How is the invasive zebra mussel influencing roach populations?

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Abstract

Previous studies have found differences in fish morphology between individuals of the same species living in different microhabitats of the same waterbody. It has been hypothesised that the main causes of this trophic polymorphism are trade-offs in foraging on different resources that might result in phenotypic divergence of populations. *Dreissena polymorpha*, the zebra mussel (ZM), is one of the most troublesome biological invaders in aquatic ecosystems. ZM can change the characteristics of the ecosystem and alter the availability of resources. The study was conducted in lake Erken. My results suggest that the abundances of ZM affected the availability of food resources for roach and therefore changed their diet as well as their specialisation level. Pelagic roach ate less zooplankton, more plants and more macroinvertebrates, whereas littoral roach ate less zooplankton, more plants and less macroinvertebrates. When high abundances of ZM occurred, roach developed a more littoral shape.
1. Introduction

Whenever a invasive species establishes in a new environment innumerable scientific questions arise. The introduction of alien species represents a great and generally irreversibly threat to the integrity and well functioning of the ecosystems. The zebra mussel (ZM) (*Dreissena polymorpha*) is found among the most troublesome biological invaders (IUCN 2005). Because *D. polymorpha* can filter great amounts of water, their presence implies a change in the structure of the freshwater ecosystem as a whole. They can cause significant changes to water quality, nutrients concentrations and benthic algal community structure (Thayer et al. 1997). Since zebra mussels are voracious filter feeders, a high abundance of ZM will remarkably decline the phytoplankton concentration, i.e. they cause decreased food availability for the pelagic fauna (Watzin et al. 2008). Another possible consequence of the high filtration activity might be an increase of food available for macroinvertebrates and therefore a higher abundance of macroinvertebrates in water substrate, since the mussel feces and pseudo-feces serve as nutrients for the benthic fauna (Higgins and Vander Zanden 2010). Hence a change of the food resources for the species found at higher trophic levels can be expected.

Previous studies have found differences in fish morphology between individuals of the same species living in different microhabitats of the same waterbody (also known as trophic polymorphism). It has been hypothesized that the main cause of trophic polymorphism are trade-offs in foraging on different resources that might result in a phenotypic divergence of populations (Svanbäck & Eklöv, 2004). Zebra mussels can change the characteristics of the ecosystems and alter the availability of resources in the ecosystem, therefore contribute to the changes in the morphology of the fishes. The aim of this project is to identify to which extent Zebra mussels have an effect on the morphology and/or diet of roach (*Rutilus rutilus*).

1.1 Zebra mussel (*Dreissena polymorpha*)

The zebra mussel (*Dreissena polymorpha*) is a relatively small mollusc (25-34 mm long) which is native to the Black Sea basin and can form dense colonies in the hard and soft substrates of waterbodies. Over the last decades the zebra mussel (ZM) has invaded and spread across Eurasia and North America. This mussel is an *r*-strategist meaning that it
has a short maturation time (1-2 years), has a the ability for high dispersion and a really high fecundity (large number of eggs produced) (Higgins and Vander Zanden 2010).

Higgins & Vander Zanden (2010) performed a meta-analysis of published studies to investigate the effects of both *D. polymorpha* and *D. rostriformis bugensis* (two of the most troublesome biological invaders) on fauna, flora, biogeochemistry and bacteria in Eurasia and North America. On the one hand, all zooplankton communities as well as phytoplankton biomasses were negatively affected by the invaders, decreasing their concentration. On the other hand, bacterial abundance dramatically increased in surrounding sediments, as well as benthic algal biomass and benthic invertebrate abundance.

ZM is not the only bivalve with the capacity to filter water and hence affect the benthic and pelagic habitats, most freshwater mussels bear a similar ecological function. However, *Dreissena spp*. can achieve much higher filtration rates than most native freshwater mussel communities and thus negatively affects the environment (Strayer et al. 1999).

1.2 Roach (*Rutilus rutilus*)

In this project I studied the effect of ZM on the morphology and diet use of roach in lake Erken. Roach (*Rutilus rutilus*) is abundant in lake Erken and found all over the lake. It is the most abundant fish species that can feed on zebra mussel. Other abundant species such as perch or ruffe do not commonly feed on ZM. *R. rutilus* belongs to the Cyprinidae family (Schiemer & Wieser 1992) and is typically present in mid-swedish lakes.

Many fish species can obtain their energy from both littoral and pelagic energy pathways (Vander Zanden & Vadeboncoeur 2002). The capacity to use both resources would buffer individual species from the drastic impacts of dreissenids invasion on lower trophic levels, and roach is a specimen with this capacity. Contrarily to that, the inability of some fish species to exclusively use benthic or littoral energy pathways could result in reduced individual body condition, reproduction and recruitment. Therefore the response of the fish populations to the zebra mussel invasion would depend on the intensity of the ecological changes and the ability of the whole food-web to respond to such changes (Higgins & Vander Zanden 2010).
Based on their feeding ecology and morphological characteristics, some fish species have been proposed to prey on zebra mussel. Roach have a molariform pharyngeal teeth, which enables them to crush molluscs shells and swallow them (Watzin et al. 2008). Other fish species lacking this morphology can theoretically swallow the bivalves as a whole but their predation rates might not be significant.

In Figure 1 an illustration of the dreissenid-induced shifts in the dominant energy pathways of freshwater ecosystems is shown. On the left side of the illustration the pelagic-profundal habitat is represented. All pathways (phytoplankton, zooplankton and profundal benthos) are negatively affected by the invasion of the mussel which decreases their abundances. On the other hand, all the littoral pathways (represented on the right side of the figure) appear to be positively correlated with the invasion (nutrients, plants and macroinvertebrates) resulting in an increase of littoral resources available for fishes.

Figure 1. Shifts induced by the dreissenid mussel in the main energy pathways of the waterbodies are shown. Arrows represent the direction of the energy flow. Solid lines represent increased abundance following dreissenid invasion, while dashed lines represent decreased abundances. Values under arrows represent the % of change induced by the dreissenid invasion (adapted from Higgins & Vander Zanden 2010).

It is clear that the presence of ZM influences the abundance of food resources in the two different habitats: pelagic and littoral. Due to the fact that ZM change the structure of the ecosystem, it could be expected that the roach diet use and morphology is affected by the presence of ZM.
1.3 Diet

As mentioned before, roach can feed on different resources: phytoplankton, zooplankton, benthic fauna, plants, etc. As Bolnick et al. (2003) stated, several fish species have a wide diet spectrum, although each individual might function as a specialist with a restricted diet. Moreover, it has been demonstrated that trade-offs in foraging on different resources can lead to phenotypically divergent populations where the trade-offs are hypothesised to be a main cause of trophic polymorphisms and adaptive radiations (Svanbäck & Eklöv 2004).

Bolnick (2003) demonstrated that individual specialisation occurs in a wide array of invertebrate and vertebrate taxa, most of them excluding effects of sex or age. It is expected that an individual chooses among the different resources available in order to maximize the benefit, which depends on different factors such as the amount of the resource availability, handling time, risks (predation), to name a few. Hence the individual’s preferred range will reflect the interactions between resource trait, resource abundance and individual’s phenotype (Bolnick 2003).

1.4 Morphology

The phenotypic changes of an organism induced by the environment, which occur during an organism lifetime, are known as phenotypic plasticity. This plasticity can be advantageous in some cases (Day et al. 1994), specially when there are changes in the environment, for example a change in food resources. Thus, plasticity is said to be an important strategy to cope with the environment variability (Day et al. 1996).

One of the most important aspects affecting foraging rate is the animal morphology (Svanbäck & Eklöv 2003, 2004), hence we can expect a change of morphology and diet if animals use different food resources. It has been demonstrated that some fish species can shift their diet source during their lifetime, and that some species can also change the morphology depending on their habitats, basically because of the food resources they use.

In fish, different body morphologies are optimal depending on which habitat the fish is living in. Individuals living in the pelagic zone (open waters), commonly looking for widely distributed and conspicuous prey, need a high search rate, for which a streamlined body is more efficient. For fishes in the littoral area (closer to the shore), with a lot of
vegetation and more cryptic preys, there is a need for a higher manoeuvrability, for which a deeper body morphology is optimal. For example, the morphologies of perch individuals have been found to be correlated with their diet (Svanbäck & Eklöv 2002). This resource polymorphism between individuals living in the littoral area and individuals in the pelagic area has also been found in different studies (Eklöv (1992), Hjelm et al. (2003) & Svanbäck & Eklöv (2004)).

1.5. Aim and hypothesis

The goal of the thesis is to study the relationship between the zebra mussel abundance and the possible shift in diet content as well as in morphology of roach. As shown in figure 1, the presence of *D. polymorpha* can alter the availability of food resources for roach in both habitats: in the littoral zone it mainly increases the abundance of benthic fauna and in the pelagic area decreases phytoplankton concentration. According to this I formulated different hypothesis.

(1) Do high abundances of zebra mussels affect the diet (gut contents) of roach in the two different habitats?

**a.** According to Higgins & Vander Zanden (2010) an increase of benthic fauna and plants in the littoral habitat will occur, hence we expect to find a higher proportion of those resources, specially molluscs, in the intestines of fishes in the littoral area. Littoral fishes will be feeding on macroinvertebrates and plants, mostly, since the concentration of the zooplankton will decrease. Hence fishes will increase their level of diet specialisation.

**b.** Also according to Higgins & Vander Zanden (2010) a decrease of the planktonic organisms will occur due to the presence of ZM in the pelagic habitat. Therefore a decrease of the proportion of plankton in the intestines of fishes living in this habitat is expected. Fishes in the pelagic habitat are expected to start feeding on a wider range of food as the concentration of the plankton is decreasing. Hence fishes will also feed on plants and macroinvertebrates more frequently. Therefore a lower specialization level is expected, so their diet will become less specialised.
(2) **Does the high ZM abundance affect the phenotype of Roach?**

According to Svanbäck & Eklöv (2002) resource polymorphism is influenced by the resources the fish feed upon. Moreover, as it has been hypothesised the ZM will affect the diet use of the fish, which in turn may affect the fish phenotype. If pelagic roach increases the use of benthic prey in the presence of ZM, then it is expected that roach in the pelagic stations with high abundance of ZM will develop a more littoral phenotype.

(3) **Are the abundances of the roach related to the abundances of ZM?**

According to Naddafi et al. (2010) roach could regulate the zebra mussel abundances since they prey on ZM and they could induce a rate of predation. For this reason a higher abundance of ZM is expected at stations with lower abundance or roach.
2. Materials and methods

2.1 Field study

The lake survey was carried out in summer 2008 in Lake Erken, situated in south-eastern Sweden with an area of 24,2 km². Erken is a meso-eutrophic, dimictic lake with a maximum elongation of 10.2 km and maximum width of 2.6 km. The greatest depth of the lake is 21 m with the mean depth being 9 m. Sampling took place in summer, since fishes are more active during this period and they should not be caught during spawning season. Moreover Erken is generally covered by ice from December to mid April.

Nine different sites were sampled for this project. Those sites were equally distributed along the shoreline of the lake in order to assess spatial variation in density of zebra mussels and roaches. These sites will be called stations from now on. Each station has two different sampling points, one in each habitat (littoral and pelagic). The littoral area is close to the shore and the nets were set outside and parallel to the reed belt at a water depth of about 2 m. The pelagic net was set roughly 200 m out in the open water (where a minimum depth of 8 m was reached).

The station number one is located north of the field station of Norr Malma and the stations were assigned numbers from one to nine counter-clockwise (see Fig. 2).

![Figure 2. Location of the 9 stations in lake Erken. Pelagic stations are marked in blue, and littoral stations are marked in green.](image)
Fish sampling

Nets used for the littoral habitat were 25 m long and 1.5 m high, whereas the nets set in the pelagic habitat were 6 m high (with an identical length of 25 m). All nets used were standardized multi-mesh Nordic gill-nets in order to catch fish from all different sizes. They were set in the afternoon and raised the morning of the following day. 2 nets were set in each habitat per station.

Sampled fishes were stored in plastic bags and kept frozen at -20 °C until the beginning of the studies.

The number of individuals caught differed among stations, thus a maximum of 60 individuals were analysed per station. In stations were more than 60 roaches were caught only a total number of 60 individuals were randomly picked and analysed.

Mussel abundance

Video transects were employed to record and study the abundance of zebra mussel on the different stations. One transect per station was driven parallel to the shoreline for 200 -250 m long at a depth of 1.5 meters. Videos were taken from a boat running at a speed of 2 km/h. The video footage was transmitted to a computer later on and the consecutive frames taken approximately every 2 seconds were used to count the number of mussels. The area the camera recorded was 0,1 m².

2.2 Morphometrics

In the laboratory, fishes were measured to the nearest 1 mm (total length: measuring from the mouth until the very end of the caudal fin) and weighted to the nearest 0.1 g. In order to describe the important habitat-specific changes in morphology, different head-structures were measured; Gape widths from all fishes were measured with a calliper rule to the nearest 0,01 mm. Mean inter-raker distance was measured on the medial side of the first right gill arch. In addition to that, the longest gill raker length was measured as well. Both gill raker measurements were made using a stereo-microscope Olympus SZ61 with an ocular micrometer.

All fishes were photographed for the subsequent study of the morphology. Images were captured with a digital camera CANON Power Shot G9, (12.1 Megapixels). Artificial
light was used to avoid shades. A standard colour scale (TIFFEN GrayScale) and a 30 cm ruler were placed next to the fishes. Fishes were photographed with their fins spread and fixed to a Styrofoam surface.

Landmarks used have to be relatively easy to identify, yet representing the global shape of the fish in two dimensions. Fig. 3 shows the 15 landmarks chosen for this study.

**Figure 3.** Distribution of the landmarks used in the morphology analysis of Roach (*Rutilus rutilus*) (from Svanbäck et al. 2008).

In order to quantify the morphological variation of the fish body shape between individuals, a multivariate geometric shape analysis was carried out. To study the changes in the morphology of the fish, digitized landmarks on the left side of the individuals and a two-dimensional Thin-plate spline Relative Warp (TPSRW) were used. Thin-plate spline (TPS) is a powerful tool to study geometric morphometrics (Zelditch et al. 2004). By applying (TPS) to morphological studies it is possible to visualize shape differences as well as deformations (Bookstein 1991). With this software (TPSRW) the relative position of the landmarks for each individual can be studied and the partial warp and uniform scores of the individuals can be calculated. This partial warp, for example, would show the local extension/contraction of a localised point of the fish, while the uniform scores measure the whole shape variation of the animal along some axis. Afterwards, the partial warps and uniform scores were analysed with a multivariate discriminant function analysis for all individuals and classified according to their habitat. This method allows to maximally discriminate between the two habitats, and combines all partial warp and uniform scores into a single score, called Morphological Index (MI). Another software, TPSREGR, was used then in order to visualize the deformation and shape variation of the pelagic and littoral fishes.
2.3 Diet use

In order to analyse the short term diet use of the fishes, each individual was thawed, the intestine was removed and the contents were extracted and analysed under a dissection microscope (zoom x10 mm). Six different categories of prey types were found in the intestine: zooplankton, macroinvertebrates, plants, molluscs, chironomids, and terrestrial organisms. The intestine contents were put on a petri dish to assess the volumetric content. The percentage of each category was visually estimated with the help of a millimetre paper. Fishes without prey items in the intestine were noted as well.

The fish diet (i.e. the content found in the intestines) was used to assess the diet variation of the population as well as the individual specialization (IS) and the proportional similarity of the population according to Svanbäck & Persson (2004). There are different methods to study the within population diet variation (Bolnick et al. 2002).

To study the diet variation within a population the individual distribution of the resource used was compared to its population using the index of proportion similarity $PS$ (Bolnick et al 2002) which shows the diet overlap between individuals and the population.

\[
PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j| = \sum_j \min(p_{ij}, q_j)
\]  

(1)

where $p_{ij}$ is the frequency of the diet category $j$ in the diet of individual $i$, and $q_j$ is the frequency of the diet category $j$ in the population as a whole. For the individuals that use the resources in the same proportion as the averaged population, $PS$ will have a value of 1.

The individual specialization (IS) in a population is expressed by the mean $PS$ value (Svanbäck & Persson 2004).

\[
IS = \frac{1}{N} \sum_i PS_i
\]  

(2)

IS is equal to 1 when there is no individual specialization and meaning that all individuals use the same resources. IS values close to 0 indicate a strong individual specialization (Svanbäck & Persson 2004). For a more intuitive value the individual diet specialization I used the index $V$ (Bolnik et al. 2007):

\[
V = 1 - IS
\]  

(3)
The range of $V$ values is between 0 and 1. Populations with a diet specialisation of 1 ($V=1$) are those with very specialised individual, whereas populations with a lower value have less individual specialisation.

2.4 Statistics

Since the aim of the project was to study how ZM are affecting roach, only individuals larger than 150 mm (standard length) were used when analysing the effect of ZM on diet use and morphology variation. 150 mm was used as a cut-off point since this was the size at which roach started to include ZM in their diet in this study (Fig. 7).

The densities of ZM found over the 9 different stations were not following a continuous increase. For a better analysis of the morphology, the stations were classified in 3 groups classes according to their ZM abundances (Table 1). Not all the groups had the same number of stations.

Table 1. Classification of the different stations according to the number of zebra mussels, in concentrations per m$^2$:

<table>
<thead>
<tr>
<th>Class</th>
<th>mussel concentration (m$^2$)</th>
<th>Station</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>9 – 39</td>
<td>6 – 3</td>
</tr>
<tr>
<td>2</td>
<td>132 – 136 – 172</td>
<td>5 – 4 – 8</td>
</tr>
</tbody>
</table>

For the statistical analysis SPSS Statistics 17.0 was used. To look for changes in diet use and morphology in relation to ZM abundances I used both linear and quadratic regressions as well as one way ANOVA with ZM class as the predictor.
3. Results

3.1 Fish captures and mussel abundances

The total fish capture in lake Erken during this study amounted to 7123 individuals and those belonged to 7 different species: perch (*Perca fluviatilis*), roach (*Rutilus rutilus*), ruffe (*Gymnocephalus cernuus*), smelt (*Osmerus eperlanus*), white bream (*Abramis bjöörkna*), common bream (*Abramis brama*), bleak (*Alburnus alburnus*), pike (*Esox lucius*), tench (*Tinca tinca*) and rudd (*Scardinius erythrophthalmus*).

Perch was the dominant species at all the stations and roach was the second most abundant species in all stations, except in littoral station number 1 and pelagic station number 8, where ruffe and smelt, respectively, were more abundant than roach. Hence roach could have an important role in the ecosystem of lake Erken. A total of 1282 roach individuals were caught during the sampling. 960 roaches were captured in the pelagic habitat and 322 in the littoral (Table 2). Zebra mussel abundances were estimated per square meter in table 2, but for statistics the value obtained on the field was used. As the littoral and pelagic nets were of different sizes I converted the roach captures into individuals/m² of the net to make the values comparable between the two habitats.

**Table 2.** The number of roach caught in the nets and their abundance converted into individuals per square meter of net. ZM abundances are also represented per square meter to have a better visualization of the data.

<table>
<thead>
<tr>
<th>station</th>
<th>Individuals / 2net</th>
<th>Individuals / m²</th>
<th>ZM/m²</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>pelagic roach</td>
<td>littoral roach</td>
<td>pelagic</td>
</tr>
<tr>
<td>1</td>
<td>47</td>
<td>15</td>
<td>0.16</td>
</tr>
<tr>
<td>2</td>
<td>207</td>
<td>31</td>
<td>0.69</td>
</tr>
<tr>
<td>3</td>
<td>96</td>
<td>28</td>
<td>0.32</td>
</tr>
<tr>
<td>4</td>
<td>101</td>
<td>47</td>
<td>0.34</td>
</tr>
<tr>
<td>5</td>
<td>102</td>
<td>26</td>
<td>0.34</td>
</tr>
<tr>
<td>6</td>
<td>218</td>
<td>36</td>
<td>0.73</td>
</tr>
<tr>
<td>7</td>
<td>41</td>
<td>12</td>
<td>0.14</td>
</tr>
<tr>
<td>8</td>
<td>21</td>
<td>65</td>
<td>0.07</td>
</tr>
<tr>
<td>9</td>
<td>127</td>
<td>62</td>
<td>0.42</td>
</tr>
</tbody>
</table>

Littoral abundances seemed to decrease with the increase of ZM, but no clear trend was found for pelagic roach (Figure 4), although there were higher global (littoral + pelagic) abundances in areas with low ZM.
3.2 Diet of the fish

The intestines of a total of 765 individuals were analysed (460 from pelagic area and 305 from the littoral zone, see materials and methods). Food content found in the intestines of the fishes is represented in a column graph below. Results were obtained from

![Column graph showing diet content of littoral and pelagic fishes](image)

**Figure 5.** Analysis of the mean proportion of the diet content per station found in the guts of the roaches analysed. On the top intestines content for littoral fishes are shown, and below the content for the pelagic fishes. Food content is shown as percentage.
the mean proportion of each category per station and habitat (Figure 5). A clear difference in food resources between the individuals living in the different habitats (littoral and pelagic) was found. In most cases (except for station 9) plankton made up 2/3 of the gut content in fishes caught in the pelagic area. In addition to that, some plant or macroinvertebrates could be found in pelagic fishes. Fishes in the littoral zone mainly had plants and macro invertebrates in their stomach. Plants and macroinvertebrates were the only resources showing significant differences between groups (ANOVA p<0.01 & p=0.04 respectively).

Presence of ZM in the gut content was marked every time to see if a correlation with the ZM abundance exists. Only 6 individuals in the pelagic area were found to be eating ZM (not included in the graph below). Figure 6 shows the percentage of fishes in each littoral station eating zebra mussels in correlation with the ZM abundance. It can be seen that there is a significant increase (p=0.042) of the percentage of fishes that include ZM in their diet when ZM abundance increases.

![Figure 6](image.png)

**Figure 6.** The increase of the percentage of littoral fishes eating ZM in correlation with the ZM abundances, the trend line is also shown.

As it can be seen in the following graph, (Fig. 7) that roach (except two individuals) started eating ZM when they reached the size of 150 mm.

![Figure 7](image.png)

**Figure 7.** Shows the length at which fishes start including ZM in their diet use, and the % of it found in the stomach.
The following statistical analysis will be carried out using only the individuals larger than 150 mm. 

Food resources used

In this part of the project the results from the gut contents are shown. Not many chironomids could be found, and they were included into the macroinvertebrates group as well as the ZM. On the Y axis the mean proportion of the diet for each station is shown, and on the X axis the ZM concentration in 1/10 m² is represented.

A decrease of the consumption of zooplankton (Fig. 8) was found for fishes in both habitats, although the trend in more obvious for fishes caught in the pelagic habitat. The quadratic R² (littoral: 0.187, pelagic: 0.175) showed a negative pattern correlated with ZM abundances.

![Figure 8. Mean proportion (%) of plankton consumed per station.](image)

The mean proportion of macroinvertebrates in the intestines of roach for all stations (Fig. 9) was always lower for fishes in the pelagic habitat. The mean proportion of macroinvertebrates in littoral fishes decreased in (R² of 0.272), whereas the mean proportion for pelagic fishes increased, (but not significantly) with increasing ZM abundances.

![Figure 9. Mean proportion (%) of all the macroinvertebrates consumed per station.](image)
A positive correlation with the ZM abundance was found for plants. Roach seemed to eat much more plants at higher ZM concentrations (Fig. 10). The quadratic R² is 0.329 for roach in the littoral and 0.297 for the ones in the pelagic zone. Plant was the food resource that showed the best positive correlation with the increase of ZM. Terrestrial organisms were not that commonly found in the intestines of roaches, and were not used for the statistical analyses, although it should be pointed out that there were more fishes from the littoral that were using terrestrial as a resource than pelagic.

![Figure 10. Mean proportion (%) of plants consumed per station.](image)

**Diet specialisation**

The mean diet specialisation for each station and habitat was calculated. Diet specialisation for littoral fishes slightly increased when ZM concentration increased but decreased again when ZM was high, meaning that those fishes became less specialised (R²: 0.509) (Fig. 11). Pelagic fishes showed the opposite pattern, their specialisation decreased a bit when the concentration of ZM increased, but it turned out to be higher when ZM densities were even higher, which means that pelagic fishes were more specialized, but the pattern was not that strong. (R²: 0.295).

![Figure 11. Trends in the diet specialisation for all stations and habitats, with a quadratic trend line for each subgroup.](image)
3.3 Morphology

Morphological Index

From the 15 landmarks analysed with different software (see materials and methods) a thin-plate spline (TPS) could be obtained for each habitat. The TPS in figure 12 summarise all fishes in the nine stations. The deformation grid plots have been exaggerated to a score of -10 and 10 in order to visualize the differences easier. Fig. 12 a) shows the morphology of the littoral roach for a morphological index value of -10, showing a deeper body morphology with the gape pointing downwards. On the right side, Fig 12 b), the shape of the roach in the pelagic habitat is presented with a morphological value of 10, showing that pelagic roach are more streamlined and their gape is pointing upwards.

Figure 12. Thin-plate spline for fishes in the littoral habitat (a) and pelagic habitat (b), the grids show a deformation for a fish with a MI score of -10 (a) and +10 (b).

In figure 13, it can be observed that the MI decreases significantly (ANOVA p <0.01), with increasing concentrations of ZM when the stations are classified in three different groups (see Table 1, materials and methods). The more negative the MI the more littoral shaped are the fishes. Individuals used were at least 150mm long.

Figure 13. Mean value for each classification (depending on ZM abundance) for all stations and both habitats. Negative values indicate a littoral shape of the fish, positive values represent pelagic body shapes. Error bars within 95% confidence interval.
**Fish morphology**

Roach in the littoral area were generally larger than the ones in the pelagic habitat (Fig. 14). The roach caught at the stations with low ZM abundances were larger, specially in the littoral habitat. But no overall trend is clear.

![Figure 14](image)

*Figure 14.* Shows the mean length of the fishes according to the ZM abundances classification. Error bars within 95% Confidence Interval

Neither the raker space or inter raker space seemed to be affected by ZM abundance (data not shown). Gape width was correlated with length ($R^2 = 0.801$) (Fig. 15). Biggest gape widths belonged to the littoral fishes, and the smallest ones were from both habitats, but were clearly related to the total length of the fish.

![Figure 15](image)

*Figure 15.* The length of all fishes is plotted against their gape width for both habitats ($R^2 = 0.801$).

Mean gape width was always smaller for fishes in the pelagic habitat, but seemed to increase with the abundance of ZM. In the following graph (Fig. 16) the mean residual
values per all stations in the pelagic habitat are plotted. To avoid any influence of the
bigger size of littoral fishes on the analysis we chose to use residuals to get preciser results
on the gape width relative to the length. Residuals were calculated with the length as
independent variable. Residuals show how big or small the gape was corrected for the
length of the fish, since a clear relationship with gape width and fish length has previously
been demonstrated (Fig. 15). An increase in gape width in relation to ZM abundance was
found in the pelagic habitat, but not in the littoral habitat (though neither relationships were
significant).

Figure 16. The mean residuals for gape width of all stations in the pelagic area are plotted against the ZM
abundance classification.
4. Discussion & Conclusions

This study shows that the abundances of zebra mussel can affect the availability of food resources for roach and therefore change their diet use as well as the specialisation level. Consequently, roach morphology can also be affected.

Morphology

Evidence that the zebra mussel abundance is affecting roach body shape in lake Erken was found in this project. To analyse the body shape, the morphological index was used. Supporting my hypothesis, roach developed a more littoral shape (p<0.01) when ZM increased in abundance. Not only the MI showed a more littoral morphology but also the gape width. Pelagic roach had wider gape widths when increasing ZM abundance occurred. This could be due to the fact that the filtering pressure of ZM significantly decreased the plankton availability in the water and fishes had to scavenge for bigger food resources (plants or macroinvertebrates). I used residuals for gape width since we found that there was a correlation between gape width and body length, and I found that littoral fishes were, in general, longer than pelagic.

Diet use

As expected, littoral roach mainly ate plants and macroinvertebrates, while pelagic roach mostly fed on plankton. However, a change in those proportions was detected when ZM increased in abundance.

The proportion of plankton consumed by roach decreased in correlation with the ZM concentration as hypothesised. This trend was more clear for pelagic roach. As stated, that is probably due to the decrease of zooplankton in the water. Littoral roach didn't feed as much as pelagic roach in zooplankton, not even in class 1 (low ZM abundance), that is the reason why the correlation is less pronounced.

More plants were found in the diet of both littoral and pelagic roach (p<0.01) when ZM increased in abundance and followed a quadratic regression ($R^2 = 0.329$ for littoral and 0.297 for pelagic roach). The trend was more obvious for plants, probably due to the fact that the higher input of nutrient in the water can raise the availability of plants in the ecosystem (Higgins and Vander Zanden 2010). Moreover, roach could feed on plants more often if other food resources were to be scarce, or less available.
The occurrence of macroinvertebrates in the environment is expected to rise with increasing ZM abundances due to the extra input of nutrients (ZM feces) (Thayer et al. 1997). The proportion of macroinvertebrates found in the intestines varied in both directions among roach in the pelagic habitat and roach in the littoral, but the proportion was always higher in the littoral roach. On the one hand, pelagic fishes in stations with high ZM abundances increased their proportion of macroinvertebrates in their stomach, meaning that they had a wider range of food resource. On the other hand, littoral fishes decreased the proportion of macroinvertebrates in their stomach. The decrease of the macroinvertebrates proportion in littoral fishes could be explained by the fact that ZM can reduce the foraging success of roach preying on benthic fauna by blocking the access to the benthos (Beekey et al. 2004) as the mollusc functions as a shelter for invertebrates and hence it is more difficult for fishes to reach them. Hence although we expected a higher increase of macroinvertebrates in the environment due to the presence of ZM that would not be reflected in the intestines content of the roach.

An increase of fishes eating ZM when ZM increased in abundance could be expected, and I found significant results (p=0.04) for the increase in percentage of roach eating ZM. Despite this, the total proportion of ZM in the stomach was not correlated with ZM abundance. The higher percentage of littoral roach feeding on ZM when ZM abundances were high could be caused by the wider gape widths of individuals living in those sites, since it has been shown that the gape width is a limiting factor for preying on ZM (Ray & Corkum 1997). However, the mean gape widths of littoral roach in class 3 (highest ZM abundance) was lower than in the other classes. Probably most of the roach in class 3 were mainly eating plants, thus they don't need to have a big gape width. Contrarily, only roach feeding on ZM would need a bigger gape width, although no previous studies have specified the size required to feed on plants.

**Diet specialisation**

Regarding the individual specialisation, pelagic roach became less specific at intermediate ZM abundances since the concentration of zooplankton decreased and hence they had to look for other resources. Littoral roach became more specialised at intermediate ZM abundances, as they ate less plankton and mainly feed on macroinvertebrates and plants compared to the conditions with low ZM abundance. Both followed a quadratic trend ($R^2 0.295 & 0.509$ for pelagic and littoral respectively)
Interestingly the gape width of pelagic roach showed a positive correlation with the increase of ZM concentration. Probably due to the fact that pelagic roach consume less zooplankton (small prey) and started preying on bigger items. In class 2 they fed on macroinvertebrates and plants mainly (showing low degree of specialization). Then again, in class 3 they feed on littoral resources but with higher individual specialization. Overall the increase in gape width supports the hypothesis that pelagic fishes show a more littoral morphology when ZM concentrations are higher.

Mean littoral roach' gape width didn't vary in a significant way but was coherent with the specialization as well. Littoral roach became more specialised in (class 2) feeding in macroinvertebrates and plants and that was the category where roach had the maximum gape width. In class 1 they fed on zooplankton, plants and macroinvertebrates as well as in class 3, and ate also some terrestrial preys, but this resource was found only in few individuals (5).

The captures of fishes were irregular all over the lake, which is according to the expectations, since fishes are most abundant wherever resource availability is highest.

According to Naddafi et al. (2010) roach populations could regulate ZM density and population size at a local scale. Although I didn't find significant correlations, captures with lots of roach took place at sites with low ZM abundances. This could support the hypothesis of Naddafi et al. (2010). A possible explanation is that at high abundances of roach, ZM cannot reach high abundances. This is supported by the fact that roach abundance was low in class 3 (high ZM abundances). Unfortunately, no results based on diet support this, since it was in class 3 where the proportions of fishes eating ZM was highest. To get more reliable data on roach abundance, nets should be set more than once.

Future directions

In conclusion, I have in this study shown that ZM affected roach diet and morphological variation. However for a better ecological understanding further research is needed. I suggest some studies could be carried out using stations with different ZM concentrations (higher differences in ZM abundances between classes) and replicates for each. It would be interesting to correlate the food availability for the roach to the gut content.
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5. References


