Article for *Biological Invasions*:

Competitive exclusion after invasion? (title and running head)

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ABSTRACT

The 'Competitive Exclusion Principle' is a foundation stone in the understanding of interspecific competition and niche relationships between species. In spite of having the status of a biological law, the principle has limited empirical support. In this study, we document strong effects of competition from the invading fish species vendace *Coregonus albula* over a 14-year period in the sub-arctic Pasvik watercourse. The native d.r. whitefish, that shared food and habitat niche with the invader, was displaced from its original niche and showed a more than 90% decline in population density over the study period. The study thus provides a unique record of how an exotic fish species excludes a native species from its original niche. Our data support the competitive exclusion principle, but also indicate that the vulnerability of the inferior competitor depends on a lack of alternative resources and on indirect ecological interactions.

INTRODUCTION

The theoretical principle of competitive exclusion predicts the outcome of interspecific competition as elimination or extinction of one of two species that occur together without niche differentiation (Volterra 1931; Lotka 1932; Gause 1934; Hardin 1960; Pianka 2000; Webb et al. 2002). The reason is simply that one species will be at least slightly more efficient at capture of the shared resource or will be able to sustain a viable population at lower minimum resource levels than can the second species (Tilman 1982). The principle is described by differential equations and has obtained the status of a biological law (Ekschmitt and Breckling 1994; Weber 1999). However, the empirical support is limited, and mainly based on simple laboratory experiments (Gause 1934; Wang et al. 2002). The lack of empirical support has raised the question about its domain of application (Keddy 1989; Peters 1991), but interspecific competition is difficult to study because its effects are mostly hidden as the temporary endpoint of a complex community structure. However, during periods of change, competition can be shown or indicated empirically by a number of different measures (Ross 1991); directly on the competitors, or on any shared resource pools or prey community affected (top-down effects). More specifically, competition is supported if a study shows:

(i) interactive niche shifts (e.g. in habitat or diet) (Nilsson 1967, 1978)

(ii) density reduction or extinction (negative population growth) (Hardin 1960)

(iii) reduced individual growth (Diehl and Eklov 1995)

(iv) reduced food intake (Bøhn and Amundsen 2001; Wauters et al. 2002)

(v) altered community composition of prey towards smaller species (Brooks and Dodson 1965; Gliwicz and Pijanowska 1989)

(vi) altered size structure of prey populations towards smaller individuals (Lazzaro 1987)

Biological invasions provide ecological scenarios that may facilitate more empirical insight to competitive interactions. Subsequent to an invasion, the processes of interspecific competition, rather than its steady-state outcome, can be studied in the receiving ecosystem (Simberloff 1981; Pimm 1989). Introduced exotic species thus provide large-scale 'natural experiments' where ecological theory (e.g. the 'Competitive Exclusion Principle') may be tested empirically. Elucidative in situ studies on ecological processes require comparisons between systems or changes due to disturbance within systems. Biological invasions provide both these possibilities and may produce unique long-term datasets. Suitable data from invasion biology cannot be obtained easily from manipulated experimental systems, for a number of reasons. Firstly, exotic invaders are largely unwanted and strong measures are taken to avoid further spread of exotic species (Glowka et al. 1994; Sandlund et al. 1999). Secondly, only about 10% of the introduced exotic species establish, and only one percent produce strong effects on the receiving community (Williamson 1996). Thirdly, the effects of exotic species may come after long time delays, often too slowly for the short-term-funded researcher to follow. Finally, for most studies of exotic species that have had significant ecological impact, there are weak or no data on the pre-invasion native community structure, simply because many exotic organisms are not discovered before late in the process. Invasion biology has mainly been operating in retrospect on long time scales

with relatively low precision data. Such data may however be successfully combined with modelling of the process (Moyer et al. 2005). In the literature, we were able to find just a few long-term studies that, in a large-scale ecosystem, followed the consequences arising from an invasion, and that also provided evidence of competitive exclusion during the process (Wilson et al. 2004; Geiger et al. 2005).

This study documents the successive stages of interspecific competition between a native and an exotic fish species over a 14-year period (1991–2004) in the Pasvik watercourse in the Norwegian Subarctic. The native whitefish *Coregonus lavaretus* in the watercourse consists of two sympatric morphs, densely and sparsely rakered whitefish (hereafter denoted d.r. whitefish and s.r. whitefish), with distinct ecological and morphological differentiation (Amundsen et al. 1999, 2004). The two whitefish morphs belong to the Siberian clade (Ostbye et al. 2005) and are most likely the result of sympatric ecological speciation within the system, partly due to lack of trophic competitors (Ostbye et al. 2006). The d.r. whitefish naturally occupies the same ecological niche (in the pelagic habitat) as the closely related, introduced vendace *Coregonus albula*, whereas the sparsely rakered whitefish prefers the littoral habitat (Amundsen et al. 2004). Vendace was introduced into the Inari watercourse in Finland around 1960 (Mutenia and Salonen 1992). After a 25-year delay in Lake Inari, this exotic species reached a high population density during the second half of the 1980s, then subsequently migrated downstream into the Pasvik watercourse, where it was recorded for the first time in 1989 (Amundsen et al. 1999). The gradual expansion of vendace into the Pasvik watercourse provided the opportunity to study the mechanisms and impact of competition throughout the period of change by comparing

resource use (habitat and food choice), growth and density of the invader and its native ecological counterpart. We test the following hypotheses:

1) the native d.r. whitefish is excluded from its original habitat niche due to asymmetric competition with vendace, the superior competitor

2) the d.r. whitefish show a population density reduction, or extinction, following the expansion of the invading vendace

3) the d.r. whitefish show reduced individual growth following the expansion of the invading vendace

4) the vendace show reduced individual growth due to increased intraspecific competition under its own population build-up

STUDY AREA AND FISH COMMUNITIES

Three countries share the Pasvik River watercourse. It originates in Lake Inari (1102 km2) 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 river system has a total area of 142 km2, a catchment area of 18,404 km2 and a mean annual water flow of about 175 m3 s−1. There are a total of seven water impoundments (hydropower reservoirs) in this part of the watercourse. Most rapids and waterfalls have disappeared so 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. The Secchi-depth ranges from 2 to 6 m.

Altogether, 15 species of fish have been recorded in the Pasvik watercourse. Whitefish (*Coregonus lavaretus* (L). sensu lato), perch (*Perca fluviatilis* L.), pike (*Esox lucius* L.), burbot (*Lota lota* L.) and brown trout (*Salmo trutta* L.) are the most abundant native species.

METHODS

Gill net sampling was performed in September of all years 1991–2004 except 1994 and 1996, in Lake Ruskebukta in the upstream part of the Pasvik watercourse. Lake Ruskebukta (69°13′ N, 29°14′ E; 52 m a.s.l.) has an area of 5.3 km^2, has a maximum depth of 15 m, and is stratified into three main habitats: pelagic, profundal and littoral. The pelagic was defined as the upper 6 m of the open water, above the deepest part of the lake; the profundal was defined as the zone up to 2 m above the bottom of the lake, in the deepest part of the lake; and the littoral was defined as areas close to the shore at depths down to 4 m. 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. Benthic gill nets with a mesh size of 10, 12.5, 15, 18.5, 22, 26, 35 and 45

mm were used in the profundal and littoral habitat. The total sample of vendace and d.r. whitefish consisted of 2670 and 1515 fish, respectively.

The catch per unit effort (CPUE) was calculated as the number of fish per 100 m^2 gill net per 12 h. CPUE is used as an indicator of relative fish density in different habitats. Some 0+ (age zero) fish were occasionally caught, but these were not included in the CPUE estimates as only the largest specimens of this age-class were retained by the size-selective gill nets. All fish were measured in terms of fork length (mm) and weight (g). The sex and stage of maturity were determined, and a sub-sample of female gonads was weighed (mg). The age of the fish was determined by counting the number of winter zones on the otoliths (Skurdal et al. 1985).

RESULTS

The development and consequences of the invasion can be summarized in *five stages* demonstrating a complex array of direct and indirect interactions, including competitive exclusion of the d.r. whitefish from the pelagic habitat (see Fig. 1 for a community overview).

In *stage I* (the pre-invasion situation – up to 1991), the native pelagic fish communities in the lakes of the Pasvik watercourse were predominantly inhabited by one zooplanktivore, the d.r. whitefish morph. In 1991, the first recorded year of sympatry between the native d.r. whitefish and invading vendace, about 75 % of the d.r. whitefish were found in the pelagic habitat and it predominated over the vendace (Fig. 2). The s.r. whitefish were found in relatively low density in the littoral habitat (Fig. 2).

In *stage II* (interactive habitat segregation of the native d.r. whitefish – 1991-1993), during the establishment and increasing population density of the invader, the native d.r. whitefish shifted from the pelagic habitat over to littoral and profundal habitats (Fig. 2) as the vendace took over the dominance of the pelagic habitat (Fig. 3). The s.r. whitefish showed a stable density and was caught in littoral and profundal habitats (Fig. 2.). The growth (length attained at age) of d.r. whitefish decreased in the zooplankton-feeding age groups, especially in the 1-year-old fish. For vendace, the growth reduction was substantial, with mean length reduced by 40–50 mm (25–35%) within age groups 1+ and 2+ (Fig. 4).

In *stage III* (boom phase of the invader / reduction of the d.r. whitefish – 1993-1998), a steady increase of the invader lasted until 1998, and almost exclusively in the pelagic habitat. During the same period, the native d.r. whitefish kept to littoral and profundal habitats, but decreased sharply (86 % combined for all habitats) in population density (Fig. 2). The s.r. whitefish showed an increase in the catches in 1995, but decreased thereafter (Fig. 2). Whereas the d.r. whitefish showed decreasing length attained at age in all age groups, the vendace seemed to stabilize its growth pattern at a new asymptotic length (about 115 mm) (Fig. 4).

In *stage IV* (bust of the invader – 1998-2000), the density of the vendace population dropped sharply (93 % combined for all habitats) (Fig. 2). Both whitefish morphs also showed reduced density (Fig. 2). The growth of the d.r. whitefish was relatively stable in this period, while the vendace showed a trend toward reduced growth (Fig. 4).

In *stage V* (after the bust – 2000-2004), the density of vendace first kept at relatively low level before increasing again in 2004 (Fig. 2). The d.r. whitefish has stabilized at a density less than 10 % of its pre-invasion value (stage I). The s.r. whitefish increased in catches after 2000 (Fig. 2). Both d.r. whitefish and vendace showed a tendency to increased length attained at age for the 1- and 2-year-old fish after 2000 (Fig. 4).

DISCUSSION

This study followed the consequences from the invasion of vendace over a 14-year period in the sub-arctic Pasvik watercourse. The native d.r. whitefish, that shared food and habitat niche with the invader, was displaced from its original niche and showed a more than 90% decline in population density over the study period. The invading vendace showed a clear boom-and-bust development and hence contributed a strong, but potentially fluctuating, impact in the native fish and zooplankton community.

In the pre-invasion situation in the Pasvik watercourse, the native zooplanktivorous d.r. whitefish completely dominated in the native pelagic fish communities of the lakes. In contrast, by 2004, more than a decade later, the invading vendace had taken over the ecological role of the native species. The event of the vendace invasion and its interactions with the receiving ecological community, had rearranged the native community structure. We followed the change in structure by a unique series of year to year empirical data in order to analyse the underlying ecological processes.

The data provided empirical support for resource limitation and competition after the vendace invasion:

Hypothesis 1: exclusion of the native d.r. whitefish from its original habitat niche
In 1991, early in the process of establishment for the vendace, a high density of d.r. whitefish was found in the pelagic zone and the habitat overlap between the species was

high. We argue that this situation with increasing pelagic fish density and increased zooplankton feeding was not sustainable. Increased exploitative competition by shared feeding on zooplankton caused a decline in food resources which forced the d.r. whitefish from the pelagic zone to littoral and profundal habitats. This observed interactive habitat segregation of the d.r. whitefish was accompanied by a shift in diet, from zooplankton to benthic invertebrates (Bøhn and Amundsen 2001). In contrast to selective segregation, where species segregate in their resource utilisation because of evolutionarily developed differences, interactive segregation is explained by present interspecific competition (Brian 1956; Nilsson 1967; Wootton 1998). If potentially competing species are distantly related, it may be difficult to distinguish if resource partitioning comes from taxonomic difference or from present interactions (Ross 1986). Interspecific competition should therefore preferably be studied in closely related species that use similar resources (Werner 1986), criteria met by the situation in Pasvik. The transition period for the niche shift of the vendace was quite short, about two years (1991–1993; Figs. 2 and 3). Since only the native species changed its use of habitat, the competition for zooplankton is asymmetrical, with vendace showing its competitive edge (Bøhn and Amundsen 2001). The strong specialization of vendace, including its many, long and densely packed gill rakers to retain small-sized food particles (Sanderson et al. 2001; Amundsen et al. 2004), combined with early maturation and high fecundity, is consistent with its competitive advantage over other zooplanktivore fish species, including d.r. whitefish (Svärdson 1976; Nilsson 1978; Bøhn et al. 2004).

Hypothesis 2: density reduction in, or extinction of, the d.r. whitefish

The d.r. whitefish decreased sharply (91%) in population density between 1991 and 2004, mostly during the boom-period of the vendace (1993–1998). This density decline did not seem to be caused by only direct food competition with vendace, but can also be related to food competition to the s.r. whitefish and to a high number of size-selective fish predators (pike, perch and burbot) in the littoral and profundal habitats into which the d.r. whitefish had been displaced (Bøhn et al. 2002; Amundsen et al. 2003). Hence, competition-mediated indirect effects put additional pressure on the d.r. whitefish. Different whitefish morphs have been found to stay in the predation window of gape-limited predators for different amounts of time, depending on the growth rate of each morph (Næsje et al. 1998). In Pasvik, the growth rate of the two whitefish morphs differ greatly; the s.r. whitefish grows faster and leaves the predation window of the littoral predators five years earlier than the d.r. whitefish (Bøhn et al. 2002). Even the invader population density declined 93% over two years (1998–2000), suggesting that the resource level of zooplankton in the pelagic was depleted below the maintenance level of the peak population of vendace.

Hypothesis 3: the d.r. whitefish show reduced individual growth following the expansion of the vendace

The length attained at age of d.r. whitefish decreased about 15–20 mm in all age groups from 1991 to 2000. In 2001, the 1- and 2-year-old fish showed higher growth rates. The overall negative trend in growth for the d.r. whitefish supports the hypothesis of food competition with vendace. However, the growth rates attained after the shift to other habitats imply feeding on other food categories, i.e. the competition with vendace was

relaxed. Therefore the growth data rather showed the ability of the 1- to 3-year-old d.r. whitefish to grow in an alternative food and habitat niche. This niche had previously been solely occupied by the other whitefish morph which supposedly was the superior competitor there. As the s.r. whitefish have evolved into this particular niche over evolutionary time (c.f. Ostbye et al. 2006), it should be no surprise that this morph was the superior competitor for benthic prey.

Hypothesis 4: the vendace show reduced individual growth due to increased intraspecific competition under its own population build-up

The growth (length attained at age) of vendace decreased substantially in the age groups from 1 to 3 years during the establishment of the invader (1991–1993). For vendace, the reduction in length within age groups 1+ and 2+ fish was 40–50 mm in just two years. The observed rapid decline in growth over the first three years indicates that both interspecific and intraspecific competition for zooplankton were intense. Even though the density of the vendace was intermediate during these years, the individual size was much larger. In fact the total biomass of vendace in 1991 was higher than in 1993 and comparable to the population peak in 1998 (Bøhn et al. 2004). We have previously interpreted the growth reduction of the vendace as a combination of (i) a density-dependent response mediated by food depletion; and (ii) a pioneer strategy that allocates resources to favour reproduction at early developmental stages and a high number of offspring, trading off growth and size of offspring (Bøhn et al. 2004).

Additional support of competition between vendace and d.r. whitefish from previous studies

Reduced food intake

In a parallel study in the Pasvik watercourse, comparisons of the diets of vendace and whitefish were made in 1993 between lakes of low and high competition, respectively. In the downstream lake, where the vendace had just arrived and had a low population density (low competition), both vendace and whitefish had a stomach fullness of about 55–70%. In contrast, in the upstream lake (Lake Ruskebukta—high competition), the stomach fullness was about 10% for the vendace and about 20–40% for the whitefish (Bøhn and Amundsen 2001).

Altered community composition of prey towards smaller species

A comparison of the zooplankton community composition between two lakes in the Pasvik watercourse, upstream and downstream, was made in 1993. Whereas this was the first year vendace was observed in the downstream lake, the species was well established with a high population density in the upstream lake (Lake Ruskebukta) (Bøhn and Amundsen 1998). The downstream lake (weak predation pressure) was dominated by larger zooplankton species, i.e. *Holopedium gibberum, Eudiaptomus graciloides* and *Daphnia cristata*, compared to the upstream lake (strong predation pressure) where *Bosmina longirostris*, the smallest zooplankton species in the watercourse predominated (Bøhn and Amundsen 1998).

Altered size structure of prey populations towards smaller individuals

Within the three dominant cladoceran zooplankton species in the watercourse (*B. longirostris, B. longispina* and D. cristata), significantly smaller individuals were found in

the upstream Lake Ruskebukta (strong predation) compared to the downstream lake (weak predation), especially during mid-summer (Bøhn and Amundsen 1998). Predation of zooplankton is positively correlated to temperature and strong predation from fish in summer often leads to reduced size of individual zooplankters (Gliwicz and Pijanowska 1989). Furthermore, both vendace and whitefish selected significantly larger zooplankton individuals from these three cladoceran species in the low predation, downstream lake (Bøhn and Amundsen 1998).

Summing up the empirical data, we show that the native d.r. whitefish was displaced from the pelagic habitat and declined dramatically over a ten-year period. The primary cause of this decline was asymmetrical competition with the invading vendace. However, indirect interactions arising from the habitat shift of the d.r. whitefish (competition with s.r. whitefish and selective predation on small-sized d.r. whitefish from pike in the littoral habitat) also seemed to contribute to the d.r. whitefish decline. All six identified ways to show resource limitation and competition were supported by our long-term data about the invasion. We thus consider the empirical evidence of (exploitative) interspecific competition to be extraordinarily well documented.

So how does the complex time sequence of the vendace invasion, including its effects on the native community, conform to the theoretical models of competitive exclusion? We have linked the empirical data from the vendace invasion in Pasvik to the graphical models on resource-dependent population growth and competition for one and two resources developed by Tilman (1980, 1982). According to these models, also called resource-ratio

theory (reviewed in Miller et al. 2005), the species that can maintain a positive growth rate at a lower resource level will be the better competitor for that particular resource.

Starting with the single resource of the pelagic habitat and the two competing zooplanktivorous species, we follow the dynamic change in the resource during the different phases of the vendace invasion (Fig. 5). The pre-invasion situation (stage I) may be assumed to closely resemble the stable equilibrium point for the native species, called the R^*_{native}, where the growth rate of the predator population (the d.r. whitefish) is zero, because the consumption of the resource (the zooplankton) by the predator equals the supply rate of the zooplankton resource (Tilman 1982). During establishment and boom of the invader (stages II and III), the predation pressure increased and the resource was depressed below the R^*_{native}, causing competitive exclusion from the overlapping pelagic niche. This lead to the observed interactive habitat shift (1991–1993) and density reduction (1993–1998) of the native d.r. whitefish. The boom of the vendace lasted until 1998. At that point the zooplankton resource was possibly depressed, at least temporarily, below the $R^*_{invader}$, causing the bust in that species' population over the next two years (stage IV). After 2000 the fish density stayed low with a slight increase towards 2004, indicating a possible increase in the resource (stage V).

A more realistic approach to the situation under study in the Pasvik watercourse includes a second resource axis, representing the benthic habitat. The competitive dominance of vendace over the d.r. whitefish in the pelagic, and its higher degree of specialization on zooplankton as food (Svärdson 1976; Helminen and Sarvala 1994; Bøhn and Amundsen

1998), substantiate a lower resource demand of vendace on the first resource axis as
compared to d.r. whitefish (i.e. the invader has a lower R_1*) (Fig. 6). However, the
specialization of the vendace on one resource most likely means a trade-off with feeding in
the benthic zone, leaving the benthic organisms at the second resource axis available for the
d.r. whitefish (i.e. the native species has a lower R_2*). This is substantiated by more
generalistic feeding and habitat use, including higher feeding rates of d.r. whitefish on
benthic organisms (Bøhn and Amundsen 1998, 2001). Thus the two species may
theoretically be allowed to coexist as competitors only through pelagic-benthic habitat and
food resource partitioning (Fig. 6). However, the situation for the whole community must
be admitted to be considerably more complex due to the competition and possible
hybridization between the two whitefish morphs in the littoral habitat, the size selective
top-predators like perch, pike and brown trout and a diverse littoral community of prey. All
these factors are less well studied and require further investigations. Nevertheless, we argue
that the present study represents a comprehensive and consistent empirical support for
competitive exclusion of a native species after the introduction of an invasive species. The
outcome of the competitive interaction supports the competitive exclusion principle as
relevant in nature, but also indicates that a complete exclusion, i.e. extinction, of the
inferior competitor depends on a lack of alternative resources and on indirect ecological
interactions.

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Figure legends

Figure 1. Direct (bold arrows) and indirect effects (dashed arrows) of the invading vendace into the food-web of the Pasvik watercourse. Negative and positive effects are denoted by − and +, respectively. The main constituents of the native fish community include two whitefish morphs (d.r. whitefish and s.r. whitefish), pike, perch, burbot and brown trout

Figure 2. Long-term (1991–2004) development in catch per unit effort (CPUE) and habitat use of the invading vendace and the two native whitefish morphs from 1991 to 2004, following the different stages of the invasion (see text for explanation)

Figure 3. Community contribution (based on numbers of fish) to the pelagic habitat by vendace and d.r. whitefish (1991–2004).

Figure 4. Mean length attained at ages 1+, 2+ and 3+ for vendace (1991-2002) and d.r. whitefish (1991-2001).

Figure 5. A graphical model on population growth rates (dashed line = invader; solid line = native) at different resource levels of zooplankton, including the suggested resource dynamics during the vendace invasion. Below the R^*_{native}, only the invader is able to exist over time. Stages as in text.
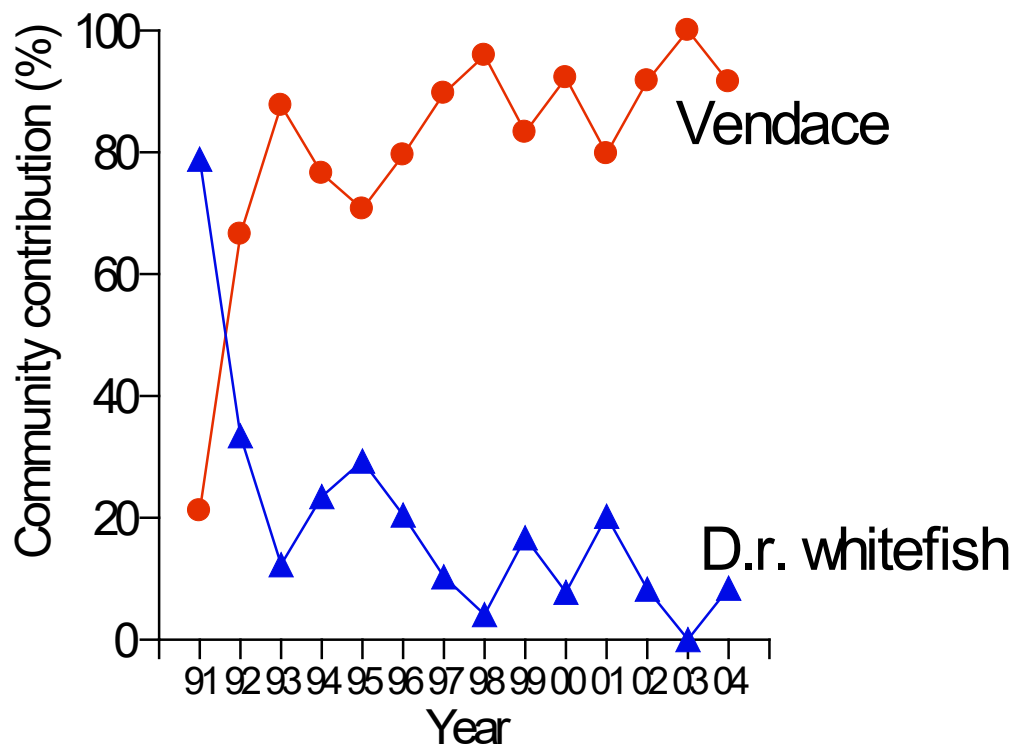
Figure 6. Zero net growth isoclines (ZNGI) (dashed line = invader; solid line = native) and areas of coexistence, competitive dominance and the single stable equilibrium point of two competitors along two resource axis; zooplankton in the pelagic habitat (R_1) and benthic organisms in benthic habitats (R_2) (adopted from Tilman 1982).
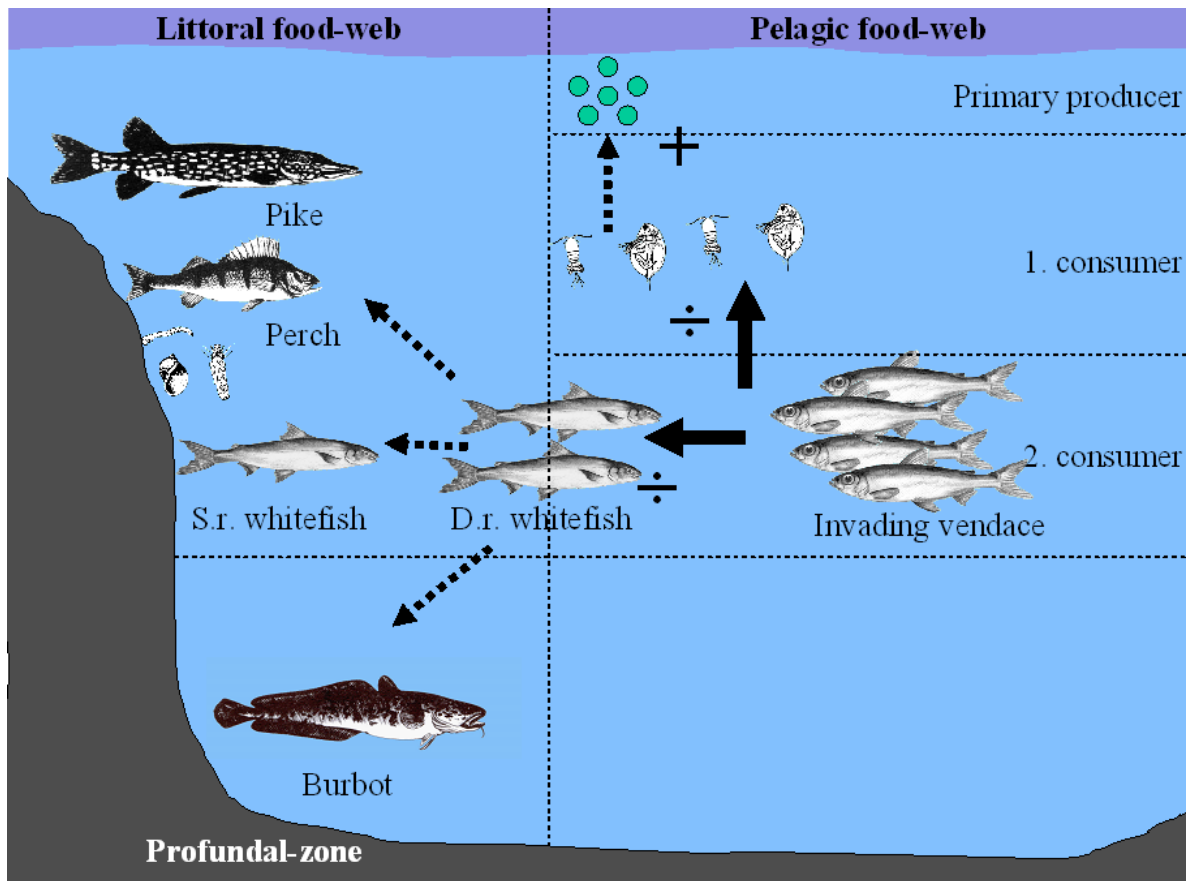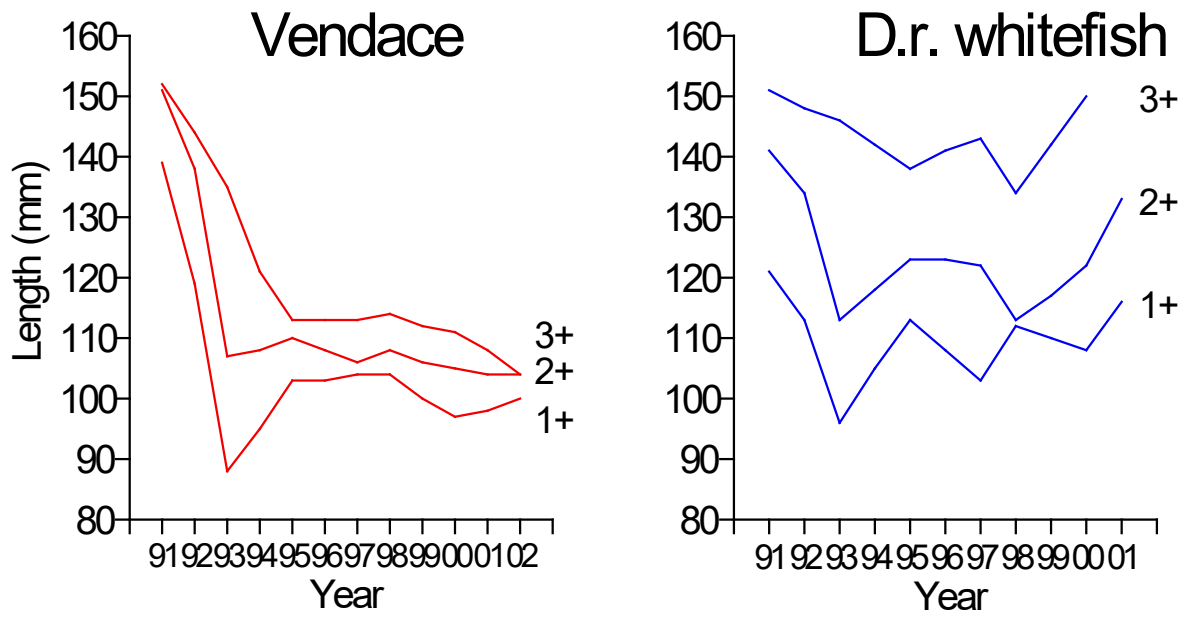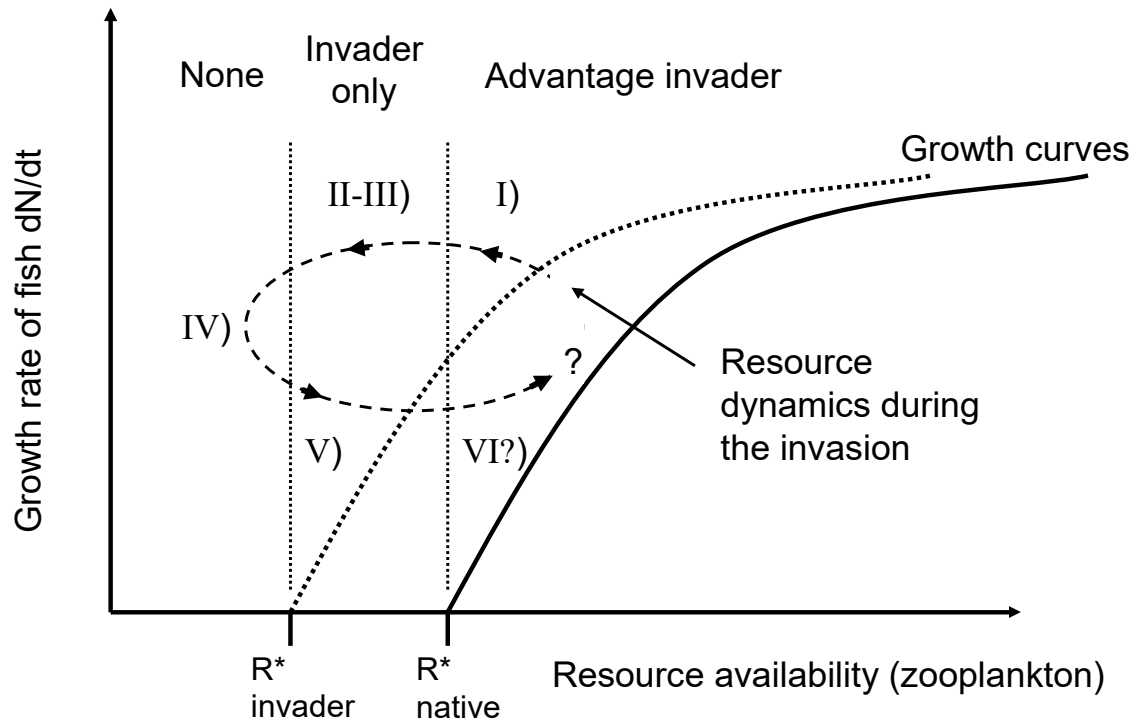
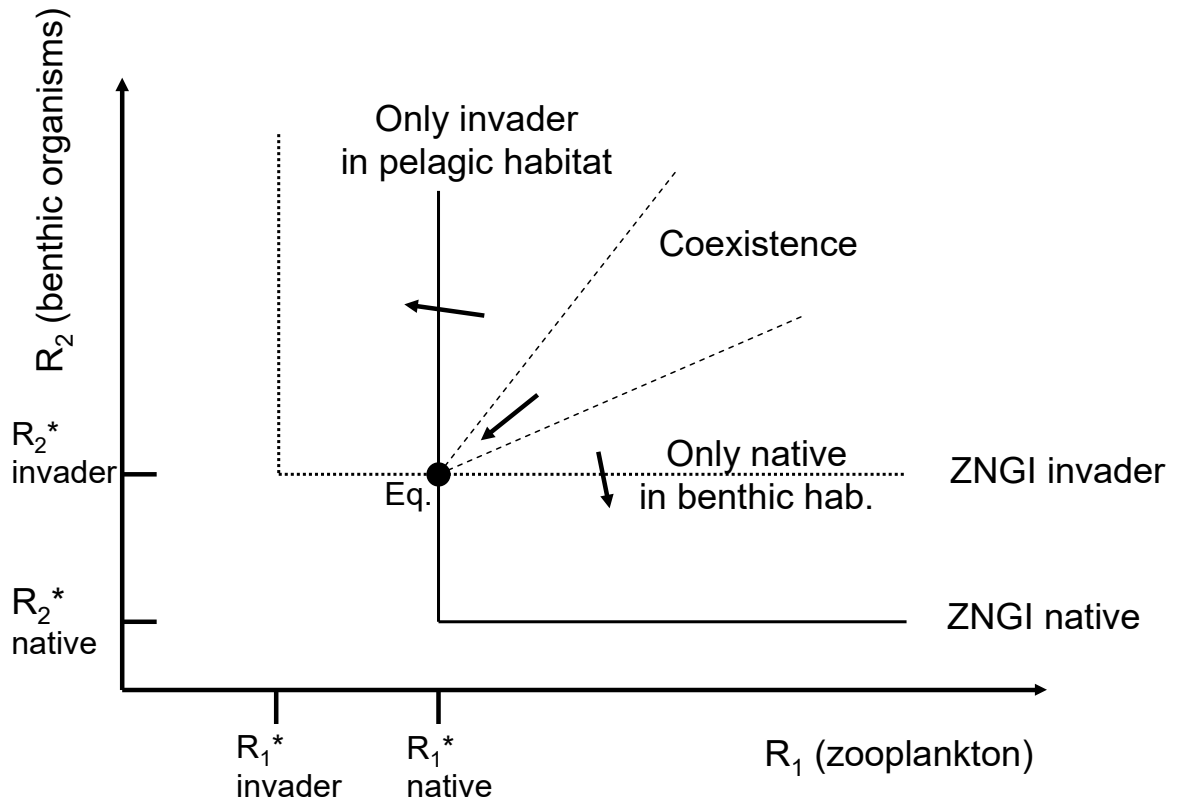Bøhn et al. Fig. 1
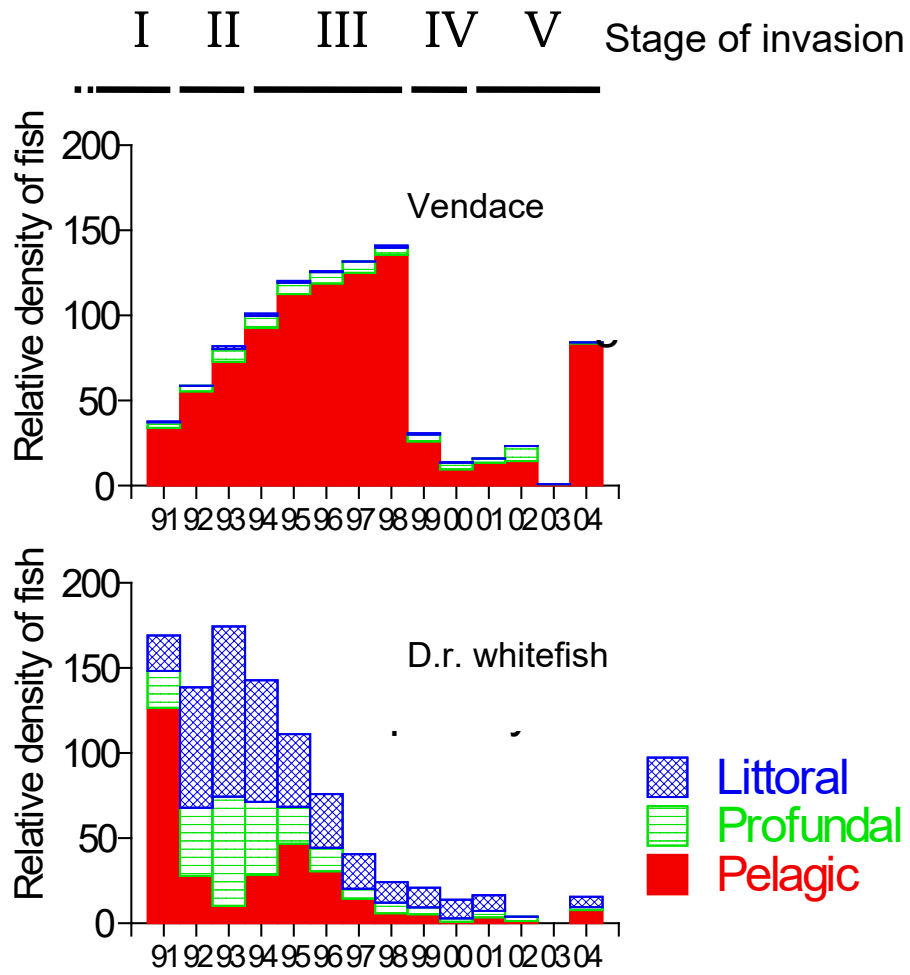
Bøhn et al. Fig. 2

Bøhn et al Figure 3.

Bøhn et al Figure 4.

Two species competing for one resource

Bøhn et al. Fig. 5

Two species competing for two resources

Bøhn et al. Fig. 6