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Effects of habitat and food resources on morphology and ontogenetic growth trajectories in perch

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Abstract Studies on resource polymorphism have mainly been considered at the end stage of ontogeny, whereas many species undergo diet changes as they grow. We conducted a field survey to analyze the role of adaptive variation during ontogeny in Eurasian perch (*Perca fluviatilis*). We caught perch from the littoral and pelagic zones of a lake to investigate whether perch differ in morphology and diet between these habitats. We also investigated whether there were any differences in morphological trajectories during the ontogeny of perch collected from the two habitats. We found that perch caught in the littoral habitat, independently of size, had a deeper body, larger head and mouth and longer fins than perch caught in the pelagic zone. Macroinvertebrates and fish dominated the diet of littoral perch, whereas the diet of the pelagic perch consisted mainly of zooplankton and to some extent fish. Independently of size, the more streamlined individuals had a larger proportion of zooplankton and a smaller proportion of macroinvertebrates in their diet than the deeper-bodied individuals, indicating a relation between diet and morphology. Some morphological characters followed different ontogenetic trajectories in the two habitats; e.g. the changes to a deeper body and a larger head were faster in the littoral than in the pelagic perch. The relationship between the length of perch and the size of the mouth and fins also differed between perch from the two habitats, where the increase in the length of the pelvic fin and the area of the mouth increased faster with size in the littoral perch. Our findings show that variation in morphology between habitats dif-

fers during ontogeny in a way that corresponds to functional expectations for fish species that occupy these habitats.

Keywords Allometry · Phenotypic plasticity · Trophic polymorphism · Ecological differentiation · Within-population variability

Introduction

Adaptations to maximize foraging intake have long been recognized to be dependent on specific habitats or prey types (e.g. Webb 1984; Webb and Weihs 1986; Smith 1990; Wainwright and Richard 1995; Wainwright 1996; Huckins 1997). Differences in morphology among species and between populations of the same species can often be interpreted as adaptations to different ecological conditions. For example, fish species that are specialized for living in open water and searching for widely dispersed prey have fusiform bodies that minimize drag and allow for efficient cruising (Webb 1984; Webb and Weihs 1986). In contrast, fish that are adapted for searching for prey in structurally complex habitats have a deep and laterally compressed body and extended fins and are well suited for slow and precise maneuverability (Webb 1984; Webb and Weihs 1986; Norton 1995).

Several studies have shown that intraspecific resource polymorphism is probably much more common than has been previously recognized (Skúlason and Smith 1995; Smith and Skúlason 1996). Resource polymorphism within a species (i.e. the occurrence of intraspecific forms displaying differential niche use), has been found in various vertebrate species and has been interpreted as occurring when there is an “open” niche (Robinson and Wilson 1994; Wimberger 1994; Skúlason and Smith 1995; Smith and Skúlason 1996). Most of the cases of resource polymorphism have been found in organisms that subdue, manipulate and process their prey, using only their mouth, such as birds and fish (Wimberger 1994).

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Studies of fish, in particular, suggest that the resource polymorphism arises as a function of habitat-specific foraging abilities (Ehlinger and Wilson 1988; Ehlinger 1990; Schluter 1993, 1995; Robinson et al. 1996; Robinson and Schluter 2000). The examples of resource polymorphism in fish may be examples of the earliest stages of adaptive radiation yet studied, and show that in lacustrine systems most of the segregation occurs between the littoral and the pelagic habitats (Robinson and Wilson 1994; Skúlason and Smith 1995; Smith and Skúlason 1996). However, most of the studies of resource polymorphism have only considered the end stages of ontogeny (but see Ehlinger and Wilson 1988; Skúlason et al. 1989; Wainwright et al. 1991; Robinson et al. 1993, 1996; Snorrason et al. 1994), and have neglected the fact that many fish species undergo diet changes as they grow (Werner and Gilliam 1984). Diet changes in growing individuals are thought to occur because growth imposes a number of scaling constraints in foraging performance and energy demands (Werner and Gilliam 1984; Werner 1986, 1988; Sebens 1987; Persson 1988; Persson et al. 1998). Furthermore, organisms that change their niche during ontogeny are often subjected to different and often conflicting selection pressures which may result in reduced performance compared to organisms that specialize in one niche throughout their ontogeny (Werner and Gilliam 1984; Persson 1988; Werner 1988).

In this study we focus on the morphological development and resource use in relation to habitat choice of the Eurasian perch (*Perca fluviatilis*). This perch may undergo two ontogenetic niche shifts during its life (Persson 1988), and is considered to have a generalist body morphology (Webb 1984), capable of foraging for a wide variety of prey in the vegetation and in open water. As a juvenile, the perch is a zooplankton feeder, then shifts to feeding on macroinvertebrates at an intermediate size and, when large enough, to a diet mainly consisting of fish (Persson 1988; Hjelm et al. 2000). Owing to possible trade-offs in efficiency of foraging for zooplankton and macroinvertebrates among habitats, a phenomenon that has been suggested for other fish species (Webb 1984; Ehlinger and Wilson 1988; Ehlinger 1990; Schluter 1993, 1995; Robinson et al. 1996), we expected perch to experience conflicting selective pressures leading to morphological trade-offs.

Therefore, perch caught in the two habitats (littoral, pelagic) should differ both in morphology and diet during ontogeny. We predicted that, independently of size, slender individuals will have a diet dominated by zooplankton, and deep-bodied individuals will have a greater proportion of macroinvertebrates in their diet.

Materials and methods

The study was carried out in lake Trehörningen, in central Sweden (latitude: 64°00'50"N, longitude 20°08'00"E). The lake's area is 2.37 km² and its maximum depth is 17 m. In addition to perch, Lake Trehörningen also contains roach (*Rutilus rutilus*), pike (*Esox lucius*), and vendace (*Coregonus albula*).

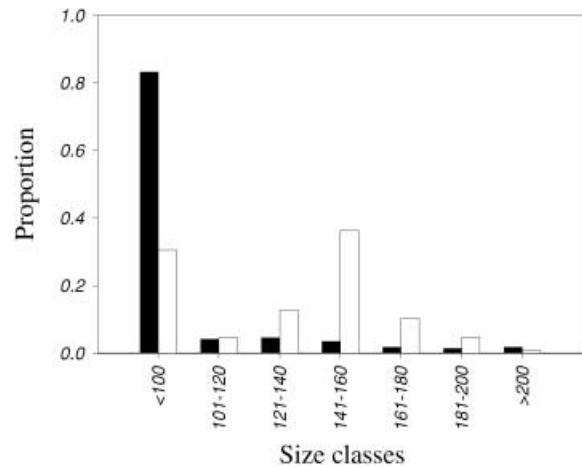


Fig. 1 Size distribution of all the perch caught in Lake Trehörningen from the littoral (black bars, $n=291$) and the pelagic habitats (white bars, $n=515$). The size distribution is expressed as proportions of the total catch in each habitat

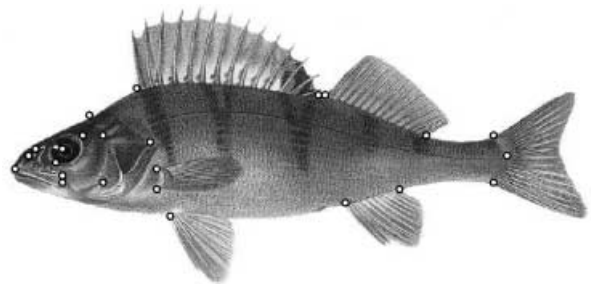


Fig. 2 Landmark configuration on the perch used in the morphological analysis

Perch were sampled in late July 1998 using pelagic and benthic gill nets of standard survey-link type. The pelagic nets were 25 m long and 3 m high and the benthic nets were 25 m long and 1.5 m high. Three pelagic nets were set at the surface (1 m) at 10 a.m. and were lifted at 10 a.m. the following day. The pelagic nets were set about 150 m offshore where the water had a depth of more than 10 m. The benthic nets were used to catch fish from the littoral zone and were placed just outside the vegetation, followed by scaring the fish inside the vegetation into the nets. Fish that came from outside the vegetation zone were easily identified by which way they pointed in the net and were not included in the analysis. The nets were then immediately emptied and the fish were deep-frozen for later analysis.

From the total catch of perch (291 littoral and 515 pelagic) a random sample of 20 specimens from each habitat and 20-mm size-class (see Fig. 1) was subjected to morphological analysis. In size-classes for which fewer specimens were caught, all specimens were used. In total, the morphology of 71 littoral perch and 142 pelagic perch was analyzed using a Polhemus digitizing tablet and Ds-digit (Slice 1994). Twenty-four landmarks on the left side of each specimen were digitized (Fig. 2). Each specimen was defrosted and placed on a bed of glass balls and the fins were fixed to the frame of the bed with needles.

We used multivariate geometric shape analysis to acquire a synthetic quantification of morphological variation in body shape among individuals (Rohlf and Marcus 1993). The digitized landmarks were used to analyze the relative position of each landmark and variation in body shape, using thin-plate spline relative warp analysis (TPSRW; Rohlf 1993a). TPSRW transforms all speci-

mens to a centroid size to avoid differences in landmarks due to body size, and TPSRW was used to calculate relative warps. Relative warps represent principal-component vectors in a multivariate-shape space, and each relative warp can be thought of as representing a unique multivariate-shape dimension, orthogonal to all other relative warps. For a more detailed description and discussion of thin-plate spline relative warp analysis see Bookstein (1991), Rohlf (1993b) and Marcus et al. (1996).

Five traits were also measured, including the length of the fins, buccal volume and gape area. The fins were measured from the base of the fin to the tip. For the anterior dorsal fin, fin rays number 1, 5, 10 and 14 were measured and an average was calculated. For the posterior dorsal fin and the anal fin, an average length was estimated from the length of the anterior and the posterior part of the fin. To quantify the buccal volume we made casts of the buccal cavities by pumping silicone sealant into the mouth. Each cast of the buccal cavity was allowed to harden inside the fish and then dissected out. The cast was then allowed to cure for one week before trimming off any silicone that had gone through the gill bars or into the esophagus. The silicone was then weighed and its volume calculated using the density of the silicone. Gape area was measured on the fish by inserting a cone-shaped probe into the mouth. The probe was inserted into the mouth until the angle between the maxilla and the lower jaw was 90° and was repeated three times, from which a mean value was calculated.

The stomach content of every fish was analyzed under a dissecting microscope and the zooplankton and macroinvertebrates were identified to the lowest possible taxonomic level, counted and measured to the nearest tenth of a millimeter. The fish found in the stomachs were identified to species and measured to the nearest millimeter (total length). The lengths of all prey types were then converted to biomass (dry weight) using our own length/weight relationships. The proportion of dry weight of four functional diet categories (zooplankton, macroinvertebrates, fish and terrestrial prey) was then used in all analyses concerning diet. We analyzed all correlations between morphology and diet, including all fish in the analysis. Since the diet of the individuals could be biased towards habitat rather than their morphology, we also analyzed perch from the littoral and pelagic zone separately.

To determine the size at which the fish changed diet, they were sorted into 10-mm length classes and the diet was divided into the three major resource types: zooplankton, macroinvertebrates and fish. The size at which perch shifted from zooplankton to macroinvertebrates (S_1) was examined for perch caught in the littoral and in the pelagic habitats and was defined as the size at which the percentage dry weight of macroinvertebrates in the diet exceeded 50% (sensu Hjelm et al. 2000). Similarly, the size for the diet shift from macroinvertebrates to piscivory (S_2) was defined as the size at which the percentage dry weight of fish in the diet exceeded 50%.

Age of individual perch was determined from the opercula bones by counting the number of winter bands. Variation in growth was then determined by a non-linear regression ($y=a \times \ln x + b$) of total length on age at capture for each fish, and differences in residuals were used to test for differences in growth related to the habitat in which the fish were caught.

Statistics

We analyzed the overall change in morphology by combining morphological dimensions into one analysis, with the total length of the fish as covariate (MANCOVA; Bookstein 1991). However, in the sequential analysis in which we explore the morphological changes during ontogeny in the two habitats, we used ANCOVA on each morphological variable. Since ANCOVA requires the slopes of the regression lines to be parallel (Sokal and Rohlf 1981), we first tested for significant interaction effects between the habitat and the covariate for each morphological variable. We interpreted a significant interaction effect as evidence of different ontogenetic trajectories and, for those morphological variables for which we found no interaction effect, we carried out ANCOVA without an interaction term. The relationship between morphology

and diet was analyzed in three steps. First, the proportion of dietary groups (arcsine square-root transformed) was regressed against total length, and residuals were estimated in order to remove the effects of body size from diet. Second, each relative warp was linearly regressed against total length and its residuals estimated in order to remove size variation from shape variation. Third, the relationship between morphology and diet was then analyzed with multiple regression, for which residual relative warp variation was used to predict variation in residual diet proportions. Multicollinearity of relative warps is not a problem in this case, because shape variation represented by each relative warp is orthogonal to the other relative warps. To make the metric characters linear, they were transformed to their natural logarithms before analysis. Proportions were arcsine square-root transformed before analysis and the two-tailed significance level was set at $\alpha=0.05$.

Results

Perch size distribution and diet

The perch caught in the two habitats were of the same size range (66–237 mm), but the size distribution of perch differed between the littoral and the pelagic habitats (Fig. 1; chi-square test: $\chi^2=228$, $df=6$, $P<0.001$). The difference was due to a higher proportion of smaller perch in the littoral zone than expected and a higher proportion of larger perch in the pelagic zone than expected.

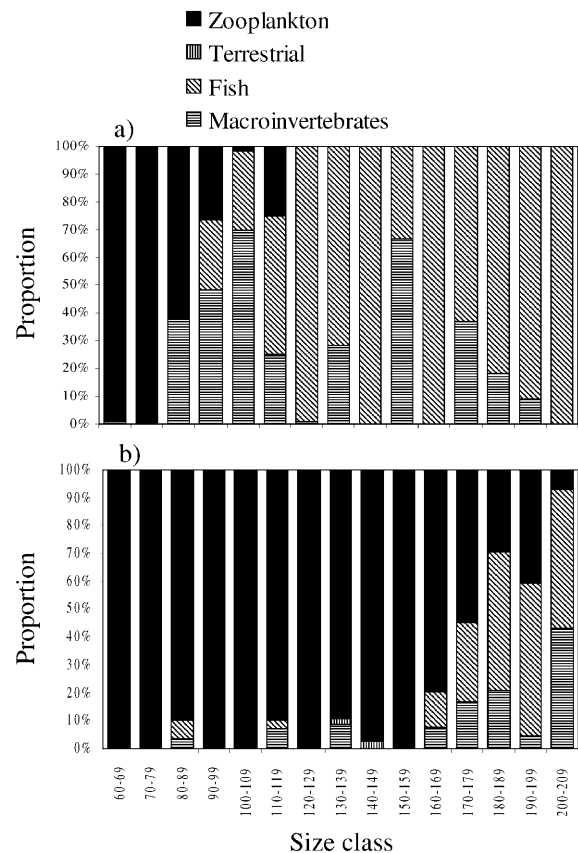


Fig. 3 Proportion of prey types in the diet of perch of different size classes from **a** the littoral and **b** the pelagic zones of Lake Trehörningen

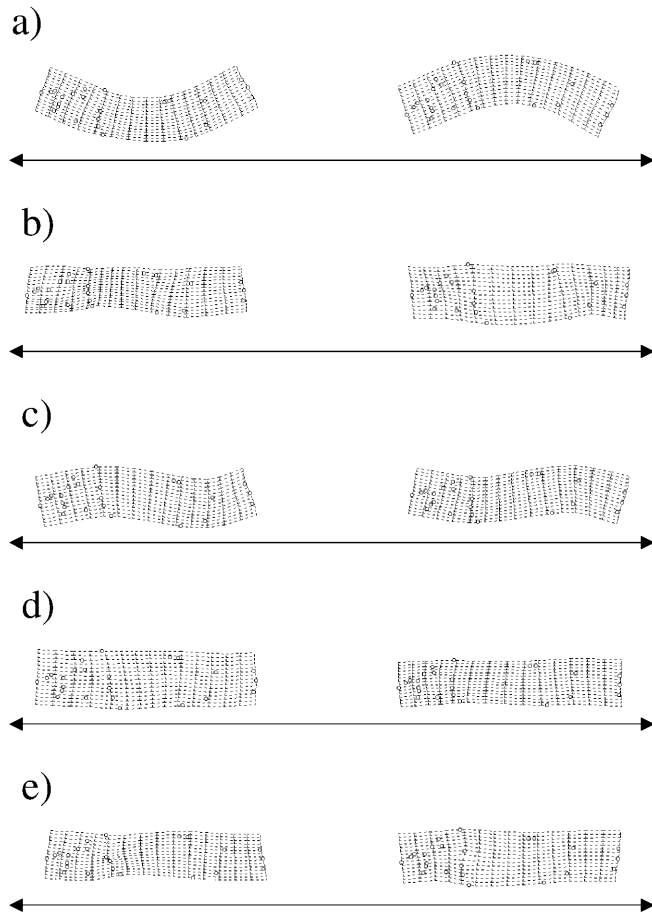


Fig. 4 Visualization of **a** RW1, **b** RW2, **c** RW3, **d** RW4 and **e** RW5 as grid plots obtained from TPSRW (Rohlf 1993a). Grid plots represent the individual with the lowest relative warp score (left panel) and the highest relative warp score (right panel) for each relative warp. Habitat is not related to the observed morphological variation in **a** and **c**, but is related to variation shown in **b**, **d** and **e** (see Table 1 and Fig. 5). On average, littoral fish had more positive scores than pelagic fish in **b** and **e**, and more negative scores in **d**

Littoral perch had a higher growth rate (total length at age) than pelagic perch (ANOVA, habitat: $F_{1,197}=9.31$, $P=0.03$; age: $F_{7,197}=4.76$, $P<0.001$; habitat×age: $F_{7,197}=2.77$, $P=0.009$). The effect of habitat relates to the fact that littoral perch of age 2+ had a higher growth rate than that of pelagic perch (Tukey, $P<0.05$), whereas in all other age classes there was no difference, in growth rate, between habitats (Tukey, $P>0.05$ for all age classes). We found no difference between the habitats in the weight of the perch at a given size (ANCOVA, habitat: $F_{1,210}=0.329$, $P=0.329$; length: $F_{1,210}=30,742$, $P<0.001$).

The diet of pelagic perch consisted mainly of zooplankton, whereas that of littoral perch consisted mainly of macroinvertebrates and fish (Fig. 3). The proportion of zooplankton in the diet of pelagic perch was higher than in the diet of littoral perch (ANCOVA of all size classes combined, habitat: $F_{1,195}=173$, $P<0.001$; length: $F_{1,195}=86.07$, $P<0.001$), whereas the proportions of fish

Table 1 Results of the final ANCOVA models comparing relative warps 1 through 5 between habitats, with total length as covariate. The full model included an interaction term (Habitat×Length) which was removed from the final model if it was not significant (indicated by interaction results given in parenthesis). Where the interaction term was significant, it was left in the full model (indicated by no parenthesis)

	<i>df</i>	<i>F</i>	<i>P</i>
(a)	RW1		
Habitat	1, 210	2.880	0.091
Length	1, 210	3.519	0.062
(Habitat×length)	1, 209	2.523	0.114
(b)	RW2		
Habitat	1, 210	16.046	<0.001
Length	1, 210	526.227	<0.001
(Habitat×length)	1, 209	1.700	0.194
(c)	RW3		
Habitat	1, 210	0.034	0.855
Length	1, 210	10.259	0.002
(Habitat×length)	1, 209	0.543	0.462
(d)	RW4		
Habitat	1, 209	13.941	<0.001
Length	1, 209	19.791	<0.001
Habitat×length	1, 209	4.268	0.040
(e)	RW5		
Habitat	1, 209	13.838	<0.001
Length	1, 209	0.199	0.656
Habitat×length	1, 209	25.446	<0.001

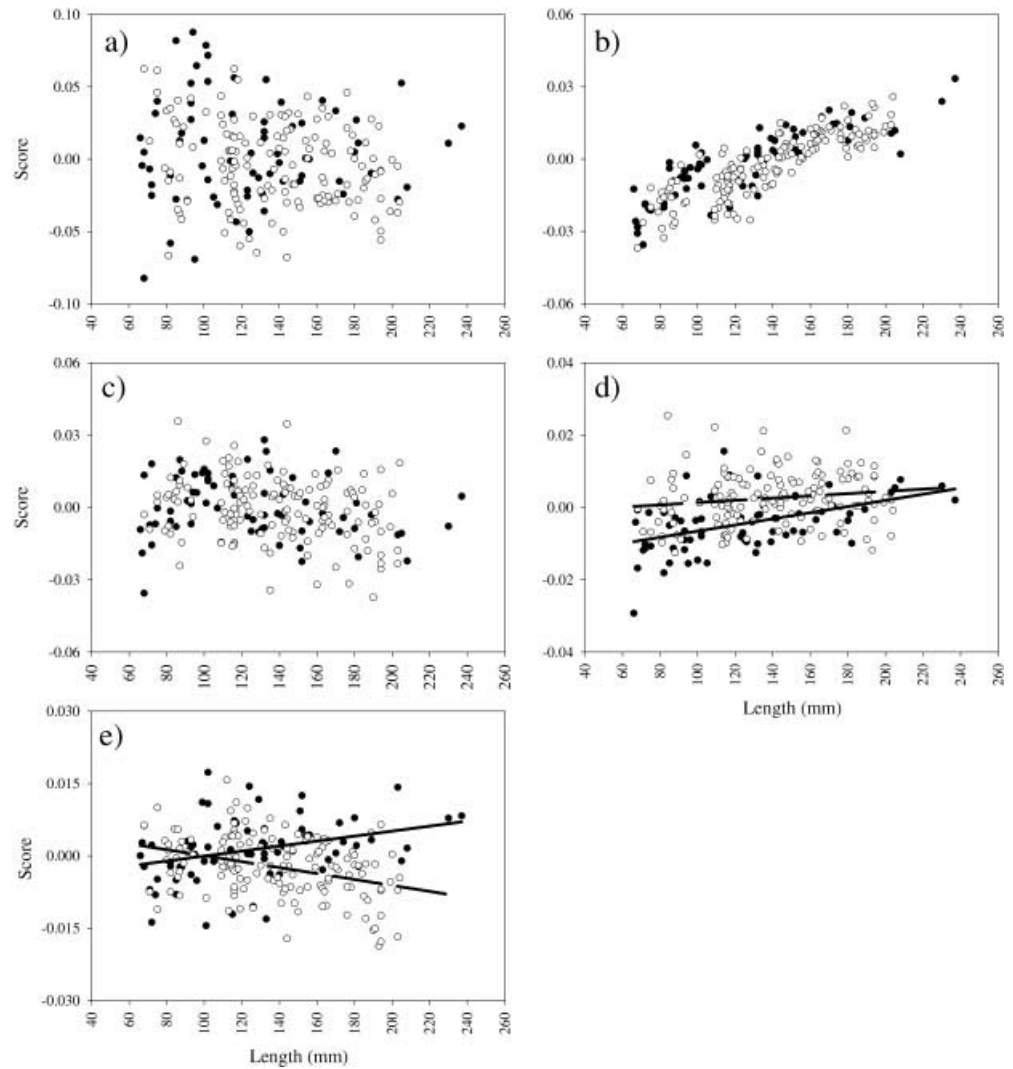
and macroinvertebrates in the diet of pelagic perch were lower than in the diet of littoral perch (ANCOVA macroinvertebrates, habitat: $F_{1,195}=26.5$, $P<0.001$; length: $F_{1,195}=2.31$, $P=0.131$; fish, habitat: $F_{1,195}=68.9$, $P<0.001$; length: $F_{1,195}=58.6$, $P<0.001$).

The change in diet from zooplankton to macroinvertebrates (S_1) in littoral perch occurred at 95 mm, whereas there was no such diet change in the pelagic perch. The proportion of macroinvertebrates in pelagic perch never exceeded 43%. The diet change to fish (S_2) occurred at a length of 115 mm in the littoral perch and at a length of 185 mm in the pelagic perch.

Landmark-based morphology

Of the 44 relative warps (RW) from the TPSRW, the first 5 described 82.5% of the total variation (RW1 explained 54.00%, RW2 12.02%, RW3 9.53%, RW4 3.88%, RW5 3.03%, respectively) and we focus on these 5 relative warps (Fig. 4). There were morphological differences between littoral and pelagic perch that were related to body length, indicating different growth trajectories (MANCOVA on RW1 to RW5, habitat: $F_{6,204}=8.93$; length: $F_{6,204}=148$; habitat×length: $F_{6,204}=8.24$, $P<0.001$ for all F values). Separate ANCOVAs were carried out on RW 1–5, in which RW2, RW4 and RW5 reflected dif-

Fig. 5 The relationship between the total length of the fish and morphology expressed as the score of **a** RW1, **b** RW2, **c** RW3, **d** RW4 and **e** RW5, respectively. *Open symbols and dashed lines* represent individuals from the pelagic habitat, whereas *solid symbols and solid lines* represent individuals from the littoral habitat. Regression lines are only present when there is a difference in slope between littoral and pelagic samples. For visualization of the morphological axis, see Fig. 4



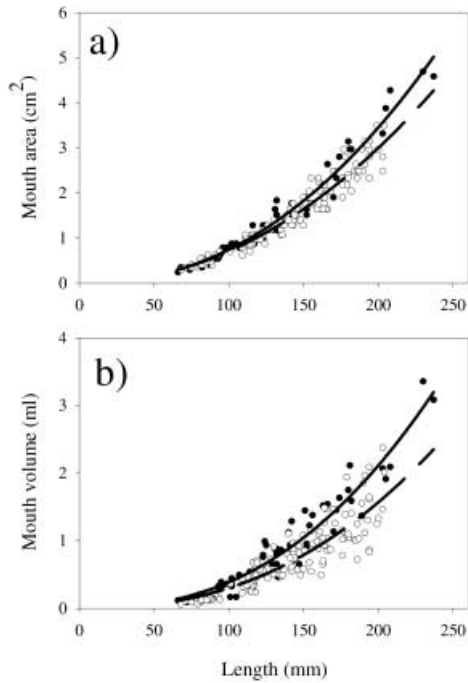
ferences in morphology between perch from littoral and pelagic habitats (Table 1; Fig. 5). Variation in morphology in RW2 indicated that littoral perch had a deeper body, longer base of the anterior dorsal fin and a shorter caudal peduncle (Fig. 4b). These three RW2 components were positively related to length in the same way in both habitats (Fig. 5b).

Differences in ontogenetic trajectories between littoral and pelagic perch were indicated in RW4 and RW5 (Table 1 d, e; Fig. 5d, e). For RW4, the littoral perch had a relatively larger head at smaller sizes, but with increasing length the relative head size decreased faster compared to the pelagic perch (Fig. 4d, 5d). There was also a difference in ontogenetic trajectories in body depth of the anterior part of the fish, as indicated by RW5. At small sizes, littoral and pelagic perch both seemed to start with a similar morphology in RW5, but, with increasing size, the littoral perch became relatively deeper in the anterior part of the body, whereas pelagic perch became more slender (Fig. 4e, 5e).

Morphological measurements using metric characters

Variation in the metric characters depended both on the habitat in which the fish were caught and on the length of the fish, indicating different growth trajectories (MANCOVA, habitat: $F_{7,201}=3.53$, $P=0.001$; length: $F_{7,201}=3.077$, $P<0.001$; habitat \times length: $F_{7,201}=3.38$, $P=0.002$).

Separate ANCOVAs revealed that the littoral perch had longer fins and larger mouth volume and gape than the pelagic perch (Table 2). Furthermore, there was an allometric relationship between habitats in the length of the pelvic fin and mouth area (Table 2). The pelvic fin increased proportionally more in length in the littoral perch than in the pelagic perch. In contrast, there were no differences in growth trajectories in the pectoral fin, the first and second dorsal fin and the anal fin between the habitats (Table 2 a–e). Mouth area also exhibited a more rapid growth with increasing length in the littoral perch than in the pelagic perch. There was no difference in the growth trajectories of mouth volume between the habitats (Fig. 6; Table 2 f, g).



Correlation between morphology and diet

The proportion of macroinvertebrates in the diet increased with RW1 and RW2 (Table 3 a) indicating more macroinvertebrates in the diet of perch with a deeper body (e.g. RW2) and with heads that are directed downwards (e.g. RW1). The proportion of fish in the diet decreased with RW4, whereas the proportion of fish in the diet increased with RW5 (Table 3 a), showing that perch with a deeper body had more fish in their diet. The positive correlation between RW4 and the proportion of zooplankton in the diet, and the negative correlation between RW1 and RW5 with zooplankton (Table 3 a) demonstrates that zooplanktivory is related to a more streamlined body with a mouth that is directed upwards.

Fig. 6 The relationship between total length of the fish and **a** mouth area and **b** buccal volume from the littoral and pelagic habitats in Lake Trehörningen. *Open symbols and dashed lines* represent perch from the pelagic habitat, whereas *solid symbols and solid lines* represent perch from the littoral habitat

Table 2 Results of the final ANCOVA models comparing metric characters (transformed to natural logarithms) between habitats with total length as covariate. The full model included an interaction term (Habitat×Length) which was removed from the final model if non-significant. Non-significant interaction results are given in parenthesis. Adjusted group means (in millimeters for fin lengths and in milliliters for mouth volume) for individuals of a total length of 134 mm are given for the metric traits where the interaction term was non-significant

	<i>df</i>	<i>F</i>	<i>P</i>	Adjusted means	
				Littoral	Pelagic
(a)	Pectoral fin				
Habitat	1, 208	61.04	<0.001	18.0	17.1
Length	1, 208	9.642	<0.001	–	–
(Habitat×length)	1, 207	1.378	0.242)	–	–
(b)	Pelvic fin				
Habitat	1, 207	4.030	0.046	NA	NA
Length	1, 207	3691	<0.001	–	–
Habitat×length	1, 207	5.033	0.026	–	–
(c)	First dorsal fin				
Habitat	1, 208	36.97	<0.001	12.2	11.6
Length	1, 207	8.548	<0.001	–	–
(Habitat×length)	1, 207	0.071	0.791)	–	–
(d)	Second dorsal fin				
Habitat	1, 208	24.35	<0.001	10.4	10.1
Length	1, 208	6.720	<0.001	–	–
(Habitat×length)	1, 207	0.656	0.419)	–	–
(e)	Anal fin				
Habitat	1, 208	30.54	<0.001	9.4	9.0
Length	1, 208	6.485	<0.001	–	–
(Habitat×length)	1, 207	1.723	0.191)	–	–
(f)	Mouth area				
Habitat	1, 207	10.23	0.002	NA	NA
Length	1, 207	5.670	<0.001	–	–
Habitat×length	1, 207	12.00	0.001	–	–
(g)	Mouth volume				
Habitat	1, 208	51.38	<0.001	0.91	0.66
Length	1, 208	1.873	<0.001	–	–
(Habitat×length)	1, 207	0.136	0.713)	–	–

Table 3 Signs of significant coefficients from a multiple regression analysis using morphology to predict diet. Signs indicate the direction of the correlation, and a 0 indicates no significant correlation. No significant correlations were found between morphology and diet in the pelagic perch

	RW1	RW2	RW3	RW4	RW5
a) All perch					
Macroinvertebrates	+	+	0	0	0
Fish	0	0	0	-	+
Zooplankton	-	0	0	+	-
b) Littoral perch					
Macroinvertebrates	0	+	0	0	0
Fish	0	0	0	0	0
Zooplankton	-	0	-	0	-

When analyzing perch from the two different habitats separately, we found no relationships between morphology and diet in any prey category in pelagic samples. However, in the littoral sample, morphology was often related to zooplanktivory, such that more-littoral forms exhibited less zooplanktivory (RW1 and RW5) and a greater reliance on macroinvertebrates (RW2) (Table 3 b).

Discussion

Differences in morphology between habitats

Our study shows that perch caught in the two habitats of Lake Trehörningen differed in morphology and diet. Furthermore, differences in morphology between habitats were consistent over the whole size range of the perch that we caught. The difference in morphology was not related to the condition of the perch, since perch from both habitats had the same weight in comparisons for which size was corrected. Although the size distribution was biased towards smaller sizes of perch in the littoral zone, we caught fish from the same size range in both habitats and the morphological difference was still present in size-corrected comparisons: perch from the littoral zone had a deeper body, larger head and mouth, and longer fins than perch from the pelagic zone. A deep body and long fins are hypothesized to be adaptations to high maneuverability and efficient foraging in the vegetated littoral habitat, whereas a more streamlined body is hypothesized to be better adapted to searching for widely dispersed prey in the pelagic zone (Webb 1984; Webb and Weihs 1986; Ehlinger and Wilson 1988; Ehlinger 1990; Svanbäck and Eklöv, unpublished manuscript). As far as we know, this is the first example of resource polymorphism involving littoral and pelagic habitats in perch, and adds to a growing list of fish taxa inhabiting postglacial northern lakes (Robinson and Schluter 2000).

Many of the studies reporting resource polymorphism in fish show distinct morphotypes between the littoral and pelagic habitats in lakes (Smith and Skúlason 1996 and references therein). In contrast, our study showed

differences in mean morphology but also a large overlap in morphology between the fish caught in the two habitats (see also Ehlinger and Wilson 1988; Robinson et al. 1993, 1996; Dynes et al. 1999). The growing body of evidence of subtle intraspecific differences in morphology between habitats suggests that it is probably very common in nature and may sometimes be an initial stage in sympatric speciation (Smith and Skúlason 1996). Our diet data do not provide any evidence of long-term patterns of habitat use in perch, but it appears that there are only fairly limited short-term movements between the habitats, since Eklöv (1997) has found very limited movement of perch between littoral and pelagic habitats. The evidence on how movements between habitats are related to morphological changes in fish is scarce, but trends have been detected in other trophically polymorphic fish species (Kurenkov 1977; Wilson et al. 1996; Bourke et al. 1997).

Morphology and diet

Morphology is expected to influence diet in fish on a short time scale, but on intermediate or longer time scales, diet may influence morphology through phenotypic plasticity or natural selection (Wainwright 1994, 1996; Wainwright and Richard 1995; Robinson and Wilson 1996; Mittelbach et al. 1999). We found clear dietary differences between perch caught in the littoral and pelagic zones. Perch caught in the pelagic zone fed mainly on zooplankton, while perch caught in the littoral zone fed mainly on macroinvertebrates and fish. The relationships between morphology and diet are congruent with the predictions that, at any given size, the more slender individuals fed more on zooplankton, and the individuals with deeper body morphology had higher proportions of macroinvertebrates in their diet (e.g. Ehlinger and Wilson 1988; Ehlinger 1990; Schluter 1993). There was no significant correlation between morphology and diet in pelagic perch, which was likely due to reduced diet variation in pelagic perch. Interestingly, we found relationships between morphology and diet in littoral perch that were similar to correlations based on all the perch. This suggests that morphologically variable perch also separate by diet within the littoral zone. The relationship between morphology and diet within a habitat has been reported before, but only in comparisons among lakes and not within a lake (e.g. Wainwright et al. 1991; Mittelbach et al. 1992).

For perch, zooplanktivorous feeding and piscivorous feeding modes appear to be associated with a similar morphology (Eklöv and Persson 1995; Hjelm et al. 2000). Zooplanktivorous and piscivorous feeding are hypothesized to be related to a slender body which is supposed to reduce drag during steady swimming while searching for patchy prey (zooplanktivory) and during fast acceleration while attacking fish prey (Webb 1984; Webb and Weihs 1986). Benthivorous feeding has been suggested to be related to a deeper body and longer pec-

toral and pelvic fins which may enable efficient maneuvering while searching for cryptic prey in the vegetated littoral zone (Webb 1984; Webb and Weihs 1986; Ehlinger and Wilson 1988; Ehlinger 1990). We unexpectedly found a general positive correlation between the depth of the fish and the proportion of fish in their diet. The availability of small fish in the pelagic zone was lower than in the littoral zone and it is possible that this positive correlation is due to different piscivorous foraging modes in the open water and the vegetation (Eklöv and Diehl 1994). Piscivory in open water is related to high acceleration and steady swimming, whereas piscivory in the littoral zone is related to high maneuverability (Webb 1984; Eklöv 1992; Eklöv and Diehl 1994). High maneuverability may in general be important for a piscivore, since predatory perch adjust their attack speed to the prey escape speed to facilitate maneuverability during attacks (Lundvall et al. 1999). Therefore, the greater degree of piscivory in littoral habitats where high maneuverability confers an advantage may account for the positive relationship between body depth and piscivory in this study. It is also possible that feeding on macroinvertebrates and zooplankton imposes stronger selection on body depths than piscivory in perch, because only at very large sizes can perch prey on fish (Lundvall et al. 1999; Claessen et al. 2000).

Ontogenetic growth trajectories

We have demonstrated that, as perch grew in size, they exhibited a relatively deeper body, a relatively shorter and higher head, and a relative lengthening of the base of the first dorsal fin. These changes in body morphology indicate that as perch grow they attain a shape that favors higher performance in preying on macroinvertebrates and fish (see argument in the two preceding sections; e.g. Webb 1984; Webb and Weihs 1986; Ehlinger and Wilson 1988; Svanbäck and Eklöv, unpublished manuscript). Similarly Hjelm et al. (unpublished manuscript) have found that as roach (*Rutilus rutilus*) grew larger, they gradually changed toward a deeper body and a higher proportion of macroinvertebrates in their diet.

However, despite such increase in body depth with size, pelagic perch did not feed much on macroinvertebrates and tended either to feed on zooplankton or on fish. In contrast, littoral perch of intermediate size fed to a large extent on macroinvertebrates. Thus, it is possible that a higher proportion of macroinvertebrates in the diet of littoral perch had a stronger influence on body morphology than that observed in pelagic perch as they grew, indicating phenotypic plasticity. Consistent with this hypothesis is the fact that some morphological changes during ontogeny were different for the littoral and pelagic perch. For example, the littoral perch, with increasing size, changed toward a deeper morphology in the anterior part of the body, whereas the pelagic perch changed to a more slender morphology in that region of the body. Also, the pelvic fin and mouth area had differ-

ent ontogenetic trajectories in which the differences in both characters increased with size between the perch from the two habitats.

A typical fish may increase five orders of magnitude in weight over its entire life span (Werner and Gilliam 1984) and is thus often subjected to different and conflicting selection pressures. To optimize performance throughout ontogeny, growing individuals are generally expected to change their ecological niche with respect to prey type, prey size, or habitat type (Werner and Gilliam 1984; Werner 1986, 1988; Sebens 1987; Persson 1988). The timing of the niche shifts will be affected both by resource availability and predation risk (Werner and Gilliam 1984; Persson and Greenberg 1990; Turner and Mittelbach 1990) and may also be related to morphological constraints (Hjelm et al. 2000). The majority of studies on fish polymorphism have focused on adult body forms to point out the importance of trade-offs related to morphological characters (Smith and Skúlason 1996 and references therein). In this study we focused on differences in morphological characters related to resource use over the ontogeny of perch. Perch pass through a zooplanktivorous as well as a benthivorous feeding stage before becoming piscivorous (Persson 1988; Hjelm et al. 2000). The morphology favoring benthivory can be in conflict with the morphology favoring zooplanktivory (Ehlinger and Wilson 1988; Ehlinger 1990; Schluter 1993), which could lead to an ontogenetic trade-off (Persson 1988; Werner 1988). The morphological patterns of perch in our study are consistent with the prediction that foraging trade-offs in perch is the responsible mechanism. In a laboratory experiment, perch from the littoral zone, which had deeper body morphology, were more efficient and grew better on littoral macroinvertebrates, whereas perch from the pelagic zone, which had a more slender body, were more efficient and grew better on zooplankton (Svanbäck and Eklöv, unpublished manuscript). Such foraging-based trade-offs are thought to impose divergent selection leading to differences in morphology and habitat/diet choice in fish (Ehlinger 1990; Schluter 1993, 1995, 1996; Robinson et al. 1996).

Two proximal mechanisms could yield morphological divergence in this perch population, either phenotypic plasticity or genetic differences. We do not know the relative importance of these two factors, but the response of morphology to environment in fish can vary greatly, depending on which trait is considered (Robinson and Wilson 1996; Mittelbach et al. 1999). For example, Mittelbach et al. (1999) showed that the difference in jaw musculature amongst pumpkinseed sunfish (*Lepomis gibbosus*) populations experiencing different resource regimes was mainly due to phenotypic plasticity. In contrast, Robinson and Wilson (1996) have shown, in a trophic polymorphic pumpkinseed sunfish population, that the morphology of young of the year pumpkinseeds was determined both by genetic differences and by environmental induction. The relative contribution of phenotypic plasticity to morphological differences in the perch population in Lake Trehörningen is still unknown, but a

study by Hjelm et al. (2001) has shown that young-of-the-year perch display rapid plastic responses in morphology to different environmental conditions.

In conclusion, our field study has shown that perch caught in the littoral and pelagic zones of a lake differed not only in morphology and diet but also in the morphological growth trajectories. Such differences in morphology and morphological growth trajectories might be a consequence of genetic differences and/or phenotypic plasticity (Robinson and Wilson 1996). Furthermore, the mechanism that creates and maintains the differences in morphology between the habitats probably relates to trade-offs in foraging efficiency in the two habitats, suggesting that natural selection may favor divergent morphologies in these lake habitats (Ehlinger and Wilson 1988; Ehlinger 1990; Schluter 1993, 1995; Svanbäck and Eklöv, unpublished manuscript). While we found clear correlations between morphology and diet, the functional mechanisms behind the relationships are poorly understood and require further investigations.

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