



Adaptive trait utility in the feeding apparatus of European whitefish (*Coregonus lavaretus*)

Relationships between feeding morphology and maximum and minimum prey size in the diet of whitefish

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Abstract

Whitefish (*Coregonus lavaretus*) populations diverge into morphs that differ in body size along a benthic-limnetic axis and throughout the depth of the water column. This process is assumedly initiated by the presence of northern pike (*Esox lucius*) and is followed by morphological adaptations to available food resources. In this study eight populations of whitefish was studied with the purpose of increasing the knowledge about adaptive trait utility in the feeding apparatus of whitefish. This was done by analyzing the mean and absolute maximum and minimum prey size ingested by fish along four morphological trait gradients. The morphological traits was body size, gill raker number and density, and gape size. The results show clear evidence of morphological adaptations in both the benthic and limnetic habitat, furthermore, when comparing the two prey size responses (mean and absolute values) it becomes clear that none of the studied whitefish is physically constrained in terms of the largest prey they can ingest. However, large fish seem to be limited in eating small prey sizes. Interestingly, I also found strong indicators for filter feeding adaptation for one of the studied populations.

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1 Introduction

Adaptive radiation, defined as the evolutionary process behind ecological and phenotypic diversity within a multiplying lineage, occurs in a number of fish species in postglacial lakes (Schluter 2000). The European whitefish (*Coregonus lavaretus*) complex is a well-studied example that fulfill the criteria used for identifying adaptive radiations (Schluter 2000); co-existing morphs often have common ancestry (Østbye et al. 2006, Öhlund 2012), speciation is rapid (Öhlund 2012), phenotypes are associated with separated environments (e.g. phenotype-environment correlations) (Kahilainen et al. 2007, Harrod et al. 2010) and utility of feeding adaptations to different resources have been demonstrated (Kahilainen & Østbye 2006, Kahilainen et al. 2007). The speciation process is believed to originate as the result of intense intraspecific competition and extensive niche availability (Schluter 1996, Smith & Skúlason 1996, Kahilainen & Østbye 2006, Østbye et al. 2006). However, Öhlund (2012) challenged this paradigm by showing that the presence of northern pike (*Esox lucius*) is a necessary condition for ecological speciation in Scandinavian lakes.

Many species complexes diverge in body size along the benthic-limnetic habitat axis (Schluter 1996, Smith & Skúlason 1996). The limnetic morph is generally small-sized and have a dense gill raker apparatus, whereas the benthic morph possess a large body and sparse gill rakers (Svärdson 1964, Svärdson 1979, Kahilainen & Østbye 2006, Østbye et al. 2006, Kahilainen et al. 2007). In some large lakes whitefish have additionally diverged along the depth gradient, with an intermediate sized profundal morph with sparse gill rakers coexisting with a littoral large-bodied morph and a pelagic small-bodied morph (Kahilainen & Østbye 2006, Harrod et al. 2010). There may also be several morphs in the pelagic habitat, utilizing the entire depth of the water column (Svärdson 1964, Svärdson 1979). Divergence in body size is believed to initiate the speciation process, whereas divergence in gill raker morphology appears to be an adaptation to the new niches occupied after the initial split (Öhlund 2012).

Gill raker number and density is of great importance for effective utilization of small prey, e.g. zooplankton (Link & Hoff 1998). It has been suggested that gill rakers function as a dead-end filter where particles larger than the spacing between the gill rakers are retained by the fish (Hoogenboezem et al. 1993, Gerking 1994). However, Sanderson et al. (2001) showed that more than 95% of all food particles consumed by suspension-feeding fishes never come into contact with the gill rakers, as it would if the gill rakers functioned as a dead end filter. The particles are instead retained by crossflow filtration, where the water flows parallel with the gill raker surface. This mechanism allows large amounts of particles that are smaller than the pore size, i.e. the gill raker distance, to be consumed (Sanderson et al. 2001, Brainerd 2001).

A number of studies show divergence between benthic and limnetic species, and/or morphs, in feeding efficiency on small prey items like zooplankton. Generally individuals with high number of gill rakers feed more efficiently on such prey (Langeland & Nøst 1995, Day & McPhail 1996, Kahilainen et al 2007, Lundsgaard-Hansen et al. 2013). Between-species studies are however not optimal since the effects of gill raker morphology is hard to separate from the effects of other species specific traits. Bentzen & McPhail (1984) investigated the effect of gill raker spacing and fish body length on feeding performance in the limnetic habitat for sticklebacks (*Gasterosteus* sp.) and found that the specific effects of the two traits could not be separated due to high intercorrelation. The literature on the importance of gill raker morphology for benthic prey utilization is even less satisfying. Schluter (1993) showed a higher usage of a benthic food source for benthic sticklebacks but the gill raker trait utility was not tested. Also, an experimental study by Lundsgaard-Hansen et al. (2013) showed higher feeding efficiency by large benthic whitefish than small limnetic whitefish on benthic prey, but the gill raker density was not quantified. Nevertheless, as benthic whitefish typically have a low number of gill rakers (Amundsen et al. 2004, Kahilainen & Østbye 2006, Kahilainen et al. 2007) the findings by Lundsgaard-Hansen (2013) indicate an adaptive trait utility of sparse gill rakers to the benthic habitat.

The aim of this study was to increase the knowledge about the adaptive trait utility of the feeding apparatus in whitefish by studying the maximum and minimum prey sizes eaten by individuals varying in body size, gill raker numbers, and gape size. Relationships between these prey size measures and functional traits may be influenced by; 1) physical constraints, e.g., prey larger than the gape size cannot be consumed, 2) the availability of prey of different size, e.g. no relationship will be seen if prey larger than the mean maximum are unavailable, and 3) active prey selection, e.g., if prey of low energetic value are ignored.

The maximum-minimum prey size approach is a previously untested way of quantifying adaptive trait utility compared to earlier studies (i.e. Kahilainen et al. 2007, Roesch et al. 2013, Lundsgaard-Hansen et al. 2013). The prey size spectrum shown in the diet should reflect how well specific morphs utilizes prey. To reduce co-linearity between traits, a setup of eight populations covering a wide range of gill raker number and fish body length was used. If the assumption of adaptive trait utility in adaptive radiations is met, small limnetic whitefish with high density of gill rakers should feed on smaller prey while large benthic morphs with low gill raker density should preferably feed on significantly larger prey items. The utilization of different prey sizes along the benthic-limnetic axis and in the pelagic is assumed to reflect the importance of morphological variability. Also, the use of extreme prey sizes would add data concerning physical constraints.

2 Materials and methods

The maximum and minimum size of prey taken by whitefish were investigated using eight different populations. The populations were chosen with the objective to minimize correlations between body size and gill raker numbers. The study setup is displayed in figure 1. The fish were collected from; Idsjön, Storvindeln and Övre-Rissjön, henceforth referred to as Rissjön. Characteristics of the different lakes are given in table 1. Each morph is recognized by unique morphological traits (table 2).

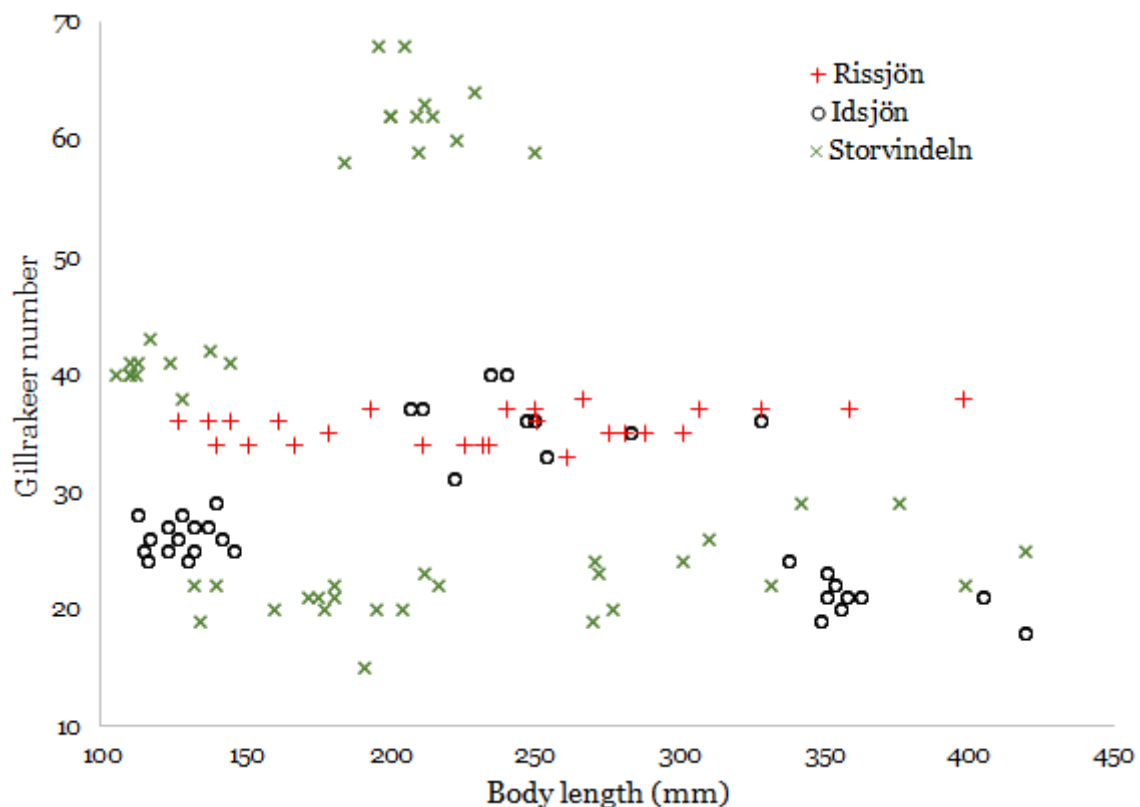


Figure 1. The relationship between body length and gill raker number for the eight study populations.

2.1 Gill net fishing and morphological data

The fish were caught during a standardized gill net fishing in the summer and fall of 2012, 2013 and 2014, both floating nets and bottom nets were used. The method is further described in Öhlund (2012). A number of individuals of the small, sparsely rakered morph was additionally fished during mating in fall 2014.

Body length was defined as fork length, i.e. the distance from tip of the snout to the end of the middle caudal fin rays. Number and density of gill rakers was determined from the left first branchial gill arch. Density (number of gill rakers/cm gill arch) was measured for 5 gill rakers starting at the central gill raker of each gill arch and moving forward. The maximum gape size (mm²) was estimated by inserting a cone into the fish mouth until a small resistance was felt (figure 2a). The measurement was taken at the upper lip of the fish (figure 2b).

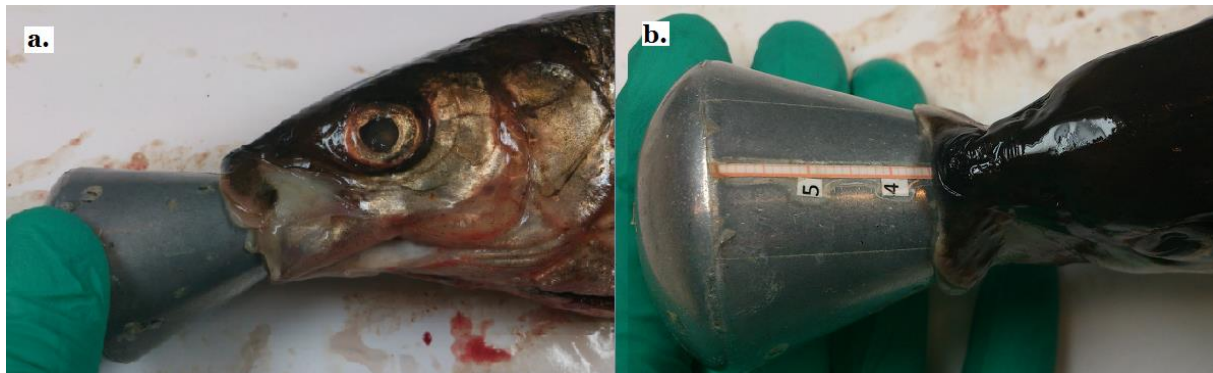


Figure 2. Gape size was measured with a calibrated cone; a) the insertion of the cone into the fish mouth, b) the measurements was taken at the upper lip of the fish.

Table 1. Characteristics of the lakes where whitefish was caught.

Lake	Long	Lat	Altitude	Area (km ²)	Max dept h (m)	No. of whitefish morphs	Other fish species present [§]
Rissjön	17.729	64.041	334	1.6	28	1	Pike, roach, burbot, brown trout, grayling, perch
Idsjön	19.603	67.490	261	9.2	33	3	Pike, roach, burbot, brown trout, grayling, perch, ide, eel, minnow
Storvin deln	17.451	65.637	359	52.1	36	4	Pike, roach, burbot, brown trout, grayling, perch, ide, minnow

[§]Pike (*Esox lucius*), roach (*Rutilus rutilus*), burbot (*Lota lota*), brown trout (*Salmo trutta*), grayling (*Thymallus thymallus*), perch (*Perca fluviatilis*), ide (*Leuciscus idus*), eel (*Anguilla anguilla*), minnow (*Phoxinus phoxinus*)

2.2 Stomach sampling and analysis of prey items

Stomachs were removed from the fish and preserved in 70% ethanol until further analysis. For the analysis, the stomachs were cut open from the esophagus down to the pyloric cecum. Stomach contents was rinsed out and each prey item was identified and counted. Prey was identified to family for insects and molluscs, and to genus level for zooplankton. However, occasionally it was only possible to determine a higher taxonomic level. All prey items was also assigned to a prey class depending on its body shape and ability to escape predators. Prey classes were; aquatic insects, terrestrial insects, molluscs and zooplankton. For all identified prey taxa the three largest and three smallest individuals were measured. When possible the full length of

the prey item was measured. For partly degraded insects the head width was measured and full body length was calculated using head width-body length regressions (Appendix 1, table 2).

Table 2. Characteristics of the eight whitefish populations.

Lake	Year of white-fish introduction	Morph [§]	N	Body length (mm)	Gill raker number
Rissjön	1927	G	26	127-398	33-38
Idsjön	Native	SDR	15	113-146	24-29
"	"	G	10	207-328	31-40
"	"	LSR	10	338-420	18-24
Storvindeln	Native	SDR	11	105-145	38-43
"	"	LSR	11	270-420	19-29
"	"	SSR	14	132-217	15-23
"	"	LGDR	12	184-250	58-68

[§]G – generalist, SDR – small, densely rakered, LSR – large, sparsely rakered, SSR – small, sparsely rakered, LGDR – large gaped, densely rakered

2.3 Data analysis

Measures of the maximum and minimum prey size were regressed on four functional traits that are expected to influence the size range of ingested prey, i.e. fish body size, gape size and the number and density of gill rakers. In order to elucidate the relative importance of physical constraints, prey size availability and active selection two different measures of maximum and minimum prey size was analyzed. In the first type of analysis the mean value of the three largest and three smallest prey items were related to feeding trait values using ordinary linear regression. These responses are henceforth referred to as “mean maximum prey size” and “mean minimum prey size”. In the second analyses the single largest and smallest prey item from each individual fish was related to the feeding traits using 95% quantile regressions. These responses are referred to as “absolute maximum prey size” and “absolute minimum prey size”. The second analysis is comparably sensitive to extreme values and will therefore reflect the influence of physical constraints or the available size spectrum better. In contrast the first analyses is expected to be more influenced by active prey selection. Additionally, the analyses described above was run for the maximum and minimum size of zooplankton. Zooplankton are present in all habitats in high abundance. Contrasting these analyses with those of all prey types therefore provided information about the role of habitat differences in prey availability.

The statistical analyses were done using the statistical software R (R Development Core Team 2010). The response variables were log-transformed to reduce heteroscedasticity. Models for maximum and minimum prey size were selected based on adjusted r^2 -values and Aikake Information Criterion (AIC). The absolute maximum and minimum prey size was regressed on functional trait values using the quantile regression function in the R-package “quantreg”.

3 Results

Gape size is highly correlated with body size (adjusted $r^2=0.9044$, $p<0.001$, figure 3, all morphs except the large gaped morph from Storvindeln). As shown in figure 3 the large gaped densely rakered morph has a significantly wider gape than other morphs within the same body length span (ANCOVA, $p<0.001$, figure 3). Also, this morph feed on considerably smaller prey than expected based on its large gape (ANCOVA, $p<0.001$, figure 4b). I hypothesize that these traits are adaptations for filter-feeding and therefore excluded this morph from the following analyses.

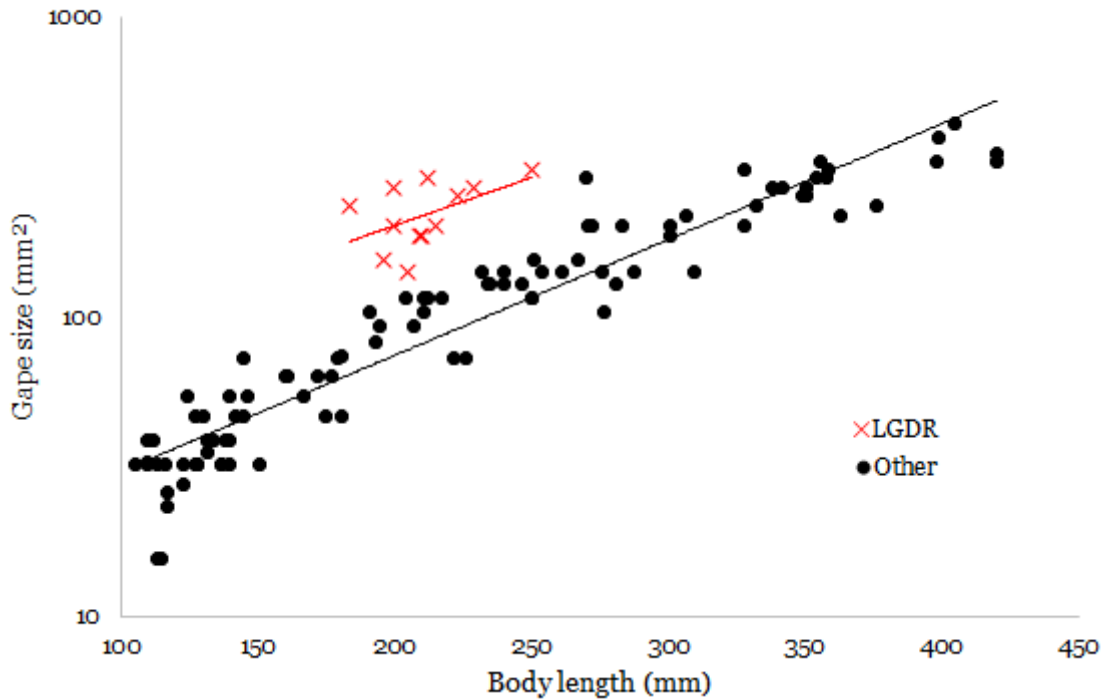


Figure 3. The relationship between gape size and body length. The large gaped densely rakered (LGDR) morph is differentiated from the other morphs by having a significantly wider mouth than other fish of the same size.

3.1 All prey

The mean maximum prey size for all prey is positively correlated with body length and gape size (figure 4a+b) but negatively correlated with gill raker number and density (figure 4c+d). The variance in mean maximum prey size is best explained by the additive effect of body length and gill raker density (table 3). However, note that the difference in r^2 -value and AIC between that model and the models for body length and gill raker number is rather small. In contrast, there was no significant relationships between the absolute maximum prey size and feeding trait values when using a 95% quantile regression (bootstrap, $p > 0.05$ for all explanatory variables, dashed black lines in figure 4a-d).

Mean minimum prey size increased with increasing body length and gape size (figure 4a+b) but decreased with increasing gill raker number and density (figure 4c+d). The model best explaining the variation in mean minimum prey size included fish body length and gill raker number (table 3). Similar relationships were observed when using the absolute minimum prey size as response variable (quantile regression, bootstrap, $p < 0.05$ for body length, gill raker number and gill raker density, but $p \approx 0.057$ for gape size, dashed red lines in figure 4a-d).

Table 3. Regression models relating maximum and minimum prey size to feeding trait values. The most relevant models are shown in this table and all investigated models are presented in Appendix 1, table 1. The feeding traits used as predictors are: BL=body length, GN=gill raker number, GD=gill raker density or GS=gape size. AIC was used to identify the models with best predictive power, marked with bold.

Response	Predictor	Adjusted r^2	AIC
Maximum prey size	BL***	0.469	258
Maximum prey size	GS***	0.3847	272
Maximum prey size	GN**	0.0897	310
Maximum prey size	GD***	0.4507	261
Maximum prey size	BL**+GD**	0.5011	253
Maximum prey size	BL***+GN*	0.4892	255

Minimum prey size	BL***	0.4119	160
Minimum prey size	GS***	0.3677	167
Minimum prey size	GN***	0.1661	194
Minimum prey size	GD***	0.4382	155
Minimum prey size	BL**+GD**	0.4631	152
Minimum prey size	BL***+GN***	0.4829	148

Level of significance; *<0.05, **<0.01, ***<0.001

3.2 Zooplankton prey

Similar patterns as for all prey were found when analyzing the maximum and minimum size of zooplankton prey as response variable. Both the mean maximum and minimum size of zooplankton are positively correlated with body length and gape size (figure 5a+b) but negatively correlated with gill raker number and density (figure 5c+d). For both mean prey sizes the additive effect of body length and gill raker number has the highest explanatory power (table 4). Also, the absolute maximum prey size was unrelated to the foraging traits (quantile regression, bootstrap, $p>0.05$ for all explanatory variables, figure 5a-d). For the absolute minimum prey size there is a significant relationship with prey size for all trait variables (quantile regression, bootstrap, $p<0.05$ for all explanatory variables, figure 5a-d).

Table 4. Regression models relating the size of zooplankton to feeding trait values. The most relevant models are shown in this table and all investigated models are presented in Appendix 1, table 1. The feeding traits used as predictors are: BL=body length, GN=gill raker number, GD=gill raker density or GS=gape size. AIC was used to identify the models with best predictive power, marked with bold.

Response	Predictor	Adjusted r2	AIC
Maximum prey size	BL***	0.3077	72
Maximum prey size	GN***	0.3299	71
Maximum prey size	GD***	0.4117	63
Maximum prey size	GS***	0.2883	74
Maximum prey size	BL***+GN***	0.5243	52
Minimum prey size	BL***	0.2227	78
Minimum prey size	GN***	0.507	52
Minimum prey size	GD***	0.4046	63
Minimum prey size	GS***	0.2332	78
Minimum prey size	BL***+GN***	0.614	39

Level of significance; *<0.05, **<0.01, ***<0.001

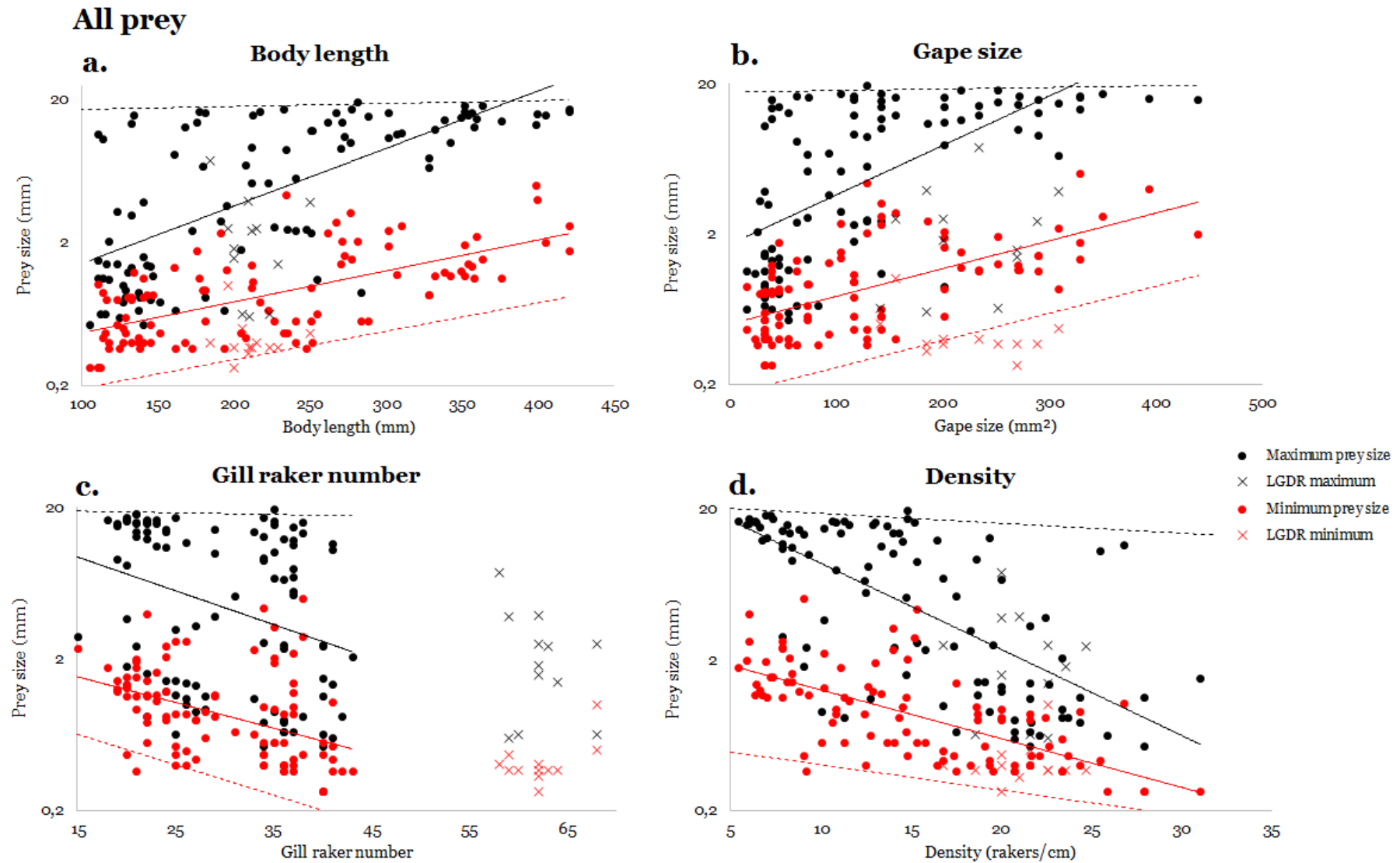


Figure 4. Relationships between mean maximum (black) and mean minimum (red) prey size, including all prey, and a) body length, b) gape size, c) gill raker number and d) gill raker density. Crosses denote maximum and minimum prey sizes of the large gaped densely rakered morph (LGDR). Dashed lines are the results of quantile regressions for the absolute maximum and minimum prey size and the solid lines are the result of ordinary regressions for the mean maximum and minimum prey size.

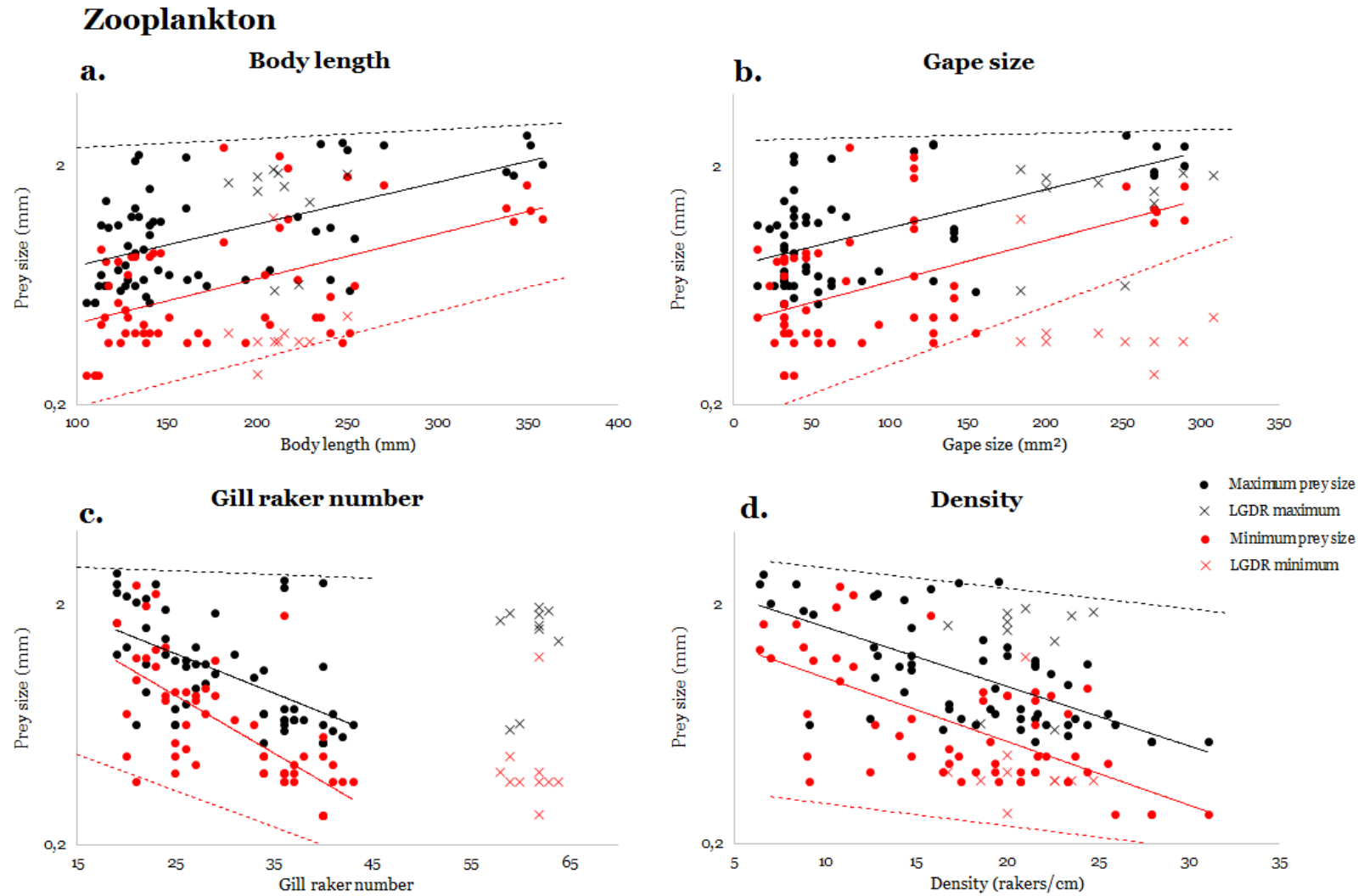


Figure 5. Relationships between mean maximum (black) and mean minimum (red) prey size of zooplankton and a) body length, b) gape size, c) gill raker number and d) density. Crosses denote maximum and minimum prey sizes of the large gaped densely rakered morph (LGDR). Dashed lines are the results of quantile regressions for the absolute maximum and minimum prey size and the solid lines are the result of ordinary regressions for the maximum and minimum prey size.

4 Discussion

The results show a difference in mean prey size utilization along each trait gradient. This result confirms adaptive trait utility within the whitefish species complex with the most important morphological traits for explaining size variation of ingested prey being fish body length and gill raker number or density. The observed patterns for both mean and absolute prey responses should be influenced by the three principle mechanisms mentioned in the introduction; 1) physical constraints, 2) prey size availability, and 3) active selection of prey. The three principle mechanisms are not independent of each other and this study was not designed to distinguish between their relative importance. However, by comparing the different responses it is possible to draw some conclusions.

The mean maximum and minimum prey size increased with body length and gape size but decreased with gill raker number and density. The observed pattern is probably explained by availability and active selection of different prey sizes in each habitat (Tolonen 1997, Kahilainen & Østbye 2006). Small and/or densely rakered fish mainly feed on small sized prey, which in figure 4a+d is displayed by a low mean maximum and minimum prey size value for small or densely rakered individuals. This pattern could be explained by findings made by Kahilainen & Østbye (2006) and Kahilainen et al. (2011) who have showed high abundance of small prey (i.e. zooplankton) in the pelagic zone and that small and/or densely rakered fish actively utilize that habitat for feeding. Moreover, as body length increase or gill raker density decrease there is an increase in mean maximum and minimum prey size, indicating an active selection for large prey by larger and/or more sparsely rakered fish. These findings could also be influenced by a higher abundance of large-sized prey in the benthic. This would be in line with Tolonen (1997) and Kahilainen et al. (2007) who showed high proportion of benthic prey in stomachs from benthic-associated whitefish morphs. Note that the quantile regression on the absolute maximum prey size show that small and/or densely rakered fish are capable of feeding on large prey when available.

Assuming that zooplankton could be available both in the benthic and limnetic habitat (Steele 1978, Jones et al. 1995), and if fish have no preference for size and/or energetic value of prey, zooplankton would be equally foraged by all fish individuals. This is however not the case as displayed in figure 5a-d; once again the result show that large and/or sparsely rakered fish feed on significantly larger prey than small or densely rakered individuals.

The quantile regression for absolute maximum prey size show that fish can feed on equally large prey items independent of fish body size, gape size, gill raker number and density. Based on this result I hypothesize that whitefish are not constrained by morphology in terms of how large prey they can ingest. If the fish were constrained by morphology the quantile regression line would follow the same pattern as the ordinary linear regression for mean maximum size since it then would be the result of a forced selection of prey in a specific size range.

For the absolute minimum prey size the pattern is however different – fish individuals show a change in absolute minimum prey size along each trait gradient. This is in line with Langeland & Nøst (1995) who showed that the minimum zooplankton prey size ingested by five facultative planktivorous fish (including *C. lavaretus*) decreased with increasing gill raker density. It is likely that large and/or sparsely rakered fish are physically constrained in feeding on small prey items, which would be in line with Roesch et al. (2013) who showed low feeding efficiency on small zooplankton by a benthic whitefish (*Coregonus* sp. “Balchen”) compared to a limnetic whitefish (*C. albellus*). Note however that it is not possible to rule out active selection towards large prey, which have been demonstrated in a number of studies, for example; Langeland & Nøst 1995 and Budy & Haddix 2005.

A high intercorrelation between gape size and fish body length was observed during this study. This type of gape size-body length relationship has also been found in *Coregonus* sp. larvae by Dabrowski et al. (1984) and Ponton & Müller (1990); studies on adult whitefish are however non-existent. Interesting, one of the morphs from Storvindeln had, compared to its

body size, an unexpectedly large gape size. Also, this morph have a higher number of gill rakers compared to all the other morphs. Furthermore, the result showed that this large gaped morph feed on prey that are considerably smaller than what would be expected based on the observed body size and gape size. These observations are indicators that the large gaped densely rakered morph from Storvindeln are displaying filter feeding adaptations. This is a reasonable conclusion based on studies reviewed in Lazzaro (1987) and Gerking (1994). According to Gerking (1994) there are two main strategies for filter feeding; 1) ram filtration means that fish swim fast forward with the mouth wide open and flaring opercles. Large amounts of water enter the buccal cavity and leave through the opercles, forcing prey items towards the esophagus, 2) in pump filtration fish instead pumps water into the buccal cavity using a series of rapid suction while being stationary. For both feeding strategies it would be advantageous to have a large mouth and high density of gill rakers. Gulping behavior, which is similar to and not distinguished from pump filtration, has been observed in two *Coregonus* species (Jansen 1978), making it reasonable to believe that the large gaped morph in Storvindeln also could engage in this behavior. From the stomach content analysis it was noticed that the large gaped morph fed mainly on zooplankton but also on benthic prey like *Chironomidae* larvae and pea clams (*Pisidium* sp.). Based on these observations the large gaped morph presumably can be suggested to be a facultative filter feeder capable of switching between particulate feeding and filter feeding depending on prey availability, size and abundance (Lazzaro 1987, Gerking 1994). This type of switching behavior has been showed in species like Atlantic herring (*Clupea harengus*) (Gibson & Ezzi 1985), alewife (*Alosa pseudoharengus*) (Janssen 1978, Crowder & Binkowski 1983) and northern anchovy (*Engraulis mordax*) (Leong & O'Connell 1969).

Without question densely rakered gills are beneficial when utilizing small prey (e.g. zooplankton) in the pelagic habitat, but what about the adaptive function of sparse gill rakers in the benthic habitats? Lundsgaard-Hansen et al. (2013) showed that benthic whitefish more efficiently use a benthic food source and this current study further strengthen this by adding data concerning morphology and prey size use of phenotypes associated with the benthic habitat. Feeding in this type of environment means that fish inevitably will take in mud (Kahilainen et al. 2003) and sparse gill rakers would allow the mud to be disposed through the gill raker slits while simultaneously be sufficiently dense to retain benthic prey (Kahilainen & Østbye 2006).

The function of the whitefish feeding apparatus is to this day not fully understood, but this study, and many others (for example Kahilainen et al. 2007, Lundsgaard-Hansen et al. 2013, Roesch et al. 2013), suggests adaptation of gill rakers towards effective utilization of available food sources in the various habitats. However, a study by Smith & Sanderson (2007) question the role of gill rakers. The study showed no change in particle movement inside the buccal cavity of blue tilapia (*Oreochromis aureus*) after removal of gill rakers and supporting filtration structures. Furthermore, another study by Smith & Sanderson (2013) tested particle size selectivity for two *Oreochromis* species before and after removal of gill rakers. For one of the species the removal of gill rakers resulted in a significantly higher proportion of small (21-70 μm) particles and smaller proportion of large (91-130 μm) particles. Removal of gill rakers could result in lower crossflow speed and inertial lift inside the buccal cavity, which in turn would lead to loss of larger particles (Cheer et al. 2012, Smith & Sanderson 2013). Both study species ingested less particles overall after removal of filtration structures, however the difference was not significant. The mentioned studies are however done on prey sizes smaller than the ones displayed in the diet of whitefish in this study, also, it has not been shown that whitefish use crossflow filtration when feeding. However, since the density of gill rakers should influence the lift force of the water flow during crossflow filtration (Cheer et al. 2012, Smith & Sanderson 2013), there should still be an effect of the gill raker trait on the ingested prey sizes.

4.1 Conclusions

The initial predator-induced split along the benthic-limnetic habitat axis and throughout the depth of the water column is simultaneously driven by a divergence in body size (Öhlund 2012). I conclude that the observed body size segregation is likely the effect of availability of different prey sizes (i.e. different energy values) in each habitat (Kahilainen et al. 2007, 2011). Also, once in respective habitats the fish may develop morphological adaptations of their feeding apparatus, i.e. the gill rakers and gape size (for the large gaped morph), in order to utilize the available food source in the most efficient way. The fact that small and/or densely rakered fish can utilize large prey is interesting, this provides additional benefit when small prey is at low densities.

Even though it is not yet understood why, it seems like studies concerning the relationship between gill raker morphology and the utilization and selectivity of different prey show the same pattern of adaptive trait utility (Langeland & Nøst 1995, Day & McPhail 1996, Roesch et al. 2013) and phenotype-environment correlations (Kahilainen et al. 2007 & 2011, Harrod et al. 2010). This study further strengthens the idea of adaptive trait utility along the entire gill raker trait axis and provide quantitative data not only on the relationships between prey size and gill raker numbers, but also for prey size in relation to gill raker density, body length and gape size.

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Appendix 1

Table 1. Model selection. All models are explaining the variation in mean extreme prey sizes using; BL=body length, GN=gill raker number, GD=gill raker density and/or GS=gape size. In the first column the included prey classes are reported, the second column indicates whether it is the maximum or minimum prey size that is modelled, the third column gives the predictors included in each model, with corresponding adjusted r²-value and AIC in the fifth and sixth column, respectively. AIC was used to identify the models with best predictive power.

Prey class	Response	Model	Adjusted r ²	AIC
All	Max	BL ^{***}	0.469	258
All	Max	GN ^{**}	0.0897	310
All	Max	GD ^{***}	0.4507	261
All	Max	GS ^{***}	0.3847	272
All	Max	BL ^{**} +GD ^{**}	0.5011	253
All	Max	BL ^{***} +GN [*]	0.4892	255
All	Max	BL ^{**} +GN+GD	0.496	255
All	Max	BL [*] +GN+GD+GS	0.4962	255
All	Min	BL ^{***}	0.4119	160
All	Min	GN ^{***}	0.1661	194
All	Min	GD ^{***}	0.4382	155
All	Min	GS ^{***}	0.3677	167
All	Min	BL ^{**} +GD ^{**}	0.4631	152
All	Min	BL ^{***} +GN ^{***}	0.4829	148
All	Min	BL ^{**} +GN+GD	0.4788	150
All	Min	BL [*] +GN+GD+GS	0.4734	152
Zooplankton	Max	BL ^{***}	0.3077	72
Zooplankton	Max	GN ^{***}	0.3299	71
Zooplankton	Max	GD ^{***}	0.4117	63
Zooplankton	Max	GS ^{***}	0.2883	74
Zooplankton	Max	BL ^{***} +GN	0.5243	52
Zooplankton	Max	GN ^{***} +GS ^{***}	0.4923	56
Zooplankton	Max	BL+GN ^{***} +GS	0.5188	54
Zooplankton	Max	BL ^{**} +GN ^{***} +GD	0.5167	54
Zooplankton	Max	BL+GN ^{***} +GD+GS	0.5119	55
Zooplankton	Min	BL ^{***}	0.2227	78
Zooplankton	Min	GN ^{***}	0.507	52
Zooplankton	Min	GD ^{***}	0.4046	63
Zooplankton	Min	GS ^{***}	0.2332	78
Zooplankton	Min	BL ^{***} +GN ^{***}	0.614	39
Zooplankton	Min	BL+GD ^{***}	0.3947	65
Zooplankton	Min	GN ^{***} +GS ^{***}	0.6047	41
Zooplankton	Min	BL ^{**} +GN ^{***} +GD	0.6125	41
Zooplankton	Min	BL+GN ^{***} +GD+GS	0.6052	43

Levels of significance; * < 0.05, ** < 0.01, *** < 0.001

Table 2. Head width-body length regressions for prey items.

Equations (HW=head width)

Tricoptera= $13.895 * HW - 0.8074$ ($r^2=0.87$)

Chironomidae= $17.831 * HW^{0.9108}$ ($r^2=0.84$)

Coleoptera= $4.7557 * (HW^{0.7654})$ ($r^2=0.80$)

Ephemeroptera= $5.1707 * HW^{0.8835}$ ($r^2=0.50$)

Ephemera= $10.345 * HW^{0.6873}$ ($r^2=0.69$)
