

# Temperature- and light-dependent ratio of energy gain to metabolic costs explains spatial and temporal habitat use of zooplanktivorous fish

Ulrika Beier

Department of Aquatic Resources, Institute of Freshwater Research, Swedish University of Agricultural Sciences, Drottningholm, Sweden

## Correspondence

U. Beier, Department of Aquatic Resources, Institute of Freshwater Research, Swedish University of Agricultural Sciences, Drottningholm, Sweden.  
E-mail: [ulrika.beier@slu.se](mailto:ulrika.beier@slu.se)

## Abstract

Understanding the forces that drive habitat selection of species in communities is important in both ecology and evolution. In nature, species face variation in competition, predation and physical characters among habitats. Vendace (*Coregonus albula* (L.)) is a specialised zooplanktivorous fish predominantly using deeper water in lakes during summer, while roach (*Rutilus rutilus* (L.)) uses mainly the shallow littoral zone as well as the upper layer of the pelagic zone. To understand mechanisms behind habitat use of these species, I first conducted a predation experiment to investigate their sensitivity to predation by perch (*Perca fluviatilis* L.). Second, I performed a foraging experiment using different temperature and light treatments. I then used metabolic calculations to estimate energetic costs when foraging. I found no difference between species regarding sensitivity to predation. Vendace was the most efficient forager on zooplankton but also swam faster spending more energy compared to roach. Roach had a comparatively high metabolic rate in the lowest temperature, where their foraging efficiency was lowest. The energy gain ratio at 6°C was highest for vendace, while it was lowest for roach. In the highest temperature (18°C) and the lowest light level (1 lux), both species were similar in their energy gain ratio. The relative energy gain ratio provides a mechanism to explain habitat distribution for the two species. An increased understanding of the role of metabolism in combination with biotic interactions and habitat use may help to foresee effects of environmental change for different species.

## KEYWORDS

competition, predation, metabolism, trade-off, zooplankton, *Coregonus albula*, *Rutilus rutilus*

## 1 | INTRODUCTION

In order to maximise their fitness, individuals will trade off the mortality risk to their possibilities of transferring food resources into biomass (Gilliam & Fraser, 1987; Hölker, Haertel, Steiner, & Mehner, 2002; Mehner, 2012). Animals may choose less profitable habitats to avoid predators, or take the risk of exposing themselves to predators if

their energy need is large enough (Rennie et al., 2010; Vijayan, Morris, & McLaren, 2012). In size-structured populations, for example fish, foraging capacities as well as predation risk vary with individual size (ten Brink, Mazumdar, Huddart, Persson, & Cameron, 2015; Byström & Garcia-Berthou, 1999; Ohlberger et al., 2013). Predation vulnerability and foraging efficiencies are both size dependent and will affect how organisms chose between habitats (Diehl & Eklöv, 1995; Werner, Gilliam, Hall, & Mittelbach, 1983). For example, Byström, Andersson,

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial-NoDerivs License, which permits use and distribution in any medium, provided the original work is properly cited, the use is non-commercial and no modifications or adaptations are made.

Persson, and De Roos (2004) showed that the habitat choice of young-of-the-year Arctic char (*Salvelinus alpinus*) depended on predation risk, while larger fish chose habitat according to food availability.

Apart from size-dependent biotic interactions, the performance of organisms in different habitats also depends on abiotic factors (Diehl, 1988; Dunson & Travis, 1991; Pekcan-Hekim, Joensuu, & Horppila, 2013). Within the species-specific temperature tolerance range, foraging capacity generally increases with temperature (Bergman, 1987; Persson, 1986b). Light conditions may also affect foraging success (Cerri, 1983; Guthrie & Muntz, 1993). Species-specific adaptations to abiotic conditions will affect the performance in different habitats (Bergman, 1988; Carmona-Catot, Magellan, & García-Berthou, 2013; Elliott, 2011). For example, light intensity and temperature may result in reversed outcomes of competition, which may facilitate species coexistence through habitat partitioning (Bergman, 1987; Mehner, Busch, Helland, Emmrich, & Freyhof, 2010; Rodtka & Volpe, 2007), or possibly lead to competitive exclusion (Carmona-Catot et al., 2013; Oyugi, Cucherousset, & Britton, 2012).

Temperature and light will thus influence the performance of fish in different habitats through mechanisms connected to search velocity and assimilation of food (Clarke & Johnston, 1999; Hölker, 2006; Persson, 1986a; Walsh, Haney, & Timmerman, 1997). Apart from mechanisms affecting energy intake, abiotic factors will also affect energy costs (Huey, 1991; Seth et al., 2013). Standard metabolic rate, although it may vary between individuals, is for ectotherms mainly affected by the temperature of the environment (Brown, Gillooly, Allen, Savage, & West, 2004; Rosenfeld, Van Leeuwen, Richards, & Allen, 2015). To better understand biotic and abiotic mechanisms underlying habitat selection of ectotherms, one way forward is to investigate how foraging efficiency in combination with net energy gain varies across habitats separated by abiotic factors. It has been shown that species and size classes within species segregate spatially in the pelagic zone (Beier, 2001; Hamrin, 1986; Rowe, 1994). Fish populations interacting in the pelagic zone, with a vertical gradient in light as well as temperature, are therefore a suitable system for studying how abiotic factors interact with biotic interactions to regulate habitat selection.

Roach (*Rutilus rutilus* (L.)), vendace (*Coregonus albula* (L.)) and perch (*Perca fluviatilis* L.) are three common fish species in temperate lakes, all using the pelagic habitat, but to varying degrees (Beier, 2001; Horppila et al., 2000; Svanbäck, Eklöv, Fransson, & Holmgren, 2008). Roach uses both the shallow habitat in the littoral zone and the upper parts of the pelagic zone (Beier, 2001; Bohl, 1980; Gliwicz & Jachner, 1992). Vendace is a specialised zooplanktivorous fish species, mostly using depth zones (>6 m) in the pelagic zone of temperature-stratified temperate lakes during summer (Beier, 2001; Hamrin, 1986; Mehner et al., 2010). It has also been shown that roach may show different relative preference for the pelagic zone in lakes with or without vendace (Beier, 2001). As both roach and vendace are planktivores but generally show different habitat affinities, they constitute a relevant example to study mechanisms governing habitat preference.

In this study, I investigate whether the observed differences in habitat use of vendace and roach can be explained by sensitivity to predation, and by relative foraging capacities together with

metabolic demands, when foraging on zooplankton in different parts of the pelagic zone. First, in a pond experiment I examine how roach and vendace are affected by predation from perch. Second, in an aquaria experiment I compare relative foraging capacities as well as swimming speeds of roach and vendace in different temperature and light conditions. Finally, I use bioenergetic models to estimate the energetic costs of foraging and derive energy gain ratios to explain the habitat distribution of these two species in the field.

Based on observations of biomass distribution in lakes, I defined possible explanatory mechanisms for the vertical separation of vendace and roach in the pelagic zone. The hypotheses tested to investigate mechanisms were as follows: 1) the two species have different costs regarding predation risk in an open habitat, 2a) the possibilities for energy gain will increase with temperature for both species, 2b) the gain in energy intake for vendace is less affected by low temperature and low light levels than for roach, 2c) the costs in terms of metabolism are higher in warmer water for vendace than for roach, and 2d) the net energy gain of vendace is higher than for roach in colder and darker water.

## 2 | MATERIALS AND METHODS

### 2.1 | Predation experiment

To study the relative sensitivity of roach and vendace to predation from perch in an open-water environment, experiments were performed in pond enclosures lacking vegetation. The size of fish used in the predation experiments matched the size interval where vendace were observed to occupy the pelagic habitat relatively more than the littoral/benthic habitat (6–9 cm) (Beier, 2001). Perch, roach and vendace were collected from Lake Mälaren during spring 1999, and species were kept separately in ponds during summer. In August 1999, I performed predation experiments in 7.3×11 m pond enclosures lacking vegetation, with 1.1 m mean water depth. In the experiments, I used four perch (mean length 196 mm, *SD* 9.5) as predators and 70 prey fish. As prey, I used only roach (mean length 63 mm, *SD* 13.3, mean weight 2.3 g, *SD* 1.4), only vendace (mean length 70 mm, *SD* 6.2, mean weight 2.3 g, *SD* 0.7) or 35 of each species together. Each treatment was performed with six replicates. Behaviour of predators and evasive behaviour of the different prey species were recorded by visual observation using Polaroid glasses, at standardised time slots (2×45 min each per day) during daylight hours, speaking observations into a tape recorder. Two observers performed the observations, at random distribution between treatments and periods. After 48 ± 2 hr, the remaining prey fish were collected and counted to determine the capture success of different prey in the different treatments.

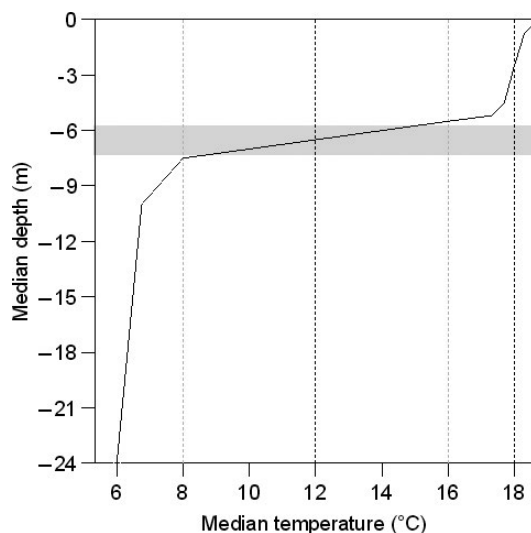
### 2.2 | Foraging experiment

From the foraging experiments, capture rates of the two species were analysed, then coupled to swimming rates when foraging. Swimming rates were further used to model energetic costs, that is active metabolic rates (AMR), and finally calculating the ratio of calculated energy intake to metabolic costs, expressed as the energy gain ratio.

To test foraging capacities, I performed experiments in aquaria with different temperature and light treatments. The size of fish used in the foraging experiments matched the predominant size interval of roach found in the pelagic zone in lakes during summer (10–13 cm TL, 10–20 g; Beier, 2001), adjusted to the same body mass interval for both species.

Roach were collected from Lake Mälaren and vendace from Lake Vättern in November 1994 and kept in large tanks before the experiments. I used roach in the same body mass range (mean length = 11.5 cm,  $SD = 0.9$ , mean weight = 13.09 g,  $SD = 3.59$ ) as vendace (mean length = 13.4 cm,  $SD = 0.95$ , mean weight = 14.58 g,  $SD = 3.80$ ), to obtain comparable foraging capacities with respect to individual body mass. Three randomly selected individuals of each species were acclimatised to temperature and light conditions in aquaria for at least 1 week prior to experiments. The experiments were performed in glass aquaria with a water column measurement of 68.8×68.8×43.8 cm (207.3 L). The aquaria were placed in climate rooms with aquarium lamps placed above the aquaria. Fish were not fed for 3 hr (12 and 18°C) or 6 hr (6°C) before the experiments. The prey used were live *Daphnia magna* filtered through a sieve, resulting in a median body length of 1.20 mm (mean = 1.4 mm,  $SD = 0.23$ ,  $N = 168$ ). In between experiments, the fish were fed with frozen zooplankton.

Temperature treatments were chosen according to a standardised situation in temperature-stratified lakes during summer (Fig. 1). At a temperature corresponding to the epilimnion, where the two species coexist in the pelagic zone of lakes, two different light treatments were used to



**FIGURE 1** Generalised thermal stratification curve based on data from 406 Swedish lakes with  $\geq 18$  m maximum depth, sampled in July–August. Median values of temperature from surface, bottom and the mid-metalimnion depth from sequential samples of each lake were used to plot median temperatures from all lakes; at surface, that is 0.2 m depth (median = 18.6°C, mean 18.4°C,  $SD = 2.6$ ), mid-metalimnion depth (median = 6.5 m, mean = 7.0 m,  $SD = 2.4$ ), temperature at mid-metalimnion depth (median = 12.0°C, mean = 12.1°C,  $SD = 3.5$ ), bottom temperature (median = 6.0°C, mean = 6.4°C,  $SD = 1.8$ ) and maximum depth (median = 24 m, mean = 28.39 m,  $SD = 13.45$ ). Data from the NORS database (SLU, 2016)

test for relative foraging efficiencies. The light treatments used, that is 10 lux and 1 lux, reflect conditions in the pelagic epilimnion and metalimnion. As an example, assuming a light extinction coefficient of 0.75 per m, approximately 10 lux can be expected at 4.5 m depth in normal daylight with 300 lux in surface water, whereas 1 lux can be expected at 4.5 m depth during twilight of 30 lux in surface water. The light intensity was measured by a lux meter with a flat surface, pressed against the centre of the front glass of the aquaria. The light intensity was adjusted by a dimmer.

Capture rates were measured for each of the two fish species at five different prey densities (0.5, 1, 2, 4 and 8 prey/L), at three different temperatures (6, 12 and 18 ± 0.2°C), and two light intensities (10 lux at all temperatures and 1 lux at 18°C). Six replicates of each treatment were performed, choosing aquaria and climate rooms with randomisation procedures. The zooplankton were counted and collected in plastic tubes and poured into a glass jar with water. Upon the start of an experiment, the fish were carefully pushed to one side of the aquarium, which was then partitioned with a flexible plastic board. The prey were poured into the part of the aquarium without fish, and as the flexible board was carefully twisted and removed, the water mixed, and fish immediately started catching prey while recording begun. One individual of the three in each aquarium was chosen at random and the capture rate for that individual was recorded. An estimate of total prey depletion was based on the number of prey caught by the studied individual multiplied by three, as it was assumed that individuals had roughly similar capture rates. To avoid satiation and effects of prey depletion on foraging performance, estimates of capture rates were made before total depletion reached 25% at maximum and in most cases before it reached 10%.

Routine swimming performance was recorded immediately following the recordings of the capture rates, with the help of a grid on the front of the aquaria made up of 14 cm squares. Additional routine swimming performance recordings were performed separately for 0.5 and 1 prey L densities, as prey were depleted quickly. Furthermore, routine swimming performance in the absence of prey (nonforaging fish) was also recorded separately at 18°C in both light treatments. Swimming speed was calculated correcting for three-dimensional movement, assuming that fish swam as much in z direction as in x and y direction.

Recording was performed by visual observation noting successful captures and grid positions A–Z on a tape recorder, and the information was transferred using event recording software. Captures could be clearly observed as movements of the mouth when the fish sucked the prey into their mouth. According to observations, the frequency of noncapture was negligible (<3%). Capture rates for each species and treatment were fitted to a simplified Holling type II functional response model (Persson, 1987). Mean body lengths and weights of fish used, as well as individual swimming speeds from experiments, were applied to models for calculating active metabolic rate (AMR) for roach (Hölker & Breckling, 2002) and vendace (Ohlberger, Staaks, & Hölker, 2007), respectively, according to the formula:

$$AMR = a \cdot M^{b_1} \cdot \exp(d \cdot T) + e \cdot M^{b_2} \cdot U^c$$

where  $a$ ,  $b_1$ ,  $b_2$ ,  $c$ ,  $d$  and  $e$  are constants (Table 1),  $M$  is body mass (g),  $T$  is temperature (°C), and  $U$  is swimming speed (cm/s). The ratio of

**TABLE 1** Constants ( $a$ ,  $b$ ,  $c$ ,  $d$ ,  $e$ ) for active metabolic rate (AMR) according to  $AMR = a \cdot M^{b_1} \cdot \exp(d \cdot T) + e \cdot M^{b_2} \cdot U^c$ , where  $M$  is body mass (g),  $T$  is temperature ( $^{\circ}\text{C}$ ), and  $U$  is swimming speed (cm/s), for roach (Hölker & Breckling, 2002) and vendace (Ohlberger et al., 2007)

	Roach	Vendace
$a^a$	0.483	0.820
$b_1$	0.760	0.930
$b_2^b$	0.600	0.930
$c^b$	0.640	2.030
$d$	0.088	0.070
$e^a$	0.994	0.430

<sup>a</sup>Oxygen consumption rates for roach converted to J/hr by the oxycaloric value 14.2 mg/O<sub>2</sub> (Hepher, 1988).

<sup>b</sup>High cost swimming applied, comparable to routine swimming when foraging in the field (Hölker & Breckling, 2002).

<sup>c</sup>Swimming speed in cm/s for roach (Hölker & Breckling, 2002), and in body lengths (cm)/s for vendace (Ohlberger et al. 2007).

energy intake from individual capture rate (prey/s converted to J/hr) to estimated individual active metabolic rate (based on individual swimming speed from experiments) was calculated. Differences in capture rates, swimming speeds, active metabolic rate (AMR, calculated from swimming speed) and energy gain ratios were analysed with ANOVA (SPSS Inc., Chicago, IL, USA). Values were ln-transformed prior to analyses to approach normal distribution.

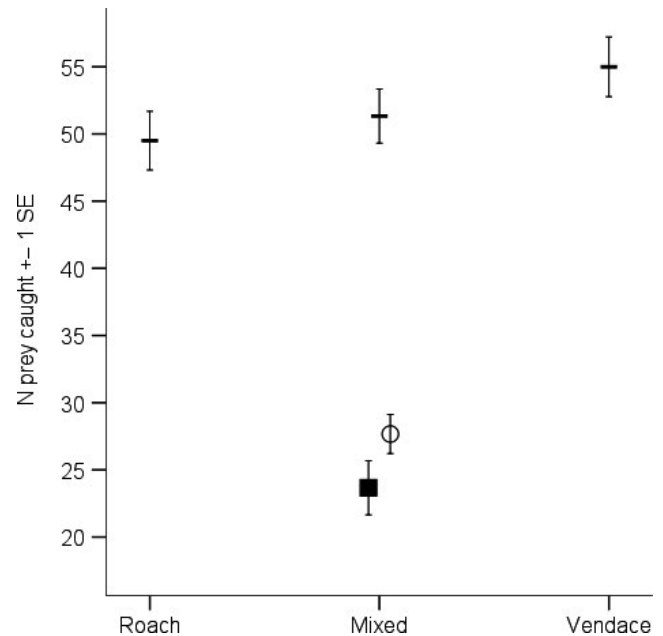
### 3 | RESULTS

In the predation experiments, no significant difference between treatments with only roach, only vendace or mixed prey species was found regarding how many prey were caught by perch (ANOVA,  $F = 1.645$ ,  $df = 2$ ,  $p = .226$ , Fig. 2). In the mixed treatment, the difference in number of prey caught depending on species was also nonsignificant (ANOVA,  $F = 2.211$ ,  $df = 1$ ,  $p = .168$ , Fig. 2). Roach and vendace showed different evasive behaviours when being pursued by perch. All prey fish normally schooled together, also in the mixed prey species treatment. Upon attack from perch, roach dispersed and jumped above the surface, while vendace schooled more tightly, that is to a tight "ball," and moved downwards.

In the foraging experiments, the effect of temperature was significant on capture rate which increased with temperature (Table 2, Figs 3 and 4a). The capture rate of vendace was higher than for roach at all temperature and light treatments (Table 2, Fig. 3). In contrast to predictions, roach capture rate was thus lower than for vendace also at 18°C (Table 2, Fig. 3). Means of capture rates, swimming speeds and resulting constants from the Holling type II model are given in Table 3.

Both roach and vendace had higher swimming speed at 12°C and 18°C compared to 6°C (Tables 3 and 4, Fig. 4b). When fish were foraging, the swimming speed of vendace was higher than for roach in all temperature and light treatments (Table 3, Fig. 4b).

Vendace capture rate was higher at 10 lux compared to 1 lux (Table 2, Figs 3 and 4a). However, the capture rate of roach did not



**FIGURE 2** Captured prey (mean  $\pm$  SE) in pond enclosure experiments with perch (*Perca fluviatilis*) used as predators and roach (*Rutilus rutilus*, black squares) and vendace (*Coregonus albula*, white circles) used as prey ( $n = 6$  for each treatment). Horizontal bold bars represent total number of prey caught in each treatment

differ significantly with light treatment (Table 2, Figs 3 and 4a). There was no significant effect of light treatment for swimming speed when foraging for either species (Tables 3 and 4, Fig. 4b).

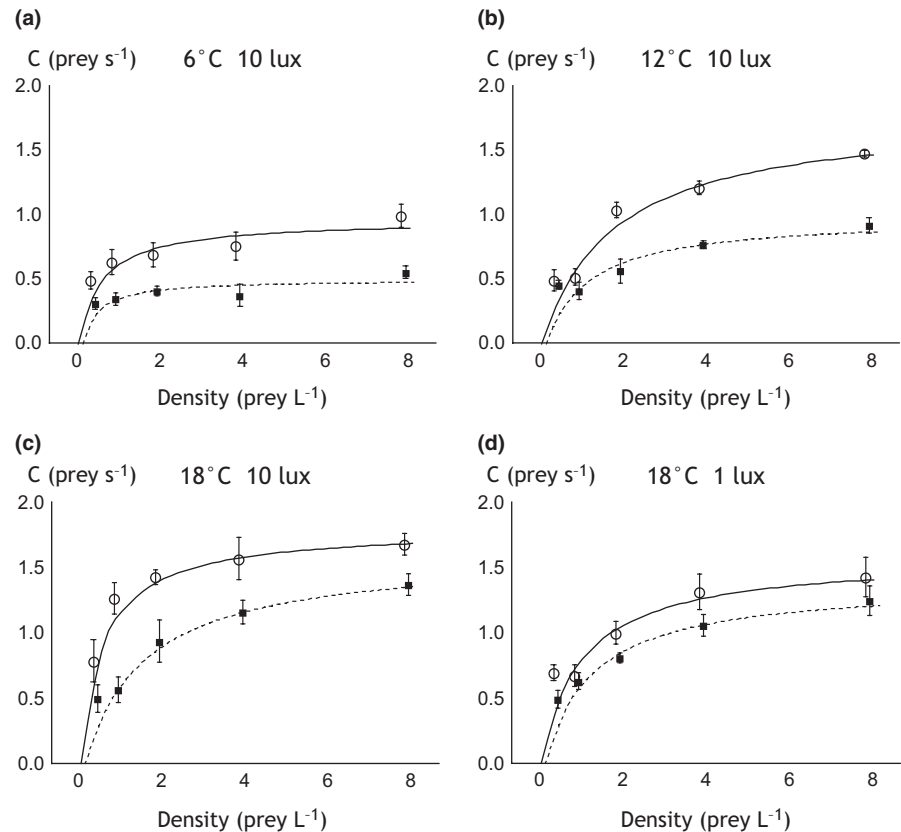
Estimated active metabolic rate (AMR) calculated from swimming speed when foraging at 10 lux was higher for roach than for vendace at 6°C (ANOVA,  $F = 61.687$ ,  $df = 1$ ,  $p < .001$ ). At 12°C, AMR estimates for both species were similar (ANOVA,  $F = 1.365$ ,  $df = 1$ ,  $p = .248$ ) while at 18°C AMR for vendace was instead higher (ANOVA,  $F = 17.609$ ,  $df = 1$ ,  $p < .001$ , Fig. 5a). However, energy gain ratio, calculated as the ratio of energy gain from intake of zooplankton to metabolic costs (AMR), was significantly higher for vendace than for roach in all temperatures when fish were foraging at 10 lux (6°C: ANOVA,  $F = 47.038$ ,  $df = 1$ ,  $p < .001$ ; 12°C: ANOVA,  $F = 6.238$ ,  $df = 1$ ,  $p = .015$ ; 18°C: ANOVA,  $F = 7.197$ ,  $df = 1$ ,  $p = .10$ ). However, at 18°C and 1 lux, the difference between the two species was nonsignificant (ANOVA,  $F = .415$ ,  $df = 1$ ,  $p = .522$ , Fig. 5b). In the treatment without prey (nonforaging fish), there was no significant difference between species in AMR in the 10 lux treatment (ANOVA,  $F = .769$ ,  $df = 1$ ,  $p = .394$ ), nor in the 1 lux treatment (ANOVA,  $F = 1.796$ ,  $df = 1$ ,  $p = .205$ ). Also, energy gain ratio was highest at 6°C and decreased with temperature for vendace, whereas it increased for roach which had the highest energy gain ratio at 18°C (Fig. 5b). The two species were similar in their energy gain ratio at 18°C and 1 lux (Fig. 5b).

### 4 | DISCUSSION

This study increases the understanding of the habitat use of two competing fish species as it separately provides estimates of mechanisms

**TABLE 2** Results from two 3-way ANOVA's testing differences in capture rates (preys/s) for roach and vendace foraging on zooplankton (*Daphnia magna*, median body length 1.20 mm) in different densities (prey/L), light and temperatures treatments. Statistical significance ( $p < 0.05$ ) indicated by \*

Comparison	Source of variation	SS (type II)	df	F	p
10 lux at 6°, 12° and 18°					
Capture rate	Species	1.676	1	112.54	<.001*
	Temperature	2.712	2	91.04	<.001*
	Species×Temperature	0.160	2	.53	.593
	Prey density	2.980	4	50.03	<.001*
	Species×Density	0.097	4	1.62	.172
	Species×Temperature×Prey density	0.649	16	2.72	.001*
	Error	2.234	150		
10 lux and 1 lux at 18°					
Capture rate	Species	3.15	1	29.25	<.001*
	Light	0.56	1	5.19	.025*
	Species×Light	0.55	1	5.07	.027*
	Prey density	14.23	4	33.02	<.001*
	Species×Prey density	0.36	4	.83	.512
	Species×Light×Prey density	0.95	8	1.10	.370
	Error	10.78	100		



**FIGURE 3** C = Capture rates (prey/s, mean  $\pm$  SE) for roach (black squares) and vendace (white circles) foraging on zooplankton (*Daphnia magna*), with densities 0.5, 1, 2, 4 and 8 prey/L. Treatments were (a) 6, (b) 12 and (c) 18°C at 10 lux, as well as (d) 18°C at 1 lux ( $n = 6$  for each treatment). Capture rates were fitted to a Holling type II functional response model for roach (broken line) and vendace (solid line) respectively

usually assumed to jointly govern habitat use, that is the trade-off between mortality risk and energy gain. Because of the different size groups used in the two sets of experiments presented, it was not possible to calculate the  $\mu/g$  ratio (mortality to growth; Gilliam & Fraser, 1987). However, the results, also including modelled metabolism, and being compared with published work on biomass distributions, provide a basis for comparing the importance of predation risk versus energetic profits for habitat use. Results from the presented

experimental studies of predation and competition could hereby identify underlying mechanisms for patterns of habitat use of roach and vendace observed in the field.

Predation is usually recognised as a principal force in ecosystems and may profoundly affect the habitat use of prey species (Lima & Dill, 1990; Sih, 2005; Werner et al., 1983). Other studies have shown that the capture abilities of predators are directly affected by abiotic factors, as well as indirectly through altered behaviour or habitat use

**TABLE 3** Mean and SE of capture rates (preys/s), swimming speeds (cm/s) and calculated AMR (active metabolic rate; J/hr) for roach and vendace foraging on zooplankton (*Daphnia magna*, median body length 1.20 mm) in different densities (prey/L), temperatures and light treatments (six replicates of each). Capture rates and densities were fitted to a simplified Holling type II functional response model (Persson, 1987). Resulting constants  $a$  and  $h$  at each prey density are given. Columns AMR treatment and Ratio treatment show mean and SE for AMR and mean energy gain ratio, where all values for each treatment (temperature, light intensity and species) irrespective of prey density were used

Treatment	Species	$a$	SE	$h$	SE	Prey dens.	Capture rate	SE	Swim. speed	SE	AMR	SE	Energy gain ratio	SE	AMR treatment	SE	Ratio treatment	SE
6°C 10 lux	Roach	1.32	0.59	2.01	0.205	0.5	0.31	0.05	11.46	0.62	27.91	0.77	6.55	1.01	24.94	0.47	9.38	0.70
						1	0.34	0.05	8.18	0.40	23.62	0.56	8.36	1.10				
						2	0.41	0.04	9.91	0.59	25.94	0.76	9.21	1.03				
						4	0.37	0.08	8.49	0.74	24.00	1.03	9.00	1.96				
	Vendace	1.73	0.58	1.04	0.100	8	0.55	0.05	7.92	0.61	23.22	0.85	13.79	1.15				
						0.5	0.49	0.07	13.81	0.55	20.68	0.44	13.55	1.82	20.25	0.39	20.48	1.42
						1	0.63	0.10	12.51	1.36	19.91	0.96	18.76	3.06				
						2	0.69	0.09	13.51	1.58	20.77	1.41	19.30	2.42				
12°C 10 lux	Roach	0.92	0.21	1.02	0.093	4	0.76	0.11	13.96	0.63	20.82	0.52	21.02	3.00				
						8	0.99	0.09	11.41	1.17	19.06	0.73	29.79	1.85				
						0.5	0.46	0.03	15.07	0.82	36.17	0.94	7.26	0.44	33.59	0.59	11.05	0.81
						1	0.41	0.07	13.31	0.37	34.18	0.44	7.60	1.12				
	Vendace	1.02	0.13	0.56	0.037	2	0.56	0.10	12.46	1.55	32.92	2.04	9.56	1.36				
						4	0.77	0.03	12.63	0.92	33.32	1.14	13.29	0.25				
						8	0.92	0.06	11.06	0.57	31.44	0.71	16.95	1.17				
						0.5	0.49	0.08	19.44	1.19	34.28	1.36	8.45	1.64	34.79	0.71	15.71	1.25
18°C 10 lux	Roach	1.09	0.24	0.62	0.065	1	0.52	0.07	17.47	2.93	33.21	2.56	8.97	1.04				
						2	1.04	0.06	21.31	1.57	36.70	1.85	16.62	1.48				
						4	1.21	0.05	19.30	0.87	34.01	1.00	20.63	1.17				
						8	1.48	0.03	20.84	0.28	35.75	0.35	23.88	0.49				
	Vendace	3.35	0.79	0.55	0.036	0.5	0.50	0.10	15.57	1.18	43.49	1.37	6.50	1.28	43.05	.64	12.30	1.09
						1	0.57	0.10	17.54	0.98	45.67	1.07	7.09	1.19				
						2	0.94	0.16	15.56	1.71	43.39	1.88	12.62	2.24				
						4	1.16	0.09	13.05	0.91	40.65	1.08	16.46	1.01				
18°C 1 lux	Roach	1.20	0.22	0.72	0.054	8	1.37	0.08	14.27	1.05	42.05	1.20	18.84	1.13				
						0.5	0.79	0.16	18.81	2.34	46.18	2.50	9.78	2.04	47.14	0.72	16.50	0.94
						1	1.27	0.12	20.00	1.42	47.02	1.63	15.67	1.54				
						2	1.43	0.06	18.90	1.20	45.67	1.44	18.12	0.60				
	Vendace	1.20	0.22	0.72	0.054	4	1.57	0.16	22.46	0.34	49.85	0.45	18.24	1.96				
						8	1.68	0.08	20.07	1.07	46.97	1.27	20.70	1.03				
						0.5	0.49	0.07	14.73	0.91	42.59	1.06	6.63	0.81	41.94	0.56	11.83	0.87
						1	0.63	0.06	15.73	1.48	43.63	1.62	8.56	1.13				

(Continues)



TABLE 3 (Continued)

Treatment	Species	$\alpha$	SE	$h$	SE	Prey dens.	Capture rate	SE	Swim. speed	SE	AMR	SE	Energy gain ratio	SE	AMR treatment	SE	Ratio treatment	SE
18°C 10 lux	Vendace	1.62	0.37	0.63	0.055	0.5	0.70	0.06	19.30	0.38	45.92	0.44	8.82	0.79	47.34	0.62	12.49	0.88
						1	0.67	0.08	18.96	1.53	45.87	1.92	8.43	0.84				
						2	1.00	0.09	22.45	1.28	50.07	1.80	11.68	1.20				
						4	1.32	0.13	21.55	0.65	48.69	0.81	15.63	1.58				
						8	1.43	0.15	19.47	0.62	46.15	0.73	17.86	1.87				
						0			11.71	1.09					38.05	1.19		
						0			12.29	1.11					39.54	0.79		
18°C 1 lux	Roach					0			9.70	1.37					36.29	1.87		
	Vendace					0			9.59	1.72					41.37	3.25		

of their prey (Einfalt, Grace, & Wahl, 2012; Eklöv & Persson, 1995; Martin, Fodrie, Heck, & Mattila, 2010). Roach and vendace showed different evasive behaviours when being pursued by perch, and vendace seemed more adapted to escaping predators in a deep water column. The different evasive behaviours of roach and vendace may also explain the principal habitat use of predation-sensitive stages of the two species. Mehner, Kasprzak, and Hölker (2007) suggested that vendace avoided the littoral/benthic zone and preferred deeper water as a response to predation risk. Horizontal migrations by roach out to the pelagic zone at night (Bohl, 1980; Gliwicz & Jachner, 1992) may be a way for roach to reduce predation risk while utilising the warm water in the epilimnion. This study's lack of corroboration for the prediction that vendace would be more susceptible than roach to predation by perch indicates that reasons for differences in habitat use between roach and vendace may also be other than solely predation. Another suggested driver for differences in the use of vertical habitat by vendace is density dependence (Mehner, 2015). However, to further clarify its role as a driving force, it is motivated to separate density dependence into actual mechanisms that determine energy gain ratio.

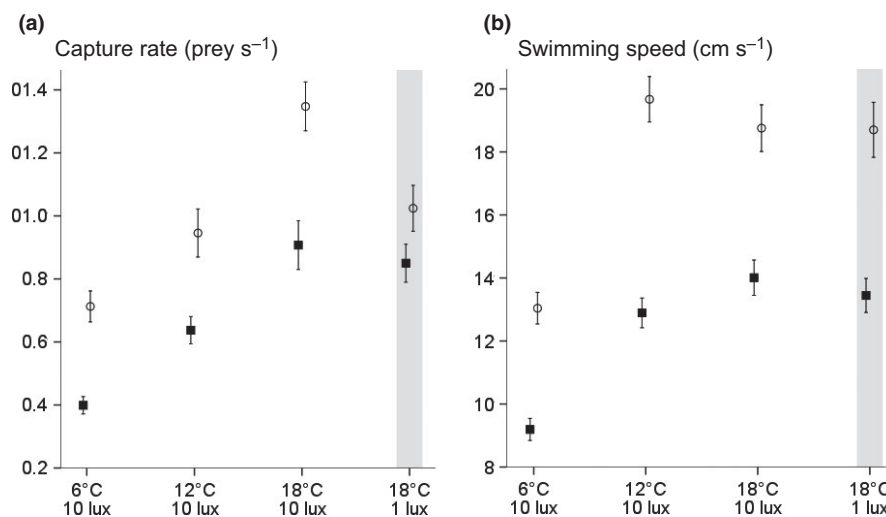
Capture rate and swimming speed increased with temperature for both species, as expected for ectotherms (Johnston & Dunn, 1987). Ohlberger, Mehner, Staaks, and Hölker (2008) previously studied capture rates of vendace at 8°C and 5 lux, however without indicating the sizes of the fish, and used slightly larger *Daphnia magna* than in the present study, which makes direct comparisons uncertain. In spite of different set-ups, Ohlberger et al. (2008) arrived at maximum capture rates in the same order of magnitude as the results from 6°C to 12°C at 10 lux, which strengthens the comparatively high capture rate of vendace estimated in the present study. The higher capture rate of vendace across all temperatures suggests that vendace could outcompete roach from the pelagic zone completely, while field studies have demonstrated that this is not the case (e.g. Beier, 2001; Bohl, 1980; Gliwicz & Jachner, 1992; Svanbäck et al., 2008). Thus, temperature-dependent foraging alone cannot explain the habitat use of vendace. Roach are hardly found below 10–12 m in lakes, which has been suggested to result from roach being adapted to warmer temperatures (Kahl & Radke, 2006). In contrast, vendace has been identified as a cold-water species (Hamrin, 1986), presumably feeding more efficiently at colder temperatures. However, as vendace was in fact most efficient in the highest temperature, this does not provide a satisfactory explanation for why the two species are spatially separated, as vendace mainly uses the deeper, colder water. Thus, the species-specific effect of temperature on foraging efficiencies did not explain the habitat use of roach and vendace.

The importance of light intensity for foraging efficiency and predator avoidance varies greatly between species (Einfalt et al., 2012; Mehner, 2012). Results from the present study showed that the capture rate of roach eating zooplankton was independent of light intensity, whereas the capture rate of vendace decreased in the lower light conditions. Similarly, no effect of light for the foraging efficiency of roach was found in previous studies, although negative effects were found for interacting species perch (Diehl, 1988) or pike (Jönsson, Ranåker, Nilsson, & Brönmark, 2012). As capture rates of roach were

**TABLE 4** Results from two 3-way ANOVA's testing differences in swimming speed (cm/s) for roach and vendace foraging on zooplankton (*Daphnia magna*, median body length 1.20 mm) in aquarium experiments using different densities (prey/L), light and temperature treatments. Statistical significance ( $p < .05$ ) indicated by \*

Comparison	Source of variation	SS (type II)	df	F	p
10 lux at 6°, 12° and 18° Swimming speed	Species	5.384	1	106.59	<.001*
	Temperature	7.339	1	72.64	<.001*
	Species×Temperature	0.129	2	1.28	.282
	Prey density	0.361	2	1.79	.134
	Species×Density	0.154	4	3.06	.019*
	Species×Temperature×Prey density	0.992	4	1.228	.253
	Error	7.526	149		
10 lux and 1 lux at 18° Swimming speed	Species	3.166	1	99.249	<.001*
	Light	0.012	1	.375	.541
	Species×Light	0.059	1	1.849	.177
	Prey density	0.120	4	.941	.443
	Species×Prey density	0.478	4	3.746	.008*
	Species×Light×Prey density	0.163	8	.637	.745
	Error	848.8	100		

Density (prey/L).



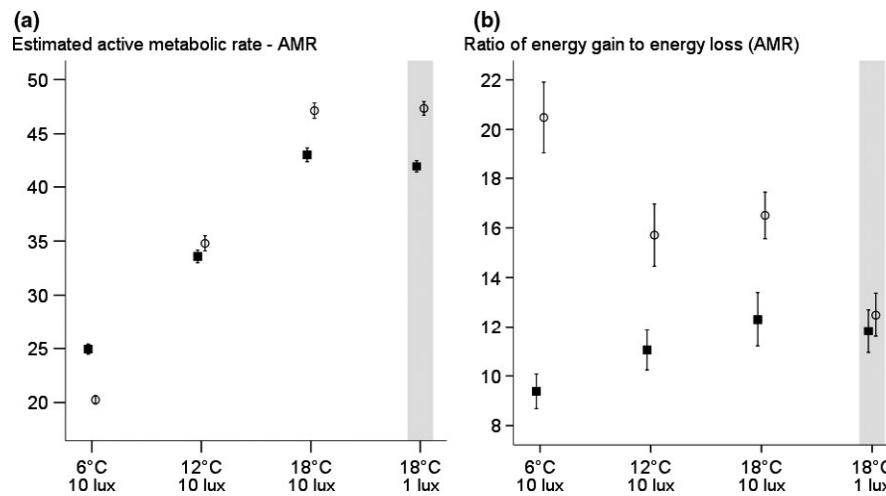
**FIGURE 4** (a) Capture rate (prey/s, mean  $\pm$  SE) and (b) swimming speed (cm/s, mean  $\pm$  SE) for roach (black squares) and vendace (white circles) in different temperature and light treatments when foraging on zooplankton (*Daphnia magna*) at varying densities (pooled data from six replicates each, using 0.5, 1, 2, 4 and 8 prey/L respectively). The light treatment of 1 lux is marked by a shaded area

not reduced by lower light, this could indicate that roach would also use deeper water, which they in fact do not (Beier, 2001). However, the relative insensitivity of roach to lower light levels when foraging could help to explain why roach migrate into the warm epilimnion of the pelagic zone at night, where their efficiency is relatively high. Furthermore, despite the use of deeper waters in the pelagic zone by vendace, results from this study show that vendace seem not to be particularly adapted to low light levels. These findings are in correspondence with that coregonids have been reported to be comparatively inactive at night in the field (Gjelland, Bøhn, Knudsen, & Amundsen, 2004; Huusko & Sutela, 1998), which may further indicate that their vision is not specifically adapted for low light levels.

Foraging abilities in different temperatures depend on the capacities to move around, and capture prey. However, swimming performance will also cost energy, which may be an energetic trap for ectothermic organisms. In this study, swimming speed and AMR did

not differ significantly depending on light level for either species, whereas swimming speed generally increased with temperature. For vendace, however, there was no difference in swimming speed between 12°C and 18°C. Vendace is thus able to consume more prey than roach, but will swim faster and spend comparatively high amounts of energy in the upper waters of the pelagic zone. This is also confirmed in this study by the highest estimated AMR for vendace found at 18°C, comparable for the same size interval with metabolic rates reported for vendace at 15°C by Ohlberger et al. (2007). Roach, on the other hand, were less efficient at reducing their metabolism in lower temperatures, and their estimated AMR was higher than for vendace at 6°C, despite that roach swam less than vendace at this low temperature. Temperature affecting the metabolic costs can thus explain why roach avoid using the cold, deeper water and why vendace avoid the upper, warm water, as their energy gain ratio was highest in the lowest temperature.





**FIGURE 5** (a) Estimated active metabolic rate (AMR, J/hr) and (b) ratio of energy intake from capture rates (prey/s converted to J/hr) to estimated active metabolic rate (AMR) (mean  $\pm$  1 SE) for roach (black squares) and vendace (white circles) in different temperature and light treatments when foraging on *Daphnia magna* (pooled data from different prey densities, six replicates of each density). AMR was estimated according to Hölker and Breckling (2002) for roach and Ohlberger et al. (2007) for vendace. Swimming speed and capture rate for each replicate were applied together with mean lengths and weights of roach and vendace respectively. Shaded area marks the treatment with 1 lux

If only metabolic costs were considered, both species would choose the coldest temperature, although roach avoids it. On the other hand, if only foraging rates were considered, both species would choose the warmest temperature, although vendace does not. Hence, neither foraging rate nor metabolic costs can on their own explain habitat use, but in light of each other they provide important information on relative habitat profitability. Thus, the net energy gain in different temperatures needs to be analysed, here calculated as the ratio of mean intake of captured prey to AMR, that is the energy cost while swimming. Energy gain ratio was indeed higher for vendace in all treatments, except in the lowest light level at 18°C, where the two species were similar. Apart from reducing predation risk, a relatively high energy gain ratio may explain why roach utilise the warmer water at times when light levels are low and performing horizontal migrations out to the pelagic zone at night (Bohl, 1980; Gliwicz & Jachner, 1992). Although migrating would increase energy expenditure (Hölker et al., 2002), this study demonstrates that the relatively high energy gain of roach at low light levels in the epilimnion may indeed compensate for energy costs. Accordingly, the relative energy gain ratio can also explain why vendace prefer colder water, in that their energy gain ratio was highest in 6°C. Altogether, results show that the main mechanism to explain the habitat distribution of vendace and roach is how their energy gain ratios are affected by temperature and light, as deduced from capture rates, metabolic costs as well as AMR. However, this study focusing on mechanisms in connection to abiotic factors has ignored the fact that zooplankton composition, abundance and production may vary vertically in lakes (e.g. Gaedke, 1992).

Other studies have related habitat use of competing species to their differences in relative foraging abilities in different habitats (e.g. Bergman, 1988; Diehl, 1988; Okun & Mehner, 2005; Persson & Eklöv, 1995). The metabolic demands of different species under different environmental conditions have also been related to habitat use on different

scales (Hölker, 2006; Huey, 1991; Mehner et al., 2010; Rosenfeld et al., 2015; Walsh et al., 1997). Furthermore, metabolism in combination with foraging efficiency has been discussed to explain habitat use of different species, exemplified with predicted consequences of climate change (Finstad et al., 2011; Seth et al., 2013). However, studies which have focused on relative gain to energy loss, that is treated both foraging efficiency and metabolism, have so far concentrated on modelling long-term intraspecific effects of changed temperature regimes for population dynamics (Ohlberger, Edeline, Vøllestad, Stenseth, & Claessen, 2011; van de Wolfshaar, de Roos, & Persson, 2008). To date, studies on quantifying metabolic requirements together with foraging efficiencies to explain habitat use are lacking. To evaluate which habitat is energetically most profitable, however, the energy gain ratio may not be the appropriate measure. Rather, the net energy intake, after subtracting energetic costs from energy gains, may further facilitate understanding of habitat use in studies of size-structured populations.

Because consumers trade off predation risk to energy gain, it is necessary to account for biotic and abiotic factors affecting the relative significance of predation mortality, food availability and net energy gain, when aiming to explain habitat selection in natural systems. Using interacting fish species as model organisms, I have shown that the sensitivity to predation in an open-water habitat did not sufficiently explain the habitat use of two competing species. Furthermore, results from capture rates and active metabolic rates, respectively, across varying temperature and light conditions could not fully explain the habitat separation between roach and vendace. Instead, foraging experiments and estimates from bioenergetic equations using data from the experiments demonstrate that the mechanisms for different habitat use can be sought in factors contributing to the energy gain ratio. As metabolic traits of competing species are connected to foraging efficiency and swimming performance, thereby attaining an estimate of net energy gain, a mechanistic explanation for the habitat

choice of roach and vendace in the pelagic zone has been provided. Including metabolic traits in studies of food webs can increase our knowledge of how the habitat use of different species may be affected by environmental change.

## ACKNOWLEDGEMENTS

I am grateful to L. Persson, M. Appelberg and P. Eklöv for helpful suggestions when setting up the study. I thank A. Gårdmark, L. Persson, M. Appelberg, J. Ohlberger, R. Svanbäck, J. de Leeuw, and two anonymous reviewers for valuable comments on the manuscript. Experiments were carried out in accordance with all applicable institutional and national guidelines for the care and use of animals. The study was financially supported by the former Swedish Board of Fisheries, University of Umeå, SLU (Swedish University of Agricultural Sciences), and a grant from the Swedish Council for Forestry and Agricultural Research to M. Appelberg.

## REFERENCES

- Beier, U. (2001). Habitat distribution and size structure in freshwater fish communities: Effects of vendace on interactions between perch and roach. *Journal of Fish Biology*, 59, 1437–1454.
- Bergman, E. (1987). Temperature-dependent differences in foraging ability of two percids, *Perca fluviatilis* and *Gymnocephalus cernuus*. *Environmental Biology of Fishes*, 19, 45–53.
- Bergman, E. (1988). Foraging abilities and niche breadths of two percids, *Perca fluviatilis* and *Gymnocephalus cernuus*, under different environmental conditions. *Journal of Animal Ecology*, 57, 443–453.
- Bohl, E. (1980). Diel pattern of pelagic distribution and feeding in planktivorous fish. *Oecologia*, 44, 368–375.
- ten Brink, H., Mazumdar, A. K. A., Huddart, J., Persson, L., & Cameron, T. C. (2015). Do intraspecific or interspecific interactions determine responses to predators feeding on a shared size-structured prey community? *Journal of Animal Ecology*, 84, 414–426.
- Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, 85, 1771–1789.
- Byström, P., Andersson, J., Persson, L., & De Roos, A. M. (2004). Size-dependent resource limitation and foraging-predation risk trade-offs: Growth and habitat use in young arctic char. *Oikos*, 104, 109–121.
- Byström, P., & Garcia-Berthou, E. (1999). Density dependent growth and size specific competitive interactions in young fish. *Oikos*, 86, 217–232.
- Carmona-Catot, G., Magellan, K., & García-Berthou, E. (2013). Temperature-specific competition between invasive mosquitofish and an endangered cyprinodontid fish. *PLoS One*, 8, e54734.
- Cerri, R. D. (1983). The effect of light intensity on predator and prey behaviour in cyprinid fish: Factors that influence prey risk. *Animal Behaviour*, 31, 736–742.
- Clarke, A., & Johnston, N. M. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology*, 68, 893–905.
- Diehl, S. (1988). Foraging efficiency of three freshwater fishes: Effects of structural complexity and light. *Oikos*, 53, 207–214.
- Diehl, S., & Eklöv, P. (1995). Effects of piscivore-mediated habitat use on resources, diet, and growth of perch. *Ecology*, 76, 1712–1726.
- Dunson, W. A., & Travis, J. (1991). The role of abiotic factors in community organization. *American Naturalist*, 138, 1067–1091.
- Einfalt, L. M., Grace, E. J., & Wahl, D. H. (2012). Effects of simulated light intensity, habitat complexity and forage type on predator-prey interactions in walleye *Sander vitreus*. *Ecology of Freshwater Fish*, 21, 560–569.
- Eklöv, P., & Persson, L. (1995). Species-specific antipredator capacities and prey refuges: Interactions between piscivorous perch (*Perca fluviatilis*) and juvenile perch and roach (*Rutilus rutilus*). *Behavioral Ecology and Sociobiology*, 37, 169–178.
- Elliott, J. M. (2011). A comparative study of the relationship between light intensity and feeding ability in brown trout (*Salmo trutta*) and Arctic charr (*Salvelinus alpinus*). *Freshwater Biology*, 56, 1962–1972.
- Finstad, A. G., Forseth, T., Jonsson, B., Bellier, E., Hesthagen, T., Jensen, A. J., ... Foldvik, A. (2011). Competitive exclusion along climate gradients: Energy efficiency influences the distribution of two salmonid fishes. *Global Change Biology*, 17, 1703–1711.
- Gaedke, U. (1992). The size distribution of plankton biomass in a large lake and its seasonal variability. *Limnology and Oceanography*, 37, 1202–1220.
- Gilliam, J. F., & Fraser, D. F. (1987). Habitat selection under predation hazard – test of a model with foraging minnows. *Ecology*, 68, 1856–1862.
- Gjelland, K. Ø., Bøhn, T., Knudsen, F. R., & Amundsen, P.-A. (2004). Influence of light on the swimming speed of coregonids in subarctic lakes. *Annales Zoologici Fennici*, 41, 137–146.
- Gliwicz, M. G., & Jachner, A. (1992). Diel migrations of juvenile fish: A ghost of predation past or present? *Archiv für Hydrobiologie*, 124, 385–410.
- Guthrie, D. M., & Muntz, W. R. A. 1993. Role of vision in fish behaviour. In: T. J. Pitcher (Ed.), *Behaviour of Teleost Fishes* (pp. 89–128), 2nd edition. (Fish and Fisheries Series 7). London, UK: Chapman and Hall.
- Hamrin, S. F. (1986). Vertical distribution and habitat partitioning between different size classes of vendace, *Coregonus albula*, in thermally stratified lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, 43, 1617–1625.
- Hepher, B. (1988). *Nutrition of pond fishes*. Cambridge, UK: Cambridge University Press.
- Hölker, F. (2006). Effects of body size and temperature on metabolism of bream compared to sympatric roach. *Animal Biology*, 56, 23–37.
- Hölker, F., & Breckling, B. (2002). Influence of activity in a heterogeneous environment on the dynamics of fish growth: An individual-based model of roach. *Journal of Fish Biology*, 60, 1170–1189.
- Hölker, F., Haertel, S. S., Steiner, S., & Mehner, T. (2002). Effects of piscivore-mediated habitat use on growth, diet and zooplankton consumption of roach: An individual-based modelling approach. *Freshwater Biology*, 47, 2345–2358.
- Horppila, J., Ruuhijärvi, J., Rask, M., Karppinen, C., Nyberg, K., & Olin, M. (2000). Seasonal changes in the diets and relative abundances of perch and roach in the littoral and pelagic zones of a large lake. *Journal of Fish Biology*, 56, 51–72.
- Huey, R. B. (1991). Physiological consequences of habitat selection. *American Naturalist*, 137, 91–115.
- Huusko, A., & Sutela, T. (1998). Diel feeding periodicity in larvae of the vendace (*Coregonus albula* L.) and influence of food availability and environmental factors on food intake. *Ecology of Freshwater Fish*, 7, 69–77.
- Johnston, I. A., & Dunn, J. (1987). Temperature acclimation and metabolism in ectotherms with particular reference to teleost fish. In: *Symposia of the Society for Experimental Biology* 41, 67–93. Cambridge: Cambridge University Press.
- Jönsson, M., Ranåker, L., Nilsson, P. A., & Brönmark, C. (2012). Prey-type-dependent foraging of young-of-the-year fish in turbid and humic environments. *Ecology of Freshwater Fish*, 21, 461–468.
- Kahl, U., & Radke, R. J. (2006). Habitat and food resource use of perch and roach in a deep mesotrophic reservoir: Enough space to avoid competition? *Ecology of Freshwater Fish*, 15, 48–56.
- SLU. 2016. National Register of Survey test-fishing - NORS. Swedish University of Agricultural Sciences, Dep. Aquatic Resources, <http://www.slu.se/sjoprovfskatedatabasen> [2016-06-06].
- Lima, S. L., & Dill, L. M. (1990). Behavioral decisions made under the risk of predation: A review and prospectus. *Canadian Journal of Zoology*, 68, 619–640.

- Martin, C. W., Fodrie, F. J., Heck, K. L., & Mattila, J. (2010). Differential habitat use and antipredator response of juvenile roach (*Rutilus rutilus*) to olfactory and visual cues from multiple predators. *Oecologia*, 162, 893–902.
- Mehner, T. (2012). Diel vertical migration of freshwater fishes – proximate triggers, ultimate causes and research perspectives. *Freshwater Biology*, 57, 1342–1359.
- Mehner, T. (2015). Partial diel vertical migration of sympatric vendace (*Coregonus albula*) and Fontane cisco (*Coregonus fontanae*) is driven by density dependence. *Canadian Journal of Fisheries and Aquatic Sciences*, 72, 116–124.
- Mehner, T., Busch, S., Helland, I. P., Emmrich, M., & Freyhof, J. (2010). Temperature-related nocturnal vertical segregation of coexisting coregonids. *Ecology of Freshwater Fish*, 19, 408–419.
- Mehner, T., Kasprzak, P., & Hölker, F. (2007). Exploring ultimate hypotheses to predict diel vertical migrations in coregonid fish. *Canadian Journal of Fisheries and Aquatic Sciences*, 64, 874–886.
- Ohlberger, J., Edeline, E., Vøllestad, L. A., Stenseth, N. C., & Claessen, D. (2011). Temperature-driven regime shifts in the dynamics of size-structured populations. *American Naturalist*, 177, 211–223.
- Ohlberger, J., Mehner, T., Staaks, G., & Hölker, F. (2008). Is ecological segregation in a pair of sympatric coregonines supported by divergent feeding efficiencies? *Canadian Journal of Fisheries and Aquatic Sciences*, 65, 2105–2113.
- Ohlberger, J., Otero, J., Edeline, E., Winfield, I. J., Stenseth, N. C., & Vøllestad, L. A. (2013). Biotic and abiotic effects on cohort size distributions in fish. *Oikos*, 122, 835–844.
- Ohlberger, J., Staaks, G., & Hölker, F. (2007). Effects of temperature, swimming speed and body mass on standard and active metabolic rate in vendace (*Coregonus albula*). *Journal of Comparative Physiology. B, Biochemical, Systemic and Environmental Physiology*, 177, 905–916.
- Okun, N., & Mehner, T. (2005). Interactions between juvenile roach or perch and their invertebrate prey in littoral reed versus open water enclosures. *Ecology of Freshwater Fish*, 14, 150–160.
- Oyugi, D., Cucherousset, O. J., & Britton, J. R. (2012). Temperature-dependent feeding interactions between two invasive fishes competing through interference and exploitation. *Reviews in Fish Biology and Fisheries*, 22, 499–508.
- Pekcan-Hekim, Z., Joensuu, L., & Horppila, J. (2013). Predation by a visual planktivore perch (*Perca fluviatilis*) in a turbulent and turbid environment. *Canadian Journal of Fisheries and Aquatic Sciences*, 70, 854–859.
- Persson, L. (1986a). Patterns of food evacuation in fishes: A critical review. *Environmental Biology of Fishes*, 16, 51–58.
- Persson, L. (1986b). Temperature-induced shift in foraging ability in two fish species, roach (*Rutilus rutilus*) and perch (*Perca fluviatilis*): Implications for coexistence between poikilotherms. *Journal of Animal Ecology*, 55, 829–839.
- Persson, L. (1987). The effects of resource availability and distribution on size class interactions in perch, *Perca fluviatilis*. *Oikos*, 48, 148–160.
- Persson, L., & Eklöv, P. (1995). Prey refuges affecting interactions between piscivorous perch and juvenile perch and roach. *Ecology*, 76, 70–81.
- Rennie, M. D., Purchase, C. F., Shuter, B. J., Collins, N. C., Abrams, P. A., & Morgan, G. E. (2010). Prey life-history and bioenergetic responses across a predation gradient. *Journal of Fish Biology*, 77, 1230–1251.
- Rodtka, M. C., & Volpe, J. P. (2007). Effects of water temperature on interspecific competition between juvenile bull trout and brook trout in an artificial stream. *Transactions of the American Fisheries Society*, 136, 1714–1727.
- Rosenfeld, J., Van Leeuwen, T., Richards, J., & Allen, D. (2015). Relationship between growth and standard metabolic rate: Measurement artefacts and implications for habitat use and life-history adaptation in salmonids. *Journal of Animal Ecology*, 84, 4–20.
- Rowe, D. K. (1994). Vertical segregation and seasonal changes in fish depth distributions between lakes of contrasting trophic status. *Journal of Fish Biology*, 45, 787–800.
- Seth, H., Gräns, A., Sandblom, E., Olsson, C., Wiklander, K., Johnsson, J. I., & Axelsson, M. (2013). Metabolic scope and interspecific competition in sculpins of Greenland are influenced by increased temperatures due to climate change. *PLoS ONE*, 8, e62859.
- Sih, A. (2005). Predator-prey space use as an emergent outcome of a behavioural response race. In P. Barbosa, & I. Castellanos (Eds.), *Ecology of Predator-Prey Interactions* (pp. 240–255). Oxford, UK: Oxford University Press.
- Svanbäck, R., Eklöv, P., Fransson, R., & Holmgren, K. (2008). Intra-specific competition drives multiple species trophic polymorphism in fish communities. *Oikos*, 117, 114–124.
- Vijayan, S., Morris, D. W., & McLaren, B. E. (2012). Prey habitat selection under shared predation: Tradeoffs between risk and competition? *Oikos*, 121, 783–789.
- Walsh, S. J., Haney, D. C., & Timmerman, C. M. (1997). Variation in thermal tolerance and routine metabolism among spring- and stream dwelling freshwater sculpins (Teleostei: Cottidae) of the southeastern United States. *Ecology of Freshwater Fish*, 6, 84–94.
- Werner, E. E., Gilliam, J. F., Hall, D. J., & Mittelbach, G. G. (1983). An experimental test of the effects of predation risk on habitat use in fish. *Ecology*, 64, 1540–1548.
- van de Wolfshaar, K. E., de Roos, A. M., & Persson, L. (2008). Population feedback after successful invasion leads to ecological suicide in seasonal environments. *Ecology*, 89, 259–268.