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## FORAGING CAPACITY AND RESOURCE SYNCHRONIZATION IN AN ONTOGENETIC DIET SWITCHER, PIKEPERCH (*STIZOSTEDION LUCIOPERCA*)

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**Abstract.** Species undergoing ontogenetic diet shifts face a risk of resource competition that delays transitions between feeding stages. Such ontogenetic bottlenecks are common in piscivorous fish because competition with future prey may retard growth and prevent a size advantage. In pikeperch (*Stizostedion lucioperca*), year class strength of 0+ cohorts is highly variable and positively related to early onset of piscivory. To identify the causes of this pattern, we experimentally quantified size-dependent planktivorous and piscivorous foraging capacity and incorporated the data into a growth model. For any given prey type and size, foraging capacity described a hump-shaped relationship with predator size. Foraging capacity on daphnids peaked at a pikeperch length of 66 mm, suggesting a narrow scope of planktivory. The highest capacity in the piscivorous niche was reached at a predator-to-prey length ratio of 5, where the ratio was an integrated measure of predator size over several prey sizes. With the growth model, we derived size distributions of 0+ cohorts as functions of resource levels. Simulations revealed two major determinants for the year class strength of pikeperch. First, discontinuous availability of prey sizes counteracted switching to piscivory within the first growing season. This was accentuated by prey fish growth, which caused the planktivory and piscivory niches to separate over time and limited the time window when diet shift was possible. Second, the hump-shaped relationship between size and foraging capacity resulted in growth reduction when growing out of the planktivorous niche. Switching to piscivory in our model occurred along a perpendicular relationship between fish prey and zooplankton density. Zooplankton density determined whether pikeperch reached a size advantage over prey, and fish prey density affected whether the foraging return of piscivory was higher than planktivory. Individuals not reaching a size advantage over prey and failing to become piscivorous were stunted at a size when consumption balanced metabolic requirements. Piscivorous individuals, however, continued to grow fast throughout the season by feeding on the wave of the prey cohort. Our results highlight the importance for predators that shift diet to be synchronized with fluctuations in resource availability, such as the pulses of new cohorts of prey fish.

**Key words:** growth model; ontogenetic diet shift; pikeperch; piscivory; planktivory; size-based model; size-structured population; *Stizostedion lucioperca*.

### INTRODUCTION

Piscivorous fish are top predators in aquatic environments and may profoundly affect community structure and dynamics (Carpenter and Kitchell 1993, Brönmark and Weisner 1996). Size and structure of piscivorous fish populations are strongly influenced by the success of the juvenile stage (Mittelbach and Persson 1998). To obtain a mechanistic understanding of community patterns it is therefore necessary to determine what constraints act on piscivore recruitment to the adult phase.

Most species of piscivorous fish pass through a phase feeding on smaller food items such as zooplankton and benthic invertebrates before switching to a fish diet (Mittelbach and Persson 1998). If resource density in this stage is low, it may constitute an ontogenetic bot-

tleneck by slowing growth and delaying the diet shift (Persson and Greenberg 1990). Thus, to reach the piscivore niche, individual fish must possess enough capacity to grow and survive in the juvenile niche in competition with, e.g., future prey fish species (Bystrom et al. 1998). This constitutes an ontogenetic trade-off, as any increase in juvenile competitive ability is likely to be at the expense of adult competitive ability in the piscivore niche. Typically, specialized piscivores switch to a fish diet at an early stage; whereas less specialized species may wait several years (Keast 1985). Early switching requires high growth rate, which implies high densities of proper resources and safe foraging opportunities. If unfavorable conditions prevail, growth is reduced and this may seriously affect recruitment into the adult stage because mortality rate due to starvation and predation is a size-dependent process (Juanes 1994, see also Mangel and Abrahams 2001). The specific requirements of specialized piscivores in their early ontogeny often result in high year-

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to-year variation in year class strength and size distribution after the first growing season (Olson 1996, van Densen et al. 1996). Thus, constraints related to the onset of piscivory, such as the size relation between individual predators and prey, will have consequences at both population and community levels.

Here, we investigate the mechanisms behind, and the consequences of, an ontogenetic trade-off in a piscivorous specialist, the pikeperch (*Stizostedion lucioperca*; see Plate 1). Field studies have shown that recruitment success of adult, piscivorous pikeperch is variable both between and within systems, and is positively correlated with year class strength, i.e., the number of surviving individuals after the first growing season (Buijse and Houthuijzen 1992). Large individual size and an early shift to piscivorous feeding characterize strong year classes. As outlined above, this suggests significant costs, i.e., low survival, associated with failure to reach the piscivorous stage during the first season. To analyze the consequences of size-based foraging performance, we first experimentally quantified the foraging rate of pikeperch as a function of predator and prey size. The parameterized foraging abilities were then used in a size-based growth model to derive a mechanistic understanding of the causes of observed variability in year class strength and size distribution of cohorts.

#### FORAGING EXPERIMENTS

Foraging capacity, in terms of attack rates, in pikeperch was determined in laboratory (planktivory) and field enclosure experiments (piscivory). *Daphnia* and fish were selected as representative prey for the planktivore and the piscivore niche, respectively. The experiments were designed as functional response experiments to derive accurate parameter estimates of the individual growth model (see *Model description*).

Pikeperch of >200 mm total length were obtained from a fishery in Lake Ringsjön, southern Sweden, and pikeperch <200 mm were delivered from a pikeperch fish farm that uses ponds and natural live prey. In total more than 100 pikeperch varying in size from 38 to 380 mm were used. Each predator was used only once for each prey size and prey density combination.

Experiments with pikeperch foraging on zooplankton were performed in 60 L tanks at a constant temperature of 18°C. One individual was introduced per tank at least 1 wk before the experiment started and was allowed to feed on zooplankton prey until the day before initiating experiments. As zooplankton prey we used *Daphnia* sp. (mean length 0.93 mm) collected from nearby ponds. An experiment started when a known number of zooplankton individuals were mixed into the water of a test tank containing pikeperch. The time from the onset of searching for the first prey item until the fifth prey item was completely ingested was recorded. We performed replicated ( $n \geq 5$ ) functional response experiments on nine different sizes of pike-



PLATE 1. Pikeperch (*Stizostedion lucioperca*) is designed for piscivory, with a large mouth and sharp teeth.

perch (38–120 mm) foraging at six prey densities (0.5–16 individuals/L).

Piscivory experiments were performed in two outdoor and one indoor pond/pool systems; experimental scales were 100 and 28 m<sup>2</sup> in outdoor and 5 m<sup>2</sup> in indoor units. The outdoor systems were used for larger predators (>135 mm) and the indoor system for the smallest predator size class (130 mm). Outdoor experiments were performed at a water temperature ranging between 16° and 20°C. The water temperature of the indoor experiments was kept at 18°C and the light–dark cycle at 14:10 to simulate summer conditions. Prey fish (roach *Rutilus rutilus* and bream *Abramis brama*) were captured with electrofishing and seining in nearby lakes. All predators were allowed to feed on fish prey for at least 1 wk before the experiments.

Each experimental unit contained one (190–380 mm length) or two predators (130–165 mm length). After predators were confined to cages, prey fish (size limits 20–150 mm) were introduced and allowed to accommodate for 1 h. The experiment started by releasing the predators, and it was terminated after 3 d when remaining fish were captured and counted. In pond experiments and for some prey sizes in pool experiments (90, 110, and 150 mm), the predator consumption rate was only determined at three prey densities. In those cases, the attack rate was determined by fitting the consumption rates to a linear functional response. In cases where more prey densities were used, attack rates were derived from a type II functional response equation (Eq. 2) using least squares nonlinear regression. Experiments were performed by either varying prey size (pikeperch sizes 130 or 350 mm) or by varying pikeperch size (prey sizes 35 or 50 mm). Consequently, estimates on attack rates were specific to each predator size and prey size combination. The estimated attack rates were fitted to the size-dependent attack rate function (Eq. 3), again using least squares nonlinear regression. This attack rate function (see Persson et al.

TABLE 1. Model variables and parameters for pikeperch (*Stizostedion lucioperca*) and its prey.

Category for variables	Symbol	Value	Unit	Description	Source†
Zooplankton	$Z$	varied	g/L	density (40 $\mu\text{g}/\text{zooplankter}$ )	a
Fish prey	$F$	varied	g/L	density	
	$l_F$		mm	length	
	$g_F$	0.5, varied	mm/d	growth rate	a, b
	$\lambda_{1F}$	55	$\text{mm}/\text{g}^{-\lambda_{2F}}$	scalar for $l$ - $w$ conversion	a
Predator	$\lambda_{2F}$	0.29		exponent for $l$ - $w$ conversion	a
	$w$		g	predator mass	
	$l_A$		mm	predator length	
	$l_R$		mm/mm	relative predator length (Prey fish are available when $l_R > 2$ )	c, d
	$\lambda_{1P}$	56	$\text{mm}/\text{g}^{-\lambda_{2P}}$	scalar of $l$ - $w$ conversion	a
	$\lambda_{2P}$	0.31		exponent of $l$ - $w$ conversion	a
Planktivory	$A_Z$	13	$\text{m}^3/\text{d}$	maximum attack rate	d
	$l_{OZ}$	66	mm	optimal predator length	d
	$\alpha_Z$	6.0		allometric exponent	d
Piscivory	$A_F$	9.6	$\text{m}^3/\text{d}$	maximum attack rate	d
	$l_{OF}$	5.3	mm/mm	optimal relative length	d
	$\alpha_F$	6.5		allometric exponent	d
Handling	$\beta$	$82 \times 10^3$	$\text{d} \cdot \text{g}^{-1} \cdot \text{mm}^{-x}$	allometric scalar	e
	$\chi$	-2.4		allometric exponent	e
Metabolism	$\delta$	0.033	$\text{g}^{(1-\epsilon)}/\text{d}$	allometric scalar	e
	$\epsilon$	0.77		allometric exponent	e
	$e$	0.61		assimilation efficiency	d

† Sources are: a, A. Persson, *unpublished data*; b, Romare and Bergman (1999); c, Turesson et al. (2002); d, this study (see *Results*); e, Persson et al. (1998), Claessen et al. (2000).

1998 for a thorough description) describes the attack rate on a specific prey type as a hump-shaped relationship with predator size. We chose this particular function for two reasons. First, a hump-shaped relationship has been found in other species to adequately describe the attack rate on specific prey (Werner 1988, 1994, Byström and Garcia-Berthou 1999, Hjelm 2000, Wahlström et al. 2000, Persson and Brönmark 2002). Second, parameter estimates were available for three species normally coexisting with pikeperch, namely perch (*Perca fluviatilis*), bream (*Abramis brama*), and roach. Hence, we could assess the competitive ability in pikeperch by comparing the parameter estimates of these species.

#### MODEL DESCRIPTION

The size-based growth model is a simplified version of the consumer-resource model described by Persson et al. (1998), with the extension of a second resource (fish). Parameter values used when modeling consumption were generated in the experimental study, whereas metabolic requirements were estimated using published relationships (Table 1).

Individual growth rate is modeled as a mass balance between intake rate ( $c$ ) and metabolism ( $m$ ), where intake rate is a function of the length relation between predator and prey ( $l$ ) and resource density ( $R$ ), and metabolic requirement is a function of predator mass ( $w$ ) according to the following:

$$\frac{dw}{dt} = ec(l, R) - m(w) \quad (1)$$

where  $e$  is a coefficient determining conversion efficiency (including specific dynamic action). Hence, the basic unit of the model is predator wet mass, but mass is converted to predator length for use in consumption equations, and to produce output data that is comparable with field data. Individual length is described as a function of body mass ( $l = \lambda_1 w^{\lambda_2}$ ) with the reservation that an individual is allowed to decrease in mass, but not in length. Starvation mortality occurs if individual mass drops below 70% of the mass predicted by the length-mass equation. If an individual temporarily decreases in mass due to starvation to thereafter increase in mass, it will not increase in length until it has reached the mass predicted by the length-mass equation. This latter case is introduced for logical reasons but it is never realized in the simulations performed in this study.

To determine the size-dependent consumption rates, we assume that individual fish captured prey according to a Holling type II functional response. The size specific consumption rate ( $c(l, R)$ ) as a function of prey density is given by

$$c(l, R) = \frac{a(l)R}{1 + a(l)h(l)R} \quad (2)$$

where  $a(l)$  is attack rate,  $h(l)$  is the handling time in-

cluding digestion, and  $R$  is the prey density. One major objective was to compare the competitive ability of pikeperch in relation to other species in the planktivorous and piscivorous niches. The attack rate for a given prey size has been shown to describe a hump-shaped relationship with predator size (Werner 1988, Persson et al. 1998 and references therein). The increase in attack rate with predator size is related to improved visual acuity and locomotion ability (Schoener 1969, Peters 1983). The decreasing part is related to decreased maneuverability with predator size compared to the prey (Domenici 2001), and decreased ability to discern small prey due to decreased cone density (Breck and Gitter 1983). Following Persson et al. (1998), the attack rate was described as a function of body length according to

$$a(l) = A \left[ \frac{l}{l_0} \exp \left( 1 - \frac{l}{l_0} \right) \right]^\alpha \quad (3)$$

where  $l_0$  is the body length at which the maximum rate,  $A$ , is achieved, and  $\alpha$  is a size-scaling exponent, which affects the rate by which the attack rate increases below and decreases above  $l_0$ . The size-dependent attack rate function (Eq. 3) is applicable to one specific prey type as in the planktivorous feeding here. However, for fish-feeding pikeperch we aimed at describing consumption rates for several combinations of predator and prey sizes. To solve this, we used the ratio of predator length and prey length ( $l_R$ ) as a measure of relative predator size (Scharf et al. 2000), instead of absolute length ( $l_A$ ), when fitting attack rates of fish feeding pikeperch to the size-dependent attack rate function (Eq. 3). The relative predator length is frequently used when describing predator and prey relations in size-structured populations (e.g., Scharf et al. 1998, Hartman 2000). Our data suggest it is legitimate to assume that the parameters are independent on predator size if corrected for prey size for the size combinations used in our experiments.

At all times, a zooplankton ( $Z$ ) and a fish resource ( $F$ ) is available. Because each resource type requires a completely different foraging mode, an individual predator is not allowed to adopt a strategy combining the two resources (i.e.,  $R = Z$  or  $F$ ). Thus, an individual is assumed to choose the foraging strategy generating the highest foraging return according to:

$$c(l_i, R) = \max \begin{cases} c(l_A, Z) \\ c(l_R, F) \end{cases} \quad (4)$$

The densities of  $Z$  and  $F$  are fixed on a wet mass basis in each simulation. However, individual fish prey grow over the season, which results in relatively large numbers of small prey in the beginning and few large prey at the end of the season (e.g., when  $F = 4$  mg/L, fish prey numbers are 1 and 0.0025 individuals/L at  $t = 0$  and 100, respectively). Individual fish prey length,  $l_F$ , is modeled as a fixed daily increment in length,  $g_F$ ,

( $dl_F/dt = g_F$ ). The initial prey length, i.e., the length of prey fish when they appear in the pelagic part of the system, was assumed to be 10 mm based on empirical observations (Hamrin et al. 1998). The gape size of the predator sets the upper limit of prey available for consumption (Hambright 1994). Based on experiments (Turesson et al. 2002; see *Results*) and field observations (Popova and Sytina 1977), this limit occurs for prey that are 0.5 times the pikeperch length. Hence, in the model pikeperch were not allowed to feed on fish prey until  $l_R > 2$ .

Metabolic demand and digestive capacity in *Stizostedion* species are largely based on the closely related and more intensively studied *Perca* species (e.g., Hewett and Johnson 1992). We used the relationships developed by Claessen et al. (2000) for perch, where metabolic demand and handling costs (including digestion) are dependent on predator mass according to allometric functions (metabolic demand:  $m(s) = \delta s^\epsilon$ , where  $\delta$  and  $\epsilon$  are constants; handling time  $h(s) = \beta s^\chi$ , where  $\beta$  and  $\chi$  are constants).

Individual growth simulations were performed using STELLA software (High Performance Systems, Hanover, New Hampshire). Each simulation was run for one season, which was assumed to last for 100 d, using a time step of 1 d. First, we tested the effects of resource densities on diet and growth in pikeperch. We used 100 pikeperch with an unimodal size distribution ranging from 9 mm (size at first feeding; McElman and Balon 1979) to 13 mm (mean 11 mm; cv 10%), to include variations related to, e.g., hatching size and time. Data were sampled at the end of each simulation and size distributions constructed using 5-mm size classes. The initial size variation used in the model is a conservative estimate in comparison with field observations, which show a coefficient of variation in length early in the season in the range of 15–20% (Hamrin et al. 1998, Romare and Bergman 1999). We also tested for interaction effects of resource densities and prey fish growth, and synchronization between pikeperch and prey fish hatching. In these simulations we used a fixed initial pikeperch size of 9 mm.

## RESULTS AND DISCUSSION

### Foraging capacity

Species with ontogenetic diet shifts face a trade-off between being a specialist forager on one resource or a generalist forager on both. Specialists trade risks associated with low competitive ability in one niche with being superior in another niche. Consequently, population densities of specialists are generally a result of their success in the feeding stage where they experience intense competition, because competition reduces growth and prevents transition between feeding stages. Specialization in one niche should be associated with costs in competitive ability in other niches (Persson 1988, Werner 1988). Based on field data showing that

pikeperch has a short planktivorous phase and early switching to piscivory (reviewed in Mittelbach and Persson 1998), pikeperch was considered a specialist piscivore. The adequacy of this statement could be evaluated by examining the quantitative estimates of foraging capacity derived from the functional response experiments, where we quantified size-dependent attack rates in pikeperch when foraging on zooplankton and fish. The attack rate first increased with pikeperch size to a maximum, and then decreased asymptotically toward zero. The shape of this relationship corresponds with earlier studies. The parameters of the size-dependent attack rate function summarize species-specific characteristics and are useful for interspecific comparisons of competitive ability between coexisting species (Byström and García-Berthou 1999, Persson et al. 2000, Persson and Brönmark 2002). Pikeperch showed a smaller optimum size (66 mm), and a lower maximum attack rate (13 m<sup>3</sup>/d; Fig. 1a) when feeding on zooplankton compared with foraging abilities estimated for both a specialist planktivore (roach *Rutilus rutilus*; Hjelm 2000) and an ontogenetic generalist (perch *Perca fluviatilis*; Wahlström et al. 2000). When comparing zooplankton feeding pikeperch and the specialist benthivore bream (*Abramis brama*), optimum size was similar, whereas maximum attack rate was twice as high in bream (Persson and Brönmark 2002). This suggests a narrow scope for planktivory in pikeperch compared with roach, perch, and bream, rendering further support to the view that piscivore specialization is related to costs in competitive ability in the planktivorous niche.

Quantification of foraging capacity over ontogeny is rare, and our data on piscivorous foraging capacity is unique. Pikeperch in the piscivory experiments were able to ingest all prey sizes used, i.e., from a predator:prey length ratio of 2 to 14, and maximum attack rate (9.6 m<sup>3</sup>/d) was achieved at a predator:prey length ratio of 5.3 (Fig. 2b). The estimated maximum attack rate for pikeperch is in the upper range of attack rates used by Claessen et al. (2000), and higher than the value suggested for perch. Interestingly, perch usually need several years to become piscivorous and rely on other resources (benthic invertebrates) until proper conditions appear. Thus, our data support the general view of pikeperch being a specialist piscivore.

#### Growth simulations

Simulations showed that resource synchronization might be crucial for the recruitment success of a predator population where individuals undergo ontogenetic diet shifts. Any mismatch in time or size availability of the second resource caused a stunted population. This mismatch was due to predators growing out of the first niche, without being large enough to fit the second niche. Thus, the origin of the stunted population was primarily discontinuous availability of prey sizes, which, in turn, was caused by the growth of prey fish that separated the two niches over time. Resource den-

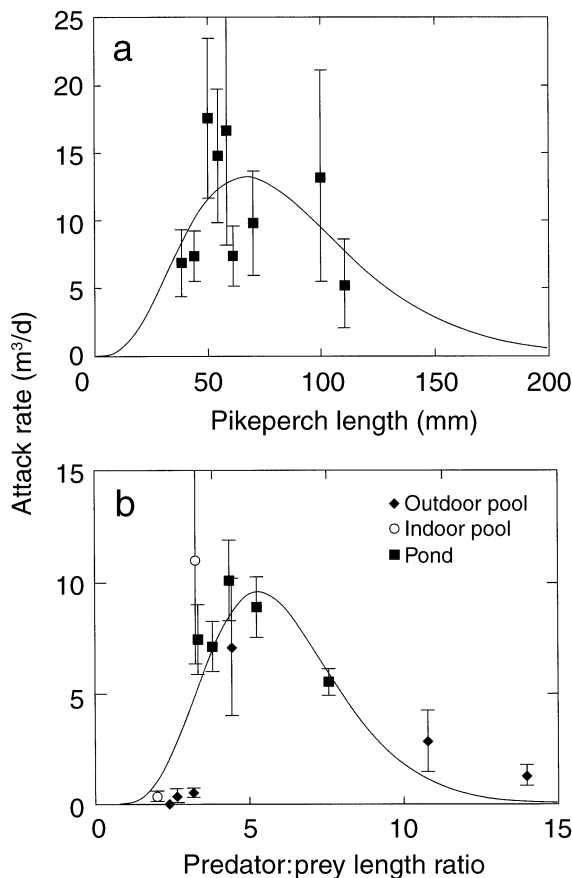


FIG. 1. Size-dependent attack rates ( $\pm 1$  SE) of (a) planktivorous pikeperch foraging on 1-mm *Daphnia* and (b) piscivorous pikeperch foraging on different sized prey fish. The attack rates describe a hump-shaped relationship with (a) pikeperch body length and (b) relative pikeperch length. Optimum size, maximum attack rate, and the size-scaling exponent of the size-specific attack rate function (based on least-squares nonlinear regression; Eq. 3) are, respectively, (a)  $l_{ZO} = 66 \pm 10$  mm,  $A_Z 13 \pm 3$  m<sup>3</sup>/d,  $\alpha_Z = 3.5 \pm 3$ ; and (b)  $l_{FO} = 5.3 \pm 0.6$  mm/mm,  $A_F = 9.6 \pm 2$  m<sup>3</sup>/d,  $\alpha_F = 6.5 \pm 3$ . Note that the data for planktivorous pikeperch assumes 12 h of feeding per day.

sity indirectly affected recruitment success by enabling a higher growth rate of the predator, and thus making a diet shift possible early in the season when the size difference between the two resources was still small.

The hump-shaped relationship (Fig. 1) between attack rate and predator size had fundamental consequences for the growth rate of the predator. When it grew into the niche there was a positive feedback as growth increased the attack rate, which in turn increased growth, and so on. This proceeded until the optimum prey-to-predator size relationship was passed (i.e., the maximum of the attack rate function), after which the opposite was true, i.e., any growth increment made the predator less efficient in this feeding niche. In the planktivorous niche this resulted in individuals attaining a size for which consumption balanced met-

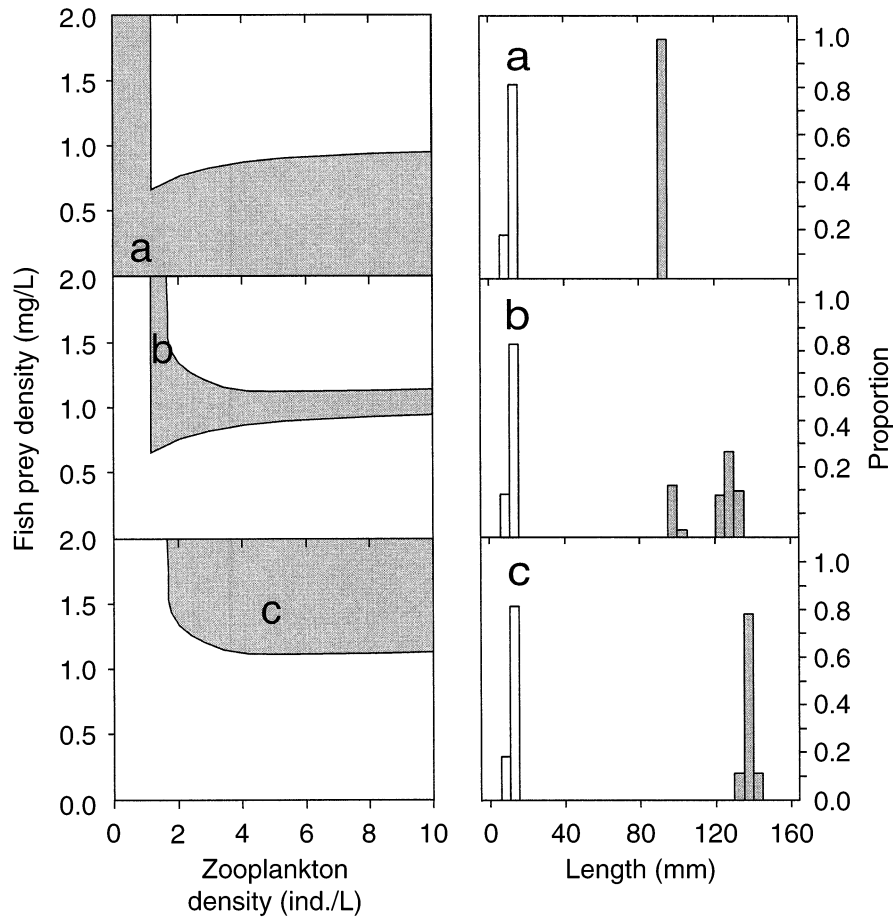


FIG. 2. Simulated pikeperch diet at different combinations of zooplankton and fish prey density (left panels), and examples of size–frequency distributions corresponding to case a–c (right panels). Open bars denote initial size distribution, and filled bars denote final size distribution. When zooplankton density  $\geq 0.05$ , all pikeperch survive, which corresponds to minimum resource requirements of 9-mm pikeperch. Shaded areas denote resource combinations where (a) pikeperch remain planktivorous the whole season, (b) the pikeperch cohort consists of both planktivorous and piscivorous individuals (the “window of bimodality”), and (c) all individuals are piscivorous. Initial fish prey size 10 mm;  $g_F = 0.5$  mm/d. Seasonal length was 100 d.

abolic requirements (Fig. 2a). In the piscivorous niche, however, pikeperch continued to grow as prey fish grew (Fig. 2c). Metaphorically speaking, pikeperch were feeding on the prey cohort wave, synchronizing their own growth in relation to prey growth.

We identified three regions in the fish and zooplankton density phase plane, representing different foraging modes (Fig. 2). Below a critical zooplankton density (0.04 individuals/L), no pikeperch survive. When resource density is just beyond this critical level, surviving pikeperch stay in the planktivore niche throughout the season (Fig. 2a). If cohorts remain planktivorous, individuals accumulate at the maximum attainable size set by zooplankton density. The size distribution is therefore narrow, with a low level of dispersion. If resource density is sufficient, diet shift to piscivory is promoted. This shift is affected by both zooplankton and prey fish density, the threshold level being a perpendicular relationship between zooplank-

ton and fish prey density (Fig. 2). In the window of bimodality (Fig. 2b), different individuals of the cohort apply different foraging modes. The size of this region is fully dependent on the dispersion of the initial size distribution. Hence, if the dispersion of the initial distribution is 0, the window of bimodality disappears. The level of dispersion of the final size distribution depends on both the initial distribution and on the difference in profitability between the planktivorous and piscivorous stage, which results in different growth trajectories. Consequently, the largest size difference is attained when zooplankton density is low and fish prey density is high, i.e., in the upper left region of the shaded area in Fig. 2b. When all individuals remaining in the cohort become piscivorous (Fig. 2c), the size distribution becomes unimodal with an intermediate level of dispersion compared to the stunted unimodal and the bimodal size distribution. It is notable that the simulated size distributions (Fig. 2) resemble patterns

shown by natural populations of pikeperch (Buijse and Houthuijzen 1992, Frankiewicz et al. 1996, van Densen et al. 1996), walleye (Madenjian and Carpenter 1991), largemouth bass (Adams and DeAngelis 1987), and Arctic char (Hammar 1998).

Switching to piscivory in our model occurred along a perpendicular relation between fish prey density and zooplankton density (Fig. 2b). Left of the vertical part of the shaded area, and below the horizontal part, pikeperch remain planktivorous. This pattern is produced by the two criteria for diet switching. First, prey size must be within the window of susceptibility to predation. Hence, left of the vertical part, pikeperch grow too slow to reach a size advantage over prey (i.e., predator:prey length ratio,  $l_r < 2$ ). The second criterion for diet switching was a higher foraging return of piscivory compared to planktivory (Eq. 4). Because the handling time is the same for both prey types, the highest intake rate could be determined by comparing the product of attack rate and resource density. Below the horizontal part, fish prey density is too low for foraging return on zooplankton to drop below that on fish (whatever the value of zooplankton density).

The most likely outcome in nature is that at least one resource, fish prey or zooplankton, is in low abundance. A large population of planktivorous fish prey would reduce the zooplankton resource. This results in different profitability in the two niches, which should reinforce any initial difference in size between pikeperch individuals. It should also be noted that if the zooplankton resource is heavily exploited, it should affect the growth rate of both pikeperch and fish prey. Consequently, slow growing prey is more likely to be found and increase the probability of diet switching at low zooplankton availability. Conversely, if zooplankton density is high (due to low abundance of planktivorous fish) there is relatively little to be gained by switching diet early because the growth opportunities in both niches are more similar. If keeping fish prey density constant, the simulations show that switching is possible above a certain zooplankton density because pikeperch reach a size advantage ( $l_r > 2$ ). Increasing zooplankton density above this threshold will initially allow switching earlier and at a smaller predator size. However, if increasing the density further, diet switching will occur later in the season and at a larger predator size. In the first case, when switching time and size are negatively related to zooplankton density, switching occurs immediately when prey fall within the window of susceptibility to predation ( $l_r > 2$ ). In the second case, when the relationship between switching time and zooplankton density is positive, foraging capacity on zooplankton is larger than on fish when pikeperch reach a size advantage over prey. Hence, switching does not occur until the foraging return on zooplankton drops below that on fish, which will occur later and at a larger size with increasing zooplankton density. In fact, pikeperch may reach a size of 166 mm the first season

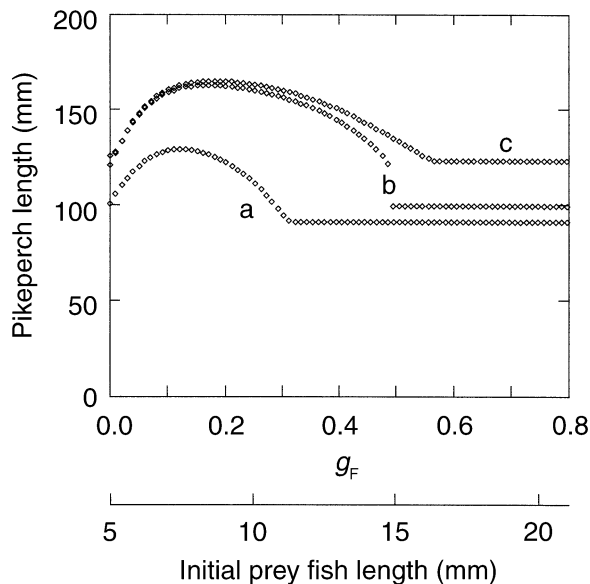


FIG. 3. Effects of initial prey fish length (lower x-axis) and prey fish growth rate,  $g_F$ , (upper x-axis) on simulated final pikeperch length. Cases a–c correspond to the combinations of zooplankton and fish prey densities marked in Fig. 2, which are: (a) 1 individual/L and 0.25 mg/L, (b) 1.5 individuals/L and 1.5 mg/L, and (c) 5 individuals/L and 1.5 mg/L, respectively. Final length is determined by zooplankton density if pikeperch fail in switching to piscivory. When the predator:prey length ratio is synchronized just beyond  $l_{OR}$ , maximum growth rate is obtained. Initial pikeperch length = 9 mm.

feeding only on zooplankton (initial length = 9 mm; zooplankton density 100 individuals/L), which exceeds the length obtained in the main part of the shaded region in Fig. 2c.

In the model, discontinuous prey size availability was caused by the growth of prey fish, which separated the two niches over time. A discontinuous availability of prey sizes may also be generated if some preferred prey sizes are removed or reduced to low levels (van Densen et al. 1996). This possibility is not specifically taken into account here as including a feedback between resource consumption and resource dynamics was beyond the scope of the study. Excluding a feedback to the zooplankton resource probably overestimates the probability of a bimodal size distribution. However, pikeperch has been shown in this study to have a low foraging capacity on zooplankton and would probably only have a minor influence on zooplankton dynamics in comparison to zooplanktivore specialists. Conversely, it is reasonable to believe that pikeperch in fact drive the dynamics of the fish resource. If we include a dynamical interaction between pikeperch and the fish resource, we would expect the smallest prey sizes to become removed first, as these individuals are the first to fall within the prey size window of pikeperch. That narrows the size range of the prey cohort, which would further increase the discontinuity in resource availability, and hence the window of bimo-

dality. In that sense, this model provides a conservative prediction of the probability of a bimodal size distribution.

We also tested how pikeperch growth is affected by prey growth rate and initial prey size (a surrogate for spawning date). Fig. 3 shows that both these factors have similar effects on final pikeperch length. Prey fish growth rate affects if and when pikeperch grow into the window of piscivory, but also the growth opportunities once in the piscivorous niche. If prey fish grow slowly, pikeperch also experience slow growth in the piscivorous niche because pikeperch growth is synchronized with prey growth at a predator: prey length ratio well beyond optimum (Fig. 3). The prey fish growth rate yielding highest pikeperch growth rate is  $\sim 0.2$  mm/d (Fig. 3), and occurs when pikeperch are able to maintain predator: prey length ratio just beyond the optimum,  $l_{OR}$ . It is notable that the simulations show pikeperch being sensitive to prey fish growth rates within the range measured in field situations, i.e., when prey fish reach 40–80 mm total length the first season. Initial prey size influenced whether or not pikeperch reached a size advantage over the prey population. If prey fish are given a head start, pikeperch only become piscivorous at high resource densities. In lakes of Sweden, pikeperch spawn simultaneously or later than most prey fish, suggesting that timing in recruitment indeed is one critical factor for recruitment success.

Whether or not pikeperch reach the piscivorous stage within the first season may have significant consequences at the population and community levels. Model simulations revealed that discontinuous prey availability and the growth rate of pikeperch in relation to prey fish determined recruitment success. In particular, the fact that the level of discontinuity increases over the season exerts further constraint on recruitment success. This points to the importance of being synchronized with predictable fluctuations in resource availability, such as the pulses of new cohorts of prey fish.

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