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1 Running Head: Density dependent individual specialization

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3 Individual diet specialization, niche width and population dynamics:
4 implications for trophic polymorphisms

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by

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1 **Summary**

2 1. We studied a perch (*Perca fluviatilis*, L.) population that during a nine-year
3 period switched between a phase of dominance of adult perch and a phase dominated
4 by juvenile perch driven by cannibalism and inter-cohort competition. We
5 investigated the effects of these population fluctuations on individual diet
6 specialization and the mechanisms behind this specialization.

7 2. Due to cannibalism, the survival of young-of-the-year (YOY) perch was much
8 lower when adult perch density was high than when adult perch density was low.

9 3. Both the individual niche breadth (if weighed for resource encounter) and the
10 population niche breadth were highest when adult population density was high, and,
11 consequently, individual specialization was highest at high adult perch densities.

12 4. When adult perch density was low, the abundances of benthic invertebrate and
13 YOY perch were high and dominated the diet of adult perch, whereas the density of
14 zooplankton was low due to predation from YOY perch. At high perch densities,
15 benthic invertebrate abundance was lower and zooplankton level was higher and some
16 perch switched to feed on zooplankton.

17 5. Our results show that individual specialization may fluctuate with population
18 density through feedback mechanisms via resource levels. Such fluctuations may have
19 profound implications on the evolution of resource polymorphisms.

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23 **Key words:** competition, density dependence, inter-individual variation, intra-
24 population variation, niche breadth

1 **Introduction**

2 Many animal populations have generalized diets but each individual function as a
3 specialist with a restricted diet (Bolnick et al. 2003). Individual diet specialization, an
4 interindividual niche variation, has been thought to reduce intraspecific competition
5 (Van Valen 1965; Roughgarden 1972; Polis 1984; Smith 1990), and in some cases,
6 diet specialization among individuals may exceed differences between conventional
7 species (e.g. Werner & Sherry 1987; Ehlinger & Wilson 1988; Meyer 1989). Within-
8 population niche differentiation can occur in a number of ways, including sexual
9 dimorphism (Shine 1989, 1991), ontogenetic niches (e.g. Polis 1984; Werner &
10 Gilliam 1984), discrete polymorphisms (Skúlason & Smith 1995; Smith & Skúlason
11 1996), or by individual-level variation (Bolnick et al. 2003).

12 Even though individual diet specialization is widespread we largely lack the
13 knowledge about the mechanisms behind this pattern. Present evidence suggests that
14 intra-specific competition may be important as it may induce rapid evolution of a
15 wider population niche breadth (Bolnick 2001). Theoretically, expansion of the
16 population niche width and adaptation to novel resources have been shown to be one
17 of the causes of resource polymorphisms and ultimately sympatric speciation (Smith
18 & Skúlason 1996; Dieckmann & Doebeli 1999; Doebeli & Dieckmann 2000). The
19 expansion of the population niche width is thought to be due to increased intra-
20 specific competition or decreased inter-specific competition (e.g. Grant 1972;
21 Robinson & Wilson 1994; Robinson & Schluter 2000). Whether the population niche
22 expansion is achieved by increased individual niche width, or increased inter-
23 individual variation is a question that theoretically has been raised repeatedly over the
24 past decades (e.g. Van Valen 1965; Roughgarden 1972; Taper & Case 1985; Bolnick
25 et al. 2003) but has received little empirical attention.

1 Although individual variation in resource use thus has attracted substantial
2 theoretical interest, it is symptomatic that the theoretical analyses of diet choice,
3 polymorphism and sympatric speciation have been restricted to consider populations
4 at numerical equilibrium. This situation contrasts to that many populations fluctuate in
5 density over time as a result of variation in resource levels (Grant 1986; Mittelbach et
6 al. 1995; Smith et al. 1999; Persson et al. 2003; Grant & Grant 2002; Klemola et al.
7 2002). These fluctuations in resource levels have been related to both external
8 environmental factors (e.g. Grant & Grant 2002) and intrinsically driven dynamics
9 (e.g. Persson et al. 2003). In both cases, population fluctuations will influence diet and
10 habitat choices and thus the selective forces on the population (Wilson & Turelli
11 1986). Existing models predict that generalist populations of individual specialists
12 will occur under conditions of high food predictability (little or no seasonality) and
13 high food availability and diversity (Roughgarden 1974, 1979; Van Valen 1965). Yet,
14 little is known of how intraspecific variation in resource use among individuals
15 changes in relation to intrinsically driven density-dependent processes in fluctuating
16 populations. Therefore, studying numerically fluctuating populations provides an
17 opportunity to test clear predictions about the role of intraspecific competition on
18 individual resource use.

19 The purpose of our study was to analyse the effect of intraspecific competition
20 on individual diet specialization in a population where the population is driven by
21 size-dependent competition and cannibalism (Persson, Byström & Wahlström 2000;
22 Persson et al. 2003). The system consisted of a population of perch (*Perca fluviatilis*
23 L.) that during a 9-year period experienced an intrinsic cycling due to size-dependent
24 inter-cohort competition and cannibalism involving a more than twenty fold change in
25 the density of adult individuals (Person et al. 2000, 2003). We focus on two main

1 issues behind individual specialization. First, we investigate the effect of population
2 density on diet choice in perch including feedbacks of perch consumption on resource
3 levels. Second, we investigate the mechanisms (individual- and population diet
4 breadth, and resource availability) that may give rise to differences in individual
5 specialization. Finally we discuss the potential implications of population dynamics
6 on evolutionary dynamics.

7

8 **Methods**

9 *Lake description*

10 The study was carried out in Lake Abborrtjärn 3, a small (9.3 ha) oligotrophic lake in
11 central Sweden (64°29' N, 19°26' E) (Persson et al. 1996). The maximum depth of
12 the lake is 12 m, and the mean depth is 6.3 m. The lake has sparse vegetation and 69%
13 of the shoreline is covered with trees that have fallen into the water. Perch was the
14 only fish species in the lake during 1992-1996. In late autumn 1996 and in spring
15 1997, roach (*Rutilus rutilus* L.) and artificial vegetation were added to the lake as a
16 part of a whole-lake experiment. However, the roach population is still very small and
17 the fish community totally dominated by perch (Lennart Persson unpublished data).
18 For more detailed information about the surrounding area and lake chemistry, see
19 Persson et al. (1996, 2000).

20

21 *Field sampling*

22 Fish were sampled with cylindrical plastic traps and fyke nets. In 1992, 60 traps (40 ×
23 100 cm, mesh size 10 and 20 mm, 30 of each mesh size), and in 1993-2000 90 traps
24 (besides the 60 traps used in 1992, 30 traps 25 × 50 cm, mesh size 5 mm) and 10 fyke
25 nets (mesh size 6 mm) were used. Traps with the two largest mesh sizes mainly

1 captured perch ≥ 2 yr old, whereas the traps with the smallest mesh size and the fyke
2 nets captured perch ≥ 1 yr and also young-of-the-year perch in August and September.
3 In this lake perch ≥ 2 yr old are > 100 mm, 1 year old perch are 60 - 100 mm, and
4 young-of-the-year perch in August and September are 30 - 60 mm (Byström, Persson
5 & Wahlström 1998, Persson et al. 2000, 2004)

6 Traps were set on four sampling dates each year (end of May and first weeks
7 in July, August, and September, hereafter May, July, August, and September,
8 respectively). The traps were set in groups of six (groups of four in 1992), including
9 two traps of each mesh size at 15 different stations. 10 of these stations were situated
10 inshore at a depth of 0.5-2 m. The other five stations were set offshore along two
11 vertical profiles, one with two stations and the other with three stations and with both
12 profiles including the maximum depth of that basin. One fyke net was set
13 perpendicular to the shore at every shore station. All sampling gear used were set at
14 13:00-14:00 and raised at 9:00-10:00 the following day. All captured perch were
15 measured (to nearest millimetre) and weighted (to nearest 0.1 g). Length-weight
16 regression at each sampling date was used to estimate the average weight of a perch of
17 size 150 and 200 mm. On every sampling date stomachs of perch were flushed for
18 dietary analyses. The stomach contents were frozen for later laboratory analyses.

19 In addition to trap-catches, in August every year, perch were sampled with gill
20 nets of standard survey link type (1.5 m high, 36 m long, mesh sizes 5, 8, 10, 12.5, 16,
21 19.5, 24, 29, 35, 43, 55 mm). Pelagic nets were set at surface (1 m) and the benthic
22 nets were set at a depth of 5 m. The nets were set at 10 am and were lifted at 10 am
23 the following day.

24 *Perch population size.* – A large trapping effort was carried out every spring
25 for three weeks (end of May and beginning of June) to estimate population size of

1 perch ≥ 2 yr old by multiple mark-recapture methods (Youngs & Robson 1978). Perch
2 were marked with blue dye injected with a Pan Jet injector (Hart & Pitcher 1969). In
3 spring 1-year old perch were electrofished from a boat along the shore where they
4 were concentrated. In years when 1-year old perch abundance was too low to allow
5 population estimates based on mark-recapture (1992, 1993, 1994), spring
6 electrofishing and the total number of 1-year old perch captured in traps and fyke nets
7 over the whole sampling season were used as abundance indices. The abundance of 1-
8 year old perch also yielded an estimate of the survival of young-of-the-year (YOY)
9 perch from the date when they had moved to the shore habitat to an age of 1-year old.
10 All data on perch population censuses represent the spring situation.

11

12 *Zooplankton and macroinvertebrate resources.* - Pelagic zooplankton was sampled 7-
13 8 times every year during the growing season at 3 pelagic stations. Zooplankton was
14 collected with a 100 μm -mesh net (diameter 25 cm). One tow was made at each
15 pelagic station from the thermocline (estimated with a thermistor) to the surface at an
16 approximate speed of 0.5 m/s. Zooplankton levels fluctuate during the growing
17 season, but the average biomass during the part of the growth period when YOY
18 perch affect zooplankton availability (July-September) was much lower in years when
19 YOY perch survival was high (adult perch density low) than in years when YOY
20 perch survival was low (adult perch density high) (Persson et al. 2000, 2003).
21 Therefore we restrict our analysis in this paper to the average (July-September)
22 zooplankton levels.

23 Macroinvertebrates was sampled in August every year. In 1992, five
24 macroinvertebrate samples were taken with an Ekman dredge (area 630 cm^2) at one
25 littoral station at a water depth of 0.5 m. In 1993-1996, the macroinvertebrate

1 sampling was extended to three littoral stations and from 1997 to 5 stations. For the
2 years 1993-2000, 6 samples were taken at each station with a core sampler (area 63
3 cm²). In this study we, concentrate on predator sensitive macroinvertebrates (PSM).
4 This group consisted of organisms living on macrophytes, branches or on other
5 substrates (Hirudinea, Ephemeroptera, Trichoptera, Odonata, Coleoptera,
6 Megaloptera). The other group (mainly chironomids) consisted of organisms living in
7 the sediment and that are less sensitive to fish predation (see Persson et al. 1996 and
8 references therein). Although chironomids are included in the diet of perch we did not
9 include them in the analysis of resource levels in this paper because it has been shown
10 that they are not related to perch population density (Persson et al. 2000).

11

12 *Diet data analyses*

13 The stomach contents were analysed under a dissecting microscope and were
14 identified to order, family, or species and lengths of the ten first prey of each group
15 were measured to the nearest 0.1 millimetre. If there were less than ten prey from a
16 group then all prey in that group were measured. The lengths of all prey types were
17 then converted to biomass (dry weight) using published length-mass relationships for
18 zooplankton (Bottrell et al. 1976) and macroinvertebrates (Persson and Greenberg
19 1990). The biomass-based diet was separated into seven different diet categories. The
20 diet categories were; 1) cladocerans, 2) copepods, 3) pelagic macroinvertebrates, 4)
21 YOY perch, 5) Predator sensitive macroinvertebrates (PSM), 6) chironomid larvae
22 and 7) Terrestrial prey types. Pelagic macroinvertebrates mainly consisted of
23 chironomid pupae and Chaoborus larvae, and terrestrial prey types included adult
24 stages of Ephemeroptera, Odonata and Gerridae.

1 There are several methods to measure within-population variation in diet
 2 (Bolnick et al. 2002). To assess the within-population diet variation we compared the
 3 resource use distribution of an individual to that of its population by using a
 4 proportion similarity index (PS) (Schoener 1968; Feinsinger, Spears & Poole 1981;
 5 Bolnick et al. 2002). The diet overlap between an individual i and the population is:

$$PS_i = 1 - 0.5 \sum_j |p_{ij} - q_j| = \sum_j \min(p_{ij}, q_j) \quad (1)$$

6

7 where p_{ij} is the frequency of diet category j in the individual i 's diet, and q_j is the
 8 frequency of diet category j in the population as a whole. For individuals that
 9 specialize on a single diet item j , PS_i takes on the value q_j . For individuals that
 10 consume resources in direct proportion to the population as a whole, PS_i will equal 1.
 11 The overall prevalence of individual specialization (IS) in the population can be
 12 expressed by the average PS_i value:

$$IS = \frac{1}{N} \sum_i PS_i \quad (2)$$

13

14 Note that if all individuals have the same diets then IS will be 1, indicating no
 15 individual specialization, whereas values close to 0 indicate strong individual
 16 specialization.

17 At each sampling date (May, July, August, and September), we calculated IS
 18 for two size classes (101-150 mm and 151-200 mm) of perch separately, comparing
 19 the individual diet within each size-class with the average diet of the size-class. We
 20 only calculated IS for the sampling dates and size-classes where more than five
 21 individuals of a size-class were caught.

1 The disadvantage of using *IS* as a measure of individual specialization is that
 2 when comparing two populations or the same population at two different times with
 3 different degrees of individual specialization, it is impossible to determine to what
 4 extent differences are due to changes in individual diet width or the population's diet
 5 width.

6 As an estimate of diet width of perch we used an index developed by Levins
 7 (1968). The index *B* is calculated as:

$$B = \frac{1}{\sum p_j^2} \quad (3)$$

8
 9 where p_j is the proportion of the diet that is represented by diet category j . The
 10 index has a minimum at 1.0 when only one prey type is found in the diet and a
 11 maximum at n , where n is the total number of prey categories, each representing an
 12 equal proportion of the diet. We used Levins' index to calculate diet width in two
 13 ways for both size classes of perch; 1) the average individual diet width in the size
 14 class on each sampling date, and 2) the total diet width of the size class on each
 15 sampling date. Diet width of individuals was calculated from the proportion of dry
 16 weight of each prey category in an individual's diet on each sampling date. The diet
 17 width of each size class was calculated from the average proportion of dry weight of
 18 each prey category in the size class' diet on each sampling date.

19 A problem with indices 1-3 is that they have not been weighed for the
 20 different availabilities of different resources (Schoener 1974). Weighing for resource
 21 availability is essential when analysing mechanisms behind individual and population
 22 diet breadths, i.e. whether individual and population feeding simply reflect resource
 23 availability or involve active selection. Furthermore, even if data on resource
 24 abundance is present for different resource categories as in our case, resource

1 densities cannot be directly transformed into availabilities that depend on encounter
2 rates with prey (Persson 1990; Mittelbach & Osenberg 1994). We quantified
3 encounter rates for 3 major prey categories of perch (predator-sensitive
4 macroinvertebrates, cladoceran zooplankton and YOY fish) for the two size classes
5 studied (Persson et al. 2004). These encounter rates were calculated as functions of
6 prey mass (see Persson et al. 2004 for functions and parameter values). These 3 prey
7 categories also showed the largest changes in availability with changes in perch
8 population density (Persson et al. 2000, 2003). We calculated an encounter based
9 resource diversity index using eqn 3 where p_j here stands for the mass encounter with
10 prey j in relation to total mass encounter (for parameter estimations, see Persson et al.
11 2004).

12

13 *Statistics*

14 Yearly values used in the analyses were calculated from averages of 4 samples (3 for
15 YOY perch in the diet and the condition factor). YOY perch were not hatched at the
16 first sampling occasion (May), hence in this case the average biomass in the diet was
17 based on the remaining 3 sampling occasions (July, August, September). For the
18 condition factor, May sampling estimates were excluded because in some years perch
19 had spawned at this sampling date whereas in some years they had not. Excluding the
20 May samplings for the condition measure meant that one year (1995) is missing in the
21 analysis of condition factor as very low samples were obtained at the other dates this
22 year. We tested the effect of the inclusion of vegetation in 1997 on all our models
23 with ANCOVA (vegetation as factor and density as covariate), but this effect was
24 never found to be significant ($P = 0.12-0.74$). As a result, we excluded vegetation
25 from our analysis although our conclusions would still be the same if vegetation had

1 been included. All data were LN-transformed before analysis, except for proportions
2 that were Arcsine-Square root transformed. Because our analyses are based on time
3 series, tests for autocorrelations were carried out using autoregressive-integrated
4 moving average (ARIMA) methods to test for the appropriateness of regression
5 analyses. As no significant time lags were observed in the ARIMA (all ARIMA tested
6 at lag 1; $P = 0.21-0.82$), we subsequently used ordinary regression analyses.

7

8 **Results**

9 *Population numbers and condition of perch*

10 During the study period perch population densities differed as much as 25 fold for ≥ 2
11 yr old perch and 120 fold for Age-1 perch. Three distinct phases with respect to perch
12 population numbers and structure were present during the study period. During the
13 first phase (1992-1993), high numbers of perch ≥ 2 yr old were present whereas the
14 density of Age-1 perch was low (Fig. 1). The low density of 1-year old perch was not
15 a result of low reproductive output but high cannibalism on YOY perch (Persson et al.
16 2000, 2003). This period can be classified as a period of cannibal-driven dynamics
17 with high cannibal control of victims (Claessen, De Roos & Persson 2000; Persson et
18 al. 2000, 2003). During the second phase (1994-1998), the density of ≥ 2 yr old perch
19 had decreased to low levels leading to high survival of YOY perch and consequently
20 high densities of Age-1 perch (Fig. 1). The number of perch ≥ 2 yr old decreased
21 because they had grown beyond the size that could be sustained on a long term by
22 their resource base (Persson et al. 2000). Increased per capita fecundity of the few
23 remaining perch ≥ 2 yr resulted in the production of new YOY cohorts, and these
24 YOY cohorts out competed Age-1 perch, in turn, leading to the reappearance of new
25 strong cohorts of Age-1 perch but continued low densities of perch of ≥ 2 yr for a

1 number of years (Fig. 1). The third phase (1999-2000) resembles the first phase with
2 high densities of ≥ 2 yr old perch, low survival of YOY perch and consequently low
3 densities of Age-1 perch (Fig. 1).

4 The length-mass relationships of perch 150 and 200 mm was negatively
5 correlated to the density of perch ≥ 2 yr old (correlation 150 mm; $N = 8$; $-r = 0.79$; $P =$
6 0.021 ; 200 mm; $N = 8$; $-r = 0.79$; $P = 0.021$). Condition of perch was low during the
7 first phase (1992-1993) with high numbers of perch ≥ 2 yr old reflecting a high
8 resource limitation (Fig. 2). The condition of both 150 and 200 mm perch increased
9 when the density of ≥ 2 yr old perch was reduced to low levels reflecting a decreased
10 resource limitation for the remaining ≥ 2 yr old perch. The condition of both sizes of
11 perch remained high during the whole second phase (1994-1998). The increased
12 condition of these perch was also reflected in an increased per capita growth, in turn,
13 increasing per capita fecundity (Persson et al. 2000, 2003). In 1999, the condition of
14 both sizes of perch started to decrease and continued to decrease during the third
15 phase (1999-2000).

16

17 *Resource densities*

18 The average pelagic zooplankton biomass differed between years with high and low
19 YOY survival, respectively, and was negatively correlated with YOY survival
20 (correlation between average zooplankton biomass and the density of Age-1 perch the
21 subsequent year; $N = 8$; $-r = 0.98$; $P < 0.001$). Overall, zooplankton biomass was high
22 in years with low YOY survival (1992-1993, 1999-2000), but low during the years
23 with high YOY survival (1994-1998) (Fig. 3).

24 The abundance of predator-sensitive macroinvertebrates differed between
25 years of high and low ≥ 2 yr old perch densities. A negative correlation between adult

1 perch density and density of macroinvertebrates has been shown before for the years
2 1992-1996 (Persson et al. 2000). The inclusion of data from the years 1997-2000
3 failed to find such relationship although there was a negative trend between the
4 density of ≥ 2 yr old perch and predator-sensitive macroinvertebrates (Correlation; N
5 = 9, $-r = 0.522$, $P = 0.146$) (Fig. 3). One reason for the non-significant result in our
6 study is that the strong one-year-old perch cohort in 1998 in contrast to previous one-
7 year-old cohorts survived the summer (Persson et al. 2003, 2004) and hence exerted a
8 substantial predation pressure on macroinvertebrates at the same time as they are not
9 included in the analysis of the relationship between macroinvertebrates and ≥ 2 yr old
10 perch density.

11 The encounter based resource diversity was negatively correlated with adult
12 perch density for both size classes of perch although the relationship was weaker for
13 larger perch (101-150 mm; $N = 9$, $-r = 0.701$, $P = 0.035$, an 151-200 mm; $N = 9$, $-r =$
14 0.606 , $P = 0.083$). For both size-classes, the encounter based resource diversity was
15 low during the first phase (1992-1993) and the third phase (1999-2000) (Fig. 4) when
16 the numbers of perch of ≥ 2 yr was high. During low numbers of perch of ≥ 2 yr
17 (phase two, 1994-1998) the encounter based resource diversity was high. For 101-150
18 mm perch, the increase in resource diversity in years with low numbers of perch of \geq
19 2 yr was due to a shift in dominance in encounter with zooplankton to a dominance of
20 both macroinvertebrates and YOY perch, whereas the increase for 151-200 mm perch
21 was due to a shift from a dominance in encounter with macroinvertebrates to a
22 dominance of both macroinvertebrates and YOY perch. These differences between
23 size-classes can, in turn, be related to differences in size-dependencies in encounter
24 rates on the two prey types macroinvertebrates and zooplankton (Byström & García-
25 Berthou 1999; Wahlström et al. 2000).

1

2 *Diet use by the population*

3 The diet of ≥ 2 yr old perch during years with low adult perch densities consisted
4 mainly of littoral prey types and in August and September also YOY perch. The
5 proportion of pelagic zooplankton (cladocerans and copepods) in the diet of both size
6 classes of perch was higher in years with high density of perch ≥ 2 yr old (1992-1993,
7 1999-2000) than in years with low density of perch ≥ 2 yr old (1994-1998)
8 (correlation between proportion of pelagic zooplankton and perch density; 101-150
9 mm perch, $N = 9$, $r = 0.845$, $P = 0.004$; 151-200 mm perch, $N = 9$, $r = 0.775$, $P =$
10 0.014) (Fig. 5). The proportion of YOY perch in the diet of both size classes of perch
11 decreased with perch ≥ 2 yr old density (Fig. 5), but was only significant for the 151-
12 200 mm size class (correlation; 101-150 mm perch, $N = 9$, $-r = 0.570$, $P = 0.109$; 151-
13 200 mm perch, $N = 9$, $-r = 0.704$, $P = 0.034$).

14

15 *Individual diet specialization*

16 During the study period, individual specialization (IS) varied between 0.36 and 1 for
17 the 101-150 mm size class and between 0.31 and 1 for the 151-200 mm size class.
18 The index of individual diet specialization (values of IS) for both size-classes was
19 negatively correlated with the density of perch ≥ 2 yr old (101-150 mm; $N = 9$, $-r =$
20 0.770, $P = 0.015$, 151-200 mm; $N = 9$, $-r = 0.883$, $P = 0.002$) (Fig. 6). After the major
21 die-off of ≥ 2 yr old perch in 1994, individual specialization decreased for both size-
22 classes and stayed low throughout the period of low densities of ≥ 2 yr old perch.
23 Following the increase in density of perch ≥ 2 yr old from 1998 to 2000, individual
24 specialization again increased for both size-classes reaching similar levels of
25 individual specialization as in 1992-1993 (Fig. 6).

1 The size-class diet breadth of both size-classes was positively related to the
2 density of ≥ 2 yr old perch (correlation; 101-150 mm; $N = 9$, $r = 0.763$, $P = 0.017$,
3 151-200 mm; $N = 9$, $r = 0.719$, $P = 0.029$). In the years with a high density of ≥ 2 yr
4 old perch, the size-class diet breadth of both size-classes was high (Fig. 6) related to
5 the inclusion of pelagic prey types in the diet. In contrast, in years with low perch ≥ 2
6 yr old densities, the size-class diet breadth of both size-classes was low (Fig. 6)
7 corresponding to that most perch were feeding on macroinvertebrates (May and July)
8 and YOY perch (August and September). These shifts in food resource use were
9 related to density dependent habitat use (see Persson et al. 2000 for habitat use
10 results). The individual diet breadth (not weighed for resource diversity) was
11 relatively constant for both size-classes throughout the study period (Fig. 6).
12 However, considering that the encounter based resource diversity was lower at high \geq
13 2 yr old perch densities than at low ≥ 2 yr old perch densities actually implies that
14 both individual niche breadth and population niche breadth was positively related to
15 the population density of perch ≥ 2 yr old.

16

17 **Discussion**

18 In this study we found that the degree of individual specialization increased with
19 increasing adult population size. This increase in individual specialization was due to
20 an increase in both population diet breadth and individual diet breadth (when weighed
21 for resource availability) with increasing density indicating that both individuals and
22 the population had more generalized diets at high perch densities. Based on these
23 changes on degree in specialization, it is relevant to ask why individuals specialize.
24 Some studies emphasize the importance of learning for foraging specialization (e.g.
25 Heinrich 1976; Pietrewicz & Kamil 1979; Lewis 1986), whereas most studies of

1 foraging specialization have been associated with morphological variation (Robinson
2 & Wilson 1994; Smith & Skúlason 1996; Bolnick et al. 2003). In many cases where
3 individuals of different morphologies have been found to specialize on different
4 niches, there have also been found evidence for efficiency trade-offs between
5 alternate niches (e.g. Ehlinger 1990; Smith 1987; Schluter 1993; Svanbäck & Eklöv
6 2003, see also review by Bolnick et al. 2003). For example, in many lakes perch from
7 the littoral zone are deeper bodied than and forage on littoral prey types more than
8 streamlined individuals, which are found in the pelagic zone and forage on pelagic
9 prey types (Svanbäck & Eklöv 2002, 2003; Peter Eklöv & Richard Svanbäck
10 unpublished data). This difference in morphology corresponds to functional
11 expectations for fish species that occupy these different habitats (e.g. Webb 1984). In
12 accordance with functional expectations, the difference in morphology and diet of
13 perch between the two habitats have been shown to be a reflection of morphology
14 dependent foraging efficiencies where deeper bodied individuals caught in the littoral
15 zone had higher foraging efficiency in experiments with structure. The more
16 streamlined individuals from the pelagic zone on the other hand had higher foraging
17 efficiency in open water trials (Svanbäck & Eklöv 2003).

18 Ecologists have traditionally predicted that foraging efficiency trade-offs
19 would favour generalist populations with individual specialists. Other conditions that
20 could lead to this are high food predictability, high food availability and diversity,
21 high intraspecific competition and low interspecific competition (e.g. Van Valen
22 1965; Roughgarden 1974, 1979). Many studies have shown individual specialists
23 within generalist populations (see review by Bolnick et al. 2003) where feeding
24 behaviour within a population can span those of several families (Werner & Sherry
25 1987). Most of these studies are, however, snapshots and only represent cases where

1 individual specialization has been detected (Bolnick et al. 2003). More importantly,
2 besides a study by Bryan & Larkin (1972) and Schindler, Hodgson & Kitchell (1997),
3 neither variation in individual specialization over time nor the mechanisms behind
4 temporal variation have been considered. In contrast to our study, Schindler et al.
5 (1997) failed to show any correlation between largemouth bass (*Micropterus*
6 *salmoides*, Lacépède) density and individual diet specialization over a 10-year period.
7 This discrepancy in results may be due to that the variation in bass density was only
8 three-fold whereas we found a more than twenty-fold difference in perch density.

9 The increase in individual and population diet breadth was because higher
10 densities of adult perch led to that a higher proportion of the population used the off-
11 shore habitat as the preferred prey types (YOY perch and macroinvertebrates) were
12 scarce, and consequently a higher proportion of perch included zooplankton into their
13 diet. In accordance with functional expectations, we have also found that it is the
14 more streamlined individuals that move out to the pelagic zone in Lake Abborrtjärn 3
15 (Svanbäck et al. unpublished data).

16

17 *Ecology and evolution of individual specialization*

18 It has been suggested that intra-specific competition is diversifying in the sense that
19 any individual able to efficiently use a new, exclusive resource, will experience
20 reduced intraspecific competition and have higher fitness (Roughgarden 1972). When
21 competitive pressure increases, selection to switch to new resources becomes stronger
22 so that previously suboptimal resources may confer a benefit (Wilson & Turelli 1986;
23 Bolnick 2001). Furthermore, population niche breadth is thought to represent a
24 balance between the diversifying effects of intraspecific competition, and the
25 constraints imposed by interspecific competition (Roughgarden 1972; Grant & Price

1 1981; Taper & Case 1985). Support for the different effects of inter and intra specific
2 competition on population niche breadth and individual specialization stems largely
3 from theory and from observational studies of character release and displacement
4 (Grant 1972; Robinson & Wilson 1994; Robinson & Schluter 2000). However, these
5 studies have not considered the effects of population feedbacks on niche breadths
6 mediated via resource levels. In our study, the increase in population niche breadth
7 and thus the increase in individual specialization with increasing adult density depend
8 on two mechanisms. First, with a high density of adult perch both YOY perch and
9 macroinvertebrate availabilities will be low due to heavy predation from adult perch.
10 In this situation, YOY perch availability is low in terms of energy as YOY perch are
11 cannibalised early on when they represent little energy to the cannibal. Second, the
12 low survival of YOY perch at high adult density releases pelagic zooplankton from
13 predation as adult perch are inferior foragers on zooplankton compared to YOY perch
14 (Byström & García-Berthou 1999; Wahlström et al. 2000; Persson et al. 2003). The
15 increase in zooplankton, in turn, allows adult perch to gain substantial energy from
16 them (Persson et al. 2004). Overall, the change in individual specialization and
17 population niche breadth over time is a result of variable cannibalism intensity and
18 inter-cohort competition.

19 It has been suggested that once a subset of the population starts to use a new
20 resource they are subject to selection pressures favouring new adaptations to use that
21 resource (Bolnick 2001). In our studied perch population all adult perch were found
22 within the littoral habitat at low adult densities (Persson et al. 2000). This means that
23 deeper bodied individuals will have the highest fitness in this phase (Robinson,
24 Wilson & Shea 1996; Svanbäck & Eklöv 2003). In contrast, at high adult densities the
25 same fitness scenario will be true for the ones staying in the littoral zone whereas for

1 the ones shifting to the pelagic zone, the slender-bodied individuals will have the
2 highest fitness (Svanbäck & Eklöv 2003). Thus, the fitness landscape for the adult
3 population will fluctuate with population density and depend on both density and
4 frequency of different phenotypes (Wilson & Turelli 1986). Based on a fluctuating
5 fitness landscape, we therefore suggest that selection will favour phenotypic plasticity
6 rather than genetically determined morphologies in this perch population. Conditions
7 under which polymorphic populations are plastic and do not diverge genetically
8 include among other things local extinction or colonization of competitors and
9 seasonal or between year environmental variation driving relative prey abundance
10 (Robinson & Parsons 2002). Our results indicate that internally driven population
11 dynamics could have the same effect and favour plasticity rather than genetic
12 diversification in polymorphic populations. Interestingly, it has been suggested that
13 Arctic char (*Salvelinus alpinus* L.) show more stable population dynamics (Johnson
14 1994; Claessen et al. 2002) than perch. Correspondingly, Arctic char also show much
15 more pronounced differences between different morphs compared to perch (Hindar &
16 Jonsson 1982; Parker & Johnson 1991; Svanbäck & Eklöv 2002, 2003). Though not
17 directly comparable, genetic studies also suggest that Arctic char populations may be
18 more genetically variable than perch populations (Hindar, Ryman & Ståhl 1986;
19 Magnusson & Ferguson 1987; Gerlach et al. 2001). However, the influence of
20 population dynamics on evolutionary dynamics in populations is a field that needs
21 further studies, both theoretically and empirically, before any general conclusions can
22 be drawn.

23

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12

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- 14

1 **Figure legends**

2

3 Figure 1. Changes in population density for one year old perch (means, filled circles)
4 and perch ≥ 2 years old (means \pm 95% CL, open circles) during the study period. Note
5 log scale on Y axis.

6

7 Figure 2. Changes in condition (average weight) of a 150 mm perch (solid symbols)
8 and a 200 mm perch (open symbols) in relation to the density of perch ≥ 2 yr old.

9

10 Figure 3. Changes in average resource biomasses (pelagic zooplankton and
11 macroinvertebrates) during the study period. Zooplankton biomasses are averages
12 over the growing season.

13

14 Figure 4. The relation between the density of perch ≥ 2 yr old and resource diversity.
15 Resource diversity is calculated from encounter probabilities on three resource
16 categories (zooplankton, macroinvertebrates and YOY perch). The resource diversity
17 was calculated for individuals of a size of 126 mm to represent the 101-150 mm size
18 class and 176 mm to represent the 151-200 mm size class and is based on size-specific
19 attack rates on the three resource categories (see text for more details).

20

21 Figure 5. Proportion of pelagic zooplankton (copepods and cladocerans) and YOY
22 perch in the diet of perch related to the density of perch ≥ 2 yr old for perch 101-150
23 mm (left panel) and perch 151-200 mm (right panel). Zooplankton is calculated as the
24 average of all samplings within a year, whereas YOY perch in the diet is an average
25 of the July, August and September samplings.

1

2 Figure 6. Top panels; changes in individual specialization (IS) within each size class
3 related to the density of perch ≥ 2 yr old for perch 101-150 mm (left top panel) and
4 perch 151-200 mm (right top panel). Bottom panels; changes in diet breadth for the
5 entire size classes (open symbols) and individual diet breath within each size class
6 (filled symbols) related to the density of perch ≥ 2 yr old for 100-150 mm large perch
7 and 150-200 mm large perch.

Figure 1.

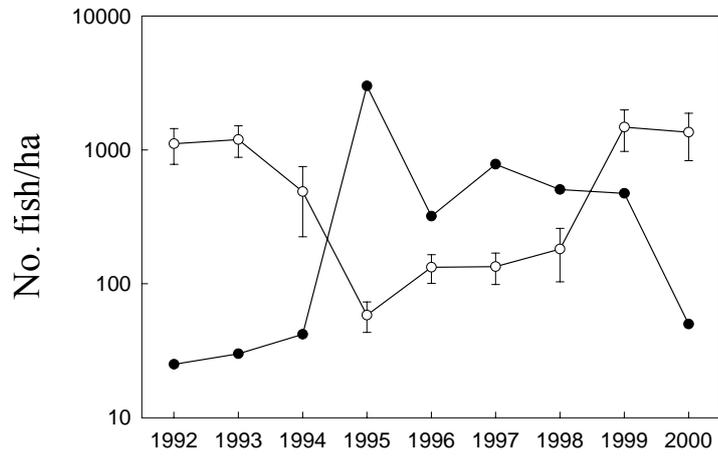


Figure 2.

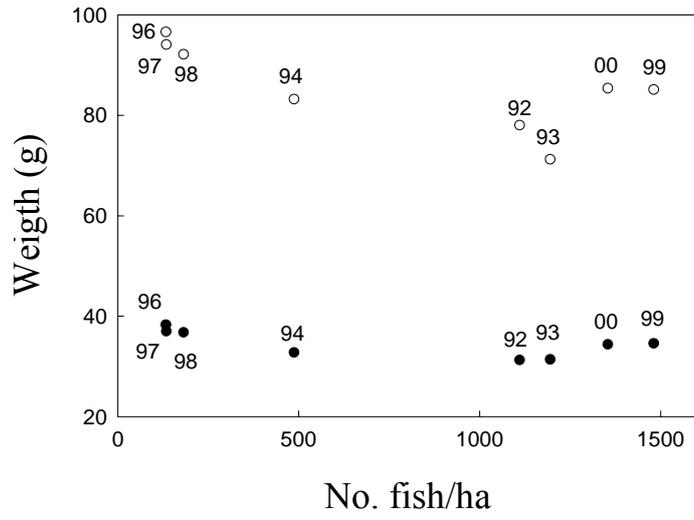


Figure 3.

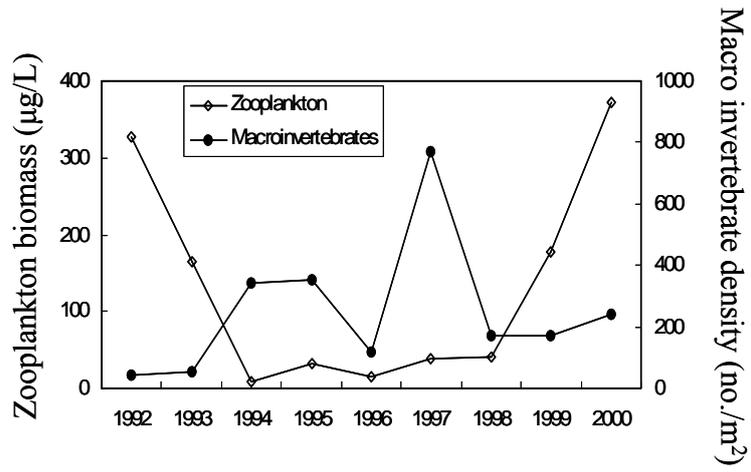


Figure 4.

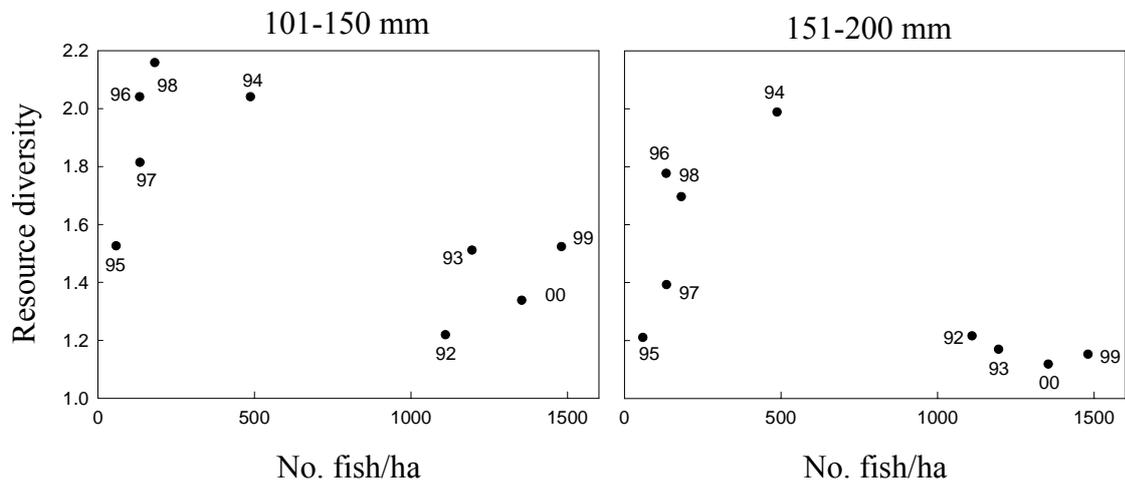


Figure 5.

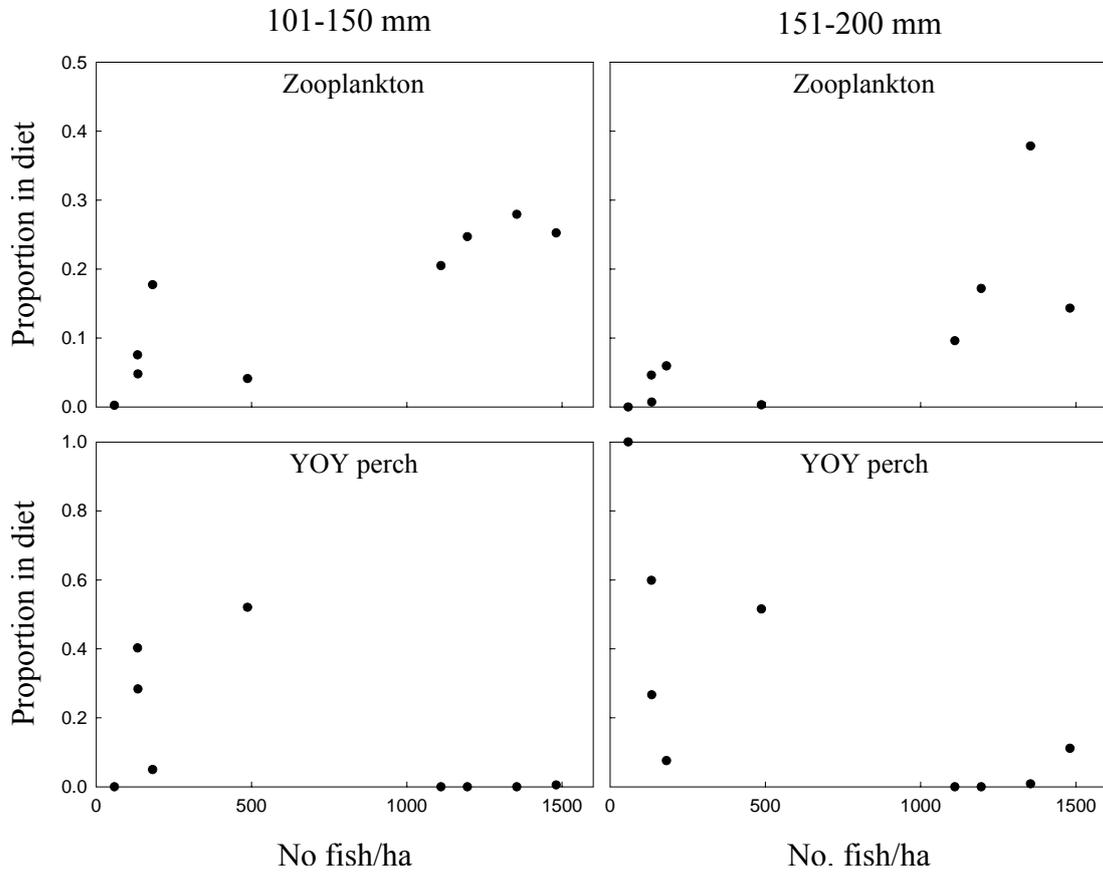


Figure 6.

