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**COEXISTENCE MEDIATED BY MICROHABITAT SEGREGATION? – AN
IN-DEPTH EXPLORATION OF A FISH INVASION**

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Running headline: Microhabitat segregation and coexistence

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1 **ABSTRACT**

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3 Vendace *Coregonus albula* has invaded the subarctic Pasvik hydrosystem, Northern
4 Norway and Russia, after being translocated from its native Finnish range into Lake
5 Inari (Finland), upstream of Pasvik. The development of the invader and the effects on
6 two native lake communities in the upstream and downstream part of the hydrosystem,
7 respectively, have been monitored since 1991. In the upstream lake location, the
8 invader relegated the native whitefish *Coregonus lavaretus* from the pelagic habitat
9 within a few years. An expected similar development in the downstream location was,
10 however, not observed. We present data on the diet and microhabitat use (vertical
11 pelagic zone) for three types of replicated situation: i) the invader versus the native
12 species; ii) upstream versus downstream lakes; and iii) early and late invasion stages
13 to explore the outcome of the competitive interactions. The use of different
14 microhabitats available within the deeper pelagic zone in the downstream location
15 was observed to have delayed the negative effects on native whitefish, possibly
16 enabling a persistent coexistence between the two species in the pelagic zone of this
17 lake.

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19 Key words: competition, *Coregonus*, interactive segregation, invasive species, lake
20 morphometry, planktivory

1 INTRODUCTION

2

3 Biological invasions and habitat loss are the primary threats to global biodiversity
4 (Diamond, 1985; Clavero & Garcia-Berthou, 2005), and examples of species
5 extirpation and extinction after the spread of non-native species into pristine
6 ecosystems are numerous worldwide (Williamson, 1996; Kitchell *et al.*, 1997; Mack
7 *et al.*, 2000). However the effects of alien species invasions are often rather complex,
8 and such case is that of vendace *Coregonus albula* L. invasions of hydrosystems of
9 northern Norway and Russia where native whitefish *Coregonus lavaretus* L. (*sensu*
10 *lato*) was previously the dominant fish species. Two morphs of the native whitefish
11 have been described: a pelagic densely-rakered (DR) morph, which forages
12 predominantly on zooplankton, and a larger benthic-dwelling sparsely-rakered (SR)
13 morph, which forages on benthic prey (Amundsen *et al.* 1999, 2004). These morphs
14 are differentiated by their genotype, morphology and ecology (Amundsen *et al.*, 2004;
15 Østbye *et al.*, 2006), potentially reflecting a process of incipient speciation seen in
16 many freshwater lakes of post-glacial areas (Schluter, 1996; Østbye *et al.*, 2006), and
17 for simplicity we will throughout this paper refer to DR whitefish as if it is a species.

18

19 The invading vendace is a specialist zooplanktivore fish species (Viljanen, 1983;
20 Hamrin, 1983). Vendace was translocated during the 1960s from its native Finnish
21 range into tributaries of Lake Inari, northern Finland (Mutenia & Salonen, 1992),
22 which lies upstream of the Pasvik hydrosystem (northern Norway and Russia). After
23 reaching high population density in Lake Inari during the second half of the 1980s
24 (Mutenia & Ahonen, 1990), vendace migrated downstream into the Pasvik
25 hydrosystem, where it first appeared in 1989 (Amundsen *et al.*, 1999). By 1993,

1 vendace dominated the pelagic areas of lakes in the upstream part of the hydrosystem,
2 and also appeared in lakes in the downstream part of the hydrosystem (Amundsen *et*
3 *al.*, 1999). A rapid increase in numbers of vendace led to increased predation pressure
4 on the zooplankton community, resulting in reduced body sizes and a shift towards
5 smaller species in the zooplankton communities (Bøhn & Amundsen, 1998). This
6 affected prey availability for the native fish species that rely on zooplankton in parts
7 or all of their life cycle, and resulted in changes in the growth, survival and life
8 history patterns of the native whitefish (Amundsen *et al.*, 1999; Bøhn & Amundsen,
9 2001, 2004) as well as of the invader (Bøhn *et al.*, 2004).

10

11 Soon after the vendace invasion in the upstream part of the Pasvik hydrosystem, DR
12 whitefish were relegated from the pelagic habitat into profundal and littoral habitats,
13 where the species rapidly diminished in numbers (Bøhn & Amundsen, 2004). There is
14 strong evidence that exploitative competition with vendace forced DR whitefish from
15 the pelagic areas by interactive segregation (Bøhn & Amundsen, 2001). The
16 suggested mechanism was the ability of vendace to forage smaller zooplankton than
17 DR whitefish, thereby keeping the zooplankton food resource at a too low level for
18 effective foraging by, and growth of, the DR whitefish (Bøhn & Amundsen, 2001).

19

20 In the downstream part of the hydrosystem, changes in the pelagic community
21 appeared to occur more slowly, and a high overlap in the diet and habitat use of
22 vendace and DR whitefish indicated that competition between the two species was
23 still negligible. This was assumed to be an effect of delayed invasion, and that DR
24 whitefish presumably could be excluded from the downstream pelagic habitats as the
25 invasion succeeded (Bøhn & Amundsen, 2001). Studies of growth and life history

1 patterns of DR whitefish have suggested that competition with vendace also began to
2 make an impact in a later invasion phase in the downstream part of the hydrosystem
3 (Bøhn & Amundsen, 2004). However, the upstream and downstream lakes studied by
4 Bøhn & Amundsen (2001) differ substantially in volume development, a physical
5 feature that is important in the structuring of lake communities (Wetzel, 2001). It is,
6 therefore, possible that the different invasion patterns may be related to this habitat
7 feature.

8

9 The success and effects of a non-native species in a recipient ecosystem is difficult
10 to predict, as several ecological interactions and higher-order interactions may be
11 involved (*e.g.* Williamson, 1999). These interactions are sometimes more or less
12 apparent, revealing themselves as direct losses through predation (*e.g.* Blackburn *et*
13 *al.*, 2004), competitive exclusion (Williamson, 1996), or losses due to spread of new
14 pathogens (*e.g.* Prenter *et al.*, 2004; Gozlan *et al.*, 2005). All of these interactions are
15 complex issues, which highlights the need for an extensive understanding of the key
16 ecological processes that may result in either extirpation or coexistence between
17 species. Community ecology and niche theory provide detailed insight into the
18 important role of ecological opportunities in determining the short term outcome of
19 invasions (Shea & Chesson, 2002; Olden *et al.*, 2006), or long term effects such as
20 speciation and adaptive radiations (Dieckmann & Doebeli, 1999; Schluter, 2001;
21 McKinnon *et al.*, 2004). The aim of the present study was to use community ecology
22 to explore further the extent of competition between the non-native vendace and
23 native whitefish in the Pasvik hydrosystem. The specific objectives were to: 1) review
24 and analyse data on the relative distribution of vendace and DR whitefish in pelagic
25 habitats from 1993 to 2006 and on the diet of the two species in 1993 (early invasion

1 phase) and 2004 (late invasion phase); and 2) assess the extent of niche overlap
2 between the two species using Schoener's dichotomous key (Schoener, 1989),
3 whereby diet and habitat use are two niche-axes frequently considered when
4 examining possible niche segregation between species. The results are discussed in
5 the view of traditional niche theory and recent developments thereof (Schoener, 1989;
6 Shea & Chesson, 2002).

7

8 MATERIAL AND METHODS

9 STUDY AREA

10 The Pasvik 'hydrosystem' (*sensu* Petts & Amoros, 1996) originates from Lake Inari,
11 Finland (69° N, 28° E), and forms the border between Norway and Russia over a
12 distance of about 120 km before entering into the Arctic Ocean (Fig. 1). The total
13 catchment area is 18 403 km². The Norwegian-Russian section of the hydrosystem has
14 a total area of 142 km², restricted to a quite narrow zone along the borderline of the
15 two countries. The mean annual water discharge is about 175 m³ s⁻¹. There are seven
16 water impoundments (hydropower reservoirs) in the hydrosystem, and these have
17 eliminated nine waterfalls and four out of five rapidly running stream sections. At
18 present, the Pasvik hydrosystem consists of a series of lakes and reservoirs linked by
19 slow-flowing river sections. The ice-free season normally lasts from May – June to
20 October – November.

21

22 Lakes Ruskebukta and Skrukkebukta in the upstream and downstream extents,
23 respectively, of the Pasvik hydrosystem were sampled either annually or biannually
24 since 1991 in order to monitor the ecological effects of the vendace invasion. These
25 lakes are henceforth referred to as the 'upstream' and 'downstream' lakes,

1 respectively, as regards the invasion time line (Fig. 1). The lakes are similar in surface
2 area, but differ in depth and volume development (Fig. 1). The native fish fauna of
3 these lakes consists of whitefish, Eurasian perch (*Perca fluviatilis* L.), northern pike
4 (*Esox lucius* L.), burbot (*Lota lota* L.), European minnow (*Phoxinus phoxinus* L.),
5 nine-spined stickleback (*Pungitius pungitius* L.), grayling (*Thymallus thymallus* L.)
6 and brown trout. Vendace and DR whitefish are the dominant pelagic zooplanktivores
7 in the Pasvik hydrosystem (Bøhn & Amundsen, 1998, 2001), whereas brown trout is
8 the dominant pelagic piscivore (Bøhn *et al.*, 2002; Jensen *et al.*, 2004, 2006). As a
9 consequence of loss of spawning habitats for the brown trout after the regulations of
10 the Pasvik River, at least 5000 brown trout (minimum fork length 25 cm) are stocked
11 annually and released into the hydrosystem in the beginning of June. About a 1000 of
12 these are released into the downstream lake, in addition there are also some natural
13 recruitment. The brown trout quickly turn to piscivory, feed mainly on vendace and
14 DR whitefish, and grow very fast (Jensen *et al.*, 2004, 2006). Perch, pike, and burbot
15 are important benthic dwelling piscivores associated with the littoral and benthic
16 profundal habitats (Bøhn *et al.*, 2002). Piscivorous waterfowl (including mergansers
17 *Mergus* spp., *Mergellus albellus*, loons *Gavia* spp., and terns *Sterna* spp.) are also
18 foraging in the lakes, but their importance in the predation on pelagic fish is not
19 known.

20

21 SAMPLING AND SAMPLE ANALYSIS

22 From a long-term dataset of multi-mesh gillnet sampling at the study sites, which
23 began in 1991, data were extracted for the eight years (1993, 1995, 1998, 2000, 2002,
24 2004, 2005, 2006) when the mesh sizes uniformly consisted of 8·0, 10·0, 12·5, 15·0,
25 18·5, 22·0, 26·0, 35·0, and 45·0 mm knot to knot (panels reaching from top to bottom

1 of the net). In the years from 1993 to 2000, 12 m deep floating gillnets with 2 m wide
2 panels for each mesh size were used. These nets were marked at 2 m depth intervals to
3 allow for depth resolution of the catches; here these catches have been combined to
4 form groups representing catches from 0—6 m and from 6—12 m depth. From 2002,
5 6 m deep floating nets with 5 m wide panels were used, without finer-grained depth
6 resolution. These nets also included 6 mm mesh size, but catches from the 6 mm mesh
7 were excluded from this study for comparison consistency with earlier years. By
8 attaching lead weights to the bottom of the floating nets, and sinking them to the
9 desired depth with a line between the weights and floatation, the 6 m deep nets were
10 also used to explore the pelagic fish community at deeper open water habitats in the
11 downstream lake. This was first carried out in 2004 at four depth intervals; 0—6 m,
12 8—14 m, 16—22 m, and 24—30 m. In 2005 and 2006, this was reduced to three
13 depth intervals; 0—6 m, 10—16 m, and 20—26 m. For simplicity, we refer to the 0—
14 6 m depth interval as the epipelagic microhabitat, but this should not be confused with
15 the term epilimnion (which is the stratum above the thermocline during stratified
16 periods; Wetzel, 2001). The term ‘intermediate depths’ refers to the following depth
17 intervals: 6—12 m, 8—14 m, and 10—16 m. The nets were set for 12 hours from the
18 afternoon until the morning during mid-September. Species and fork length (L_F)
19 distributions were established from the gillnet catches. Catch per unit effort (CPUE)
20 was calculated as number of fish caught per 100 m² nets per night (12 hours), and
21 used as density indices. Stomachs from a random sub-sample of fish were preserved
22 on ethanol in the field, and later analyzed in the lab.

23

24 Prey items were identified and categorized into 13 groups based on taxonomy and/or
25 typical habitat of the prey item (Bosminidae, Daphnidae, Holopedidae, Polyphemidae,

1 Leptodoridae, Cyclopidae, Calanoidae, Chydoridae, Mollusca, benthic insect larvae,
2 pupae (Chironomidae and Trichoptera), surface insects, and Hydracarina). Stomach
3 fullness was subjectively determined on a scale from 0 (empty) to 100 % (full), and
4 the contribution of each prey category to the total stomach fullness was determined in
5 the same manner. Pair-wise comparisons of diets were made between species in each
6 lake, between lakes within each fish species, and within species between early and
7 late invasion phase. The degree of diet overlap D was calculated using Schoener's
8 index, expressed as percentage (Schoener, 1970):

9

$$10 \quad D = 100 \left(1 - 0.5 \sum_{i=1}^n |p_{x,i} - p_{y,i}| \right)$$

11

12 where $p_{x,i}$ denotes the mean proportion of diet category i in the stomachs of species x ,
13 and $p_{y,i}$ the same for species y . For between-species comparisons x and y were DR
14 whitefish and vendace, respectively. Using Schoener (1989)'s dichotomous
15 competition key, and assuming that competition does occur, two possible outcomes
16 were expected. Firstly, if competition was high, then niche overlap in fine-grained
17 dimensions (diet, microhabitat) should be high, or overlap in coarse-grained
18 dimensions (macrohabitat) should be low. Secondly, and conversely, if competition
19 was low, then niche overlap in fine-grained dimensions should be low and overlap in
20 coarse-grained dimensions should be high. Here, we treated vertical position in the
21 water column as a fine-grained environment dimension (microhabitat), whereas the
22 littoral zone, the benthic-associated profundal zone, and the overall pelagic zone
23 comprised a coarse-grained environment dimension (macrohabitat). Within the fine-
24 grained environment, the prey species may be more or less randomly distributed, and

1 interaction strengths may vary as a consequence of environmental gradients (e.g. light
2 intensity, temperature). The coarse-grained environments differ in prey and predator
3 species composition, and hence differ in the set of species interactions.

4
5 Three pairs of comparisons were undertaken using the niche overlap data: i) the
6 invader versus the native species; ii) upstream versus downstream lakes; and iii) early
7 and late succession stages of the invasion to explore the outcome of the competitive
8 interactions between invading vendace and native DR whitefish. These comparisons
9 were undertaken separately for each lake, and for early and late invasion phase. For
10 the comparisons of DR whitefish between lakes, x and y were DR whitefish in the
11 upstream and downstream lake, respectively, and likewise for vendace. Separate
12 comparisons were made for the early and late invasion phase. When comparing DR
13 whitefish between early and late invasion phase, x and y were DR whitefish in 1993
14 and 2004, respectively, and likewise for vendace. Again, comparisons were made
15 separately for each lake.

16
17 **RESULTS**

18
19 The gillnets captured a total of 1772 vendace and 341 DR whitefish in the upstream
20 lake from 1993 to 2006. Vendace dominated the catches from 0—6 m and 6—12 m in
21 all years, except for 1995 when there were also substantial catches of DR whitefish
22 (Fig. 2). The pattern of vendace dominance was evident although density in terms of
23 CPUE varied by more than an order of magnitude for both species, with notable peaks
24 in 1998 and 2004 for vendace. In the downstream lake, 1502 vendace and 2050 DR
25 whitefish were captured. Vendace increased in density through the study period, and

1 replaced the DR whitefish as the dominant species in the epipelagic microhabitat (0—
2 6 m depth) from 2004 and onwards (Fig. 2). DR whitefish decreased in density in the
3 epipelagic microhabitat, however at intermediate depths (6—16 m depth interval) DR
4 whitefish kept being the dominant species throughout the study period, with fairly
5 similar densities in early and late invasion phase. The catches of DR whitefish were
6 consistently largest at this depth interval. In both lakes, median L_F was between 10
7 and 12 cm for both vendace and DR whitefish.

8

9 In the early invasion phase of the downstream lake, vendace occurred in higher
10 densities at intermediate depths than in the epipelagic microhabitat (Fig. 2). By the
11 late invasion phase, in contrast, vendace occurred in similar densities in the epipelagic
12 microhabitat as at intermediate depths, implying that there was a shift in the relative
13 distribution of vendace towards the surface from early to late invasion phase.

14 Combining the catches from 0—16 m (excluding deeper catches due to lack of
15 comparisons in early invasion phase), there was a trend of overall increasing vendace
16 abundance, increasing total abundance of vendace and DR whitefish combined, and
17 decreasing DR whitefish abundance from early to late invasion phase. However, this
18 decreasing trend in DR abundance depended solely on the 1993 catches. At depths
19 deeper than 16 m, the species generally contributed more or less equally to the
20 catches, but in lower numbers. The density variations for the species combined was
21 lower in the downstream lake as compared to the upstream lake (Fig. 2).

22

23 Dietary analysis of 174 vendace and 91 DR whitefish stomachs from the upstream
24 lake, and 139 vendace and 164 DR whitefish stomachs from the downstream lake
25 revealed that DR whitefish had stomach fullness levels as high or higher than vendace

1 in the upstream lake both in the early and late invasion phases. However, stomach
2 contents were very different, with DR whitefish consuming zooplankton to a smaller
3 degree than vendace (Fig. 3a). This was reflected also in the diet overlap, with a low
4 overlap between the species both in the early (1993) and late (2004) invasion phases
5 (Fig. 4a). In the downstream lake, the stomach contents of the two species differed
6 much less. Zooplankton was the most important prey type for both vendace and DR
7 whitefish, but the latter fish species had a more diverse diet (Fig. 3). Dietary overlap
8 between the species was consistently high in early and late invasion phases of the
9 downstream lake, at all depths (Fig. 4a).

10

11 Within species, dietary overlap between lakes was much higher for vendace than for
12 DR whitefish (Fig. 4b). This reflected the consistently high proportion of zooplankton
13 taken by vendace in both lakes, and the large proportion of benthos and insects in the
14 diet of upstream DR whitefish, which contrasts the high proportion of zooplankton
15 taken by downstream DR whitefish. In 1993, stomach fullness of both species was
16 highest at intermediate depths. In 2004, downstream vendace had its highest stomach
17 fullness in the epipelagic microhabitat, whereas DR whitefish stomach fullness was
18 still highest at intermediate depths. Both species had a reduction in stomach fullness
19 from 1993 to 2004. However, this reduction was much larger for vendace than for DR
20 whitefish (Fig. 3b). The within species diet overlap was high from early to late
21 invasion phase for both species and lakes (Fig. 4c), perhaps with the exception of the
22 upstream lake where DR whitefish diet overlap was reduced substantially by relative
23 changes within the insect prey categories.

24

25

DISCUSSION

Our results have confirmed that the pelagic dominance of vendace observed in the upstream lake in the early invasion phase continued for 13 years and that DR whitefish in low density continue to coexist with vendace in this lake. Although the proportion of DR whitefish in the catches was consistently a bit higher at 6—12 m than at 0—6 m depth, there was no clear segregation from vendace in microhabitat use. The dietary data for both species in the upstream lake in late invasion phase were very similar to those in the early invasion phase, *i.e.* low stomach fullness, similar composition between years, and limited overlap. Indeed, there was considerable diet overlap between early and late invasion phase in the upstream lake, and the observed differences were associated with relative dietary changes within the zooplankton categories or within the insect categories, rather than switching between the broader zooplankton, benthos and insect dietary categories. The inclusion of benthos in the diet moreover indicated that the DR whitefish captured in the pelagic macrohabitat spent a substantial proportion of their time foraging in benthic macrohabitats. Thus, in the upstream lake, the overall pattern of interactive segregation in diet and macrohabitat use between vendace and DR whitefish in the early invasion phase, described also by Bøhn & Amundsen (2001), seemed to be more or less replicated 11 years and a few vendace generations later. This suggests that the competition between these two species was still strong (cf. Schoener, 1989; Bøhn & Amundsen, 2001).

In the early invasion phase, vendace densities in the downstream lake were low, and there were no indications of competition between the vendace and DR whitefish populations (Bøhn & Amundsen, 2001). During the last half of the 1990s, however,

1 reduced individual growth rates and altered life history patterns suggested that both
2 the invader and the native species began to suffer from increased competition,
3 although vendace densities were relatively stable in contrast to declines in DR
4 whitefish density (Bøhn & Amundsen, 2004; Bøhn *et al.*, 2004). The present study
5 documents that stomach fullness was reduced in both species in the late invasion
6 phase, relative to the early invasion phase, and this is another indication that the
7 resource availability had been reduced. Vendace gradually monopolized the
8 epipelagic microhabitat (0—6 m depth), but DR whitefish persisted in considerably
9 higher numbers at intermediate depths (6—16 m) throughout the study period. By the
10 late invasion phase, the two species thus showed a clear interactive segregation in
11 microhabitat, with the inferior competitor DR whitefish being displaced from the
12 epipelagic microhabitat. According to Schoener (1989), this is an indication of low
13 inter-specific competition. On the other hand, the consistently high dietary overlap
14 between the species at all depths is an indication of strong inter-specific competition
15 (Schoener, 1989). From these somewhat contrasting findings in the downstream lake
16 (*i.e.* increased vendace abundance, consistently high dietary overlap, altered DR
17 whitefish microhabitat use, reduced individual growth rates in both species), we
18 conclude that the two species compete and that the inter-specific competition was of
19 intermediate strength.

20

21 How inferior is DR whitefish in its inter-specific competition with vendace, and
22 under what conditions? These are timely questions, since there appear to be
23 substantial differences in the progress of the vendace invasion between the upstream
24 and downstream lakes. This is also an important aspect in the understanding and
25 prediction of the further development of the invasion. Bøhn & Amundsen (2001) have

1 demonstrated that vendace is the superior zooplankton forager in the upstream lake,
2 confirming reports elsewhere of vendace as a highly specialized zooplankton forager
3 (Svärdson, 1976; Viljanen, 1983; Hamrin, 1983). However, the overall developments
4 in the downstream lake suggest a less clear-cut asymmetry in competitive ability
5 between the species. It could even be argued that DR whitefish performed best at
6 intermediate depths where the species: 1) occurred consistently in higher density than
7 in the epipelagic microhabitat, 2) did not decrease in density between the early and
8 late invasion phases, 3) had its highest stomach fullness during both the early and late
9 invasion phases, and 4) had higher stomach fullness values than vendace during the
10 late invasion phase. Vendace, on the other hand, seemed to have the competitive edge
11 in the epipelagic microhabitat, where they had higher levels of stomach fullness than
12 DR whitefish in both early and late invasion phase, and by the late invasion phase
13 vendace had largely replaced DR whitefish in the epipelagic microhabitat. The shift in
14 vendace relative depth distribution towards the surface between the early and late
15 invasion phases, as well as the congruent substantial decrease in vendace stomach
16 fullness at intermediate depths in late invasion phase, indicate a shift in the optimal
17 habitat use of vendace towards the epipelagic microhabitat due to competitive
18 interactions with DR whitefish. Although vendace also increased in density at
19 intermediate depths between the early and late invasion phases, this increase was
20 much smaller than that in the epipelagic microhabitat. The DR whitefish population in
21 the downstream lake therefore appears to have demonstrated considerable biological
22 resistance to the vendace invasion.

23

24 Recent developments in community ecology, and in particular niche theory, provide
25 a predictive framework for invasion ecology for defining conditions that promote

1 invasions in terms of resources, natural enemies, the physical environment,
2 interactions between these factors, and how these features vary in time and space
3 (Shea & Chesson, 2002). According to this theory, a species' ecological niche is the
4 species' response to a point in niche space, and the effect of the species at each point
5 (Chesson, 2000). Tilman's R^* can be employed as the estimator of the resource level
6 at which a species' net per capita growth rate equals zero, *i.e.* the species' gains (the
7 response of the species to the resource) will equal its maintenance requirements
8 (Tilman, 1982; Chesson, 2000; Shea & Chesson, 2002). Thus, if the potential invader
9 has a lower R^* than the native competitor, then there will be an opportunity for the
10 species to create a niche and invasion will ensue (Shea & Chesson, 2002). In the
11 present study, vendace have clearly been offered a 'niche opportunity', being able to
12 exploit smaller zooplankton more effectively than DR whitefish (Bøhn & Amundsen,
13 2001). The invader's niche response was the rapid establishment of a high density
14 population, especially in the upstream parts (Amundsen *et al.*, 1999; Bøhn &
15 Amundsen, 2001). The niche effect of the invader was a reduction in zooplankton size
16 and an alteration of zooplankton composition (Bøhn & Amundsen, 1998; Bøhn &
17 Amundsen, 2001), and a support of piscivore predators (Bøhn *et al.*, 2002; Jensen *et*
18 *al.*, 2004, 2006). Another aspect of niche opportunity, which potentially facilitated
19 invasion, was the natural enemy escape opportunity, such as predators, parasites and
20 pathogens (Shea & Chesson, 2002). There is a wide array of piscivorous fishes and
21 birds that prey on vendace in the Pasvik hydrosystem, and all vendace size classes
22 may be vulnerable to predation from brown trout (Bøhn *et al.*, 2002; Jensen *et al.*,
23 2004). However, the invading vendace have a lower parasite load than the native DR
24 whitefish (P.A. Amundsen, unpublished), potentially reducing the maintenance
25 requirements for vendace as compared to DR whitefish.

1

2 An important question regarding the invading vendace is what its superiority as a
3 zooplankton forager means for the future of the Pasvik hydrosystem. The basis of
4 coexistence in the upstream lake seems primarily to be the segregation of vendace and
5 native DR whitefish in diet and in macrohabitat use, which are both stabilizing
6 mechanisms for coexistence (Chesson, 2000). Vendace is an obligate planktivore and
7 relies heavily on the zooplankton resource (strong niche response), which it
8 suppresses through its effective foraging (strong niche effect), creating a density-
9 dependent feedback loop (cf. Chesson, 2000). The stabilizing effects of segregation
10 and the feedback loop could be counteracted by large asymmetry in density (cf.
11 Chesson, 2000). As an example, even if individual vendace had a very low proportion
12 of insects and benthic prey in their diet, the cumulative consumption of a dense
13 vendace population could reduce insect and benthic prey to a level too low for DR
14 whitefish existence. This seems unlikely, though, given the almost exclusive
15 zooplankton diet of vendace. But DR whitefish also face new competitors for its new
16 dietary niche, such as SR whitefish and perch. Thus, the question of coexistence
17 between DR whitefish and vendace in the upstream lake depends on the success of
18 DR whitefish in its new resource base (cf. Bøhn *et al.* 2007), and on its potential
19 losses to predation and further indirect interactions (Bøhn *et al.*, 2002; Amundsen *et*
20 *al.*, 2003).

21

22 There seem to be qualitative differences between the upstream and downstream lake
23 ecosystems that have contributed to the relatively larger invasion resistance to, and the
24 different invasion progress of, vendace observed in the downstream lake. The most
25 obvious feature differing between the two lakes is volume development. The lakes are

1 of similar area, but the depth and volume of the pelagic area is much lower in the
2 upstream than in the downstream lake. Thus, the ability of DR whitefish to segregate
3 in microhabitat has been very limited in the upstream lake. In the downstream lake,
4 the existence of a large profundal (dark) zone provides an extensive refuge for
5 zooplankton from intensified visual predation, and for DR whitefish a refuge both
6 from competition with vendace and from visual predators. The role of the profundal
7 as a zooplankton refuge is supported by less prominent changes in zooplankton
8 community structure than in the upstream lake (Bøhn & Amundsen, 1998; A.
9 Siwertsson & P.A. Amundsen, unpublished data). The relatively greater availability of
10 zooplankton sizes suitable to DR whitefish implies that the resource effect of vendace
11 is less severe in the downstream lake, and thus a reduced interspecific competition can
12 be inferred.

13
14 According to Chesson (2000), intra-specific competition must be greater than
15 interspecific competition for stable coexistence to occur, and it remains unclear
16 whether this occurs in the downstream lake. The apparently more symmetric
17 competition between vendace and DR whitefish in the larger pelagic volume of the
18 downstream lake may have implied that the DR whitefish population in this lake was
19 better adapted to a strictly zooplanktivorous life history. If DR whitefish performs
20 slightly better than vendace at intermediate depths, with vendace best suited to the
21 epipelagic microhabitat, then competitive symmetry would change with depth. This
22 remains speculative, but such a relationship could lead to stronger intraspecific than
23 interspecific competition within each species' predominant depth utilization. If so,
24 then the criteria for stabilized coexistence would be met, but could be counteracted by
25 any large asymmetry in vendace and DR whitefish densities as long as the species

1 have more or less identical diets (cf. Chesson, 2000). The stabilizing role of the
2 observed segregation in microhabitat will be of either transitory or persistent nature.

3
4 DR whitefish residing at intermediate depths largely escape from predation by
5 visually-oriented predators, thereby reducing its maintenance requirements.
6 Piscivorous brown trout is probably the most important pelagic predator in the Pasvik
7 hydrosystem, and the species occurs in relatively high densities due to the annual
8 stocking of large-sized specimens. The composition of fish species in the brown
9 trout's diet reflects that of the available prey fishes in the epipelagic microhabitat
10 (Jensen *et al.*, 2004, 2006), and in the late invasion phase, brown trout diet was
11 dominated by vendace (K.Ø. Gjelland & P.A. Amundsen, unpublished). Such
12 frequency-dependent prey selection by brown trout will have a stabilizing effect on
13 vendace and DR whitefish coexistence (Chesson, 2000). The higher metabolic costs
14 associated with the warmer epipelagic microhabitat implies a higher Tilman's R^* , and
15 although anabolic processes at deeper and colder depths would be reduced, this would
16 affect both DR whitefish and vendace residing in the same microhabitat. Hence, when
17 vendace invaded and depressed the resource level, the segregation of DR whitefish to
18 deeper, colder microhabitats was possibly a behavioural response in order to reduce
19 the maintenance requirements both in terms of metabolic costs and predation
20 mortality (cf. Shea & Chesson 2002).

21
22 In conclusion, 17 years after its first known appearance, non-native vendace appears
23 to have succeeded in invading the Pasvik hydrosystem. The species now dominates
24 the epipelagic microhabitat (0—6 m depth) in lakes in both the upstream and
25 downstream parts of the hydrosystem, and has relegated the native DR whitefish to

1 other microhabitats. Vendace is a more effective zooplankton forager than DR
2 whitefish, at least in the epipelagic microhabitats of the hydrosystem. The invasion
3 process in the upstream and downstream lakes has differed considerably, with rapid
4 colonization upstream (probably due to low biotic resistance in the DR whitefish and
5 zooplankton populations) and slow colonization downstream (probably due to greater
6 lake volume and thus greater zooplankton refugia). The question of coexistence
7 between DR whitefish and vendace in the shallower upstream lake seems to depend
8 on the success of DR whitefish in its new macrohabitat, whereas in the deeper
9 downstream lake it is facilitated by microhabitat (depth) segregation within the
10 pelagic environment. Our data shows clear microhabitat segregation between the
11 interacting zooplanktivores, potentially resulting in further coexistence mediated by
12 reduced interaction strength.

13

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- 4

FIGURE CAPTIONS:

1

2

3 Fig. 1: Geographical location and bathymetric maps of the upstream and downstream
4 lakes in the Pasvik hydrosystem (northern Norway and Russia), with hypsographic
5 curves of the lake areas at different depths in the lower left-hand corner of the figure.

6

7 Fig. 2: Relative contribution of native DR whitefish and introduced vendace in the
8 catches from 1993 to 2006 in the a) upstream lake and b) downstream lakes of the
9 Pasvik hydrosystem. The pie slices are labelled with the CPUE-values. \triangle DR
10 whitefish, \blacktriangle vendace.

11

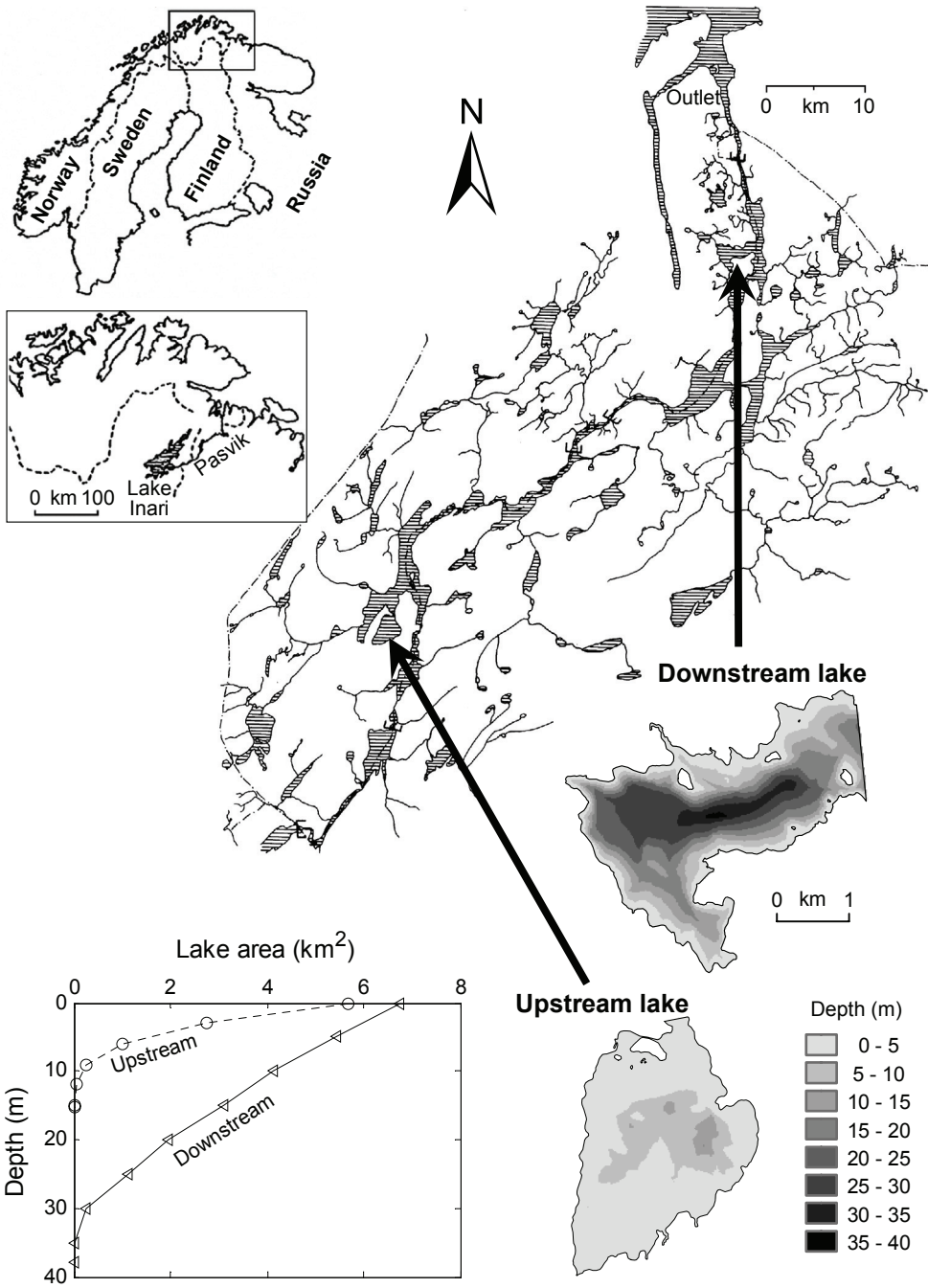
12 Fig. 3: Stomach fullness with relative contribution of zooplankton (\blacksquare), benthic prey
13 (\square), and surface insects and insect pupae (\boxplus) in the diet of native DR whitefish and
14 introduced vendace in the a) upstream and b) downstream lakes of the Pasvik
15 hydrosystem in the early (1993) and late (2004) invasion phase.

16

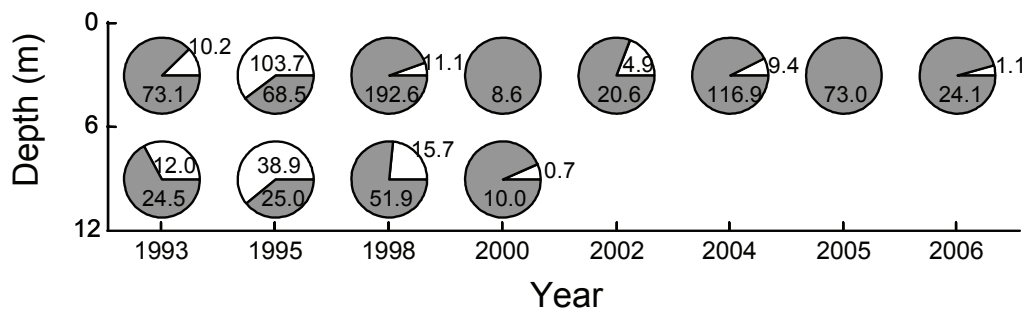
17 Fig. 4: Dietary overlap (Schoeners D) between a) species (native DR whitefish and
18 introduced vendace), b) lakes (Pasvik hydrosystem), and c) early and late invasion
19 phases (1993 and 2004, respectively). Shades of grey indicate depth intervals used in
20 comparisons (the catches at 8-14 m in 2004 is indicated as 6-12 m for simplicity): \square
21 0-6 m, \square 6-12 m, \blacksquare 16-22 m, \blacksquare 24-30 m.

22

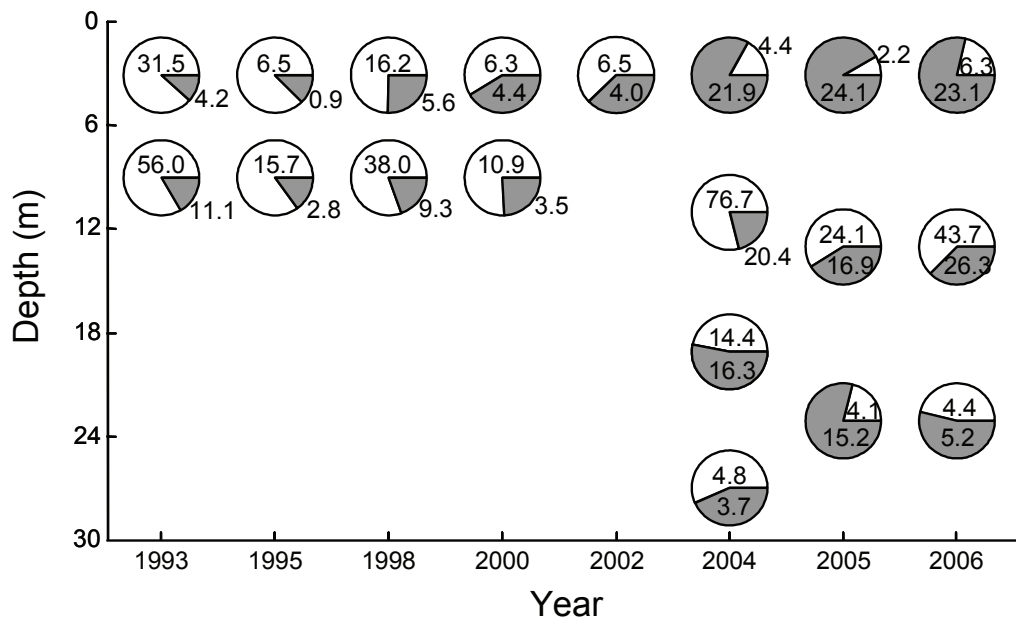
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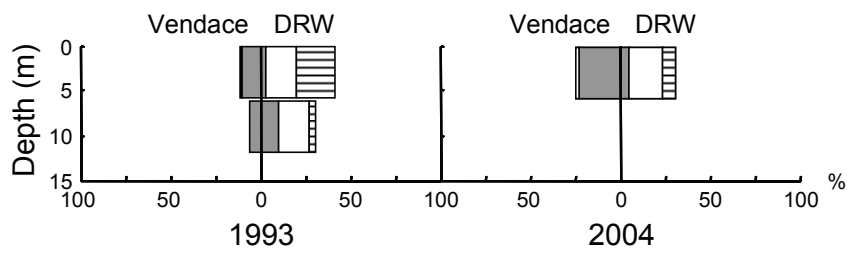
a) Upstream



b) Downstream



a) Upstream



b) Downstream

