

Invasion of top and intermediate consumers in a size structured fish community

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Till Orvar

List of Papers

This thesis is a summary and discussion of the following papers, referred to in the text by their roman numerals:

- I Byström P., Karlsson J., **Nilsson P.**, Van Kooten T., Ask J. and Olofsson F. 2007 Substitution of top predators: effects of pike invasion in a subarctic lake. *Freshwater biology* 52, 1271-1280.
- II **Ask P.**, Ask. J., Byström P., Jansson M., Karlsson J. and Persson L. Temperature mediated effects on top consumer populations in subarctic lakes. Manuscript.
- III **Ask P.**, Ask. J., Byström P., Jansson M., Karlsson J. and Persson L. Competition mediated coexistence of invading intermediate consumer, ninespine stickleback, and a resident omnivorous top predator, Arctic char. Manuscript.
- IV **Ask P.**, Byström P. and Persson L. Preference for cannibalism and ontogenetic constraints in competitive ability of piscivorous top predators. Manuscript.

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Abstract

In this thesis I have investigated the effects of invading top and intermediate consumers in a size-structured fish community, using a combination of field studies, a lake invasion experiment and smaller scale pond and aquaria experiments.

The lake invasion experiment was based on introductions of an intermediate consumer, nine-spine stickleback (*Pungitius pungitius* L.), in to allopatric populations of an omnivorous top predator, Arctic char (*Salvelinus alpinus* L.). The invasion experiment was performed in two tundra lakes and in two birch forest lakes to investigate the effect of climate on the invasion success. I found that the effect of sticklebacks on char was size dependent. Small char suffered reduced growth from resource competition with sticklebacks whereas the maximum size of adult char increased from the addition of a larger prey resource, stickleback. The negative effect of sticklebacks on the growth of small char suggests that sticklebacks may be a better resource competitor than char, which was also supported by the pond and aquaria experiments. The pond experiments also suggested that char were more efficient cannibals than interspecific predators on sticklebacks. Cannibalism in char may limit the recruitment of char and decrease both their predatory and competitive effect on coexisting species and thereby also promote the coexistence of char and sticklebacks. The successful invasion by sticklebacks and their subsequent increases in density suggest that the absence of sticklebacks in char lakes in this region is not caused by biotic interactions with char. Instead, it may be suggested that co-occurrence of sticklebacks and char in the region is limited by dispersal.

The char – stickleback system resembles an intraguild predation system with char as the top consumer and stickleback as the intermediate consumer. The effects of the stickleback invasion is also contrasted with a field study of a northern pike (*Esox lucius* L.) invasion into a system with coexisting char and stickleback, where pike can be viewed as the top consumer and char as the intermediate consumer both feeding on sticklebacks. In this case pike excluded char. The identity of the invading species and the relative strength of the predatory and competitive interactions in the two contrasting systems are discussed in relation to coexistence in intraguild predation systems. I found that the identity of the invading species is of crucial importance for the response at the ecosystem level, and that the inherent size dependency of competitive and predatory interactions in fish communities is important for attaining a mechanistical understanding of the effects of invasive species in lake ecosystems.

Keywords: Invasion, intraguild predation, size-structure, cannibalism, climate, temperature, Arctic char, nine-spine stickleback.

Introduction

General background

Fish grow substantially in size over their ontogeny which may change their identity as predator or prey in the food web and hence also their competitive and predatory relationships (Werner and Gilliam 1984, Persson 1988). The large variation in size present in fish populations also allows for and determines the strength of intra- and interspecific predation (Smith and Reay 1991, Claessen et al. 2002), and size also determines competitive ability (Wahlström et al. 2000, Byström and Andersson 2005) and susceptibility to predation (Werner and Gilliam 1984, Lundvall et al. 1999). Hence, individual size becomes a key determinant of the role and faith of an individual within a population, and the size dependence of individual rates become fundamentally important to the structure and dynamics of fish populations (Persson et al. 1996). The inclusion of size-structure into community level models thus offers a more detailed analysis and mechanistical understanding of some of the processes that may affect coexistence in fish communities. For example, the inclusion of size structure may either increase or decrease the scope for coexistence in intraguild predation systems (van de Wolfshaar et al. 2006, Schellekens 2010).

Climate change may affect lake ecosystems in a number of ways, one of which is by shifting the range distribution of species and hence also increase invasions of species adapted for a warmer climate into former cold environments (Walther et al. 2002, Parmesan and Yohe 2003). The effects of an invading species will depend on the strength and identity of biotic interactions between species, and also by the size relationship between invading and resident species (Persson et al. 2007, Nilsson 2010). Increasing temperature *per se* may also affect community dynamics through effects on species performance (Vasseur and McCann 2005), and hence influence the effects of invading species on community structure and dynamics in a climate change scenario (Van der Putten et al. 2010).

There is a large gap between theory and empirical data on how climate and invasive species affect lake ecosystems at the population and community level. In this thesis I investigate competitive and predatory interactions in a size-structured fish community with small scale pond and aquaria experiments to large scale field studies and lake invasion experiments. I hope to advance our understanding of how climate and invasive species affect coexistence in size structured fish communities.

Intraguild predation

In the context of food web ecology, omnivory is broadly defined as feeding on more than one trophic level (Pimm and Lawton 1978). Intraguild predation involves omnivory within a guild of predators and prey that compete for a shared resource (Polis et al. 1989). In the simplest form it involves one top consumer (TC) feeding on an intermediate consumer (IC) and a shared resource (R) (fig. 1a). Intraguild predation thus involves a mix of predatory and competitive interactions that differs from ordinary predation, in the sense that the TC benefits not only a direct energetic gain but also reduced resource competition by feeding on the IC. Consequently, intraguild predation involves interactions such as resource competition and apparent competition (fig. 1b, 1c), and may have more complex effects on community dynamics compared to strictly competitive and predatory interactions.

Early theoretical work on intraguild predation systems predicted that stability would decrease with increasing omnivory, and omnivory was at that point considered to be rare in natural communities (Pimm and Lawton 1978). However, Polis (1991) empirical work on desert food webs pointed out that omnivory is common in natural communities (see also: Diehl 1993 for a review) and that omnivory is rather the rule than an exception in natural food webs. The contradicting results regarding the role of omnivory in natural food webs was considered to be an artefact of that the early empirical food webs were too low in taxonomical resolution to appreciate the extent of omnivory in natural food webs (Polis 1991, Polis and Strong 1996). The discrepancy between early theoretical predictions of the destabilizing effect of omnivory and the fact that natural communities are replete with omnivory has since inspired a range of theoretical and empirical work on the role of omnivory in foodwebs and of the stability of intraguild predation systems.

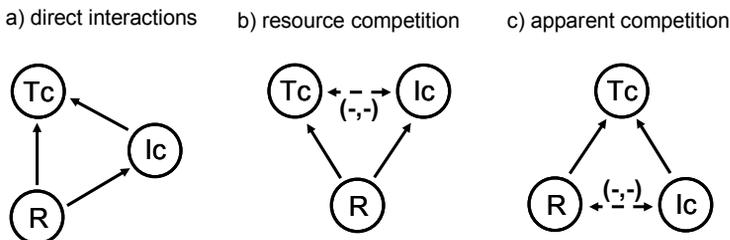


Figure 1. Redrawn in part from Polis et al. 1989. Interactions in a three species food web of an omnivorous top consumer (TC), an intermediate consumer (IC) and their common resource (R). a) Direct interactions. b) Resource competition. c) Apparent competition. Solid arrows represent direct interactions (+,-) with a positive effect on the consumer and a negative effect on the consumed resource. Bi-directional hatched arrows represents mutually negative (-,-) indirect effects.

McCann and Hastings (1997) showed theoretically that increasing omnivory may actually bound system dynamics further away from zero densities and switch an unstable equilibrium to a locally stable equilibrium, i.e. stabilize food chains. However, they also pointed out that too strong omnivory may destabilize food webs and that increased efficiency of the TC decreases the amount of omnivory that can be sustained before the system loses its interior attractor. The findings of McCann and Hastings (1997) also received empirical support strengthening the idea that omnivory may indeed stabilize natural communities (Fagan 1997, Holyoak and Sachdev 1998, Morin 1999). Further theoretical explorations of dynamics in intraguild predation systems demonstrated that coexistence was dependent on the competitive superiority of the IC and that coexistence was limited to intermediate levels of productivity (Holt and Polis 1997, Diehl and Feissel 2000, Mylius et al. 2001). At low productivity, the TC was excluded by the competitively superior IC, and at high levels of productivity the TC was predicted to exclude the IC through apparent competition.

Diehl (1993) proposed in his review of omnivorous feeding relationships that the relative sizes of IC and TC determine the role of omnivory in communities. A large size difference between resource and the IC would direct TC predation towards the IC, and thus strengthen indirect effects of TC on the resource and hence also the role of omnivory for food web dynamics. The inclusion of size-structure and food dependent growth in recent theoretical extensions of intraguild predation models have demonstrated that the scope for coexistence may either increase or decrease depending on the type of regulatory mechanisms that are present in the system. The mechanism that demotes the coexistence between TC and IC in intraguild predation systems arises from the positive feedback induced by TC predation on IC that relaxes resource competition and increases the growth of juvenile TC and their per capita predation rate later in life (van de Wolfshaar et al. 2006). Conversely, size-structure may promote coexistence in a competition situation between TC and IC when maturity and reproduction in the TC becomes dependent on the IC as a prey (Schellekens 2010). Hence, the effects of consumer relative size and the possible feedbacks arising from size-structure may be of crucial importance to understand patterns of coexistence in intraguild predation systems.

Cannibalism

Cannibalism is widely distributed in the animal kingdom and is particularly common in arthropods, amphibians and fish (Polis 1981, Smith and Reay 1991). Cannibalism in fish populations is inherently size dependent, related to the ontogenetic changes of piscivores and size dependent limitations in prey catchability. The upper size limit of prey that a piscivore can handle is related to limitations in gape size (Werner 1974, Hambright 1991), and to the

relative swimming speed of predator and prey (Christensen 1996), whereas the lower size limit of prey is dependent on problems with retention (Persson 1987) and the visual detection of small prey (Lundvall et al. 1999).

Cannibalism has strong impacts on the structure and dynamics of fish populations (Persson et al. 2000, Claessen et al. 2002, Byström 2006, van de Wolfshaar 2006). The population dynamic effect of cannibalism is strongly dependent on the strength and size limits of cannibalism and of the offspring size at hatching (Claessen et al. 2002, van Kooten et al. 2010). Essentially, large offspring sizes and/or a low size limit of cannibalism induce cannibal driven dynamics, where cannibalism is associated with a strong dynamical effect by numerical control of recruiting cohorts (Claessen et al. 2000, Persson et al. 2000). In this situation, cannibals are numerous and consume the offsprings during a short time period and do not gain significantly in growth from feeding on the small recruits. Relaxing the regulatory effect of cannibalism induces size dependent resource competition in dense recruiting cohorts that may allow for the emergence of a few giant individuals that feed on the dense and slow growing cohort and gain substantially in size but, on the other hand, have a limited impact on system dynamics (Claessen et al. 2002). Cannibalism has been empirically shown to regulate recruitment in fish populations (Persson and De Roos 2003, Byström 2006, Nilsson 2010). This regulatory mechanism of cannibalism has also been suggested to facilitate coexistence in communities with competing predators and prey (i.e. intraguild predation systems, sensu: Polis et al. 1989) (Claessen et al. 2004, van de Wolfshaar 2006, Rudolf 2007).

Climate effects on lake ecosystems

Climate influences lake ecosystems directly through variation in water temperature and length of the ice free season (Magnuson et al. 2000), but also through indirect effects on lake productivity via variation in loading of allochthonous dissolved organic carbon (DOC) and inorganic nutrients from the catchment (Karlsson et al. 2005, Jansson et al. 2008). Trophic feedbacks mediated by changes in top predators within lake ecosystems may alter lake carbon fixation and thus also the carbon exchange between lakes and the atmosphere (Schindler et al. 1997). Such trophic feedbacks within ecosystems have also been shown to change the expected outcome of climate change on ecosystems structure and function (Lensing and Wise 2006, Wilmers et al. 2006, Suttle et al. 2007).

Studies of lake productivity has been focused on the nutrient limited pelagic habitat and to a large degree overlooked the importance of production in the benthic habitat to overall lake productivity (Vadeboncoeur et al. 2002). Increasing input of nutrients and coloured DOC may shift the relative contribution of benthic and pelagic production in small oligotrophic lake ecosystems and also decrease overall lake productivity (Ask et al. 2009).

Fish species in small oligotrophic lakes are strongly dependent on benthic production (Sierszen et al. 2003, Karlsson and Byström 2005). The production of fish biomass in these systems have also been demonstrated to decrease with an increase in nutrients and DOC due to the shift from benthic to pelagic productivity and a subsequent decrease in total lake productivity (Karlsson et al. 2009). Since a large proportion of the worlds lakes are small (Downing et al. 2006), such climate induced changes in lake productivity can be expected to have strong effects on lake ecosystems on a global scale.

Increasing temperature has been shown to have disparate effects on different trophic levels, potentially interrupting energy flows and destabilizing ecosystem dynamics (Beisner et al. 1997, Strecker et al. 2004, Winder and Schindler 2004a, Emmerson et al. 2005, Wagner and Benndorf 2007). Increased temperature will also directly influence the vital rates of all consumers in the food web including their consumption, metabolism and search efficiency (Persson 1986; Harrison & Fewell 1995; Jiang & Morin 2004; Reim *et al.* 2006). Ecological mechanisms, such as gape size limitation, may also feedback on the effects of temperature on individual growth affecting population level responses and potentially also the effects of climate on ecosystems (Armstrong et al. 2010). The effects of temperature on individual species performance also differ between different species and trophic levels which has strong effects on the structure and dynamics of communities (Voigt et al. 2003, Vasseur and McCann 2005, Barton et al. 2009). Furthermore, climate change may increase invasions of species adapted to a warmer climate into present cold water lake ecosystems (Magnuson et al. 1997), provided that habitat connectivity allows for the migration of invasive species into lake ecosystems (Spens et al. 2007). Depending on the strength and identity of biotic interactions between invading and resident species, species invasions may have strong effects on the dynamics and composition of lake communities (Magnuson et al. 1998, Englund et al. 2009, Sharma et al. 2009).

Hence, the response of lake ecosystems to increasing temperature is a multifaceted problem that poses a challenge to scientists and management efforts trying to understand and mitigate the effects of climate change. Not only will the ecosystem status be affected by inherent properties within the system, lake communities are also under considerable influence by allochthonous input and species invasions that may affect the overall dynamics of lake ecosystems in a climate change perspective.

Aims

The overall aim of this thesis was to investigate the impact of invading top and intermediate consumers on size structured fish communities, and to increase our understanding of the underlying mechanisms that may affect the impact of species invasion and climate on size structured fish communities.

Specific topics considered:

- Effects of temperature on Arctic char populations and individual performance in natural systems (II).
- Ecosystem consequences of species invasion in size structured fish communities (I, III)
- Cannibalism vs. interspecific predation: Arctic char as an omnivorous top predator (IV).

Methods

To investigate the effects of invasions of top and intermediate consumers in size structured fish communities, this thesis includes data from aquarium scale experiments on foraging capacity to pond scale experiments on competition and piscivorous efficiency to field studies and large scale lake invasion experiments on interactions in natural communities. Below I give a brief description of the study species and present the main features of the methods and procedures in field studies, experimental lake manipulations and of the pond and aquaria experiments.

Study species

Arctic char (*Salvelinus alpinus* L.) has a circumpolar distribution and is a typical cold water species that is well adapted to their low grade environment (Klemetsen et al. 2003). Char is a substrate spawner that spawns in autumn and the egg stage completes over the winter period and the fry emerges in early spring. Char can reach sizes up to several kilos in lake ecosystems and it is a generalist predator that feeds on zooplankton and benthic invertebrates as well as on fish prey including conspecifics (Klemetsen et al. 2003). Cannibalism in char is frequent, and has been demonstrated to have strong effects on the structure and dynamics of char populations (Amundsen 1994, Svenning and Borgström 1995, Byström 2006, Berg et al. 2010).

Ninespine stickleback (*Pungitius pungitius* L.) is a small bodied species (adult size ~ 64mm) that is generally distributed in fresh and saltwater environments throughout the northern hemisphere (Scott and Crossman 1973). Spawning takes place in a nest built and guarded by the male in which

several females may deposit their eggs (Scott and Crossman 1973). Sticklebacks feed mainly on zooplankton (Gray et al. 2005), but may include a range of prey in their diet; benthic macroinvertebrates, fish eggs and even small fish fry (Hynes 1950, Gray et al. 2005). Sticklebacks has also been shown to have strong effects on zooplankton community structure and biomass density (Hansson et al. 1990, Bizina 2000, Olofsson 2003). It is also a common prey species of piscivorous fishes (Griswold and Smith 1973, Scott and Crossman 1973, Byström et al. 2007).

Northern pike (*Esox lucius* L.) has a holarctic range distribution and is commonly occurring in freshwater lakes and streams as well as in weakly saline waters throughout its range of distribution (Craig 2008). Spawning takes place during early spring in shallow or flooded areas with dense vegetation, eggs develop fast and fry hatch shortly after the spawning period (Scott and Crossman 1973). Fry grow fast and switches to piscivory already in their first summer of life (Mittelbach and Persson 1998, Wootton 1998). Pike is a highly efficient specialist piscivore that have strong effects on the behaviour and abundance of their prey species with cascading effects in aquatic food webs that may affect the overall structure and dynamics of aquatic communities (Byström et al. 2007, Persson et al. 2007, Englund et al. 2009).

Field study (I)

We conducted a comparative field study to investigate the effects of an invasion of the top predator pike on community composition in Lake 6 (Karlsson and Byström 2005), a small subalpine lake that had char and sticklebacks before the pike invasion. We investigated the densities of char, sticklebacks, benthic macroinvertebrates and zooplankton before and after the pike invasion and we also sampled an adjacent lake (Lake Stavlussukjavri) with char and sticklebacks to control for other factors not included in our study that may have affected the response of the community to the invasion of pike. Fish populations in Lake 6 was sampled with live traps (OY Ella Fishing AB, Hangö, Finland) and small minnow traps with similar sampling protocols in the years 2002, 2004 and 2005, and with additional gillnet (Nordic 12) samplings in the years 1999, 2002, 2004 and 2005. Lake Stavlussukjavri was sampled in 2005 with live traps and gillnets. Benthic macroinvertebrates and zooplankton was sampled in 2002 and 2005 in Lake 6, and in 2005 in Lake Stavlussukjavri for comparison to a system without pike invasion (for further details on sampling procedures cf. I).

Lake Experiments (II and III)

The central part of the work in this thesis has been conducted in 4 oligotrophic lakes in the north of Sweden close to Abisko (68°21' N, 18°49' E). Two of the lakes were situated in the subalpine birch forest (lake

Almberga and lake Tjabrak) and two of the lakes on the subalpine tundra (lake Ruozut and lake Vuorejaure). The altitudinal difference between lake types (266 m) corresponded to an average difference in water temperature of 1.4 ± 0.5 (average \pm 1SD). The catchments are small (25-65 ha) and differs in their vegetation between lake types. Forest catchments have birch forest and the low shrub vegetation is characterized by *Vaccinium myrtillus* with contributions of herbs and grasses while the tundra catchments lack birch forest and are dominated by alpine heath vegetation characterized by *Empetrum nigrum* and *Betula nana* with some contributions of herbs and grasses. The lakes are small (3.4-6.2 ha) seepage lakes that had allopatric populations of char as the only fish species present. We started the work in 2005 with an initial sampling and investigation of the lake ecosystems and char populations prior to the stickleback introductions (II). Sticklebacks were collected from a nearby lake with coexisting char and stickleback (Lake Stavlussukjavri, see I) and introduced in one tundra lake and one forest lake (Lake Tjabrak and Lake Vuorejaure) at the end of the growth season in 2005 and in the remaining 2 lakes in 2007 (Density average \pm 1SD, 493 ± 27 no. ha⁻¹) (III). Following the stickleback introductions we monitored densities of zooplankton and benthic macroinvertebrates and the change in the stickleback and char populations over the study period, 2005-2009.

The fish populations of the lakes were sampled at 2 (2005, 2008) or 3 (2006, 2007, 2009) occasions per year using both live traps (OY Ella Fishing AB, Hangö, Finland) and electrofishing. Multimesh gillnets (Nordic 12) were used once per year at the last sampling occasion in each year to estimate the size-structure of the populations and to collect samples for age determination. Densities of char were estimated using the Petersen mark recapture method. Char caught with traps and electrofishing were marked at the first sampling occasion in each year with blue dye using a Panjet injector (Hart and Pitcher 1969) and then released back into the lakes and recaptured in the successive samplings within that year.

Benthic macroinvertebrates were sampled with an Ekman grab in the profundal and littoral soft bottom habitats, and by collecting and brushing fist sized stones in the stony nearshore habitat. Benthic macroinvertebrates were divided into predation sensitive macroinvertebrates and other macroinvertebrates, based on their way of living and exposure to fish predation (Persson et al. 1996). Zooplankton were sampled in both pelagic and littoral habitats of the lakes with zooplankton net (\varnothing 25cm, mesh size:100 μ m) (cf. II and III for a more detailed description of material and methods).

Pond and aquaria experiments (IV)

To analyse competitive and predatory interactions between char and sticklebacks in more detail, I performed different pond and aquaria

experiments. The pond experiments were conducted in two ponds (32 × 10.8m, mean depth 0.9m) in Umeå, Sweden, each pond divided with green tarpaulin into 8 experimental enclosures (4 × 10.8m). Each pond had a water inflow and an outlet in the opposite end of the pond, openings (width 0.2m × height of water column) in the tarpaulin covered with mesh (mesh size 3mm) allowed for water to flow through the experimental enclosures. Experiments were typically short in duration and performed during the spring period to avoid high water temperatures. Ponds had a well developed belt of *Carex* sp. along the edge of the water. In general, experiments were terminated with a seine net and enclosures were considered empty when 3 subsequent empty hauls of the seine net had been obtained, caught fish were stored cold and brought to the lab for further analysis. For a detailed description of experimental designs and procedures for each pond experiment see manuscript **IV**.

The aquaria experiments were conducted in climate chambers at a constant temperature of 14 °C, aquaria were 30L in size with back and sides covered with black plastic and lit from above with fluorescent tube (11W). Four size groups (0.1 ± 0.02 , 0.22 ± 0.04 , 0.54 ± 0.09 and 1.5 ± 0.20 g, average \pm 1SD) of wild caught sticklebacks (Lake Hamptjärn, 63°52'34"N, 20°12'51"E) were trained in the experimental procedures for 2 days prior to the estimation of size dependent foraging efficiency on zooplankton prey (*Daphnia* size: 1.11 ± 0.08 , mm \pm SD) (for detailed experimental procedures cf. **IV**).

Major results & Discussion

Invasion of top and intermediate consumers

Species invasions is predicted to increase following climate change (Walther et al. 2002), and the identity of invading species can be expected to have strong effects on the outcome of species invasion on the dynamics and structure of fish communities (Magnuson et al. 1998, Englund et al. 2009). In paper **I** and **III** we investigate the effects of an invading top consumer (pike) and of an invading intermediate consumer (stickleback), two species with widely different roles in the community they invaded (see Methods, section: study species). In paper **I** pike excluded char from the system, with cascading effects down the food web, strongly decreasing the density of sticklebacks with subsequent positive effects on resource densities. The change of top consumer in the system demonstrates the importance of the strength of predation on the structure of the community, i.e. compare the weak predatory effect of char with high densities of sticklebacks to the strong predatory effect of pike resulting in very low densities of sticklebacks. Sticklebacks may function both as a resource competitor to small char and as

a prey to large char, and the char –stickleback system can thus be viewed as an intraguild predation system (**I**). In paper **III** the invasion of sticklebacks into allopatric populations of char, show that sticklebacks were able to depress resource levels more than the native char populations which resulted in decreased growth of small char. Sticklebacks also had a positive effect on the growth of large char and increased the maximum size of char. The increased maximum size of large char may reflect that sticklebacks constitute a new resource and niche shift possibility available to large char, allowing for growth to larger sizes compared to macroinvertebrate resources (Werner and Gilliam 1984). However, the increased growth of a few large char can be expected to have a very limited impact on the overall stickleback population density (similar to cannibalistic dynamics in Claessen et al. 2000, Claessen et al. 2002, Byström 2006). The fact that sticklebacks successfully invaded and increased in density in all experimental lakes and co-occur with char in the birch forest zone in the region also suggests that sticklebacks do coexist with char (**I**, Olofsson 2003).

The different outcomes on the persistence of the systems in the case of the pike invasion compared to the stickleback invasion demonstrate the importance of the relative strength of predation and competition for coexistence in intraguild predation systems. In the case of the pike invasion, the system can be characterized as an intraguild predation system with pike as a top consumer and char as an intermediate consumer both feeding on the shared resource, sticklebacks. Pike may be regarded as a much more efficient piscivore than char when reviewing the life history characteristics that are associated with piscivory (Mittelbach and Persson 1998). Hence, the top consumer in this configuration can be expected to be a much more efficient resource competitor than the intermediate consumer, which based on theoretical expectations from studies of coexistence in intraguild predation systems would render coexistence of the two species very unlikely (Holt and Polis 1997, Diehl and Feissel 2000, Mylius et al. 2001, van de Wolfshaar et al. 2006). The exclusion of the intermediate consumer, char, is thus likely a combination of predation and competition from the top consumer, pike (**I**). In contrast, the invasion of sticklebacks into char populations, where the competitive effect of the intermediate consumer, sticklebacks, is strong (**III**, **IV**) and the predation by the top consumer, char, appears weak (**I**, **III**, **IV**), can be expected to promote the coexistence of the two species in the system (Holt and Polis 1997, Diehl and Feissel 2000, Mylius et al. 2001). In the case of the stickleback - char system, it may be suggested that sticklebacks are better competitors for small sized prey than char and that char may be better than sticklebacks feeding on larger macroinvertebrates. Resource partitioning in combination with weak predation by char on sticklebacks can be expected to promote the coexistence between the two species, and relaxing the predatory impact on the intermediate consumer has also been

demonstrated to increase the range of coexistence in intraguild predation systems (Mylius et al. 2001).

Recent theoretical work has also demonstrated the importance of size – structure for the coexistence of top and intermediate consumers in intraguild predation systems. The inclusion of size-structure may either decrease or increase the range of coexistence depending on how the system is regulated (van de Wolfshaar et al. 2006, Schellekens 2010). The different effect of sticklebacks on large and small char in our invasion experiments also emphasize the importance of taking size-structure into account to better understand how invasive species affect lake ecosystems.

Cannibalism

Cannibalism in char is well documented and has been suggested to have important implications for the structure and dynamics of char populations (Svenning and Borgström 1995, Byström 2006, Andersson et al. 2007, Berg et al. 2010). Our results in paper **IV** suggests that cannibalism in char is strong and may be preferred over interspecific predation, both in char and among piscivores in general.

Cannibalism has a strong population dynamical effect and matters the most for the structure of the system when many small to medium sized cannibals exert strong predation pressure on the recruiting cohorts, thus killing the majority of their own offspring. In this situation, cannibal prey appears in the diets only during a very limited time window and is not a significant energy source to cannibals (Claessen et al. 2000, Persson et al. 2004). In contrast, the conspicuous large but few cannibals that have accelerated in growth from feeding on the breakthrough of an abundant slow growing cohort have a very weak impact on recruiting cohorts, and the overall system dynamics is characterised more by cohort dynamics (Claessen et al. 2000, Persson et al. 2004). This may lead to that the importance of cannibalism in natural systems may be overlooked, as cannibal driven dynamics may not give rise to the conspicuous large individuals associated with cannibalism and piscivory in general.

Density dependent cannibalism decreases the competitive and predatory impact of top consumer species on coexisting species (Claessen et al. 2004), and thereby also increases the likelihood of coexistence in intraguild predation systems (van de Wolfshaar 2006, Rudolf 2007). A preference for cannibalism over interspecific predation in piscivorous top consumers may thus be a mechanism for coexistence in fish communities in general (**IV**). Nonetheless, despite extensive cannibalism in the top consumer, exclusion of the intermediate consumer by strong predation of the top consumer in intraguild predation systems may still be the case (Persson et al. 2007).

Climate

Climate may have strong effects on the structure and dynamics of lake ecosystems through effects on phenology (Winder and Schindler 2004b), allochthonous input (Jansson et al. 2007), light (Diehl 2007), ice cover duration (Magnuson et al. 2000) and lake water temperature (Magnuson et al. 1997).

In paper **I** we show that the air temperature has increased over the past decade in the study region, and demonstrate the strong effect that climate induced species invasion may have on the community structure of lake ecosystems. In our experimental lake study we tested the effects of climate by comparing lakes on the alpine tundra and in the birch forest, where the birch forest lakes were consistently warmer than the tundra lakes during the experimental period (**III**). This difference in temperature caused char to grow faster in the warmer birch forest lakes, via effects on both foraging efficiency and on resource productivity (**II**). Because resource densities were similar between lake types, we argue that the resource production must be higher in the birch forest lakes compared to the tundra lakes to support the higher metabolic costs and growth rates of char in these lakes due to the higher temperature (**II**). When later analysing the effects of temperature on resource densities in paper **III** we could also see that there was a positive effect of temperature on the density of predation sensitive macroinvertebrates in the stony nearshore habitat. Our results thus indicate that climate affects both the resource production and the individual performance of char in our lakes.

The effect of increasing temperature on the ecosystem level depends on the temperature scaling of resource production and consumer foraging efficiency and metabolic demands. In consumer resource systems increasing temperature may decrease the biomass of both resource and consumer and destabilize system dynamics (Vasseur and McCann 2005). In our case, biomass of resources and consumer did not decrease with increasing temperature (**II**), which suggests that resource production in our system actually increased more with increasing temperature compared to that used in the study of Vasseur and McCann (2005). The size-structured nature of char populations also allows for cannibalism, which increases the number of interactions and possible feedbacks compared to a linear consumer resource system. The internal regulation of the char populations via cannibalism (Claessen et al. 2000, Andersson et al. 2007), may thus cause the increase in resource production to be expressed in increased individual growth rather than as an increase in population density and biomass (**II**).

There are few empirical studies detailing the interactions and mechanisms involved in determining the effects of temperature in natural communities, which undoubtedly will be a key component for our understanding of how natural communities will respond to climate change.

Concluding remarks

I found that the identity of the invading species affected the strength of predatory and competitive interactions in the fish communities and was fundamentally important to the overall effect on the investigated lake ecosystems. I also found that size-structure was a key component for understanding the mechanism behind the response of the native char population to the stickleback invasion. I further conclude that sticklebacks were not limited by biotic interactions in the region for their co-occurrence with char. I found that temperature *per se* may increase individual growth in char and that productivity had to increase with temperature in our system to sustain resource levels and support the increased growth and metabolic demands of char. I suggest that the regulating effect of cannibalism may promote coexistence in fish communities in general, and that cannibalism in char may be important for the response of char populations to both the effects of increasing temperature and invading species. Taken together, the effects of invasive species and climate on lake ecosystems is a complex field of research that is affected by both inherent properties of the ecosystem as well as by external factors, making predictions of how lake ecosystems will respond to climate change difficult. This thesis emphasize the importance of considering internal processes, like cannibalism and size-dependent interactions, to better understand the mechanisms by which lake ecosystems change in response to climate and invading species.

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