Stabilization of Population Fluctuations due to Cannibalism Promotes Resource Polymorphism in Fish

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abstract: Resource polymorphism is a well-known phenomenon in many taxa, assumed to be a consequence of strong competition for resources and to be facilitated by stable environments and the presence of several profitable resources on which to specialize. In fish, resource polymorphism, in the form of planktivore-benthivore pairs, is found in a number of species. We gathered literature data on life-history characteristics and population dynamics for 15 fish species and investigated factors related to the presence of such resource polymorphism. This investigation indicated that early cannibalism and low overall population variability are typically associated with the presence of resource polymorphism. These findings match previously reported patterns of population dynamics for size-structured fish populations, whereby early cannibalism has been shown to decrease temporal variation in population dynamics and to equalize the profitability of the zooplankton and macroinvertebrate resources. Our study suggests that competition alone is not a sufficient condition for the development of resource polymorphism because overly strong competition is typically associated with increased temporal variation (environmental instability). We conclude that although resource competition is an important factor regulating the development of resource polymorphism, cannibalism may also

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play a fundamental role by dampening population oscillations and possibly by equalizing the profitability of different resources.

Resource polymorphism, defined as the occurrence of different morphotypes within a single population using different resources, has been found in many different taxa (Collins and Cheek 1983; Smith 1987; Thompson 1992; McPhail 1993; Padilla 2001) and may constitute and provide an example of ongoing evolution (Schluter 2000), possibly associated with ecological selection (Skúlason and Smith 1995). Resource polymorphism is assumed to develop in response to severe competition for a certain resource because adaptation to alternative resources under such circumstances increases the fitness for individuals (Schluter 2000). Morphological differences between groups using different resources have been shown to depend on phenotypic plasticity as well as genetic divergence (Nordeng 1983; Gíslason et al. 1999), and the two factors have also been suggested to act together (Adams et al. 2003). Although many studies of resource polymorphism exist, few discuss its development in a broader ecological context. It has been suggested that the development of resource polymorphism is favored in environments that are temporally stable with respect to both abiotic and biotic factors (Jónasson et al. 1998; Egas et al. 2004; Snorrason and Skúlason 2004) and by the occurrence of several niches of relatively high productivity capable of supporting different specialists (the habitat heterogeneity argument; Lavin and McPhail 1986; Walker 1997; Grant 2001). A further important factor is community composition, because new morphs are expected to be able to develop only in the presence of open (i.e., unoccupied) niches, as a result of the absence of one or several functional species (Schluter and McPhail 1992; Robinson et al. 1993; Böhn and Amundsen 2001). Finally, predation may also facilitate resource polymorphism, either by strengthening trade-offs between different strategies (Andersson 2003; Andersson

and Persson 2005) or by decreasing the effects of resource population feedbacks (Rundle et al. 2003).

A large number of studies on resource polymorphism have been performed on fish (Svärdson 1979; Ehlinger and Wilson 1988; Sandlund et al. 1992; Schluter and McPhail 1992; Robinson et al. 2000). These studies include many different types of specializations, but a frequently reported type of resource polymorphism concerns benthic-limnetic (benthivorous-planktivorous) pairs (Robinson and Wilson 1994; Smith and Skúlason 1996). However, studies have hitherto mainly restricted themselves to morphological differences between morphotypes per se; relationships among diet, morphology, and performance; and trade-offs as a result of morphology (Ehlinger 1990; Malmquist 1992; Malmquist et al. 1992; Schluter and McPhail 1992; Schluter 1995; Robinson et al. 1996; Svanbäck and Eklöv 2003).

We investigated the hypothesis that stable environments promote the development of resource polymorphism and relate this to results from work on the effect of density-dependent life histories on population dynamics in size-structured populations. We propose that cannibalism is a candidate ecological factor that facilitates resource polymorphism. Previous work has shown that the population dynamics of consumer-resource systems are characterized by large-amplitude cycles if the consumer is size structured and lacking cannibalism (Hamrin and Persson 1986; Persson et al. 1998; Sanderson et al. 1999; Lammens et al. 2002). Large-amplitude cycles in resources imply that specialization on a certain resource is associated with long periods of very low resource levels, forcing specialists to change their diet in order to survive and hence promoting the existence of generalists. The effect of cannibalism on population stability depends on several aspects, but, in general, strong cannibalism that targets newborn individuals stabilizes both consumer and resource dynamics (Claessen et al. 2000, 2002). Another effect of cannibalism is that resources consumed by cannibalized size classes are released from predation and thereby increase in relative availability (Persson et al. 2004a). Hence, cannibalism can equalize or differentiate the relative profitability of different resources, allowing for specialization on resources previously exploited by smaller size classes.

To test our hypothesis that a decrease in temporal variability as a result of cannibalism promotes the development of resource polymorphism, we performed a literature survey that considered species-specific foraging traits and population dynamics. Our literature survey included ecological characteristics in fish species in which resource polymorphism is known as well as those for which it is not. On the basis of factors typically proposed to facilitate resource polymorphism and the ecological relationships previously described, we predicted that species displaying resource polymorphism should be characterized by can-

nibalism in early life stages, resulting in low temporal variation in population densities and possibly also equalization of resource levels.

Material and Methods

We used three criteria to select species for inclusion in our review of resource polymorphism in fish. First, we considered only resource polymorphism with regard to lake-dwelling planktivore-benthivore pairs, to be able to look at a set of parallel examples of resource polymorphism and to exploit the large body of information on resource use and foraging ability that already exists for such species. Second, species were included only for which there were extensive data on dietary shifts at different sizes. Finally, data on population size over time were required so that the presence/absence of resource polymorphism could be related to differences in population dynamics.

We gathered data for the following seven variables. (i) Maximum size for planktivory: the maximum body size when zooplankton can still be the main resource. (ii) Benthivory potential: confirmative data showing that the species uses benthic resources during ontogeny and hence that the species could potentially develop a benthivorous morph. (iii) Minimum size for piscivory: the smallest body size at which the species starts to include fish in its diet (inter- or intraspecific prey). (iv) Minimum victim-cannibal size ratio: the minimum body length ratio between victims and cannibals reported. In cases where the relationship could not be found, we used the lower size relation between the predator species and other prey fishes. If the species was cannibalizing on eggs or newly hatched larvae, the ratio was set to 0. (v) Maximum fish size: reported maximum body size in natural systems. (vi) Population abundance variation: the coefficient of variation in numbers of individuals 1 year old and older. We searched for data from relatively undisturbed environments and for surveys lasting at least 4 years. In some studies, we could not find actual numbers of individuals but only catch per unit effort (CPUE) data. In these cases, CPUE values for different years were used to compute the coefficient of variation. (vii) Resource polymorphism: to be classified as displaying resource polymorphism, we had to find at least five lakes from which different morphotypes have been reported to coexist.

We first performed a principal component analysis (PCA) on the data from the literature survey in which the following factors were included. (1) The ratio between maximum size and maximum size for planktivory: we use this ratio as an estimate of the importance of planktivory over the ontogeny (a low value close to 1 indicates that planktivory is important). (2) The ratio between maximum size and minimum size for piscivory: a high value

indicates that piscivory is important. For nonpiscivorous species, this ratio was set to 1. (3) The maximum fish size. (4) The minimum victim-cannibal size ratio. For species with no cannibalism, this ratio was set to 1. (5) The coefficient of variation for population abundance. To homogenize the data, the ratios between (i) maximum size and maximum size for planktivory and (ii) maximum size and minimum size for piscivory and maximum size were $\ln(x+1)$ transformed. Data on the cannibalistic lower limit were arcsine transformed before conducting the PCA analysis. We could not find any data for the minimum size for piscivory in pumpkinseed (*Lepomis gibbosus*); therefore, we used the same value as for bluegill (*Lepomis macrochirus*) because of their close taxonomic relationship. In order to test our hypothesis that cannibalism, especially when it targets smaller individuals, stabilizes population dynamics, we performed a one-sided test using linear regression for the coefficient of variation in number of individuals on the minimum victim-cannibal size ratio. Thereafter, to further explore the effects of the different variables on the presence of resource polymorphism, and because of the small sample size, we performed a binary logistic regression with resource polymorphism as the dependent factor (present/not present) and the two principal components produced in the PCA analysis as independent. With respect to our hypothesis that variation in population size and a small minimum victim-cannibal size ratio promote resource polymorphism, the B coefficient (analogous to the slope in a linear regression) for the binary logistic regression should be negative when testing resource polymorphism and principal component (PC) 2.

Two possible caveats in our analysis of the literature data should be mentioned. First, no concern was given to phylogeny and past evolutionary history in our analyses because the aim of our article was not to unravel taxonomic relationships but to look for functional traits that may also co-vary within families. However, it is worth noting that for each of the species displaying resource polymorphism, there is almost always another species within the same family not displaying resource polymorphism, the only exception being threespine sticklebacks (*Gasterosteus gasterosteus*). Another potential weakness in our analyses is that it is not always a simple task to conclude that a species does not display resource polymorphism. A species classified as nonpolymorphic may simply constitute a less thoroughly investigated taxon that may be classified as polymorphic in the future. However, this is unlikely to be a major problem in our data set because almost all species that we classified as polymorphic display quite dramatic differences, with their polymorphic nature first having been observed visually before undertaking morphometric analysis, with the exception of bluegill. Thus, we argue that even if polymorphism will be found

in other species in the future, these species would already have been found if the morphological differences had been as large as for the species that we classified as polymorphic.

Results

Data used in the literature survey are summarized in table 1. Seventy-nine percent of total variation was accounted for by the first two PC axes (fig. 1; table 2). PC1 was predominantly associated with the ratio of maximum fish size to maximum size for planktivory, the ratio of maximum size to minimum size for piscivory, and maximum size per se. PC2 reflected the minimum victim-cannibal size ratio and the coefficient of variation in population abundance (table 2). Four groups could be discerned in the PC1-PC2 plane (fig. 1). First, all species that lack evidence of cannibalism (i.e., bream [*Abramis abramis*], vendace [*Coregonus albula*], and roach [*Rutilus rutilus*]) occur in the upper left corner of the PC plot (group A; fig. 1). These species have not been reported to display resource polymorphism but are characterized by high-amplitude population cycles, driven by intercohort competition dominated by recruiters (Hamrin and Persson 1986; Perrow et al. 1990; Lammens et al. 2002; table 1). Yellow perch (*Perca flavescens*) was also associated with this group of species, reflecting common occurrence of intercohort competition-driven cycles and the lack of resource polymorphism (Sanderson et al. 1999; Persson et al. 2004*b*). Remaining species clusters are all characterized by cannibalism, but the extent of polymorphism differs substantially between the groups. The group B species (largemouth bass [*Micopterus salmoides*], northern pike [*Esox lucius*], and pikeperch [*Sander lucioperca*]) are found to the far right in figure 1, reflecting a large maximum fish size, a low ratio of maximum fish size to minimum size for piscivory, and a low ratio of maximum fish size to maximum size for planktivory. Generally, these species have been classified as obligatory piscivores characterized by a short planktivorous life stage and an early shift to piscivory (Keast 1985; Mittelbach and Persson 1998), which is in accordance with the results of our PCA. Of the remaining species, those in group D (Arctic char, bluegill, pumpkinseed, threespine stickleback, and whitefish [*Coregonus lavaretus*]) all display resource polymorphism (fig. 1). This group is characterized by relatively low population variability and a low value for the minimum victim-cannibal size ratio (all species in group D are reported to cannibalize on egg and larvae). Finally, group C (brown trout [*Salmo trutta*], Eurasian perch [*Perca fluviatilis*], and lake trout [*Salvelinus namaycush*]) represents a quite heterogeneous group. Eurasian perch displays relatively high population variability and a relatively high minimum victim-cannibal size ratio, placing it closer to group A. In contrast, brown

Table 1: Species traits and characteristics from literature survey

Species	Maximum size for planktivory (g)	Benthivory	Minimum size for piscivory (g)	Minimum victim-cannibal size ratio	Maximum size[1] (g)	Coefficient of variation for population size	Resource polymorphism
No cannibalism:							
Abramis brama	275[2]	Yes[2]	…	…	6,300	>1[3,a]	…
Coregonus albula	125[4]	Yes[5]	…	…	1,000	.86[6]	…
Rutilus rutlilus	40[7]	Yes[7]	…	…	2,500	.59[8]	…
Cannibalism:							
Piscivores:							
Esox lucius	.4[9]	Yes[9]	1.0[9]	.03[10]	28,400	.40[11,a]	…
Micropterus salmoides	.25[12]	Yes[12]	.5[12]	.05[13,a]	10,100	.44[14]	…
Stizostedion lucioperca	1.0[15]	Yes[15]	2.0[16]	.07[17,18]	20,000	.94[19]	…
Omnivores:							
Coregonus lavaretus/							
Coregonus clupeaformis	500[20]	Yes[20]	500[20]	0[21]	10,000	.21[22]	Yes[20]
Gasterosteus aculeatus	10[23]	Yes[23]	.8[24]	0[25]	10	.43[26]	Yes[27]
Lepomis gibbosus	35[28]	Yes[28]	…	0[29]	630	.43[30]	Yes[31]
Lepomis macrochirus	50[32]	Yes[32]	40[33]	0[34]	2,150	.56[35]	Yes[36–39]
Perca flavescens	20[40]	Yes[40]	35[41]	.08[10]	1,910	.80[42]	…
Perca fluviatilis	35[43]	Yes[43]	40[10]	.05[10]	4,750	.62[44]	…
Salmo trutta	300[45]	Yes[45]	35[46]	.07[47]	20,000	.23[48]	…
Salvelinus alpinus	200[49]	Yes[49]	40[46]	0[50]	15,000	.25[48]	Yes[51]
Salvelinus namaycush	245[52]	Yes[52]	5.0[53]	.08[54,a]	32,700	.15[55]	…

Note: Maximum size for planktivory, minimum size for piscivory, and maximum size reported as weight. Victim-cannibal size ratio reported as the minimum size of the victim in percentage of the cannibal with respect to lengths. Coefficient of variation is for the density over time. The presence of benthivory and resource polymorphism reported only as confirmative data. A more detailed description of the different categories is given in "Material and Methods."

Sources: Superscript numbers refer to the following sources: 1 = Froese and Pauly 2004; 2 = Persson and Brönmark 2002*a*; 3 = Lammens et al. 2002; 4 = Hamrin 1983; 5 = Böhn and Amundsen 2001; 6 = Hamrin and Persson 1986; 7 = Hjelm et al. 2003; 8 = Perrow et al. 1990; 9 = Skov et al. 2003; 10 = Persson et al. 2004*b*; 11 = Persson et al. 2006; 12 = Olson 1996; 13 = Pierce et al. 2001; 14 = Schindler et al. 1997; 15 = Frankiewicz et al. 1999; 16 = Buijse and Houthuijzen 1992; 17 = Keskinen and Marjomaki 2004; 18 = Persson and Brönmark 2002*b*; 19 = Willemsen 1977; 20 = Svärdson 1979; 21 = Skurdal et al. 1985; 22 = Healey 1980; 23 = Schluter and McPhail 1992; 24 = Mori 1995; 25 = Whoriskey and FitzGerald 1985; 26 = Wootton and Smith 2000; 27 = McPhail 1993; 28 = Robinson et al. 1993; 29 = Scott and Crossman 1973; 30 = Huckins et al. 2000; 31 = Robinson et al. 2000; 32 = Werner and Hall 1988; 33 = Breck 1996; 34 = Neff 2003; 35 = Schneider and Lockwood 1997; 36 = Ehlinger and Wilson 1988; 37 = Layzer and Clady 1987; 38 = Yonekura et al. 2002; 39 = Chipps et al. 2004; 40 = Keast 1977; 41 = Knight et al. 1984; 42 = Sanderson et al. 1999; 43 = Persson et al. 2004*a*; 44 = Persson et al. 2000; 45 = Gray 2001; 46 = L'Abée-Lund et al. 1992; 47 = Kahilainen and Lehtonen 2002; 48 = Saksgard and Hesthagen 2004; 49 = Nilsson and Filipsson 1971; 50 = P. Byström and J. Andersson, unpublished manuscript; 51 = Skúlason et al. 1996; 52 = Konkle and Sprules 1986; 53 = Dryer 1965; 54 = Madenjian et al. 1998; 55 = Mills et al. 2002.

[a] Additional information given personally by the authors.
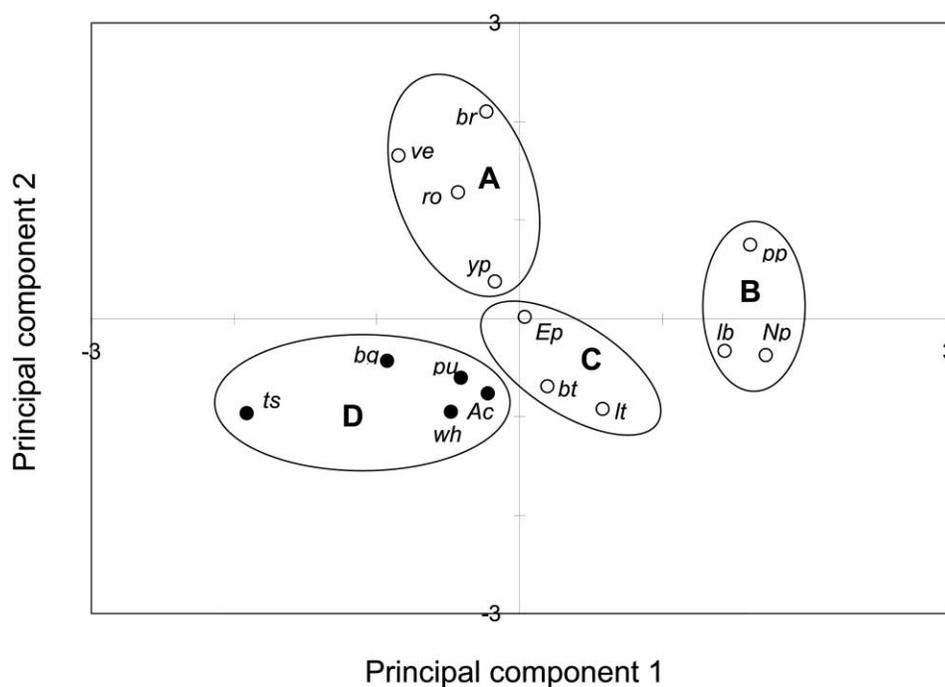
Figure 1: Two first principal components of the principal component analysis on the literature data. Filled circles show species displaying resource polymorphism, and open circles show species not displaying resource polymorphism. Four groups are recognized: *A*, high-amplitude dynamics and noncannibalistic/low-degree cannibalistic species; *B*, true piscivore species; *C*, cannibalistic but not egg/larvae cannibalistic species; *D*, egg/larvae cannibalistic species. The species are bream (*br*), vendace (*ve*), roach (*ro*), northern pike (*Np*), largemouth bass (*lb*), pikeperch (*pp*), whitefish (*wh*), threespine stickleback (*ts*), pumpkinseed (*pu*), bluegill (*bg*), yellow perch (*yp*), Eurasian perch (*Ep*), brown trout (*bt*), Arctic char (*Ac*), and lake trout (*lt*).

trout and lake trout display relatively stable dynamics but because of larger maximum fish size and minimum size for piscivory are more associated with group B (fig. 1). A higher minimum victim-cannibal size ratio was positively related to high population variability (linear regression, slope $= 0.253$, $F = 6.0$, df $= 1, 13$, $P = .015$). Finally, we found that PC1, mainly described by maximum size for planktivory, minimum size for piscivory, and maximum size, could not explain resource polymorphism (Wald coefficient $= 2.3$; $P > .1$). In contrast, PC2, mainly described by population variation and minimum victim-cannibal size ratio, relates the presence of resource polymorphism to small population variations and small minimum victim-cannibal size ratios ($B = -1.66$; Wald coefficient $= 3.87$; $P = .025$).

Discussion

Population Variability and Resource Polymorphism

Resource polymorphism did not occur in any noncannibalistic species in our analysis. Noncannibalistic fish populations and their resources have been shown previously to exhibit high-amplitude cycles driven by cohort competition (Hamrin and Persson 1986; Perrow et al. 1990; Lammens et al. 2002). This is also true for species with low cannibalistic voracity, such as yellow perch (Sanderson et al. 1999; Persson et al. 2004*b*). On the basis of these results, we propose that noncannibalistic species do not display resource polymorphism due to the large temporal variation in population densities leading to periods during which conditions are unfavorable for specialist strategies because of low resource availability. Our finding of the absence of resource polymorphism in noncannibalistic species, in association with large-amplitude population dynamics, is also in accordance with the general idea that a temporally unstable environment reduces the likelihood that resource polymorphism will develop (Egas et al. 2004; Snorrason and Skúlason 2004).

Although the remaining species were all cannibalistic, we found resource polymorphism only in those exhibiting early cannibalism (especially cannibalism on eggs and larvae). Theory predicts that early cannibalism in size-structured populations stabilizes population dynamics (Claessen et al. 2002), a prediction supported by the literature

Table 2: Factor loadings of the first two principal components (PCs) explaining 79% of the variation

Factor	PC1	PC2
Maximum size planktivory	.95	−.04
Minimum size piscivory	.80	−.45
Cannibalistic lower limit	−.14	.89
Population variation	−.047	.86
Maximum size	.80	−.007

data on temporal variation in numbers in species with early cannibalism relative to non- or weakly cannibalistic species. However, we also found cannibalistic species that do not display resource polymorphism despite their relatively stable population dynamics (e.g., pike, largemouth bass, and lake trout). This suggests that population stability is not a sufficient condition for the development of resource polymorphism in fish. Pike, largemouth bass, and lake trout can all can grow to very large sizes. In order to do so, they become piscivores at a small size and use zooplankton resources for only a very short period early in development (Hudson et al. 1995; Mittelbach and Persson 1998; Skov and Koed 2004). We suggest that the lack of resource polymorphism involving zooplankton and benthic resources in the piscivore species in our study, despite their relatively stable population dynamics, reflects the importance of entering the piscivore niche as early as possible for an obligate piscivore's future success. Consequently, an early shift to a fish diet is typically associated with special morphological adaptations to catch, handle, and ingest large prey (Webb 1984; Mittelbach and Persson 1998; Huskey and Turingan 2001), which reduces the scope for parallel adaptation for handling small prey, such as zooplankton.

Relative Resource Profitability

Another effect of size-specific cannibalism is that the relative availability of resources used by the cannibalized size classes increases concomitantly with reduced consumption from these size classes (Claessen et al. 2002). Fish generally undergo one or two ontogenetic niche shifts: new hatchlings feed predominantly on zooplankton before shifting to benthic macroinvertebrates, with some species further becoming piscivorous when older (Persson and Brönmark 2002*a*; Persson et al. 2004*a*; Byström and Andersson 2005). The size-dependent nature of cannibalism has an indirect effect on the relative profitability of different resources. Cannibalism on the smallest size classes leads to an increase in the profitability of the zooplankton resource as a result of reduced consumption by small fish, whereas the benthic resource will be less affected, which results in

a greater gain for larger fish using the zooplankton resource (Persson et al. 2004*a*). In contrast, cannibalism on intermediate size classes leads to an increase in the availability of the benthic resource, enhancing its relative profitability.

On the basis of the stronger positive effect of early cannibalism (i.e., on larvae and eggs) on zooplankton compared with benthic resources and the observed association between early cannibalism and resource polymorphism, we suggest that the availability of zooplankton is a crucial ingredient in the development of polymorphic planktivore-benthivore pairs. If this hypothesis is true, we anticipate patterns whereby exploitation of zooplankton is additional to a more fundamental dependence on benthic resources in species displaying resource polymorphism. In accordance with this hypothesis, several diet studies on benthivore-planktivore pairs indicate that complete specialization on zooplankton resources is not common, whereas benthic morphs normally are highly specialized for macroinvertebrate feeding and essentially exclude zooplankton from their diet (Malmquist et al. 1992; Schluter and McPhail 1992; Robinson et al. 1993).

Competition and Population Stability

Hypotheses on resource polymorphism generally assume that strong competition is the crucial factor behind morphological divergence, with individuals able to escape competition by switching to an alternative resource (Schluter 2000). However, cannibalism, besides having the potential to stabilize dynamics, also has the potential to reduce competition by favoring higher overall resource densities (Claessen et al. 2002; Persson et al. 2004*a*).

Both empirical and modeling results clearly suggest that if competition is the only regulating factor, this leads to high-amplitude dynamics (Hamrin and Persson 1986; Perrow et al. 1990; Persson et al. 1998, 2004*b*; Sanderson et al. 1999; Claessen et al. 2000; Lammens et al. 2002), which we suggest should also reduce the possibility for resource polymorphism to evolve. Although the stabilizing effect of early cannibalism has been shown to release competition for shared resources (Claessen et al. 2000; Persson et al. 2004*a*), stable (fixed-point) dynamics in competition-regulated systems without cannibalism, which would support both the stability and the competition arguments for resource polymorphism, is possible. But this is expected to occur only within a narrow range of attack rate values, a fundamentally important size-scaled parameter (Persson et al. 1998). In contrast, all existing experimental data on the size scaling of foraging rates in fish are well outside this range and point to exploitative cohort competition leading to high-amplitude cohort cycles (Mittelbach 1981; Byström and García-Berthou 1999; Hjelm and Persson

2001; Persson and Brönmark 2002*b*, 2002*a*; Byström and Andersson 2005). Finally, interference competition favoring larger individuals could potentially stabilize dynamics at intermediate values (Persson et al. 1998), but this is an explanation not generally discussed or explored in the context of resource polymorphism, as far as we are aware.

Results for Eurasian perch provide particularly strong evidence for the idea that both predator population stability and the relative profitability of different potential prey influence the possibility for resource polymorphism to develop (Svanbäck and Persson 2004). According to both theory and empirical data, the value of the minimum victim-cannibal size ratio for perch is in a critical range that causes population dynamics to shift between periods of relatively stable cannibal-driven dynamics and periods characterized by large-amplitude population cycles driven by cohort-competition (Persson et al. 2000, 2003; Claessen et al. 2000, 2002). Diet analyses of perch over a 10-year period in relation to population dynamics show that individuals were more specialized on either resource during periods with cannibal-driven population dynamics than during periods with competition-driven dynamics (Svanbäck and Persson 2004). This fine-scaled behavioral pattern supports the hypothesis advanced above, that a control of recruitment through cannibalism has a positive effect on the likelihood of diversification into different morphotypes but that interruptions by periods with recruit dominance and severe competition impose a strong constraint on the development of a true planktivore-benthivore pair. The co-occurrence of higher resource densities (and weaker competition) and cannibalism together with the suggested relationship between cannibalism and resource polymorphism do contrast with most previous hypotheses on the evolution of resource polymorphism. However, a recent experimental study suggests that predation can facilitate diversification despite decreased competition (Rundle et al. 2003). Finally, Svanbäck and Persson (2004) also found that larger individuals consumed zooplankton to a greater extent during periods with cannibal-driven dynamics than periods with competition-driven dynamics, which supports the hypothesis that zooplankton is the limiting resource for the development of resource polymorphism.

Extensions to Additional Species Configurations and Future Perspectives

Our results have relevance for additional types of resource polymorphism. We have, for example, found studies showing that pike, lake trout, and brown trout can have benthivore-piscivore specialists in the same lake, which could be argued to be an effect of cannibalism and the consequential stabilization of resource dynamics (Ferguson

1986; Beaudoin et al. 1999; Henderson and Anderson 2002). In a broader context, resource polymorphism is expected to occur more frequently in populations in which recruitment is strongly regulated at an early stage (e.g., by cannibalism, interspecific predation, or limited breeding habitats) compared with other populations lacking such regulation. Our hypothesis could thus be tested by comparing populations of the same species found in different ecological settings with respect to early regulation. Overall, our study suggests that the evolution of resource polymorphism is best understood by considering population feedbacks and is hence in line with the rapidly growing theoretical framework of adaptive dynamics where evolution in ecologically dynamical systems can explicitly be explored (Dieckmann et al. 2004). In particular, a theoretical investigation into the effect of cannibalism on individual resource use and morphology in size-structured populations should yield new insights into the evolution of resource polymorphism.

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