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Invasion-mediated changes in the population biology of a dimorphic whitefish *Coregonus lavaretus* population

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Population biology changes in native dimorphic whitefish *Coregonus lavaretus* were studied over a decade in the subarctic Pasvik watercourse, where large biotic changes occurred due to an invasion by vendace *C. albula*. Although initially recorded in the upstream part of the watercourse, where it is now the dominant pelagic species, the vendace subsequently also colonised the downstream area. We hypothesized that the impact of the invader would affect the population biology (density, habitat choice, growth, size- and age-structure and size and age at maturation) of the native whitefish populations, especially upstream in the watercourse, late in the invasion phase, and in the pelagic whitefish morph. Strong effects from the invading vendace were observed on the native dimorphic whitefish populations. Effects on the densely-rakered whitefish, which are ecologically similar to vendace, ranged from numerical responses (strong density decline in the population), habitat use (shift from pelagic to littoral) and individual growth (significant growth reduction in zooplanktivorous life stages). For the benthic sparsely-rakered whitefish, effects were more restricted and recorded mainly on growth.

Introduction

Introductions and establishment of exotic invasive (or "alien") species are among the major global threats to native biodiversity (Diamond 1985, Glowka *et al.* 1994, Williamson 1996). Freshwater ecosystems are among the most susceptible to invading species (Mills *et al.* 1993, Cohen & Carlton 1998), and the rate of introductions is continually increasing due to both intentional and accidental releases of exotic species (Welcomme 1992, Moyle 1999). In spite of the recent research interest in the impact of introductions, several aspects of invasions and species establishment are poorly understood. For example, the population dynamics and life history changes of both invaders and species in the receiving community are only weakly documented (Williamson 1999, but *see* Bøhn 2002).

Fish have indeterminate growth (Wootton 1998) and changes in life history traits are particularly relevant in taxa that may respond both numerically (on the population level) and/or in somatic growth (on the individual level). Long time series covering the complete invasion and establishment process may contribute to the understanding of ecosystem responses to invasions, thereby helping humans to respond to artificially high rates of species transfer (e.g., Mooney & Hobbs 2000).

This paper documents life history changes in two native fish morphs of whitefish *Coregonus lavaretus* (a zooplanktivorous pelagic morph and a benthivorous littoral morph) during the invasion and establishment of the ecologically similar vendace (*Coregonus albula*), in the Pasvik watercourse. The vendace population has become the dominant species in the upstream part of the watercourse, and since 1990 has expanded extensively downstream (Amundsen *et al.* 1999, Bøhn 2002). As a *predator* it has grazed down the zooplankton, strongly reducing the edible food resources in the pelagic habitat upstream in the watercourse (Bøhn & Amundsen 1998, Bøhn & Amundsen 2001). Thereby, as the superior pelagic *competitor*, it has also excluded the native pelagic whitefish from its zooplanktivore food niche (Bøhn & Amundsen 2001). In addition, as a small-sized fish with very high population density upstream, the vendace has become the most frequent *prey* of pelagic piscivorous fish (Bøhn *et al.* 2002). In the downstream part of the watercourse, the establishment of vendace has been delayed and the present situation resembles earlier stages of the process in the upstream part.

Here we contrast the population biology of the whitefish morphs between early and late invasion phase, upstream and downstream in the watercourse, respectively. Along the time and space gradients of the vendace invasion, it has been possible to study the population biology of the two native whitefish morphs under low impact conditions (early invasion phase) and high impact conditions (late invasion phase). During the early invasion phase (low density of vendace, relatively abundant pelagic food resources and presumably low interspecific competition), we expected the two whitefish morphs to display a density and life history close to that of the undisturbed pre-invasion situation. During the late invasion phase (higher density of vendace, relatively scarce pelagic food resources and presumably higher competition), the density and life history of whitefish is expected to change according to the new biotic conditions. This impact is expected to increase with the density of vendace, and the pelagic nature of this species suggests a stronger impact on the pelagic densely-rakered whitefish as compared with the more benthic sparsely-rakered morph, due to the higher ecological overlap of the former.

We hypothesized that the impact of the invader would affect the population biology of the native whitefish morphs in the following manner:

H1: Density declines.
H2: Altered use of habitat.
H3: Changes in size and age structure.
H4: Changes in size and age at maturation.

These effects should further be expected to be of greater importance upstream in the watercourse, late in the invasion phase, and in the pelagic whitefish morph.

Study area and fish community

Three countries share the Pasvik River watercourse. It originates in lake Inari (1102 km^2) in Finland, runs into Russia and then forms the border between Norway and Russia over a distance of about 120 km (Fig. 1). The Norwegian–Russian part of the watercourse has a total area of 142 km^2, a catchment area of 18 404 km^2 and a mean annual water flow of about 175 m^3 s^{-1}. There is a total of seven water impoundments (hydropower reservoirs) in this part of the watercourse. Most rapids and waterfalls have disappeared such that the river system today consists primarily of lakes and reservoirs linked by slow-flowing river sections. The bedrock in the region is dominated by gneiss, and surrounding forest is mainly birch (*Betula* sp.) and pine (*Pinus sylvestris*) with significant areas of *Sphagnum* bogs. Annual mean air temperature is –3 °C and minimum and maximum monthly mean temperatures are –13.5 °C (January) and +14.0 °C (July), respectively. The annual mean precipitation is 358 mm. The water level fluctuations are small, usually less than 80 cm. The ice-free season in the lakes and reservoirs lasts from May/June to October/November. The lakes and reservoirs are oligotrophic with relatively humic waters with a Secchi depth range from 2 to 6 m.

Two lake localities situated about 50 km apart in the watercourse were investigated: Ruskebukta in the upstream part (henceforth called the upstream lake), and Skrukkebukta downstream (the downstream lake) (Fig. 1). Both basins are located adjacent to the main path of the Pasvik watercourse and have negligible water flow. The upstream lake (69°13´N, 29°14´E; 52 m above sea level) has an area of 5.3 km^2 and a maximum depth of 15 m. The downstream lake (69°33´N, 30°7´E; 21 m above sea level) has an area of 6.6 km^2 and a maximum depth of 19 m. The water chemistry of the two lakes is similar (Langeland 1993).

Altogether, 15 species of fish have been recorded in the Pasvik watercourse. The two lake localities have similar fish communities, with whitefish, perch (*Perca fluviatilis*), pike (*Esox lucius*), burbot (*Lota lota*) and brown trout (*Salmo trutta*) being the most abundant native species. The whitefish occur as two morphs, differentiated by the morphology and number of gill rakers, here referred to as densely- and sparsely-rakered whitefish. The densely-rakered whitefish have numerous long and narrowly spaced gill rakers (mean number 33.0), whereas the sparsely-rakered form has fewer, shorter and more widely spaced rakers (mean number 23.1) (Amundsen *et al*. 1999, 2004). According to Reshetnikov (1980), the two forms may be referred to as *Coregonus lavaretus mediospinatus* (densely-rakered whitefish) and *C. lavaretus pidschian* (sparsely-rakered), whereas Svärdson (1976) described these forms as two different species; *C. lavaretus* and *C. nasus* respectively. The densely-rakered whitefish usually occupy the pelagic zone, feeding predominantly on zooplankton, whereas the sparsely-rakered form feeds mainly on zoobenthos in littoral and profundal habitats (Amundsen 1988).

The natural distribution of vendace in Scandinavia and Finland is restricted to the low altitude watercourses which at present or previously drained into the Baltic Sea (Svärdson 1966, Rask *et al*. 2000). Due to its postglacial immigration history, the species was originally absent from freshwater systems in the northern and western parts of this region. However, during the 1950s and 1960s, vendace was deliberately introduced into upstream tributary river systems of Lake Inari in northern Finland (Mutenia & Salonen 1992). As might be expected, the vendace was later observed in lake Inari (first observation in 1973), building up high population densities and commercial fisheries during the late 1980s (Mutenia & Salonen 1994). Lake Inari drains into the Pasvik watercourse and the first specimens of vendace were caught in the upstream part of the river system in 1989. In the downstream part of the Pasvik system, the first vendace were caught in 1993 (Bøhn & Amundsen 1998).

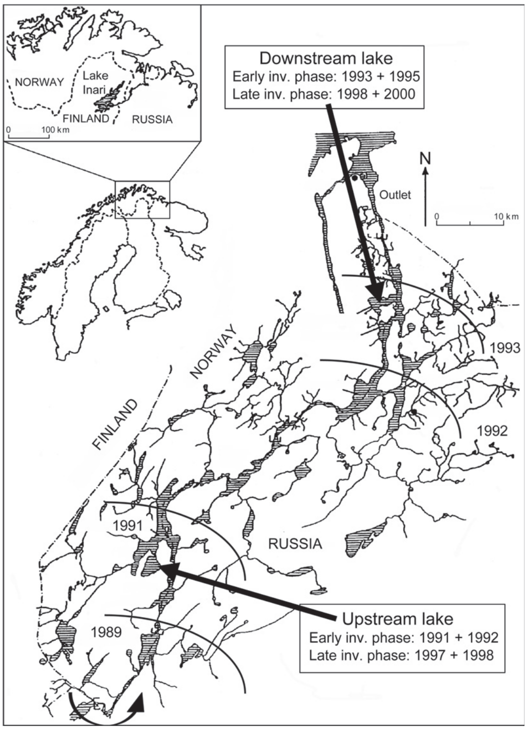

Fig. 1. The Pasvik watercourse, with arrows indicating the upstream and downstream sampling sites and arcs indicating the downstream limits of vendace distributions in 1989, 1991, 1992 and 1993.

Methods

Sampling for the present study was performed intermittently during the ice-free season between 1991 and 2000. Sampling took place in June/July, August and September 1991, 1993, 1998 and 2000, in July and September 1992, and in September 1995 and 1997. Gill nets with mesh sizes of 8, 10, 12.5, 15, 18.5, 22, 26, 35 and 45 mm (knot to knot) were used in the pelagic habitat. Pelagic gill nets consisted of two differ-

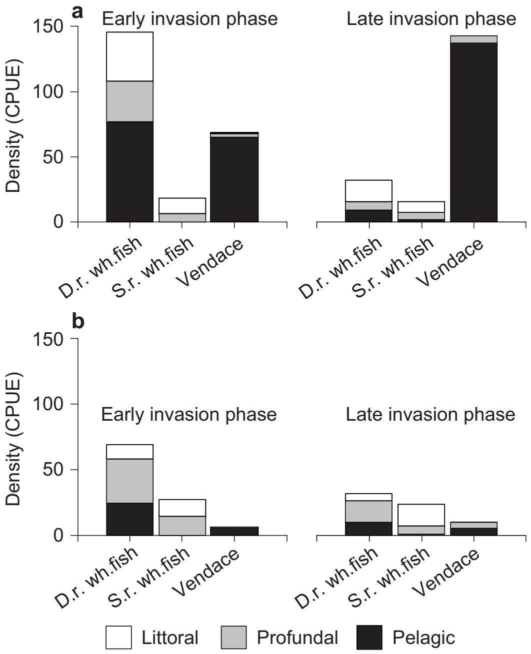

Fig. 2. Population density (CPUE = number of fish per 100 m^2 gillnet per 12 hours) of densely-rakered (D.r.) whitefish, sparsely-rakered (S.r.) whitefish and vendace in different habitats in early and late invasion phase, (**a**) upstream and (**b**) downstream in the watercourse.

ent types: 40-m long and 4-m deep; and 16-m long and 12-m deep. Additional benthic gill nets, 40-m long and 1.5-m deep with mesh sizes 10, 12.5, 15, 18.5, 22, 26, 35 and 45 mm, were used in the profundal and littoral.

The catch per unit effort (CPUE — number of fish per 100 m^2 per 12 hours — cf. Fig. 2.) of vendace and whitefish was calculated from comparable September samples only, due to large seasonal variation. CPUE is used here as an indicator of population density in the pelagic, the profundal and the littoral zone.

All fish were measured in mm (fork length) and weighed in grams. The sex and stage of maturity were determined by a visual examination of the gonads (only the September samples were used to evaluate the stage of maturity), and the age of the fish was determined by counting the number of winter zones on the otoliths (Skurdal *et al*. 1985).

In both localities, and within the early and late invasion phase, respectively, there were very similar growth rates and size/age at maturation between males and female, with one exception (mentioned in the results). Therefore all male and female data were pooled.

Results

Sample sizes

The total sample consisted of 4990 coregonid fish; 2624 densely-rakered whitefish, 1189 sparsely-rakered whitefish and 1177 vendace (Table 1).

Density of fish in different habitats

In the upstream locality, lake Ruskebukta, the density of the densely-rakered whitefish (the pelagic morph) as indicated by CPUE was high in all three habitats in the early invasion phase (1991–1992), but dropped dramatically (by ca.

Table 1. Catches of vendace, densely-rakered (D.r.) and sparsely-rakered (S.r.) whitefish from the early and late invasion phases in the upstream and downstream localities, classified by habitats.

		Upstream			Downstream			
		Pelagic	Profundal	Littoral	Pelagic	Profundal	Littoral	Total
Early invasion phase	Vendace	115	5		97	11	6	234
	D.r. whitefish	128	70	98	500	311	263	1370
	S.r. whitefish	0	9	33	2	130	238	412
Late invasion phase	Vendace	593	21	22	242	57	8	943
	D.r. whitefish	61	59	181	536	327	90	1254
	S.r. whitefish	15	56	118	17	290	281	777
	Total	912	220	452	1394	1126	886	4990

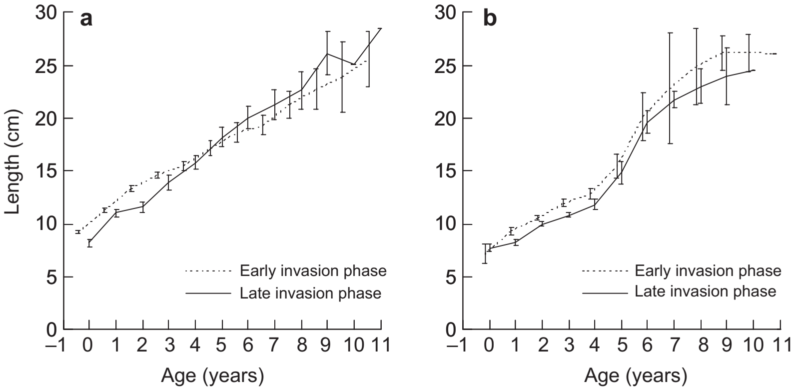

Fig. 3. Mean length at age of densely-rakered whitefish in the early and late invasion phases in the (**a**) upstream and (**b**) downstream localities. Bars show 95% confidence limits.

80%) to the late invasion phase (1997–1998). Most of the density reduction was seen in the pelagic habitat (Fig. 2a). In the sparsely-rakered whitefish (the benthic morph), only a slight reduction in density was observed from the early to the late invasion phase (Fig. 2a). The density of the invading vendace more than doubled between the early and late invasion phase, and almost all of the vendace inhabited the pelagic habitat (Fig. 2a).

In the downstream locality, lake Skrukkebukta, the overall density of coregonids was markedly lower than in the upstream locality. The densely-rakered whitefish showed a clear reduction in density (ca. 50%) from the early invasion phase (1993–1995) to the late invasion phase (1998–2000), but without a change in the use of habitat (Fig. 2b). The sparsely-rakered whitefish also showed a reduction, although less pronounced than for the densely-rakered morph. The vendace increased slightly, but remained at a relatively low density through the whole study period (Fig. 2b).

Length at age

Densely-rakered whitefish

In the upstream locality, the densely-rakered whitefish of age 0, 1, 2 and 3 were larger in the early as compared with the late invasion phase (significantly larger for ages 0, 2 and 3; *t*-test: $p < 0.001$, $p < 0.001$ and $p < 0.05$, respectively). Fish of age 4 were of similar size and older fish showed the opposite trend (Fig. 3): in the early invasion phase the fish were significantly smaller than in the late invasion phase (age 6, 7 and 9; *t*-test: $p < 0.05$).

In the downstream locality, the densely-rakered whitefish were larger at all ages (except 0+) in the early invasion phase (Fig. 3), and the differences were significant for fish of age 1–4 years (*t*-test: $p < 0.001$ for age 1 and 3, $p < 0.01$ for age 2 and 4).

Sparsely-rakered whitefish

In the upstream locality, no significant differences in length at age were found between the early and late invasion phases (Fig. 4; *t*-test: $p > 0.05$). However, the same trend in growth patterns was found as for the densely-rakered whitefish, i.e. higher growth rates for young fish and lower growth rates for older fish in the early invasion phase.

In the downstream locality, the sparsely-rakered whitefish showed a strong reduction in length at age from the early to the late invasion phase (Fig. 4), significant at ages 2–6 years (*t*-test: $p < 0.001$) and 9 years (*t*-test: $p < 0.01$).

Size distribution and size at maturation

Densely-rakered whitefish

In the upstream locality, the modal length was ca. 15 cm and the size at first maturation was 10–12 cm in the early invasion phase. In the late invasion phase, there was a tendency for a larger

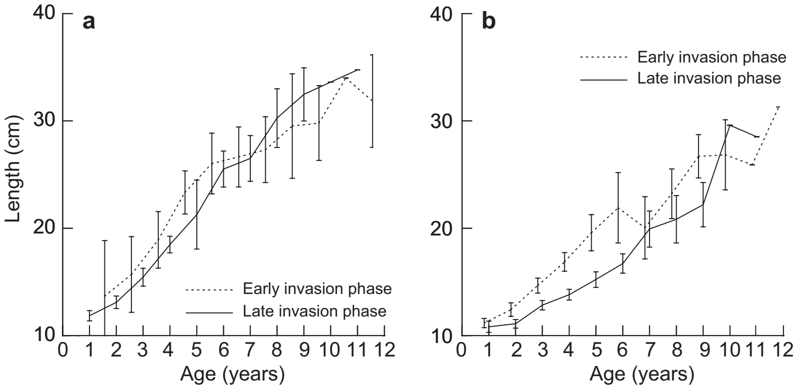

Fig. 4. Mean length at age of sparsely-rakered whitefish in the early and late invasion phases in the (**a**) upstream and (**b**) downstream localities. Bars show 95% confidence limits.

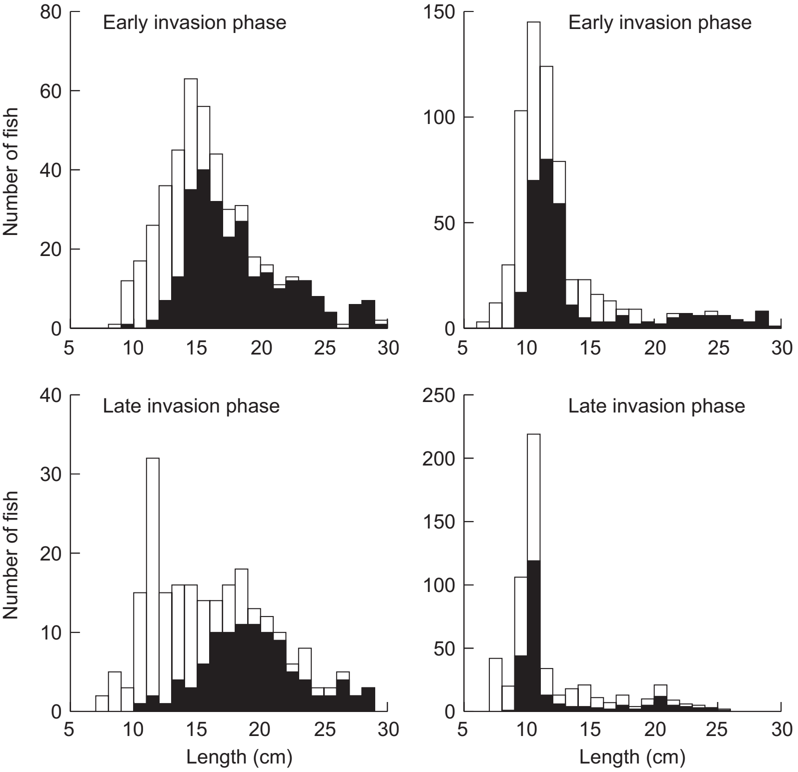

Fig. 5. Length distribution of densely-rakered whitefish in the early and late invasion phases in the upstream (left-hand side panels) and downstream (right-hand side panels) localities. Open and filled bars represent immature and mature fish, respectively.

part of the population to be small and immature fish. The size at first maturation was similar (Fig. 5), but the median size of mature fish had increased from the early to late invasion phase (Mann-Whitney test: $p < 0.001$).

In the downstream locality, the size distribution showed in general smaller fish (< 13 cm) as compared with the upstream locality, with a modal length of ca. 10 cm in the early invasion phase, dropping to 9 cm in the late invasion phase (Fig. 5). Also the size at first maturation was lower in the downstream locality (9–10 cm) as compared with upstream, dropping slightly between the early and the late invasion phase. The median size of mature fish was significantly smaller in the late invasion phase (Mann-Whitney test: $p < 0.001$).

Sparsely-rakered whitefish

In the upstream locality, most of the fish caught

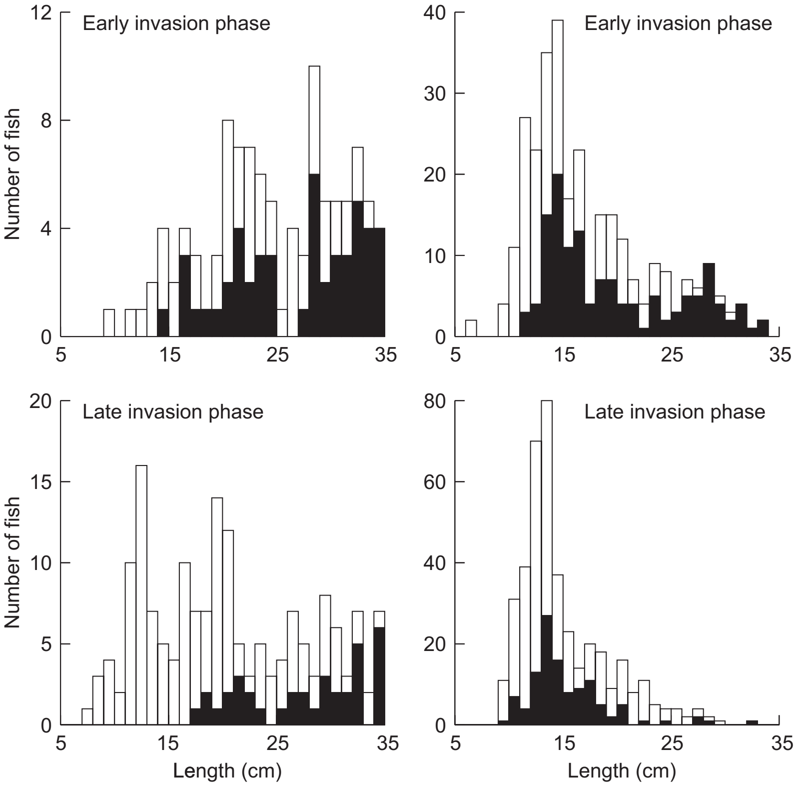

Fig. 6. Length distribution of sparsely-rakered whitefish in the early and late invasion phases in the upstream (left-hand side panels) and downstream (right-hand side panels) localities. Open and filled bars represent immature and mature fish, respectively.

consisted of individuals larger than 20 cm, with a size at first maturation at 14 cm in the early invasion phase (Fig. 6). In the late invasion phase most of the population consisted of fish smaller than 20 cm, but the size at first maturation had increased to 17 cm. The median size of mature fish was insignificantly smaller in the late invasion phase (Mann-Whitney test: $p = 0.22$).

In the downstream locality, the fish were generally smaller than in the upstream locality, and both the size structure of the population and the size at first maturation decreased from the early to the late invasion phase (Fig. 6). The median size of mature fish decreased significantly from the early to late invasion phase (Mann-Whitney test: $p < 0.001$).

Age distribution and age at maturation

Densely-rakered whitefish

In the upstream locality, dominating age-classes in the early invasion phase were 1–4 years old fish with first maturation at 2 years (Fig. 7). In the late invasion phase, there were proportionally more immature young fish (< 4 years), but a few mature males of age 1 year. The median age at maturation increased significantly from the early to the late invasion phase (Mann-Whitney test: $p = 0.003$).

In the downstream locality, the fish were younger than those in the upstream locality (Fig. 7). The pattern from the early and late invasion phase was similar (Fig. 7), and the median age at maturation decreased insignificantly from early to late invasion phase (Mann-Whitney test: $p = 0.58$).

Sparsely-rakered whitefish

In the upstream locality, dominating age-classes in the early invasion phase were 5–8 years old fish with first maturation at 4 years (Fig. 8). In the late invasion phase, more young and immature fish were represented, but age at first maturation had increased to 5 years. The median age

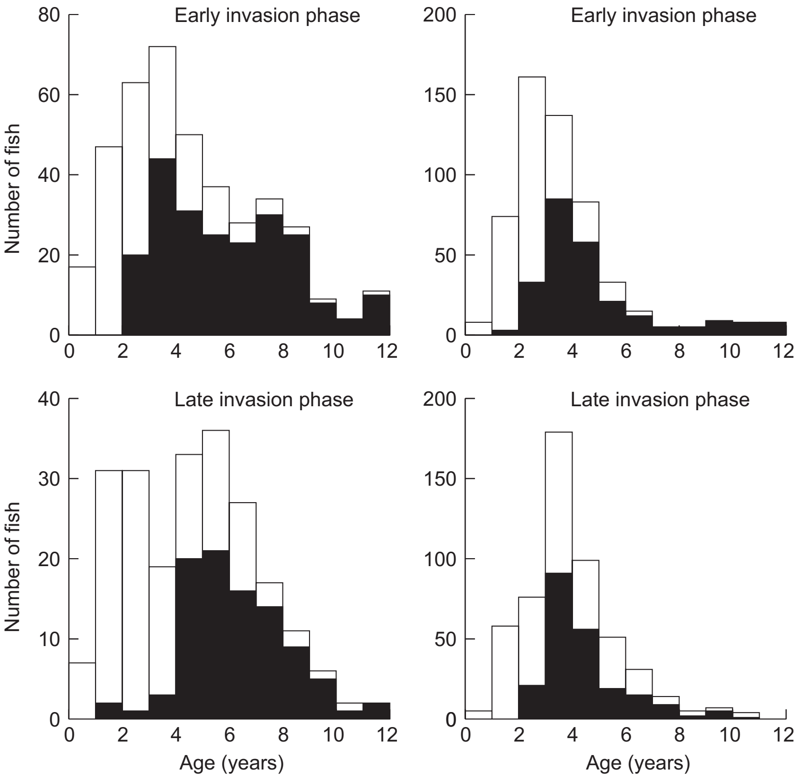

Fig. 7. Age distribution of densely-rakered whitefish in the early and late invasion phases in the upstream (left-hand side panels) and downstream (right-hand side panels) localities. Open and filled bars represent immature and mature fish, respectively.

at maturation decreased insignificantly from the early to late invasion phase (Mann-Whitney test: $p = 0.098$).

In the downstream locality, the fish were younger and matured earlier than those in the upstream locality (Fig. 8). The age at first maturation was the same for the early and late invasion phases, but the median age at maturation decreased significantly over the same period (Mann-Whitney test: $p < 0.001$).

Discussion

In the context of biodiversity losses and other threats, knowledge of the ability of invading or introduced species to transform or significantly alter native ecological communities is crucial for the understanding of biological invasions *per se*, and equally important for possible counteracting the huge problems imposed by a continuously increasing rate of exotic species transfer (Williamson 1996, Moyle 1999, Mooney & Hobbs 2000, Bøhn 2002).

The gradual downstream invasion of vendace into the Pasvik watercourse in the 1990s after introduction to its headwaters (lake Inari, Finland) around 1960 (Mutenia & Salonen 1994) has provided a rare opportunity to study many aspects of ecology in the receiving native ecosystem during times of dynamic change (Amundsen *et al.* 1999, Bøhn & Amundsen 1998, 2001, Bøhn 2002, Bøhn *et al.* 2002). Since fish have indeterminate growth and also show plastic responses in other life history traits (Stearns 1992, Wootton 1998), this taxon is particularly suitable for studying life history responses to changes in biotic or environmental conditions. In this study, life history traits of the two native whitefish morphs were followed in the early and late invasion phases of a potential competitor, representing weak and strong impacts in two replicate localities.

The population density of vendace in the upstream locality more than doubled between the early and late invasion phases. This expansion was mainly recorded in the pelagic habitat where the density of the pelagic densely-rak-

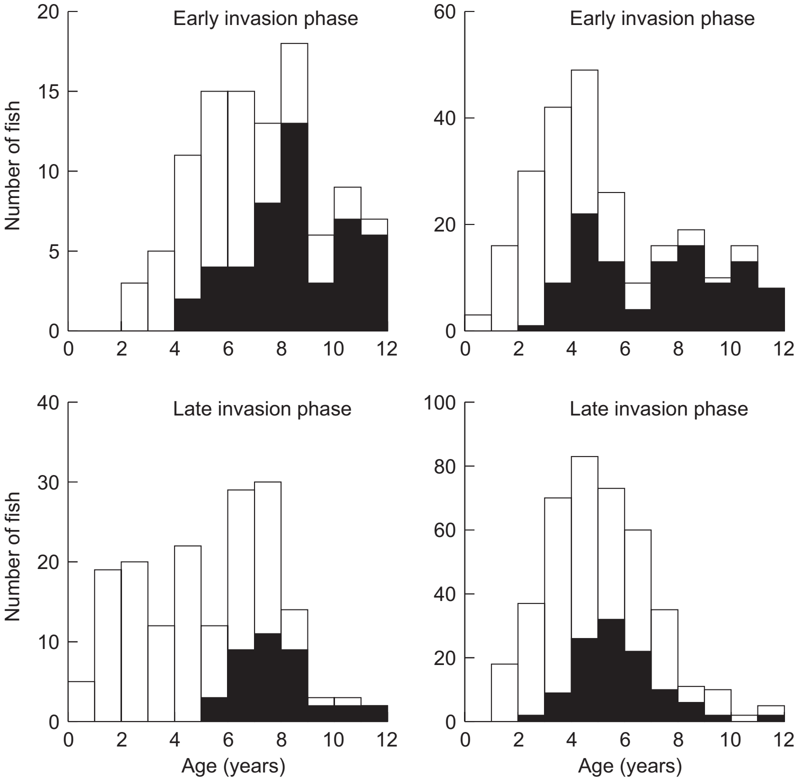

Fig. 8. Age distribution of sparsely-rakered whitefish in the early and late invasion phases in the upstream (left-hand side panels) and downstream (right-hand side panels) localities. Open and filled bars represent immature and mature fish, respectively.

ered whitefish morph was high during the early 1990s. From its initial high density, the densely-rakered whitefish declined dramatically (ca. 80%, combining all habitats) by the late invasion phase just 6–7 years later. This decline was even more marked in the pelagic zone. A pelagic substitution of densely-rakered whitefish by vendace indicates strong competitive interactions between the species, a conclusion supported by a complementary feeding study by Bøhn and Amundsen (2001). In northern Norway, densely-rakered whitefish generally feed on zooplankton (Amundsen 1988), but may also show an ontogenetic niche shift to a diet dominated by benthos later in life as observed in the Pasvik watercourse (Bøhn 2002). On top of the population density reduction of the densely-rakered whitefish, a significant growth reduction of young zooplanktivorous whitefish demonstrates a double response: density decline and lower growth rates. Interestingly, in spite of the growth reduction in young fish, older densely-rakered whitefish grew better in the late invasion phase as compared with the earlier period. This may be the result of a juvenile competitive bottleneck where originally zooplanktivorous stages were subsequently faced with a choice of feeding in a pelagic zone with a reduced level of available zooplankton (Bøhn & Amundsen 1998, 2001), or shifting to a benthic food before they became naturally adapted to it. The survivors of this bottleneck, however, experienced an intraspecific competitive release for zoobenthos. The size- and age-structure, and the size and timing of maturation of the densely-rakered whitefish, showed a change towards maturation at larger size and greater age. As most of the mature fish were five years or older in age, these fish were the same individuals that showed increased growth rates due to the suggested competitive release. High growth rates in fish are often associated with maturation at larger size and younger age. The relation between growth and age at maturity is not straightforward and responses may turn both ways, depending on if the growth rates changes from low to intermediate, or from intermediate to high (Alm 1959, Stearns & Koella 1986, Wootton 1998).

The sparsely-rakered whitefish showed only minor changes in population density, use of habitat and growth in the upstream locality. This may be expected as this whitefish morph normally occupies the littoral zone and feeds on benthic invertebrates, thereby having an insignificant niche overlap with the invading species. However, both the size- and age-structure showed that a higher proportion of the population was small and immature in the late invasion phase. There was also a tendency that size- and age at first maturation increased. The reason for this change is uncertain.

In the downstream locality, the population density of vendace remained low throughout the study period (1993–2000), i.e. there was no similar increase in population density as at the upstream site. However, a density reduction in the densely-rakered whitefish of more than 50% was observed. In addition, the growth was significantly reduced in early (zooplanktivorous) life stages. This may seem like an unreasonably strong response if we compare it with that in the upstream locality, at least before we take the size structure of the populations, the resource level and the different morphometry of the lakes into consideration. The size structure of the densely-rakered whitefish population mainly consisted of fish smaller than 12 cm in the early invasion phase, with a relatively high proportion of mature fish. By the late invasion phase the size had been further reduced and nearly all fish were smaller than 10 cm. This contrasting demography of the densely-rakered whitefish in the downstream locality may have represented a stronger community resistance to the invading vendace due to a higher proportion of zooplanktivorous individuals and thus a higher ecological overlap. In addition, the availability of edible zooplankton was lower in the downstream locality as compared with that in the upstream locality (Bøhn & Amundsen 1998, 2001). These two factors may have limited the vendace expansion in the downstream locality. However, the strong documented effects on both density and growth of the densely-rakered whitefish, even from a relatively low density of vendace, represent a counter argument to this supposed biotic resistance. Another factor that may play a role here is the morphometry of the lakes. The downstream lake is deeper and has relatively more pelagic areas as compared with the shallower lake upstream. This difference may give the densely-rakered whitefish less opportunity to shift to a benthic habitat and diet. The lack of an alternative ontogenetic pathway for the densely-rakered whitefish may have thus produced strong pelagic interactions even at a relatively low vendace density. If so, the combined effects of the limited expansion of the vendace and the reduced density and growth of the whitefish are to be expected.

The sparsely-rakered whitefish showed no numerical response in the downstream locality, but growth declined sharply in the early life stages between the early and the late invasion phase. Again, this is the zooplanktivorous stage in the life cycle and indicates an increased pressure on the pelagic food resources after the vendace invasion. The reduced growth of the sparsely-rakered whitefish may have caused both the observed reduction in the overall size-structure of the population, and the reduced size, but not age, at first maturation.

It seems likely that the invading population of vendace will establish a pattern of cyclic variation in abundance as commonly observed for this species in other systems (Hamrin & Persson 1986, Sandlund *et al.* 1991, Helminen *et al.* 1993). The strong specialization of vendace as a pelagic zooplanktivore, combined with its high fecundity, gives the species a competitive edge over other zooplanktivores (Svärdson 1976, Nilsson 1978, Auvinen 1988, Bøhn & Amundsen 1998, 2001). Thus, the potential impact of vendace on other species with similar ecological niches may therefore be substantial, as indeed observed in the Pasvik watercourse (Bøhn & Amundsen 2001, Bøhn 2002).

The vendace has not only changed the community of its zooplanktonic prey with cascading effects on primary production (Bøhn & Amundsen 1998), it has also assumed the role of the most important prey for pelagic piscivorous predators (Bøhn *et al.* 2002). This role of a key-species, in combination with a potential cyclic variation in abundance, may destabilize the aquatic ecosystem in the watercourse and thereby also greatly complicate future management.

In conclusion, this study documents strong effects, probably through competition, from the invading vendace on the native dimorphic whitefish population. The effects on the pelagic and ecologically similar densely-rakered whitefish ranged over numerical responses (strong density decline in the population), habitat use (shift from pelagic to littoral) and individual growth (significant growth reduction in zooplanktivorous life stages). For the benthic sparsely-rakered whitefish, effects were more restricted and centred mainly on growth.

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