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The effect of visibility and predators on foraging efficiency in littoral and pelagic perch



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Abstract

Phenotypic plasticity in Eurasian perch (*Perca fluviatilis*) can be driven by a trade-off for ecological specialisation to littoral and pelagic resources. Previous studies on perch have found that this specialisation can have different effects on linkage between the littoral and pelagic food web depending on water transparency. In this study I aimed to answer how foraging efficiency and prey preference of phenotypic divergent perch are affected by high and low water transparency, and the presence of a predator in a series of aquarium experiments. Two different phenotypes of perch were kept in littoral and pelagic environments in the lab. By presenting perch with *Daphnia* sp. and Ephemeroptera, either separately or combined. I found that in clear water the littoral and pelagic phenotypes were comparatively more efficient on resources that were representative of their habitats (Ephemeroptera and *Daphnia*, respectively) and that both phenotypes prefer Ephemeroptera over *Daphnia*. In low visibility the differences in foraging efficiency between phenotypes when feeding on *Daphnia* disappeared but remained similar to clear water when feeding on Ephemeroptera. When vision was constrained littoral and pelagic perch showed no sign of prey preferences. In the presence of a predator the difference in foraging efficiency between the phenotypes, and also prey preference disappeared. I found that littoral phenotypes interacted more with other group members than did pelagic phenotypes, when foraging on littoral prey. And for perch in general, when foraging for *Daphnia* the interaction among group members was markedly reduced compared to when foraging for Ephemeroptera.

In this study I show that morphological adaptation and prey choice is affected by visibility and predation. I also give suggestions how and argue why this can affect linkage of food webs and the community composition in littoral and pelagic habitats.

1 Introduction

Water transparency of lakes can change because of eutrophication, or an increase in water colour. It has been hypothesised that lower water transparency homogenises the structure in lake habitats ([1], Bartels *et al.* unpublished manuscript) and constrain visibility. Little is known about how resource and habitat specialisation is affected by low visibility variation in the environment.

Since heterogeneous environments cause different selection pressures on a single species, a single phenotype is unlikely to have the same fitness in all environments. One way to cope with this heterogeneity is through adaptations of the phenotype depending on the environment (phenotypic plasticity) that is: the phenotype is plastic in a way that a single genome can give rise to several different phenotypes [2]. In other cases the phenotypic adaptation to heterogeneous environments can be genetically fixed and in those cases it is said to be polymorphic [3]. Thus, in this case the phenotype of a specific trait is predetermined instead of being a plastic response to the environment. Polymorphism

is maintained differently than phenotypic plasticity. Phenotypic plasticity is influenced by that some alleles are expressed in different environments with various effect on the phenotype and/or gene regulation that turn genes on or off in certain environments [2]. As a response to environmental heterogeneity polymorphism is possible if there are two available niches where the extremes have higher fitness in one each of the two niches. In this case disruptive selection would be able to maintain a stable polymorphism [4][5]. Both genetic and environmental adaptations can work on a specific morphological trait [6] and which has the most profound effect varies among species [7].

Resource polymorphism is a morphological or/and behavioural response to a more efficient exploitation of certain resources or habitats. Resource polymorphism can be based on both genetic variation and on phenotypic plasticity. It is found in many taxonomic groups within vertebrates: e.g. in the amphibian *Plethodon cinereus* [8], in the mammal *Orcinus orca* [9], in the turtle *Caretta caretta* [10], and in the bird *Pyrenestes ostrinus* [11], but it seems to be especially common among fishes [7]. In a synthesis, fishes in post-glacial lakes of the northern hemisphere showed polymorphic responses often related to littoral and pelagic habitats of lakes [12]. An extensively studied organism of resource polymorphism is the three-spined stickleback (*Gasterosteus aculeatus*). In some lakes of British Columbia, where the three-spined stickleback is the only fish species, there are clear morphological differences within the species [13]. The divergence is exhibited in a “benthic” form which compared to the “limnetic” form have a larger body size, larger head, deeper body, fewer and shorter gillrakers [13]. The different morphologies have a higher growth rate in their respective niche [14], which may lead to disruptive selection and potentially adaptive radiation [15]. The heterogeneity of littoral and pelagic habitats [16] is a common cause of diversification of fishes in lakes [17][18][19][20]. In the three-spined stickleback the different niches have different selection pressures on trophic traits, which result in higher foraging efficiency and thus higher growth rate in their niche. This means that for a certain character such as body size, a large body favours foraging in the benthic habitat and a small body favours foraging in the pelagic habitat. Thus, there will be a trade-off for morphological specialization to habitat ([14] and references therein). When an organism is provided with an ecological opportunity selection can drive the population in various directions. Once different niche specialized morphologies have evolved, competition between morphologies maintains diversity [21]. And trade-off in competitive ability of morphologies can drive adaptive radiation [21].

Organisms adapt and respond to their environment, but inevitably they also affect their environment by changing their niches [22]. This can be effective for example in a co-evolutionary arms race where a predator and a prey, exert selection pressures on each other. An evolutionary change in the prey makes it more difficult for the predator to catch it’s prey, subsequently this exerts a different selection pressure on the predator enhancing the evolutionary adaptation of the predator. Over time this can be viewed as an escalating process of changing selection pressures (e.g. red queen hypothesis [23] and arms races [24]). The immediate effect of evolution on the ecosystem and the feedback again on the

organism is difficult to observe while taking place because of short periods of rapid evolution and a subsequent stable state [25]. One of the best documented evidence of eco-evolutionary feedbacks has been found in alewife (*Alosa pseudoharengus*) ([26] and references therein). Alewife populations are anadromous, and when they migrate to freshwater to spawn they also forage on zooplankton in the spawning habitat. By selectively choosing larger plankton they change the size distribution to smaller zooplankton in the spawning habitat. After the spawning the alewives migrate back to the sea and zooplankton size distribution shifts to larger individuals again. By contrast in a landlocked population, alewife spawn and stay in the same habitat implying a selection towards smaller sizes of zooplankton. Alewife that has adapted to forage on smaller zooplankton will be favoured at the expense of those adapted to forage on larger ones. The eco-evolutionary feedback is caused by that landlocked alewives develop smaller gillrakers and a decreased gillraker gape size shifting prey size selection to smaller prey sizes.

In perch (*Perca fluviatilis*), adaptive morphological responses to the littoral and pelagic habitats of lakes have been found [27]. Perch in the littoral zone have a deep body, whereas in the pelagic zone they have a more slender body [27]. This likely arise from a fitness trade-off where deeper bodied perch are favoured in the littoral, whereas slender bodied perch are favoured in the pelagic [28]. The differences in phenotype of littoral and pelagic perch are induced by the habitat and feeding mode [29]. Littoral perch have higher foraging efficiency of littoral prey items (Ephemeroptera) than pelagic perch, and pelagic perch have higher foraging efficiency of pelagic prey (*Daphnia* sp. and *Chaoborus* sp.) than littoral ones. While foraging in vegetation littoral specialists are more efficient regardless if the prey type is littoral or pelagic [28]. The phenotypes use different foraging behaviour, pelagic phenotype uses higher search and attack velocity than the littoral phenotype [30]. Since the pelagic phenotype forage more on conspicuous and elusive prey it has been hypothesised that it is favoured to fastly search the water column and attack prey at high speed in the pelagic zone. Whereas for cryptic and vegetation-attached prey in the littoral zone, slow and thorough search and a suction feeding mode is favoured. The morphological differences in perch can to the largest extent be explained by phenotypic plasticity and to a minor extent by genetic differences [31].

In aquatic food webs fishes are regarded as integrator of spatially separated food webs [32][33]. For example, fish that forage in both littoral and pelagic habitats can integrate littoral and pelagic food webs. However, individuals are different and show intraspecific differences in resource use and in phenotype [34]. If a conspecific specialise morphologically to forage in either the littoral or the pelagic habitats, this could potentially limit food web coupling [35]. It has been shown that an environmental factor such as water transparency (Secchi depth) can affect adaptive morphology in perch and that niche specialisation increase with increased water transparency [36], thus coupling of the benthic and pelagic food webs by perch decrease with increasing water transparency. Still little is known about what mechanisms that cause morphological variation in perch in relation to environmental variation and especially to water transparency. Fur-

thermore, it is not known whether resource use and resource preferences could be a key mechanism to morphological variation under varying environmental conditions.

The aim of this study was to compare the foraging efficiency of littoral and pelagic perch phenotypes on single or combined littoral or pelagic resources under different environmental conditions; clear water, low visibility, and in the presence and absence (in effect clear water) of a predator. With background to that resource specialisation in perch gives an higher foraging rate on habitat specific resources [28][30] and niche divergence between phenotypes is affected by water transparency [36]. This study tries to answer indirectly (with foraging efficiency as a proxy) how morphological differentiation in perch could affect food webs and niches under various environmental conditions. The study extends from [37] dealing with how prey can simultaneously cope with several different prey types and here addressing the question of prey selection under different environmental conditions. Three main questions were addressed:

1. How does water colour and predator presence affect the phenotypes foraging efficiency?
2. Are there any preferences (foraging efficiency used as a proxy) of prey type by the different phenotypes?
3. Is there any differences in foraging behaviour between the phenotypes and while foraging different prey?

2 Methods

2.1 Collecting and maintenance of the fish

Young-of-the-year perch were collected with a seine net in mid July 2011 at Lake Erken, and transported to the Swedish Board Fisheries laboratory at Drottningholm Stockholm. The fish were stocked into two different cylindrical 7 m^3 tanks containing either an artificial structurally complex habitat created by plastic strings attached to a grid of iron bars ($300\text{ strings m}^{2^{-1}}$) placed at the bottom (littoral), or an open water habitat without structure (pelagic). The structured artificial vegetation resembled *Sparganium* sp. The two tanks were fed by filtered lake water and the total water retention time was approximately 12 hours. The two populations were fed the same amount of food (Chironomids of approximately 15% of individual dry weight/day) which was presented in two different ways: The littoral perches were fed by placing the food on a platform that was lowered down to the bottom. On the platform, $5 \times 5\text{ cm}$ squares of plastic turf (Astroturf®) were placed into which the food was pressed. The turfs with food were then frozen so the food would stay at place during feeding. The pelagic perch were fed by spreading the food at the surface. These methods is proven to induce phenotypic plasticity in perch [29].

In August, the same year, the fish were transported from Drottningholm to the aquarium facility at the Limnology department at Uppsala University. The

perch were put into two cylindrical tanks with the same structural treatments and feeding rations as before, tanks had a height of 100 cm and a radius of 50 cm, one littoral pool with 56 fishes and one pelagic pool with 46 fishes. The mean length of thirty fishes from the littoral pool was 59.07 mm (SE \pm 0.74) and from the pelagic pool 59.13 mm (SE \pm 1.27). The temperature in all aquaria and tanks was kept at ambient temperature, approximately 16°C, and there was a 12:12 hour light:dark period. Water was kept circulating with filter pumps for the tanks and bubbling pipestone for the aquaria. Half of the water was changed once a week and occasionally when needed, at closer intervals.

In October, four young of the year northern pikes (*Esox lucius*) with a mean length of 121.75 mm (SE \pm 4.66) were caught by a seine net or a throwing net in Lake Hersen. The pike were later used to induce as a predatory threat to the perch, and were kept separated in 50 \times 25 \times 25 cm aquaria with gravel bottom and vegetation and fed with young of the year cyprinids caught at the same occasion as the pike. The cyprinids (*Carassius carassius*, *Rutilus rutilus*, *Scardinius erythrophthalmus*) were kept in 50 \times 25 \times 25 cm aquaria with gravel bottom and vegetation and feed with fish food pellets. The pike were acclimated at least two weeks to aquarium conditions, before the experiments started.

2.2 Experimental setup

The experiment was set up as a fully factorial design with two categorical variables (fish phenotype and single or mixed prey treatments) and with prey capture per second as the response variable. In the phenotype category there were two factors, littoral and pelagic phenotype. Prey type was either pelagic (*Daphnia* sp.), littoral (Ephemeroptera), or a mix of both pelagic and littoral prey. The number of replicates was 8. From the mix treatment I got two datasets one with *Daphnia* and one with Ephemeroptera. With this design I made two two-way ANOVAs for each environmental condition, one with pelagic prey and one with littoral prey. All experiments were conducted in 50 \times 25 \times 25 cm aquaria with the bottom covered by sand, the aquaria have a volume of 31.25 l but were only filled with 25 l. I conducted the experiments under three different environmental conditions: clear water, low visibility, and presence of a predator (figure 1). The clear water experiment was made up with water from the tap that was left for a couple of days to reach ambient temperature and loose chlorine by diffusion. The low visibility experiment was done by staining tap water with 20 ml Sera® Blackwater Aquatan. This colour make the water resemble dystrophic lake water. The light was scattered by the coloured water to 8.52 μ E (SE \pm 0.34) compared to 48.77 μ E (SE \pm 2.04) in the clear water experiment. The light intensity was constant during all experiments. One young-of-the-year pike was used in the predator experiments. The predator was presented non-lethally and in order to reduce the probability of an attack from the pike to zero, the pike was offered cyprinid prey until satiation. This procedure was successful and no attacks were observed.

Three perch specimen were used in each replicate, because perch are social foragers [38]. The perch were starved for 24 hours prior to the start of the exper-

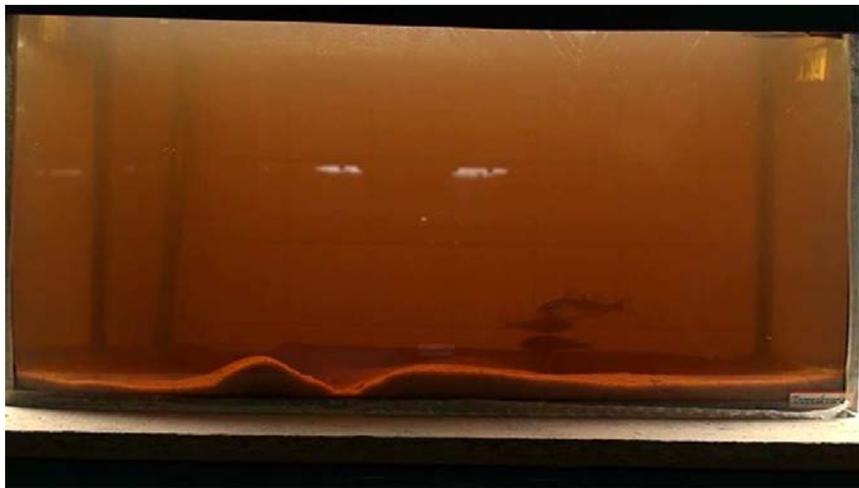
iment. In the experiment with pike the perch was starved for 72 hours prior the experiment to ensure that the perch would be enough motivated to feed. Before the experiment the perch were placed in one side of the aquarium (roughly $\frac{1}{3}$ of the total volume) and blocked off with a PVC plate. In this compartment the perch was offered ten minutes to acclimate to the aquarium conditions before the experiment started. In the experiment with pike the predator was also acclimated to the aquarium conditions on the other side of the PVC plate (roughly $\frac{2}{3}$ of the total volume) for the same time as the perch. After ten minutes of acclimation the resources were added to the side separated from the perch and the plate was lifted and the experiments began.

2.3 Behavioural measurements

All trials were video recorded and analysed later on. In the trials with pelagic resources I measured the time for 30 captured prey per fish. In trials with littoral resources I measured the time for three perch to capture 12 prey. The clock started when the first prey was captured and the consecutive capture counted as one, and so on, i.e. 31 and 13 preys was captured. In the mixed trials I used the same procedure as in the single treatment with pelagic and littoral resources respectively; thereby I got two different results from the mixed trial. This means e.g. that when observing foraging rate for *Daphnia* and a fish foraged Ephemeroptera no notion of that was taken. By this method, any other activity than foraging *Daphnia* (such as foraging Ephemeroptera) is reflected in a lower foraging rate, and vice versa. In the trials with pelagic resources the perches that started foraging after one fish had captured thirty preys was excluded from the data compilation. This was done in order to have perch foraging at similar prey densities and therefore the foraging had to be somewhat synchronised. Since initial prey density of *Daphnia* was 11 prey $dm^{3^{-1}}$, if then two fishes have captured 30 preys each, and the third start after that, the initial prey density for that fish would be 8.6 prey $dm^{3^{-1}}$. This effect is what I tried to avoid by synchronising the foraging. So in each replicate when pelagic resources was offered a possible minimum of one fish and a maximum of three fishes was foraging, and from their resulting prey captured per second a mean of each replica was calculated. The reason that I used different methods to measure foraging efficiency depending on prey type is that the perch I used were small and Ephemeropterans are in comparison a large prey. Because of this a single fish cannot eat many before satiation. Also the aquaria I used were small, and the number of Ephemeropterans could not be much higher without making the density unreasonably high. Since the fish is supposed to search, detect, and attack the prey and all these components of foraging are affected by prey density. In the predator experiments, four pike were used and alternated in a way that each pike was used in two replicates in each set of eight replicates. As pelagic resource I used *Daphnia* and as littoral resource I used Ephemeroptera. The densities of resources were as follows, for pelagic resources 11 prey $dm^{3^{-1}}$ or 275 preys per replicate, and for littoral resources 0.8 prey $dm^{3^{-1}}$ or 1.6 prey $dm^{2^{-1}}$ or 20 preys per replicate. In the mixed resource trial I simply added the



(a) Clear water



(b) Low visibility



(c) Predator presence

Figure 1: Images of the three different experimental conditions.

pelagic and littoral number of prey.

To document group foraging behaviour I counted the number of followers per captured prey in clear water. A follower was defined as a fish that either oriented itself towards a fish that captured a prey, chased the same prey, or chased a fish that was chasing a prey. In experiments with Ephemeroptera as prey I observed the number of followers for the first thirteen captured prey. In experiments with *Daphnia* as prey I used the number of followers per captured prey for each foraging fish and for 30 preys per fish. Each replicate from Ephemeroptera and *Daphnia* trials resulted in a mean that was used for statistical analyses. I also observed the duration of each stop the fishes made after each captured *Daphnia*, this in order to examine if the littoral phenotype took longer stops after capturing *Daphnia* than the pelagic phenotype. To do this I played videos of the trials at 0.3× speed and clocked the time from prey capture until the fish paddled away or oriented on a new prey. I used a mean of ten stops between the eleventh and twentieth prey for each fish, for statistical analyses.

2.4 Statistical analyses

All data for ANOVA and t-test was checked for normality and standardised residuals, and transformed when needed. The ANOVAs where factorial two way ANOVAs, I made six separate ANOVAs, three for each prey taxa and one within each environmental condition per prey taxa. I used Levene's test for homogeneity of variance to test for differences in variance between groups. Levene's test was bootstrapped, which randomly sample with replacement the data within each group. The bootstrap procedure was iterated 100,000 times. Thus instead of a sample size of 1 in each group I reused my own data to get a sample size of 100,000 and from that sample I did a Levene's test of homogeneity of variance. All statistical analyses were made with statistical software R, (R Development Core Team (2011). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>).

3 Results

3.1 Clear water

For a visual overview see figure 2. In clear water the pelagic phenotype had a higher capture rate of *Daphnia* than the littoral phenotype in the single prey treatment (table 1, $P = 0.0397$). Also capture rate was consistently higher for both phenotypes in the single treatment than in mixed treatments (table 1, $P = 0.0015$,). In the mixed treatment the littoral phenotype have more variation in their foraging efficiency of *Daphnia* than the pelagic phenotype does (table 3, $P = 0.02801$).

The littoral phenotype had a higher foraging rate on Ephemeroptera than the pelagic phenotype (table 2, $P = 0.0005$). In the mixed prey treatment both

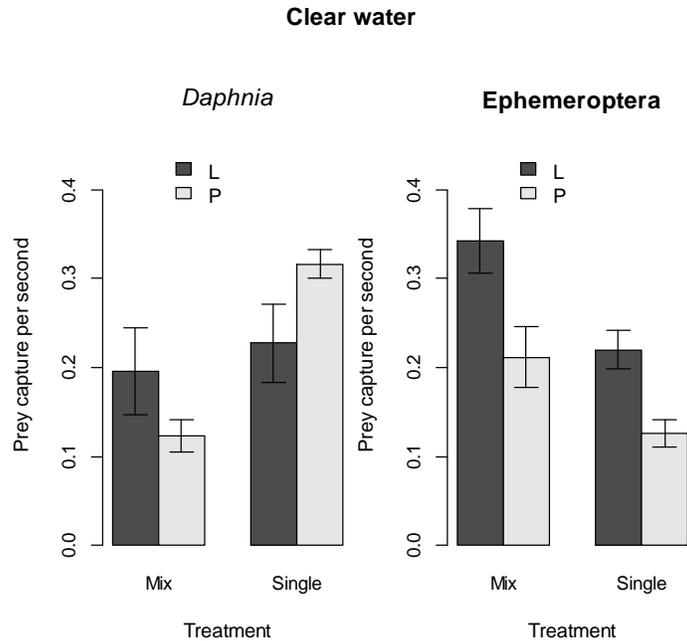


Figure 2: Prey captured per second for littoral and pelagic perch phenotypes (see legend), foraging on *Daphnia* and Ephemeroptera and a mix of *Daphnia* and Ephemeroptera in clear water. Bars indicating mean and error bars indicating standard error ($n = 8$).

phenotypes had a higher foraging rate than in the single prey treatment (table 2, $P = 0.001$), which is opposite to that of the results with *Daphnia* in the mix treatment, indicating a preference of Ephemeroptera over *Daphnia*. Also the pelagic phenotype had a higher variation in foraging efficiency of Ephemeroptera in the mixed treatment than in the single treatment (table 4, $P = 0.01476$), whereas the the littoral phenotype had no difference in foraging efficiency with the same comparison (table 4, $P = 0.3025$).

3.2 Low visibility

For a visual overview see figure 3. There is no difference in foraging efficiency of *Daphnia* between the two phenotypes in low visibility (table 1, $P = 0.1355$). There was close to significance in comparison of mixed and single treatment, were there is a trend towards higher foraging efficiency in the single treatment (table 1, $P = 0.0623$).

In low visibility the littoral phenotype had a higher foraging rate of Ephemeroptera than the pelagic phenotype (table 2, $P = 0.0288$). This was due to that the

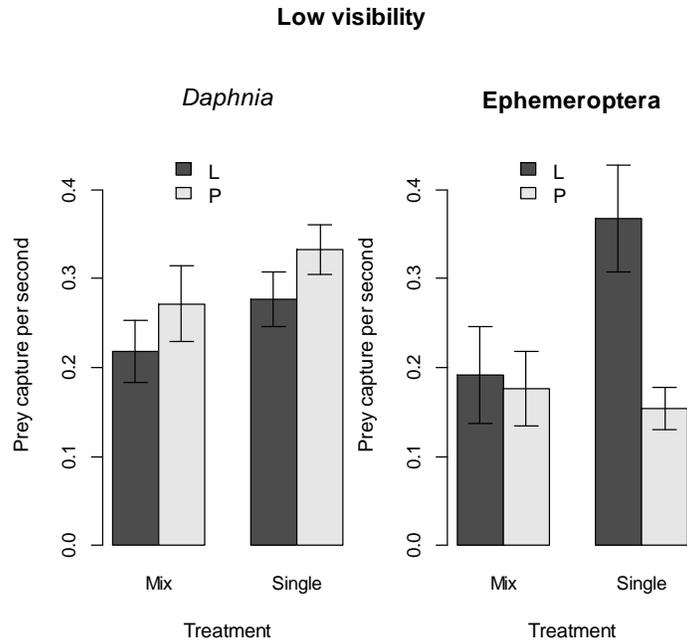


Figure 3: Prey captured per second for littoral and pelagic perch phenotypes (see legend), foraging on *Daphnia* and Ephemeroptera and a mix of *Daphnia* and Ephemeroptera in low visibility. Bars indicating mean and error bars indicating standard error ($n = 8$).

littoral phenotype had a higher capture rate (table 2, $P = 0.0497$) than the pelagic phenotype in the single treatment. In the single treatment the littoral phenotype had higher variance in foraging efficiency of Ephemeroptera than the pelagic phenotype (table 3, $P = 0.03392$). As well, the pelagic phenotype had higher variance in foraging efficiency of Ephemeroptera in mixed treatment than in single (table 4, $P = 0.03291$), whereas there is no difference for the littoral phenotype when the same comparison is made (table 4, $P = 0.6158$).

3.3 Predator presence

For a visual overview see figure 4. There is no differences in foraging efficiency between the phenotypes when a predator is present (table 1, table 2). A predator also homogenise variation in foraging efficiency between phenotypes (table 3) and between single and mixed treatment within phenotypes (table 4).

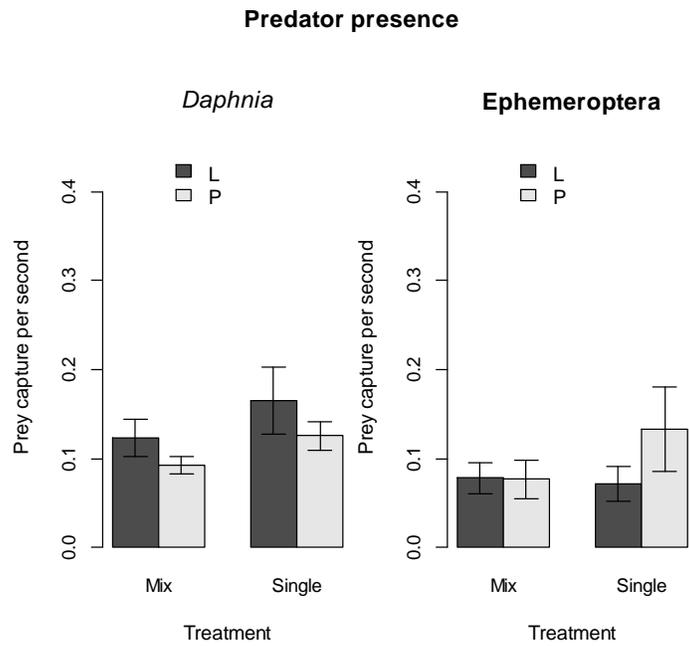


Figure 4: Prey captured per second for littoral and pelagic perch phenotypes (see legend), foraging on *Daphnia* and Ephemeroptera and a mix of *Daphnia* and Ephemeroptera in presence of a predator. Bars indicating mean and error bars indicating standard error ($n = 8$).

Table 1: Results of analysis of variance of the effect of phenotype and treatment on foraging efficiency of *Daphnia*.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)*
<i>Clear water</i>					
Phenotype	1	0.00078	0.00078	0.116	0.7365
Treatment	1	0.08350	0.08350	12.299	0.0015
Phenotype x Treatment	1	0.03160	0.03160	4.655	0.0397
Residuals	28	0.19010	0.00679		
<i>Low visibility</i>					
Phenotype	1	0.01051	0.010515	2.362	0.1355
Treatment	1	0.01678	0.016778	3.769	0.0623
Phenotype x Treatment	1	0.00001	0.000007	0.002	0.9693
Residuals	28	0.12464	0.004452		
<i>Predator Presence</i>					
Phenotype	1	0.00833	0.008326	1.903	0.1787
Treatment	1	0.01263	0.012633	2.887	0.1004
Phenotype x Treatment	1	0.00006	0.000064	0.015	0.9044
Residuals	28	0.12251	0.004375		

*Note: $\alpha = 0.05$

Table 2: Results of analysis of variance of the effect of phenotype and treatment on foraging efficiency of Ephemeroptera.

	Df	Sum Sq	Mean Sq	F value	Pr(>F)*
<i>Clear water</i>					
Phenotype	1	0.1007	0.1007	15.608	0.0005
Treatment	1	0.0862	0.0862	13.363	0.0010
Phenotype x Treatment	1	0.0026	0.0026	0.399	0.5327
Residuals	28	0.1806	0.0065		
<i>Low visibility</i>					
Phenotype	1	0.1091	0.10912	5.316	0.0288
Treatment	1	0.0553	0.05529	2.693	0.1120
Phenotype x Treatment	1	0.0864	0.08641	4.210	0.0497
Residuals	28	0.5748	0.02053		
<i>Predator Presence</i>					
Phenotype	1	0.0038	0.003814	0.258	0.6153
Treatment	1	0.0031	0.003111	0.211	0.6498
Phenotype x Treatment	1	0.0057	0.005698	0.386	0.5395
Residuals	28	0.4136	0.014770		

*Note: $\alpha = 0.05$

Table 3: Bootstrap (n = 100,000) classical Levene’s test based on the absolute deviations from the mean. Test of homogeneity of variance between littoral and pelagic phenotype in foraging efficiency of *Daphnia* and Ephemeroptera in mix and single treatments. Significant values in bold.

	Dap. Mix	Dap. Single	Eph. Mix	Eph. Single
	P-value			
Clear water	0.02801	0.1130	0.7339	0.80120
Low visibility	0.39210	0.4352	0.7309	0.03392
Predator presence	0.12630	0.2361	0.6123	0.09015

Table 4: Bootstrap (n = 100,000) classical Levene’s test based on the absolute deviations from the mean. Test of homogeneity of variance of the foraging efficiency between mix and single treatment of pelagic and littoral separately. Significant values in bold.

	Dap. Littoral	Dap. Pelagic	Eph. Littoral	Eph. Pelagic
	P-value			
Clear water	0.5945	0.5178	0.3025	0.01476
Low visibility	0.8590	0.1422	0.6158	0.03291
Predator presence	0.4596	0.5735	0.8519	0.13650

3.4 Foraging behaviour

The littoral phenotype and the pelagic phenotype interacted with other individuals to a different extent when foraging on Ephemeroptera (figure 5, Welch Two Sample t-test: $t = 3.1142$, $df = 14$, $p\text{-value} = 0.007614$). Both phenotypes behaved differently when foraging on *Daphnia* compared to Ephemeroptera (figure 5). The pelagic phenotype: Welch Two Sample t-test: $t = 6.0496$, $df = 12.896$, $p\text{-value} = 4.245 \times 10^{-5}$. The littoral phenotype: Welch Two Sample t-test: $t = 9.1318$, $df = 13.981$, $p\text{-value} = 2.873 \times 10^{-7}$.

I could observe that while foraging for *Daphnia* the littoral phenotype waited longer until resuming swimming after capturing a prey. While the pelagic phenotype waited shorter until resuming paddling after capturing a prey. When observing the fishes forage, the littoral phenotype behaviour look jagged with start and stop for most of their prey captures. While the the pelagic phenotype foraging behaviour looks smooth, as swimming while feeding. However the experimental setup I used was not efficient enough to spot a difference between these two groups even if one existed (Two sample t test power calculation: $n = 19$, $d = 0.561804$, $\text{sig.level} = 0.05$, $\text{power} = 0.3919643$; Welch Two Sample t-test: $t = 1.5994$, $df = 27.493$, $p\text{-value} = 0.1212$).

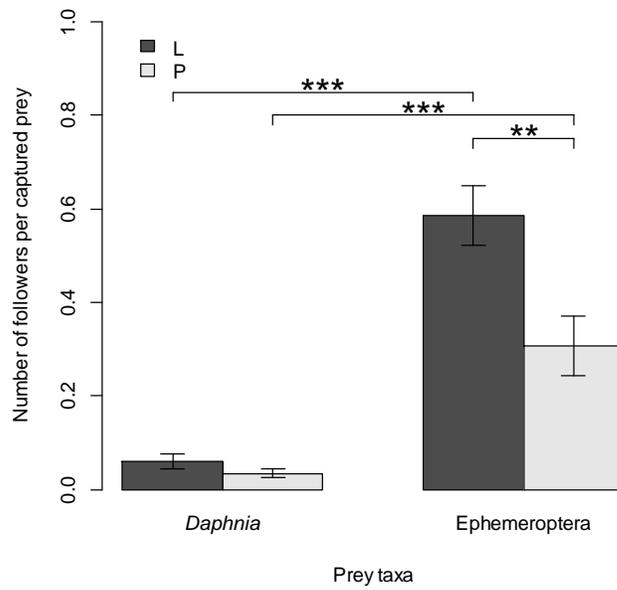


Figure 5: Number of followers per captured prey, for different prey taxa and different phenotypes (see legend). Bars indicating mean and error bars indicating standard error. Stars show significance: ** = $P \leq 0.01$ and *** = $P \leq 0.001$ ($n = 8$).

4 Discussion

In this study I found the littoral phenotype to be more efficient in foraging on littoral prey (Ephemeroptera) and the pelagic phenotype to be more efficient in foraging on pelagic prey (*Daphnia*) in clear water. As other studies and this study show, pelagic and littoral perch phenotypes are more efficient in foraging of prey that are representative for their habitat [28][30]. The foraging efficiency of the two phenotypes when foraging on *Daphnia* were similar in low visibility, but littoral phenotypes still were more efficient foragers of Ephemeroptera. These results were confirmed by results from the field. [39] found that planktivorous perch in dark coloured lakes were prohibited by low visibility and were forced to forage on macroinvertebrates earlier in life than in less coloured lakes. Other results show that the reliance of littoral resources of littoral perch of lakes was positively correlated with water transparency, whereas the pelagic population was not [36]. This implies a segregation of resource utilisation of perch populations in clear water lakes and an integration of resource use of populations in coloured lakes. This pattern could likely be influenced by the differences between phenotypes in foraging efficiency of pelagic prey (*Daphnia*) that I found in clear water and the lack thereof in coloured water.

My results show that the influence of predators was strong and any difference in foraging efficiency due to phenotypic plasticity disappeared in the presence of predators. The perch were still feeding but to a lower and for the phenotypes similar efficiency. However there is evidence that foraging latency of bluntnose minnows (*Pimephales notatus*) decrease as shoal size increase [40]. It is thereby possible that fish in the wild are less affected, because they can form larger shoals, than the three perch I used in each trial during my experiments.

I found that both the littoral phenotype and the pelagic phenotype prefer Ephemeroptera over *Daphnia*. This was clear because foraging efficiency was higher for Ephemeroptera in the mix treatment with *Daphnia* than when the perch only were feeding on Ephemeroptera. This result did not appear in low visibility, plausibly because here the perch had more difficulties in assessing available resources. In a study of optimal foraging in bluegill sunfish (*Lepomis macrochirus*) [41] found that depending on prey abundance, fishes choose different size classes of prey. If prey abundance was low all size classes were included in the diet, if prey abundance was high fishes dropped lower size classes and focus on larger prey. These results suggest that what could be considered optimal depends on the density and the profitability of the available prey[41]. Therefore, in low visibility the perch is less likely to follow optimal foraging rules because the perches cannot make the necessary assessment of available resources. When a predator is present the perches did not have any preferred prey, likely they pick whatever prey is easiest to take. Since they have to weigh profit of selectively choose prey against risk of being killed [42].

[43]found that individuals show a for the individual characteristic foraging behaviour, some bluegills had short hovers and some had long hovers. But by learning which hover duration (depending on prey density or structural complexity) was optimal for prey detection the individuals variation in hover duration

could be homogenised. However the individuals with short and long hovers still after learning had relatively short and long hovers. This is in alignment to my results: in clear water the littoral phenotype show more variation in foraging efficiency than the pelagic phenotype while foraging *Daphnia* and also can choose to forage Ephemeroptera. The pelagic phenotype have more variation while foraging Ephemeroptera and also can choose to forage *Daphnia* than when only Ephemeroptera is present. Also in low visibility the pelagic phenotype had a higher variation in foraging efficiency of Ephemeroptera in mix with *Daphnia* compared to when Ephemeroptera was the only prey.

Contrary to [43] who found that specialisation homogenises variation in foraging behaviour. Littoral phenotypes were more effective in foraging on Ephemeroptera but also showed a higher variation in foraging efficiency of Ephemeroptera in low visibility than pelagic ones (table 4). One explanation could be that group foraging is especially premiered in low visibility, and also as I found in this study more common among littoral perch (figure 5). Since the perch can take advantage of each other and don't have to see the prey themselves. And when only one fish forage alone in the dark in some trials and in other trials they forage as a group, it's likely the cause of the large variation in the littoral population. Pelagic perch don't show this group foraging behaviour as often so the variation in foraging efficiency between one fish and three fishes foraging is likely not as high as it is in the littoral population.

Presence of a predator homogenises the variation in foraging efficiency between mix resource and single resource treatments and littoral and pelagic phenotypes. [44] found that the three-spined stickleback compromised between foraging efficiently and avoid a predatory threat, and preferred to forage at longer distances from the predator. This compromise between a threat and a food resource is likely what cause the homogenisation of foraging efficiency of the phenotypes.

I found that the littoral phenotype forage more in a group than the pelagic phenotype while foraging on Ephemeroptera, a large and cryptic prey that can evade predatory attacks. Also, perch foraging for widespread conspicuous prey such as *Daphnia* do not interact in other fishes foraging at the same extent as when they forage Ephemeroptera. That the littoral phenotype interact more in other individuals foraging is likely a good strategy while foraging for prey in a patchy environment, where they can benefit from the visual contact with other individuals at prey detection. [38] found a similar pattern when he compared group versus solitary foraging by piscivorous perch. Perch foraging in groups of five individuals grew better, captured more prey, and spend less energy than perch foraging alone.

Another feature in foraging behaviour that might distinguish littoral and pelagic phenotypes is that the pelagic phenotype possibly make a shorter stop after capturing *Daphnia* and thus move on foraging faster. If this is the case then this could be one reason to why they have a higher foraging efficiency of pelagic prey. [30] found that the pelagic phenotype forage on *Daphnia* at higher search velocity than littoral ones. [43] found that bluegill could adapt their hover duration depending on prey type, and shorter hovers while forag-

ing of *Daphnia* enhanced detection rate. This in sense is in alignment with what I could observe (however without statistically reliance), that the pelagic phenotypes with shorter stops also have a higher foraging efficiency of *Daphnia*.

It has been found that intraspecific resource specialisation can have the effect that different foraging efficiencies or prey preferences selectively remove certain prey, and thereby cause changes in community composition [45]. In my study I did not directly test the effect of phenotypic specialisation of perch on habitats. However some predictions on how phenotypic plasticity in perch could affect ecosystems can be made from my results. In clear water littoral and pelagic perch likely have a high predation rate on the resources they are adapted to feed on. In low visibility, according to my results pelagic prey (zooplankton) would not be as affected by phenotypic specialisation in perch as littoral prey (macro-invertebrates) would be. When perch forage in the presence of predators littoral and pelagic phenotypes have no difference in foraging efficiency on either pelagic or littoral prey, and thus there is likely no difference in their affect on the resource consumption. These somewhat trivial predictions could be a good basis for empirical tests were cascading effects on community composition could be investigated.

[16] found in a survey throughout North America that on average 55% of fish diet were of benthic origin. Because fishes can use both littoral and pelagic prey a number of studies have highlighted the importance of fishes in coupling the pelagic and benthic food web [16][32][33]. However studies have shown that within many species conspecifics can have different ecological implications depending on individual specialisation [34]. It has been found in perch that individual habitat specialisation or resources specialisation can potentially limit habitat coupling [35]. Furthermore it has been found that the extent of habitat coupling (niche overlap) can be affected by environmental conditions, such as water transparency (which is positively correlated to niche divergence) [36]. In clear water my results point in the direction of that phenotypic specialisation in perch would limit habitat coupling, because the phenotypes are more efficient on their respective prey. In low visibility there is no difference in foraging efficiency between phenotypes on pelagic prey but when they forage on littoral prey, this suggest more linkage of food webs of perch in lakes with low water transparency. When a predator is present all differences in foraging efficiency are gone and as a direct inference of my results, presence of predators would make perch couple food webs.

In conclusion this study have shown that both morphological adaptation and prey choice is affected by visibility and predation, this can potentially affect linkage of food webs and the community composition in the littoral and pelagic habitats of lakes.

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