Age matters—Experienced predation risk affects behavior and morphology of juvenile 0+ and 1+ perch

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ABSTRACT

Empirical field studies have shown relations between predation risk and differences in anti-predator behavior and morphology between and within perch populations. The present study used juvenile 0+ and 1+ perch in an experimental approach to vary the factor predation risk. Predators were able to feed on perch during the experimental period in large outdoor tanks. Perceived predation risk affected the behavior and the morphology of both age classes of perch, with perch being deeper bodied and shyer with increasing intensity of predation. Changes in morphology were somewhat more pronounced in the 0+ age group, while the 1+ age group exhibited significantly stronger changes in behavior, but behaved less conform within groups. Though it remains unanswered if the predator induced these changes by selective predation, or if perch adjusted their behavior and morphology in response to the predator, the results indicate that perceived predation risk can have a fast and strong direct effect on amount and distribution of phenotypes within a prey population. The results further suggest that balance and use of anti-predator strategies on different response levels may be differential over age-classes in European perch.

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Introduction

Predators may have multifarious direct and indirect effects on their prey, influencing the distribution and abundance of phenotypes within a prey population (e.g. Sih et al., 1985; Eklöv and Hamrin, 1989; Langerhans et al., 2004; Sharma and Borgström, 2008; Soykan and Sabo, 2009). Most predators hunt selectively. This favors characteristics in prey that facilitate the avoidance of predation and increases the prey's probability of survival and reproduction (Lind and Cresswell, 2005). Studies on fish have shown that e.g. increased body depth (e.g. Nilsson et al., 1995) and a shyer (Moodie et al., 1973) and a more vigilant behavior (Godin and Davis, 1995) decreases the likelihood for an individual to fall victim to predation. Hence, rainbow trout (*Oncorrynchus mykiss*) were found to preferably consume bold threespined sticklebacks (*Gasterosteus aculeatus*) (Bell and Sih, 2007) and acara cichlids (*Aequidens pulcher*) selected for non-vigilant stickleback (Godin and Davis, 1995), while pike predators (*Esox lucius*) were found to more often attack slender bodied crucian carp (*Carassius carassius*) than deeper bodied individuals, when given the choice (Nilsson et al., 1995).

Behavioral and morphological defences are often plastic, where expression of a defence trait is induced by sensation of predation risk (e.g. Brönmark and Miner, 1992; Eklöv and Jonsson, 2007; Robinson et al., 2008). The potential plasticity of morphological and behavioral traits has been documented for many taxa (Agrawal, 2001; Price et al., 2003; Crispo, 2008). For example, pumpkinseed sunfish (*Lepomis gibbosus*) were found to increase spine length, body depth, and their behavioral reaction to a predator when previously exposed to the odor of walleyes (*Sander vitreus*) (Robinson et al., 2008). Similar, juvenile perch (*Perca fluviatilis*) were found to increase in body depth (Eklöv and Jonsson, 2007) and to behave shyer in response to piscivorous predators (Magnhagen, 2006b).

Due to gape size limitations of many piscivores, vulnerability of prey changes also with size (Lundvall et al., 1999; Svanbäck and Eklöv, 2011). The size range during which growing juveniles have the highest predation risk, termed vulnerable size window, is shaped by the structure of the associated predator community (Claessen et al., 2002; Borcherding et al., 2010). Correspondingly, strength and effect of selective predation and the intensity of defence expression over ontogeny should also be influenced by the size structure of the predator community, i.e. the distribution and abundance of phenotypes within a prey population should be related to the intensity of predation risk. Indeed, boldness of perch from two nearby Swedish lakes differed between lakes and age classes and their behavioral patterns were not consistent but were connected to the actual experience of cannibalistic predation (Magnhagen and Borcherding, 2008).

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Table 1
Scheme of outdoor tank stocking with sizes of prey perch and predators, numbers of prey perch at the start and the end of the mesocosm treatment (duration), and mean values of condition, growth and daily predation on the prey perch. The latter values were used to obtain predation risk classes ($-$ = no predator, + = low risk < 0.006, ++ = high risk).

Age class	Prey $L_T \pm SD$ (mm)	Treatment	Predator L_T (mm)	Prey to predator ratio	N_{start}	Duration (days)	N_{end}	Condition factor	Growth (mm day^{-1})	Daily predation	Predation risk class
0+	75.8 ± 7.0	No pred			30	42	30	0.95	0.14	0.000	$-$
0+	75.8 ± 7.1	No pred			29	48	29	1.04	0.20	0.000	$-$
0+	75.1 ± 6.8	No pred			30	54	30	0.99	0.17	0.000	$-$
0+	80.8 ± 6.4	Small pred	198	0.41	39	42	17	1.11	0.17	0.013	++
0+	77.2 ± 7.4	Small pred	185	0.42	50	48	43	1.06	0.17	0.003	+
0+	73.0 ± 8.0	Small pred	198	0.37	50	54	36	1.02	0.22	0.005	+
0+	78.4 ± 7.3	Large pred	250	0.31	70	42	58	1.07	0.18	0.004	+
0+	77.8 ± 7.6	Large pred	247	0.31	70	48	59	1.06	0.22	0.003	+
0+	77.1 ± 8.1	Large pred	242	0.32	68	54	31	1.05	0.26	0.010	++
1+	113.9 ± 10.2	No pred			16	42	16	1.10	0.19	0.000	$-$
1+	123.6 ± 7.6	No pred			14	48	14	1.17	0.16	0.000	$-$
1+	116.5 ± 9.7	No pred			17	54	17	1.14	0.19	0.000	$-$
1+	114.6 ± 8.4	Small pred	205	0.56	15	42	10	1.12	0.21	0.008	++
1+	115.6 ± 11.0	Small pred	200	0.58	17	48	15	1.15	0.24	0.002	+
1+	120.0 ± 10.0	Small pred	215	0.56	17	54	17	1.14	0.17	0.000	+
1+	112.7 ± 8.7	Large pred	360	0.31	37	42	24	1.10	0.22	0.008	++
1+	115.6 ± 10.0	Large pred	345	0.33	32	48	15	1.13	0.20	0.011	++
1+	113.4 ± 9.9	Large pred	360	0.31	36	54	28	1.12	0.21	0.004	+

The disadvantage of such empirical field studies is, however that numerous factors like different habitat structures (Brown and Warburton, 1997; Svanbäck and Eklöv, 2002), different nourishment (Heermann et al., 2007; Borcherding and Magnhagen, 2008; Heynen et al., 2011) or different water transparencies (Skov et al., 2007; Bartels et al., 2012) may influence the results. Thus, basic functionality of a certain ecological phenomenon should be analyzed additionally with a defined experimental approach, in which only the independent factors of interest are varied and all other possible factors are kept constant.

Based on the results outlined by Magnhagen and Borcherding (2008), we used also 0+ and 1+ perch. Groups of perch were held in large outdoor tanks with and without predatory perch and the predators were able to prey on the juvenile perch. Previous studies showed that piscivores often selectively hunt for shallow bodied and bold prey and that juvenile perch might also plastically adapt to predation with increasing in body depth and decreasing in boldness. Therefore, it was hypothesized that the surviving perch would differ in their behavior and their morphology according to the perceived predation risk. With increasing risk of predation it was expected (1) that perch should become shyer in the trade-off between food and shelter (Magnhagen, 2006b), and (2) should develop deeper body morphology (Eklöv and Jonsson, 2007).

Methods

Field samples

500 young-of-the-year (0+) perch (size: up to 88 mm L_T) and 250 1+ perch (1+, size: 100–135 mm L_T) were caught in Lake Speldrop (latitude: 51°46′50.70″N, longitude: 6°22′42.11″ E), a gravel pit lake at the Lower River Rhine (Beeck et al., 2002), Germany, by electrofishing (Bretschneider), beach seining (net mesh size: 4 mm, length: 10 m) and angling. Prior the experiments fish were held in two large tanks (2×1.17 m^3). Predatory perch were caught with gillnets in Lake Speldrop and Lake Reeser Meer (latitude: 51°45′01.03″N, longitude: 6°27′27.37″E; Borcherding et al., 2007) and held in two separate tanks (2×0.7 m^3) for acclimatization.

Tank treatments

18 round outdoor tanks (Ø 1.8 m, 1.65 m^3, 50% cover with artificial vegetation, T mean 16.0 °C) were used for the experiments. The bottom of the tanks was covered with gravel and a filter with a recirculation pump was placed in the center of every tank to support aeration. Four weeks prior the start of the experiments, the predators were introduced to the tanks. 6 tanks were stocked with a small predatory perch (i.e., to create a prey-predator size ratio on the border of ingestability, cf. Persson et al., 2004), 6 tanks with a large predatory perch (i.e., well below the critical size ratio for ingestability) and 6 tanks were left without a predator. Predators were not fed during the acclimatization time, to generate a standardized and high hunger level.

The tank-experiments all started at the same time, by stocking half of the tanks with 0+ perch and the other half with 1+ perch (Table 1). All juvenile perch used in the tank-experiments were measured to the nearest mm (total length, L_T). During the tank-experiment, prey perch were fed daily with deep frozen red chironomid larvae (15% prey perch body weight), distributed over three temporally random feeding events, to prevent habituation of prey and predators.

The tank-experiments were stopped in three successive rounds, after 42, 48 and 54 days, with one replicate of each treatment (0+ no, 0+ small, 0+ large, 1+ no, 1+ small and 1+ large predator) being stopped in each of the three rounds (Table 1). After the tank-experiments, 12 randomly chosen prey individuals from each tank (except one tank with only 10 surviving prey perch) participated in behavioral experiments and the same individuals were subsequently used for morphometric analysis (Table 1).

To account for differences between individual predators (Smith and Blumstein, 2010) and the resulting differences in imposed predatory threat, the actual experienced intensity of predation was calculated for each tank (number consumed prey fish × number stocked prey fish^{-1} × number tank-treatment days^{-1}). This real experienced daily predation was then classified (no, low < 0.008 and high predation risk; Table 1), and used in the following analyses as the independent variable "predation risk".

Behavioral studies: aquaria experiments

Prior to the behavioral experiments juvenile perch were anaesthetized (Aquacalm), weight (to the nearest g), measured (to the nearest mm) and marked with an individual color tattoo on the base of its caudal fin. Fulton's condition factor ($K = 10^5 m L_T^{-3}$, where m = biomass in g and L_T = total length in mm; (Bagenal and Tesch,