a noteworthy contribution to the pelagic diet (fig. 6).

The relative abundances of *Daphnia, Bosmina* and copepods in Gräsvattnet remained constant throughout the study. In Ringsjön the *Daphnia* showed a dramatic change as it was driven to less than 1% in 1990, with the copepod and *Bosmina* populations increasing slightly (Fig. 7).

Zooplankton biomass in Gräsvattnet varied insignificantly over the study period (Fig. 8, Gräsvattnet linear regression: t=0.79, N=4, p=0.51). In Ringsjön biomass zooplankton decreased throughout the study but was also insignificant (Fig. 8, Ringsjön linear regression: t=-2.64, N=4, p=0.12).

Gräsvattnet showed a positive correlation between fish size and selection on zooplankton size. Small fish selected small and medium zooplankton, medium fish selected medium zooplankton and large fish selected large zooplankton (Fig. 9). In Ringsjön there is a similar trend, however medium fish select highly on large zooplankton and large fish only select for medium size zooplankton. The latter result may be explained by the small and biased sample size of large fish in Ringsjön; large fish were only caught the first (N=12) and second (N=1) sampling occasion.

Fig. 4. The relative abundance in the diet of prey originating from different habitats. Each whitefish individual is represented by three data points, denoting the proportion of resource from each habitat. Trend lines represent an ordinary linear regression line and are used to visualize the patterns seen in the data.

Fig. 5. The relative abundance in the diet of prey originating from different habitats in Ringsjön from 1986 to 2001. Each whitefish individual is represented by three dots denoting the proportion of food from each habitat. Key is found in figure 4. Trend lines represent an ordinary linear regression line and are used to visualize the patterns seen in the data.
Fig. 6. The relative abundance of zooplankton taxa in the diet of whitefish in Ringsjön and Gräsvattnet.

Fig. 7. Changes over time in the relative abundance of zooplankton in the environment in Gräsvattnet and Ringsjön.

Fig. 8. Changes over time in zooplankton biomass in Gräsvattnet and Ringsjön.

Fig. 9. Ivlev’s electivity index for small, medium and large sized whitefish feeding on zooplankton prey of different sizes. Positive values characterise positive selection and negative values characterise negative selection. Small fish are <200mm, medium fish are 200-300mm and large fish are >300mm.
The size of zooplankton in the environment and in the diet of the whitefish in Gräsvattnet did not vary over the study period (Fig. 10). In Ringsjön the size of Bosmina and copepods remained constant but Daphnia size fluctuated with a large drop in size in the lake population (Fig. 10, ANOVA: $F=212.0$, $p=3.15 \times 10^{-06}$). The size in the stomach remained large throughout the majority of the study period.

4. Discussion

It has been proposed that by using the pike–whitefish system as a model, the initiation of speciation can be studied (Öhlund 2012). For this system it is hypothesized that pike, as a large-gaped predator, can induce a between-habitat trade-off in whitefish that cause them to mature in a safe place away from predators or at a safe size out of the gap size of predators. This trade-off is thought to lead to the formation of two morphs; a large benthic morph which is relatively safe from predation as they have out grown the gape size of the littoral predator pike and can now predate on the larger food items found in the littoral zone and a small pelagic morph which avoid predation by staying in the pelagic (Öhlund 2012). This is thought to be a novel mechanism for the initiation of sympatric speciation (Öhlund 2012). The above described selection regime is believed to cause divergence in whitefish size, habitat use and diet with a common feature being the evolution of a benthic giant feeding on macroinvertebrates and a pelagic dwarf feeding on zooplankton.

As size is a key element in this model of speciation, I focused the analyses on changes in size and size-dependent traits in this study. There was a significant change in average size over time in both whitefish populations, with a small but significant increase in Gräsvattnet and a highly significant decrease in Ringsjön. Size can affect the risk of predation, with small individuals having a higher predation risk than large individuals due to the gape limitation of the predators creates an upper limit on prey size that can be ingested (Persson et al. 1996). This in turn may lead to different habitat use of small and large individuals due to the predation regimes differing between littoral and pelagic habitats; the pelagic zone is usually relatively safe from pike whereas the littoral zone is where pike can be found (Öhlund 2012). Habitat use is thought to be a contributing factor for divergence in this system. Indeed we found that the relatively small whitefish fish in Ringsjön were mainly caught in the pelagic, possibly because the whitefish are being forced to stay the pelagic due to the presence of pike in the littoral habitat. On the other hand in Gräsvattnet most whitefish were found in littoral and benthic habitats, which may be explained by the absence of pike and more productive littoral zone (Zohary & Gasith 2014).
I have also shown that in Ringsjön, the size of an individual becomes a more important factor when determining resource use. Throughout the study larger individuals had a more benthic diet whereas at the beginning of the study there was very little variation in the diet and size of individuals. Using different resources such as benthic prey items (e.g. macro invertebrates) and pelagic prey items (e.g. zooplankton) can favour different foraging behaviours and morphology (Nagel and Schluter 1998). Dietary niche differences can be an important component driving ecological speciation, and have been shown to be a key element of divergence in many freshwater fish species such as sticklebacks (Schluter 1993), Arctic char (Gislason et al., 1999) and whitefish (Kahlainen et al. 2003). A bimodal resource distribution such as the benthic/pelagic resources can cause spatial separation leading too disruptive selection, which may promote ecological divergence and could potentially lead to reproductive isolation in Ringsjön. This however does not occur in Gräsvattnet as there is no habitat restriction caused by pike and all individuals can use any food resource without fear of predation from pike. This is shown in my results as there is very little difference in the diet of small and large individuals and this does not change over time.

The results discussed so far supports the model proposed by Öhlund 2012 for divergence in the pike-whitefish system. However, it cannot be used to solely explain the observed changes seen in the Ringsjön whitefish population. My results suggest that over the study period the majority of whitefish in Ringsjön switched to a benthic diet. This seems to contradict the findings that whitefish size decreased over time and that the use of the pelagic habitat increased over time. One explanation for this result could be that the benthic prey we found in the whitefish diet was caught in the profundal. The profundal is also believed to be a habitat with low predation risk from pike that could be utilised by whitefish, although chironomids are thought to be one of the only prey available (Præbel et al. 2013). However the whitefish in this study consumed less than 2% of the total benthic biomass in chironomid’s (Data not shown) and so this explanation can be excluded. With that said I hypothesize that this change is a result of resource competition between smaller and larger individuals. As previously discussed the size of an individual can be an important factor when determining resource use; large whitefish feed efficiently on larger prey items like macroinvertebrates but are less efficient feeding on small prey items such as zooplankton (Roesch 2013). In contrast small individuals are more efficient at consuming small zooplankton rather than benthic invertebrates (Kahlainen 2003). This is supported by my results as that the size of the whitefish is positively correlated with the size of the zooplankton that is being selected for. The larger individuals in Ringsjön have changed their diet to a more benthic diet over time this may be due to increasing resource competition in the pelagic. Diet data also suggests strong resource competition in Ringsjön, as it shows that the pelagic resource is found less in the diet of whitefish over time due to decreased availability of resource. This could be explained by the fact that the pelagic resource is less abundant in the environment compared to that of the benthic resource due to resource competition in the pelagic. This result is mirrored in Gräsvattnet and may suggest higher resource competition for benthic resource as it is found less in the diet of whitefish and is less available than the pelagic resource. This could imply the importance of both predation pressure and resource competition in the process of speciation, as the population in Gräsvattnet only lacks predation from pike and shows limited to no change in behavioural and phenotypical changes.

If resource competition is the cause of a diet shift in Ringsjön there should be a corresponding change in total zooplankton abundance or in the relative abundance of key taxa in the environment (Hanazato et al. 1990). The change in pelagic resource seen in both Ringsjön and Gräsvattnet were insigificant and may be explained by changes in the climate or time of sampling. Despite this there was an overall decrease by almost 40% over the course of the study period biomass of zooplankton in Ringsjön and in Gräsvattnet there is varying levels of zooplankton. This could suggest a less stable system due to the lack of pike (Andersson 2007) or the whitefish in Gräsvattnet are not using the pelagic resource
consistent due to the availability of the benthic resource and other factors such as climate could be the cause of these variation. This may indicate that once again there is little or no competition for pelagic resource in Gräsvatnet (Casini et al. 2008). Resource competition could also be supported by the electivity results in Ringsjön, the medium sized whitefish are selecting highly on large zooplankton possibly due to a resource competition. This could reduce the number of large zooplankton that is available for larger whitefish individuals and thereby forcing them to change diet to larger invertebrate prey. Resource competition for the pelagic resource should also affect the relative abundances of zooplankton taxa in the environment (Berg et al. 1994). Whitefish are positively selecting for Bosmina and Daphnia and these taxa make up the majority of the whitefish diet, with Bosmina dominating in Ringsjön and Daphnia in Gräsvatnet. The relative abundances of different zooplankton taxa in the environment were negatively correlated to whitefish electivity, this suggests that whitefish have a top-down effect on zooplankton abundance (data not shown). There are no large changes in the relative abundances of zooplankton taxa in Ringsjön and Gräsvatnet, except for a reduction in Daphnia in Ringsjön, which coincides with an increase in selectivity for Daphnia and an increase in the size of Daphnia found in the diet compared to that found in the environment. Thus it seems that that the whitefish population in 1990 in Ringsjön were highly selective for large daphnia. However the overall effect of Daphnia on the whitefish population in Ringsjön should, be minimal as Daphnia is not a major part of their diet. The top-down effects on zooplankton in this study was also found in an investigation by Berg et al. 1994 where whitefish were introduced into a lake with pike. The Daphnia population density and mean body size was decreased and the copepod population increased, due to the release of resources (Phosphorus and chlorophyll-a concentration increased) (Bartell 1981 and Berg et al. 1994). Another possible top-down effect of whitefish could be seen in Ringsjön with the noticeable change in Bythotrephes found in the diet of the whitefish. In Ringsjön in 1986 Bythotrephes made up 50% of the diet and then dramatically dropped in 1990 to around 5%. This could imply that the Bythotrephes population suffered a large decrease due to high predation from the whitefish in 1986. This change in diet could suggest a change in the relative abundance of Bythotrephes found in the environment. It has been shown that lakes with no/small population of Bythotrephes have a higher abundance of small cladocerans and larger Leptodora populations (Foster et al. 2012). Although in Ringsjön and Gräsvatnet, the data for the relative abundance of both Bythotrephes and Leptodora found in the lake was inaccurate and so could not be used, we can see possible indications of this change in relative abundance with the reduction in average body size of cladocerans from 1986-1990 by 57%. This possible change in relative abundance would further reduce the amount of available resources for larger whitefish individuals (Bohn and Amundsen 1998).

In Ringsjön the presence of pike appears to force the whitefish into the pelagic, which should intensify competition for zooplankton between smaller and larger individuals. Small individuals should be selected for as they use pelagic resources more efficiently. Smaller individuals may also do better over time as the zooplankton may be reduced in size, by a release of resources from larger zooplankton due to reduced competition caused by whitefish predation (Bartell 1981, Berg et al. 1994) and the possible change in zooplankton relative abundance to a Leptodora dominated system. Large individuals seem to be selected against as they are less efficient at ingesting small zooplankton and could be forced by resource competition in to a more benthic diet to avoid starvation and move to the littoral habitat which has a higher predation risk. My results found in Ringsjön suggest that a combination of predation pressure and resource competition increase the importance of size for resource use which could promote divergent selection on the whitefish population and ultimately lead to sympatric speciation into a pelagic dwarf morph and a benthic giant morph. Whitefish in Gräsvatnet had a slight increase in size but overall have remain at an average whitefish size, uses more pelagic resources and spend most of the time in littoral habitat. This could imply strong competition for benthic invertebrates as these are the opposite results found in Ringsjön. However there is no change in diet overtime and small and large individuals have
very similar diets as a result of no habitat restriction from pike, implying no size dependent diet division in the population.

4.1. Conclusion

I found changes in both behaviour and phenotypes in Ringsjön which is believed to be caused by the pike–whitefish interactions and little to no change in Gräsvattnet where pike is absent. The changes seen in Ringsjön have been suggested to be the first steps towards sympatric speciation and my hypothesis is largely confirmed by the data. The changes in Ringsjön are thought to be initiated by the predation pressure from pike which forces the whitefish population into the pelagic zone, which was also the case in this study. However, the presence of a littoral predator cannot explain the change in diet found in the whitefish population, as individuals in Ringsjön switched to a benthic diet, even though average size decreased and thus risk of predation in the littoral should increase. The change in diet observed in Ringsjön is likely caused by resource competition between large and small individuals and a change in zooplankton composition which can be seen in the results. It has been shown that without predation pressure no divergence can occur (Öhlund 2012) as seen in Gräsvattnet and without resource competition there would be no need to change to a benthic diet in Ringsjön. Consequently, in the possible speciation process of the whitefish population in Ringsjön, it seems that both selection pressures are acting against larger fish; the larger fish do not compete well for small pelagic resource being forced to change to a more benthic diet where they are also at risk of predation as the population has not grown out of the pike’s gap range. This could explain the reduction in average size and may be the first steps in speciation that will lead to the divergence into two morphs and ultimately sympatric speciation.

5. Acknowledgement

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